FISHERIES RESEARCH BOARD OF CANADA
BULLETIN 162

the Sockeye Salmon,

Oncorhynchus nerka

R. E. Foerster

Ottawa 1968

THE SOCKEYE SALMON,
ONCORHYNCHUS NERKA

Female sockeye salmon, 61 cm fork-length, age 6_3, caught in the central part of the Gulf of Alaska on May 18, 1967, on longline gear during tagging and sampling operations of the MV *G. B. Reed.* (Photo by C. E. Turner of the Fisheries Research Board of Canada Biological Station, Nanaimo.)

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By R. E. Foerster

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

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PREFACE

Around the whole periphery of the North Pacific Ocean where sockeye salmon occur and are commercially fished—from the Columbia River on the east to the streams of the west coast of Kamchatka on the west (Fig. 2)—there has taken place a gradual but marked decline in the sockeye salmon stocks. The reason or reasons for such decline are by no means clear; investigations have been and continue to be directed in Canada, Alaska, and the Kamchatka area of the USSR, to discover the responsible factors.

Two major causes have been suspected—overfishing, on the one hand, and a general reduction in rate of natural survival of young, on the other. Under conditions of overfishing, the escapement of maturing fish to the spawning grounds becomes insufficient to maintain the stocks of sockeye. When the rate of production of young sockeye from the eggs laid by the parent fish drops, whether due to changes in the freshwater environment or from other causes, the numbers of recruits to the stock become fewer and the population declines. If both factors are at work, the situation can become very serious. This seems to be the case in many areas.

One of the first requirements for a study of sockeye production in any area and its present-day trend or status is a full understanding of the life history from egg through to spawning adult stages. In addition, it is necessary to know what losses occur at each stage and why. Since the environmental conditions, to which the sockeye at each stage are subjected, play so important a role in their well-being and survival, it is necessary to know what a normal environment is, how widely the conditions may fluctuate, and how profoundly they affect the sockeye.

This Bulletin attempts to bring together all that is presently known about sockeye. All studies carried out in the North Pacific sockeye area have been reviewed and their results incorporated in order to present sockeye production under a variety of climatic and environmental conditions and to assess overall survival, as well as at each stage of the life cycle from egg to adult. Only when knowledge of this kind is available can we know, for increase of stocks, where improvements in natural production can be made and what regulatory measures are most effective. Such a review reveals the extent of our present knowledge and the significance of the findings. Of equal importance, it will bring to light what we do *not* know and must still investigate.

In all Pacific areas where studies have been conducted, the pattern of investigation has been the same. First to be undertaken was a qualitative study of the fish landed, to determine the sizes, sex ratios and ages, and the numbers taken each season. Comparisons were made, in some instances, between populations caught in different river estuaries or coastal areas. Some attention was directed to that part of the population which proceeded to the spawning grounds in order to find out where the fish went and in what numbers. During this period some tagging of adult fish in coastal fishing areas was undertaken in order to ascertain the coastal movement of the fish and to which river systems they were headed.

The second phase involved a more or less intensive investigation of the freshwater stages of the life history and the percentage survival up to the seaward migrant stage from known egg depositions. It had become apparent that losses during the freshwater period of the life cycle were extremely heavy. It was desired to know at what stages these occurred and what were the causative factors. A thorough study of the environment was required in order to know the conditions under which the fish lived at each stage.

Great variations in climatic and environmental conditions and in the numbers of fish present occur from year to year in all of the various widely differing geographic habitats of the sockeye. These have a profound effect on the well-being and survival of young sockeye. In order to evaluate them, long-term studies, embracing a wide range of conditions, are required. Either this is needed, or a number of studies in a variety of localities which may together achieve the same objective.

It is indeed remarkable—and most unfortunate—that whenever investigations of this kind have been initiated, circumstances—finances, lack of trained personnel, changes in degree of interest, etc.—have intervened to curtail, terminate, or break the continuity of the studies. As a result there is nowhere available a steady, continuous, long-term series of pertinent data which, covering a wide range of prevailing conditions, will reveal either an average state or establish trends. For this reason we can, at the present time, only put together all the results obtained from investigations carried out in Canada, Alaska, and Kamchatka, and endeavour to analyze their general significance.

The third phase, now coming to the fore, is a study of the ocean life of the salmon, their distribution, and growth. Heretofore, the ocean phase of the life history has been looked upon as a relatively stable one. While changes obviously occurred, the fluctuations were considered to be within narrow limits and to have no real significance so far as survival, growth, and distribution were concerned. Observations within recent years have raised doubts in this regard. Investigations are now being made. Concurrently, oceanographic studies are being instituted to define the conditions in the areas where the salmon dwell, and to plot the seasonal and annual fluctuations. Ocean current patterns are being charted and the changes in water-mass movements recorded.

Furthermore, with the initiation in recent years of a high-seas salmon fishery by the Japanese, it has become very apparent that each Pacific country possessing a coastal salmon fishery which it strives to regulate and foster, must know where, in the ocean areas, the fish bred in its rivers dwell. This calls for exploratory high-seas fishing and a study of the place of origin of the fish caught, either by tagging and subsequent recovery in fishing areas or on the spawning grounds, or by some method of racial analysis of the fish.

Such information on ocean residence, the prevailing conditions there, and the abundance of salmon, may become of value also in the further refinement of the techniques of predicting the return of runs to the coastal fishing areas each year, i.e., the number of fish likely to be available for capture by fishermen. At present such predictions are made on the basis of the size of the spawning parent run or, where feasible, on the size of the seaward migrations of the young fish. Any pertinent indices as to the development and survival of these fish during the period of ocean residence are valuable additional guides.

At the present time, while researches and observations are adding further information and are giving us a better understanding of sockeye production and the significance and relative importance of the many limiting factors to survival, some degree of management of the fishery to assure maintenance of the stocks at as high a level as possible must be practised. The basic requirement in any salmon fishery is to have, on the spawning grounds, that number of mature and spawning fish which will produce the greatest number of young going to sea. Therefore, with declining runs in almost every stream, the main problem is to assure passage through the fishery of as many fish as possible, consistent with maintenance of the commercial fishery, in order that the runs may gradually build up.

Nevertheless, at least for the Canadian Pacific coast, as the valleys of the major river systems become more densely populated and developed for agriculture, industry, etc., stream and lake conditions are bound to change from the natural state. Increasingly then, "hopes for continued abundance of salmon to support a flourishing industry and to maintain an important food resource seem to hinge on our ability to develop a sort of semi-cultivation of salmon whereby inroads into primitive habitats are balanced by well-planned improvements in other places" (Neave and Foerster, 1955).

In restoring the sockeye populations in the North Pacific to their former state, and in maintaining them against, on the one hand, the deleterious influences of a highly efficient commercial fishery, and, on the other hand, a changing freshwater environment for production of young fish, the results of researches, observations, and experiments, wherever undertaken, become of great value. Hence, the importance of the present review and summary.

Chapter 1. Systematics, distribution, general life history

THE GENUS *ONCORHYNCHUS*

The Pacific salmon of the British Columbia coast belong to the genus *Oncorhynchus*, a name given to this group of fish in 1861 by the American ichthyologist, Suckley, and derived from the Greek words for "hook" and "snout," thus referring to the conspicuous hooked snout which the male Pacific salmon develop at spawning time.

Jordan (1925, p. 292) records that "the species were first made known nearly one hundred and fifty years ago by that most exact of early observers, Steller, who, almost simultaneously with Krascheninnikov, another early investigator, described and distinguished them with perfect accuracy under their Russian vernacular names. These Russian names were, in 1792, adopted by Walbaum as specific names in giving to these animals a scientific nomenclature." Walbaum (1792), in his classification, considered the Pacific salmon as belonging to the genus *Salmo* along with the Atlantic salmon and trout, but Suckley (1861), noting conspicuous differences between these species and those of the genus *Salmo*, placed them in the new genus *Oncorhynchus*.

The number of species belonging to the genus *Oncorhynchus* varies from six to eight, depending on which authority one follows. According to Vladykov (1962, p. 9), Nikolsky (1954, p. 135) recognizes six species. Vladykov himself adds one more, *O. rhodurus*, making seven in all:

1. *O. gorbuscha* (Walbaum): pink salmon (Canada and United States), karafuto-maru (Japan), gorbuscha (USSR).
2. *O. keta* (Walbaum): chum salmon (Canada and United States), sake (Japan), keta (USSR).
3. *O. kisutch* (Walbaum): coho (Canada and Alaska), blueback (Strait of Georgia, Canada), silver salmon (United States), gin-maru (Japan), kizhuch (USSR).
4. *O. masou* (Brevoort): masu (Canada and United States), masu or yamama (Japan), sima (USSR).
5. *O. nerka* (Walbaum): sockeye (Canada and United States), red salmon (Alaska), blueback (Columbia River), beni-masu (Japan), krasnaya or nerka (USSR).
6. *O. rhodurus* (Jordan and McGregor): Biwa salmon (English name suggested by Oshima, 1934), amago or amego (Japan).
7. *O. tshawytscha* (Walbaum): spring salmon (Canada), chinook or king salmon (United States), masunosuka (Japan), chavycha (USSR).

To these, Hikita (1962) adds an eighth, *O. kawamurae.* The validity of this species may be in question. It may prove to be a variety of the freshwater form of *O. nerka,* usually referred to as *O. nerka kennerlyi,* which dwells entirely in lakes.

IDENTIFICATION OF SPECIES

Five of the above species are common to the Pacific coast of North America and may, in the adult stage, be separated, according to Clemens and Wilby (1961, p. 31–32), as follows:

Large fleshy appendage at base of each pelvic fin .... Family Salmonidae

Rays in anal fin, 13 to 19 .... Genus *Oncorhynchus*
Black spots on back and caudal fin.
Spots large; scales in first row above lateral line, 170 or more ....
.... Pink salmon, *Oncorhynchus gorbuscha*

Spots small, irregular; scales in first row above lateral line, fewer than 155, moderate:
Black spots on caudal fin usually on upper lobe only; light silvery pigment along bases of teeth; pyloric caeca, fewer than 100 .... Coho salmon, *Oncorhynchus kisutch*

Black spots on both lobes of caudal fin; black along bases of teeth; pyloric caeca, 120 or more .... Chinook salmon, *Oncorhynchus tshawytscha*

No large black spots on caudal fin, small black speckling usually present:
Rakers on first gill arch, 19 to 26, short, stout, smooth, widely spaced ....
.... Chum salmon, *Oncorhynchus keta*

Rakers on first gill arch, 30 to 39, long, slender, rough, closely-set ....
.... Sockeye salmon, *Oncorhynchus nerka*

When the salmon are quite young, i.e., in the fry or fingerling stage, identification can readily be made by the distinctive markings or colouration, or both. As pointed out by Foerster and Pritchard (1935a)—see also Carl and Clemens (1948)—ready separation of the fry may be made as follows:

No parr marks present. Fry deep blue to greenish on back ....
.... Pink salmon, *Oncorhynchus gorbuscha*

Parr marks present as vertical bars or oval blotches.
Parr marks short, elliptical or oval, extending little, if any, below lateral line:
Row of definite black spots on back; bluish or greenish on back; no green iridescence on sides below lateral line .... Sockeye salmon, *Oncorhynchus nerka*

Black spots on back may be present but not as large and position irregular; bright, mottled green on back and faint green iridescence on sides below lateral line ....
.... Chum salmon, *Oncorhynchus keta*

Parr marks large vertical bars, almost bisected vertically by lateral line:
First rays of anal fin not elongated; back with much black stippling; no brassy iridescence; fins not usually coloured .... Chinook, *Oncorhynchus tshawytscha*

First rays of anal fin elongated, producing a concave posterior margin to fin; back, brown to brownish-orange, with heavy black stippling; sides and belly tinged with brassy iridescence. Fins tinged with orange and tipped with white .... Coho salmon, *Oncorhynchus kisutch*

PLATE I. Sockeye salmon, male and female, *Oncorhynchus nerka* (Walbaum).

(Photo courtesy of Dr Loyd Royal, Director, International Pacific Salmon Fisheries Commission.)

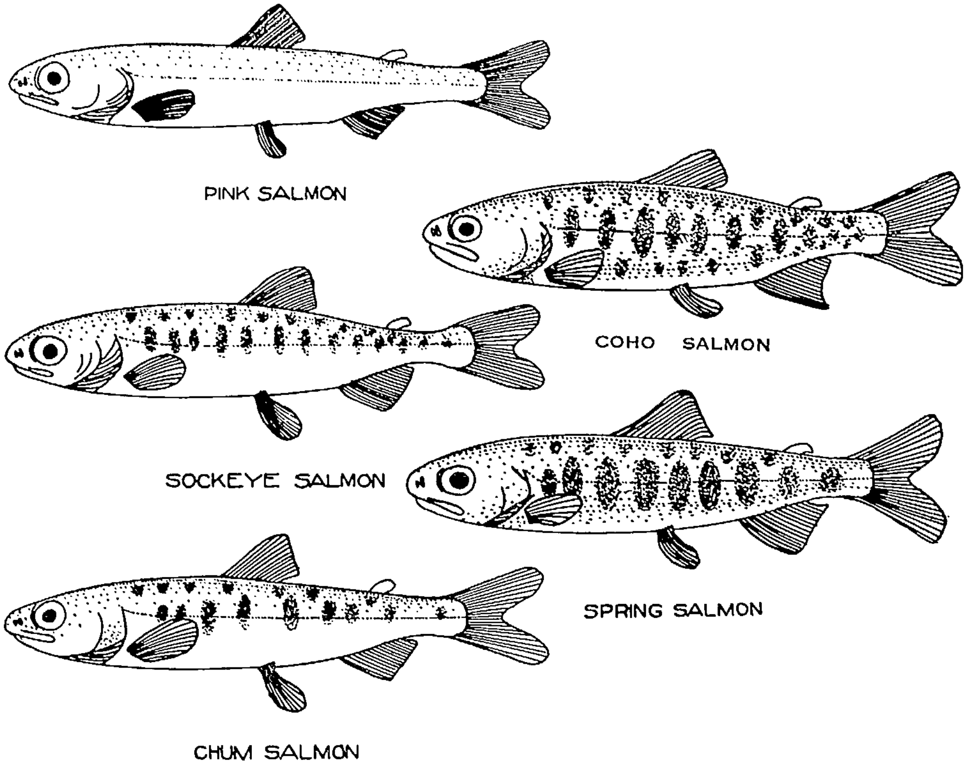

PLATE II. Line drawing of young Pacific salmon occurring in British Columbia waters. (From Foerster and Pritchard, 1935a.)

Hikita (1962, p. 48) separates the species of *Oncorhynchus* into two groups "on the basis of differences in external form in the parr fingerling: one is represented by an elongate or rather slender form and lower depth, while the other is shown by non-elongate form and deeper depth in appearance." Thus, of the five species, referred to above as common in eastern Pacific waters, the pink, chum, and sockeye would belong to the first group, the slender, elongate type, while the chinook and coho would represent the second group, the shorter, stumpy parr. Of the first group, the pink and chum fry proceed to sea shortly after emergence from the gravel whereas the sockeye tend to remain, except in a few rare instances, in lakes for 1 year or more. Consequently, any likelihood of finding pink, chum, and sockeye fry together would occur only in the spring of the year and separation on the basis of the colour markings should be easy. Coho and chinook fry can be readily distinguished by the conspicuous parr marks and the colouration outlined in the key above.

At the time of smolt migration from lake to sea, coho and sockeye migrants may occur together. Here again, the colour markings and the shape of the anal fin should make identification quite easy.

EVOLUTIONARY ORIGIN

It is now generally accepted that the genus *Oncorhynchus*, the Pacific salmon, was developed in pre-Glacial Epoch times from the genus *Salmo*, to which the trout and Atlantic salmon belong. It is believed that at one time this genus *Salmo* was distributed around the whole northern section of the northern hemisphere when North America was connected with northern Asia by a land bridge across the Bering Strait. This would be prior to the Pleistocene Period, which period has been variously estimated by geologists to have begun some 600 thousand or 1 million years ago.

It has been suggested (Neave, 1958) that early in the Pleistocene Period a large stock of the genus *Salmo* became isolated geographically in one of the farthest regions to which it penetrated southward. There it developed certain characteristics which make it distinctly different from the populations of *Salmo* which continued to inhabit the other coastal areas of the north Pacific. The suggested region of isolation and development of this new type, the genus *Oncorhynchus*, is that now occupied, in part, by the present Sea of Japan. In support of this theory it is pointed out (1) that the Japan Sea region is the only coastal area of the North Pacific where *Salmo* is not present today except where introduced by man, although it occurs in areas immediately to the north, and (2) that the species of *Oncorhynchus* seemingly most primitive and most like *Salmo*, namely *O. masou*, is found mainly in the Japanese region.

During the Pleistocene Epoch repeated glaciations took place. Geologists generally agree that at least four major ones occurred in the northern hemisphere. During one of the early interglacial periods, when the Pacific Ocean was opened up to the area behind the land barrier, the early forms of *Oncorhynchus* broke out and broadly extended their range. Subsequently, as the land areas now occupied by the Sea of Okhotsk and Bering Sea became, in turn, elevated and submerged, with periods of geographical isolation extending over 50,000–150,000 years, further evolution of the genus may have occurred and the various species split off.

Just when and where the various separate species originated is not clear but it is apparent that the availability of much greater quantities of food in the ocean was a prominent factor in the adoption of an anadromous behaviour. Berg (1940) states that "anadromous fish obviously originally dwelt in fresh water. Their residence in the sea must be considered as a secondary adaptation brought about by the richness of the food supplies in the ocean." Since the sockeye salmon seem, in one respect, namely one or more years' residence of the young in freshwater lakes, to have departed least (except for *O. masu*) from the primitive *Salmo*, they may have been developed at an early period, but this is mere conjecture. Milne (1948) is inclined to consider the coho salmon (*O. kisutch*) as the most primitive since it is very similar to the steelhead trout (*S. gairdneri*). The other species split off independently at later periods in the order of chinook salmon (*O. tshawytscha*), sockeye (*O. nerka*), chum (*O. keta*), and pink salmon (*O. gorbuscha*).

At the present time we can but agree with Neave (1958) that:

> "Assuming, however, that *Oncorhynchus* diverged from *Salmo* at or near the beginning of the Pleistocene, the subsequent repeated appearance and disappearance of land and ice barriers in

the North Pacific would seem to have created favourable conditions for rapid development of a series of divergent forms and for rapid dispersal of the latter."

SPECIES EVOLUTION

The evolution of the various species of *Oncorhynchus* from the originally wholly freshwater resident *Salmo* presents a fascinating study. According to Hoar (1958), three groups of behaviour changes are involved in the development of the characteristic downstream migration to the sea by the juveniles and the extended ocean residence. These are (1) the smolt transformation, (2) increased nocturnal activity, and (3) a schooling behaviour, all of which, in due course, bring about migration downstream into the sea.

The development of species separation is considered as brought about in four steps (Hoar, 1958, p. 425). The first step is "the separation of a type ancestral to the sockeye, pink, and chum salmon, but more like the sockeye than the other two. This ancestral type developed from trout-like salmonids of the present-day coho type but before the evolving genus *Oncorhynchus* had lost its ability to complete successfully its life cycle in fresh waters."

The second step in evolution occurred before the smolt transformation was lost and perhaps before an obligatory marine life was necessary to the success of any species. It is assumed that at this stage some Pacific salmon had acquired the behaviour of migrating to the estuary as fry.

The third step occurred in the estuary "where the ancestral type with early fry migration acquired progressively earlier resistance to hypertonic sea water and an abbreviation of the pre-smolt period." Here would, then, take place the separation between (1) pink and chum salmon which go to sea as fry, and (2) the sockeye and coho which tarry in fresh water until smoltification occurs, usually after 1 year's residence in fresh water.

The fourth step involves a split between the chum and pink salmon, the pink being considered the more specialized and requiring a minimum of freshwater life.

These observations of Hoar may be considered as supporting the order of evolution of *Oncorhynchus* species suggested by Milne (p. 4). Consideration must be given to evidence more recently provided by Simon (1963) based upon a study of chromosome numbers.

From counts of the diploid chromosome numbers, as follows: (*O. keta*—74; *O. tshawytscha*—68; *O. kisutch*—60; *O. nerka*—56; *O. gorbuscha*—52), and their morphology, it is suggested (Simon, 1963, p. 93) that "the chum salmon may be thought of as the most primitive, with the remaining species occupying positions of increasing specialization characterized by decreases in chromosome numbers."

Further studies are required. Consideration must be given also, however, to the geographic development of the country—the evolutionary changes that took place. For the probable situation along the Pacific coast of North America, the remarks of Clemens (1953, p. 3) are of interest. He states that:

" . . . it may be conceived that a number of species of *Oncorhynchus* evolved early in the Pleistocene and became distributed along the west coast of North America from Alaska to California.

What may have been the distribution of the various species during most of this period is difficult to visualize. . . . However, from the time of the last glacial period onward, a reasonably clear picture of events may be developed. At the height of the last glacial period, about 15,000 years ago, there could have been no streams from the southern area of Alaska to the northern section of the State of Washington. The Yukon Valley was not glaciated and it is possible that some species of Pacific salmon were able to spawn in, and the young to survive in, the Yukon River. To the south, the Columbia and other rivers, at least as far south as the Sacramento, were available and undoubtedly were utilized. If northern and southern populations existed, they probably remained isolated as distinct stocks for many thousands of years. As the glacial ice retreated, innumerable streams came into existence in the region between the Yukon and the Columbia River, and gradually became occupied by the various species."

GEOGRAPHIC DISTRIBUTION OF SOCKEYE SALMON

Sockeye salmon,* first known as *Salmo nerka* by Walbaum and then from 1861 as *O. nerka* (Suckley, 1861), are native to practically all the temperate and subarctic waters of the North Pacific Ocean. They are found along the North American coastline from the Klamath River in California to the Yukon in Alaska but occur in considerable number, i.e., in commercially important quantities, only from the Columbia in the south to Bristol Bay, Alaska, in the north (Cobb, 1917, p. 10–11). On the Asiatic side they are reported from Cape Chaplina in the northern part of the Bering Sea southward around the Kamchatka Peninsula to the northern shore of the Okhotsk Sea (Anon., 1955, p. 26–28), though most abundant in Kamchatka waters.

Up until quite recent years the sockeye have been fished chiefly in coastal areas and in river estuaries. Their coastal distribution is thereby well known. How far they move off shore and what areas of the high seas they frequent during their 2–5 years' residence in the ocean are only now becoming more clearly understood as a result of the researches being conducted by Canada, the United States, and Japan for the International North Pacific Fisheries Commission (INPFC, 1954). When these researches are concluded, the Commission's report will show the ocean-wide distribution (Manzer et al., 1965).

Relating the known distribution of sockeye salmon to the environmental conditions prevailing in these areas, such as ocean temperatures and salinities, as reported by Davidson and Hutchinson (1938), Fleming (1955), and J. P. Tully (unpublished data), it appears that they are found where the summer surface temperatures range from around 5 to 16 C and where the summer surface salinities are generally less than 32.2‰. Gill net catches by the Japanese commercial fishery in high seas areas, and by Canadian and United States exploratory fishing vessels, indicate that salmon are taken mostly in the upper 10 m (30 ft) of the net. Since the netting is done chiefly at night it may be inferred, therefore, that salmon occupy normally the

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* This species is known popularly by a number of names: for example, red salmon in Alaska, sockeye salmon in British Columbia and Washington, and blueback in Oregon. An endeavour has been made through the American Fisheries Society to reach some accord in the use of common names for Pacific salmon; the common name "sockeye" was recommended for adoption (Anon., 1953). How generally this will be observed remains to be seen.

upper 20–30m (60–100 ft) strata but, as the observations conducted for the International North Pacific Fisheries Commission are continued, more precise information will become available.

It is of interest to record that attempts to transplant sockeye salmon to other parts of the world (Davidson and Hutchinson, 1938) have been generally unsuccessful, if success of a transplantation is measured by the extent to which the introduction has produced subsequent sea-running populations. No sockeye runs have been developed in either Chile or Argentina. In New Zealand transplantation has resulted in the development of "a single small stock, which seems to have abandoned its seagoing habit, and migrates only between Lake Ohau and its tributaries" (Allen, 1956, p. 7). It seems clear that the failures of transplantations into foreign areas have been due to unfavourable environmental components of the new habitat, to the lack of either suitable fresh water or satisfactory marine conditions. Davidson and Hutchinson (1938) thus conclude that "owing to the dependence of the Pacific salmon on particular environmental conditions, there are no oceanographic regions in the world that can support populations of these fish as great as those supported by the North Pacific region."

LIFE HISTORY OF THE SOCKEYE SALMON

Sockeye salmon are an anadromous fish; that is, they spend most of their life in the ocean but, when approaching maturity, they return to fresh water to spawn. They select, usually, those coastal streams or tributaries of major river systems which originate in lakes. Spawning takes place either in the small streams flowing into the lakes, in the gravel areas along the lakeshore where seepage flows (underground springs) occur, or in the upper reaches of the lake outlet stream.

Spawning occurs in late summer and autumn, August–November, with the runs to individual areas quite consistent, from year to year, as to time of arrival. Some of the larger areas, such as the Shuswap and Stuart on the Fraser River and Babine Lake on the Skeena, have both early (late July and early August) and late (September and October) runs, while in Kamchatka there occur "spring" (June and early July) and "summer" (late July and August) runs. All of these runs normally proceed to separate and distinct spawning grounds. The eggs are deposited in nests or "redds" which have been excavated by the female fish in selected parts of the stream bed, they are fertilized by the accompanying male fish, and then are covered up by the subsequent activities of the female parent. The period of egg incubation depends primarily on the temperature of the water flowing through the "redd" and under normal conditions may vary from 80 to 140 days. The fully formed and free-swimming fry emerge from the gravel in early spring (April and May), the time of hatching and emergence also depending on the water temperature.

Proceeding downstream (if hatched above) or upstream (if hatched below) to the adjacent lake, the young fry are resident there for a period of 1, 2, or, more rarely, 3 years before setting out on their seaward migration in April to June—at the beginning of their 2nd, 3rd, or, more rarely, 4th year of life, as computed from the time of fry emergence. They remain in the ocean feeding areas for from 1 to 4 years and, with the onset of maturity, turn back again to coastal waters and to their natal stream.

In a number of river systems there occur "races" of sockeye which spawn in streams without associated lakes. In some of these cases the fry may drop down directly to the sea. Among returning adult fish there are found individuals with no freshwater period of residence indicated on the scales. Thus, they are termed "ocean-type" sockeye. Usually the numbers of such sockeye are small, due, it is presumed, to a heavy mortality of fry in the sea but in one river of the USSR far east, the Kamchatka River, in one year, 1932, (Krokhin and Krogius, 1937b) 81% of the sockeye were of this type. Gilbert (1919, p. 29) reports one "race" or colony spawning at Harrison Rapids—an area of the Harrison River below Harrison Lake—where the sockeye "use gravel-bars in a shallow backwater region of the river where they have no genuine lake conditions at their disposal nor any lake into which the young can drop back after hatching. They have adopted, therefore, the highly exceptional method . . . of dropping down to salt water as soon as they are free-swimming . . . and it is clear that before man disturbed the balance of nature, enough survived to keep the colony in a flourishing condition." Ward (1921, p. 241) refers to a tributary (Clear Creek) of the Copper River, Alaska, which has a sockeye run of considerable size but on which "there is no lake at any point along the part of the course that was visited. . . . Throughout the more swiftly flowing section of the stream, salmon were abundant."

Rather conflicting and puzzling evidence is provided by experiments conducted at the Port John sockeye study area (see page 135). Here all the sockeye fry produced naturally in the main sockeye spawning stream (Tally Creek, Fig. 39), and captured at the counting weir on downstream migration to the lake, were placed in shipping cans and transferred to the estuarial area of Hooknose Creek. The purpose was (FRBC, 1961, p. 99) "to explore the possibility of promoting rapid growth and obviating freshwater mortality by acclimating the fish to a low-salinity environment." All other sockeye migrating seaward from the watershed and captured, as smolts, at the weir at the mouth of Hooknose Creek, were distinctively marked for recognition upon their return as adults. "Since," as reported (FRBC, 1961) "few unmarked sockeye have returned to Hooknose Creek in the years up to and including 1960, it seems clear that the young fish did not survive well under the changed environmental conditions."

In Kamchatka, particularly in the Bolshaya River on the western coast (Semko, 1954a) and in the Kamchatka River on the eastern seaboard (Krogius, 1958) the young sockeye, hatched in the "spring" areas, do not go to sea as fry but remain for a year in the backwater lagoons and in pools in the streams. In some areas, i.e., the Paratunka River, on the southern east coast of the Kamchatka Peninsula, the young sockeye native to the "springs" stay in the river "less than a year but sometimes for several months" (Krogius, 1958, p. 61).

On the scales of the fish the life pattern is clearly portrayed, both for freshwater and marine periods of residence (Fig. 1). Throughout the year circuli or sclerites,

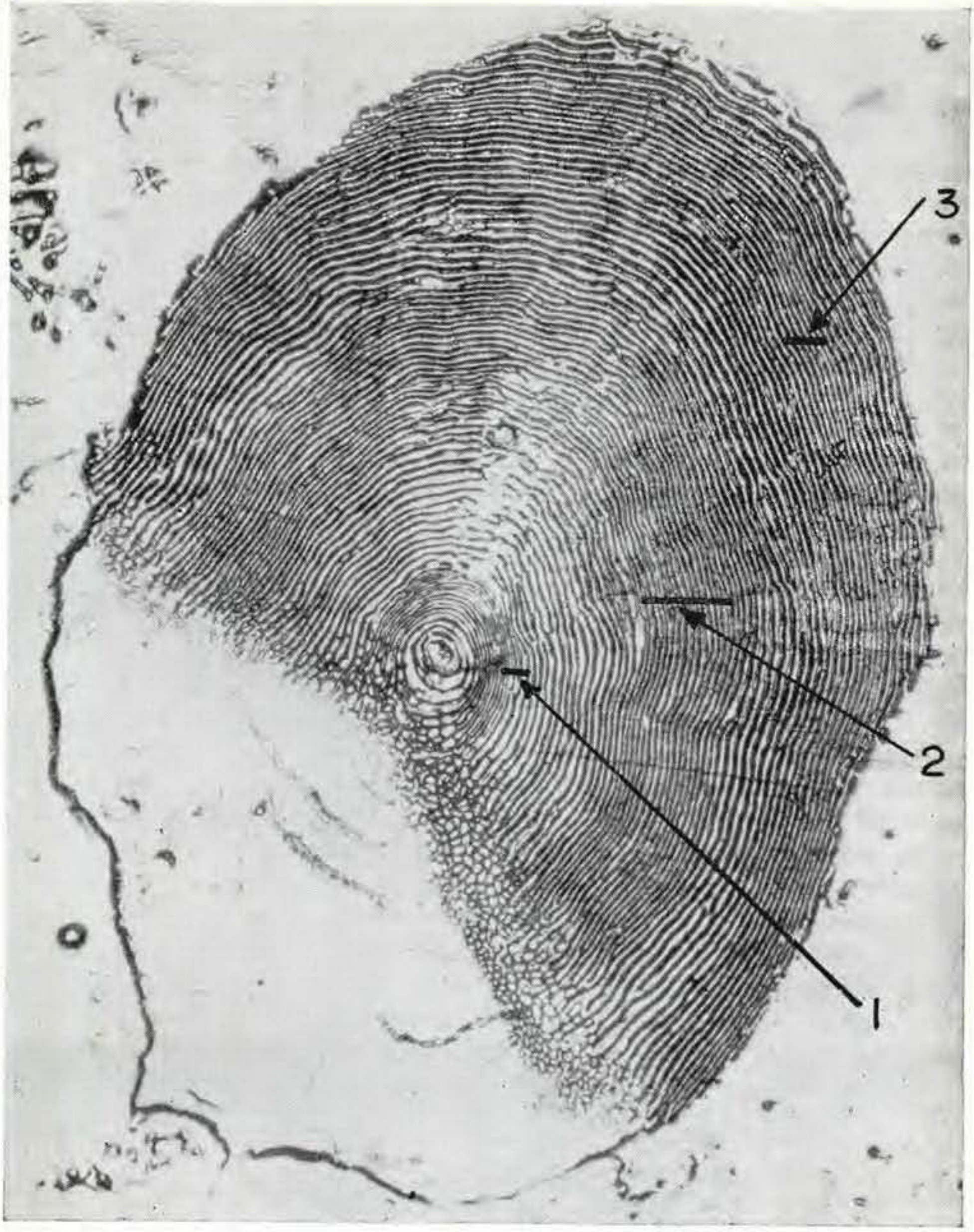

FIG. 1. A scale from a sockeye salmon, age 4_2, to show the freshwater nuclear area and the narrow winter bands or annuli denoted by the compactly packed circuli (1–3).

which look, under the microscope, like ridges, are laid down on the scale (Neave, 1936). In summer when growth is relatively rapid, these circuli or sclerites are widely separated but in winter when growth is slower they are more closely packed, forming "bands" as it were, the so-called "winter bands." By counting these latter on a scale one can determine the number of years of life. Furthermore, since growth in fresh water is appreciably less rapid than in the ocean, the circuli laid down during residence in lake or stream are more delicate, more compacted, and thus quite readily distinguished from those formed during sea life.

It is possible, then, by examining the scales, to ascertain how long a young sockeye stayed in fresh water before proceeding to sea and how long it spent in the ocean and, thus, the age. By selecting the scale from a specific area on the side of the fish where it has been found that the most uniform and reliable relationship exists between growth of scale and growth of fish (body length), the amount of growth per year can be readily computed (see page 354). Scales taken in the first row above the lateral line and in the area directly under the dorsal fin are generally acceptable. A survey of the literature reveals that the age at maturity of sockeye may vary from 2 to 7 years and that the time spent initially in fresh water may range from 0 to 4 years.

Actually the reading of the scales for age determination is relatively simple in comparison with the confusion which has been created in setting up a technique for expressing the age as and when read. One has to be very careful that one fully understands just what the symbols which are used mean. Three methods are currently in use. They are

1. An early European technique, used for Atlantic salmon, in which a large Arabic numeral denotes the total age in years, i.e., the number of annuli, and a smaller subscript Arabic numeral indicates the number of years (annuli) in fresh water. Thus, a sockeye with one freshwater annulus and two ocean annuli would be designated as 3_1.
2. A system devised by Gilbert and Rich (1927, p. 32–33) as an improvement on the European method, in which the large Arabic numeral denotes the actual year of age in which the adult is taken, while the small subscript Arabic number relates to the year of age when the young fish went to sea. Thus, a sockeye with one freshwater annulus and two ocean annuli would be designated as 4_2. The fish was in its 4th year, having gone to sea in its second.
3. A method used by Europeans for Atlantic salmon in which a decimal mark separates the number of years spent in fresh water from the number of years spent in the sea. Thus, a sockeye with one freshwater annulus and two for ocean residence would be designated at 1.2. The numeral in front of the decimal represents the freshwater period; that coming after the decimal relates to the ocean phase. This system is now commonly used by the Fisheries Research Institute of the University of Washington in its Alaskan studies (F.R.I., 1960).

The Gilbert technique (No. 2 above) has been generally accepted along the North American Pacific coast except by the Fisheries Research Institute, as just noted. It will be used in this treatise. In the USSR, for both Atlantic and Pacific salmon, the early European method is still in use. In order that there be no confusion as to the age-groups dealt with, Table 1 shows all the age-classes thus far recorded for sockeye of the North Pacific region, according to the three systems.

TABLE 1. Growth patterns observed among anadromous sockeye, and their designations in the three commonly used notation systems.

Particulars of growth pattern		Age, as designated in		
Proceeds to sea	Ocean residence	Canada	USSR	Alaska
As fry	2 years	3_1	2_0	0.2
As yearling	1 "	3_2	2_1	1.1
As fry	3 "	4_1	3_0	0.3
As yearling	2 "	4_2	3_1	1.2
After 2 years in lake	1 "	4_3	3_2	2.1
After 3 years in lake	0 "	4_4	3_3	3.0
As fry	4 "	5_1	4_0	0.4
As yearling	3 "	5_2	4_1	1.3
As 2-year-old	2 "	5_3	4_2	2.2
After 3 years in lake	1 "	5_4	4_3	3.1
As fry	5 "	6_1	5_0	0.5
As yearling	4 "	6_2	5_1	1.4
As 2-year-old	3 "	6_3	5_2	2.3
After 3 years in lake	2 "	6_4	5_3	3.2
After 4 years in lake	1 "	6_5	5_4	4.1
After 2 years in lake	4 "	7_3	6_2	2.4
After 3 years in lake	3 "	7_4	6_3	3.3
After 4 years in lake	2 "	7_5	6_4	4.2
After 3 years in lake	4 "	8_4	7_3	3.4
After 4 years in lake	3 "	8_5	7_4	4.3

Although representatives of many of the above age-groups may be found in the sockeye runs to any river system, the most common ones encountered in the various important rivers (see Fig. 2), in order of importance, are given below.

Columbia River—4_2, 3_2. Normally the 4_2's make up over 90% of the run each year but in some years, e.g., 1953 (Anas and Gauley, 1956, p. 17) the 3_2 fish may predominate.

Fraser River—4_2, 5_3, 5_2, 3_2. The 4_2 age-group greatly predominates.

Skeena River—4_2 and 5_2, 5_3, 3_2. Normally either the 4_2 or 5_2 fish predominate in varying degree. For example, in 1947 the 4_2 age-group represented 14% and the 5_2—82%, whereas in 1948 there were 80% 4_2's and 13% 5_2's. On the other hand, the representation may be less marked, e.g., 1953—48% 4_2's and 43% 5_2's; or 1954, 33% 4_2's and 54% 5_2's (Foskett, 1956, p. 37). Very few 3_2 fish are taken in the gill-net fishery because of their small size but they frequently appear in goodly numbers on the spawning grounds.

Nass River—5_3, 4_2. Normally the 5_3 fish predominate. From the Nass River north the sockeye tend to spend a 2nd year in fresh water due, presumably, to slower growth in the colder lakes.

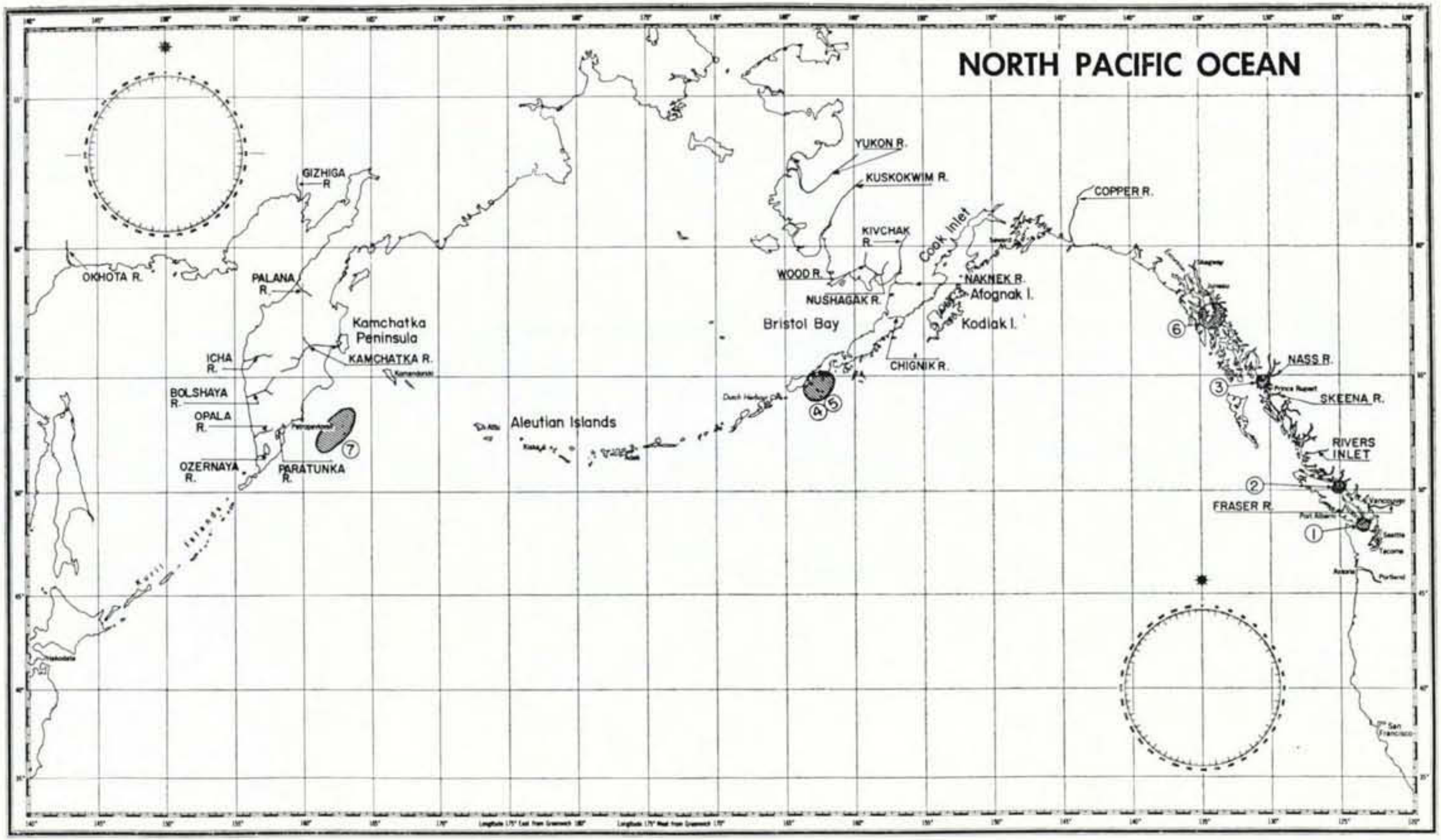

FIG. 2. The north Pacific Ocean, showing the general locations of tagging experiments 1–8 referred to in the text. The INPFC taggings—no. 8, p. 16—embrace the whole area of the north Pacific from Kamchatka to the Gulf of Alaska and on both sides of the Aleutian Island chain.

Karluk River—5_3, 6_3, 6_4.
Naknek—Kvichak—6_3, 5_2, 5_3. Average of 37 years.
Kvichak—4_2 dominant. 1956, 1960.
Egegik—6_3, 5_3, 5_2. Average of 25 years.
Ugashik—5_3, 6_3, 5_2. Average of 27 years.
Nushagak—5_2, 4_2, 6_3, 5_3. Average of 32 years.
Wood River—4_2 and 5_2 dominant.
Kamchatka—5_1, 4_1, 5_2. One year, 1932.
Paratunka—4_2, 5_2, 5_3. Average of 2 years (1932–33).
Ozernaya—5_2, 6_3, 5_3, 4_2. Average of 3 years (1930–32).
Ozernaya—6_3, 5_3, 6_4, 7_4. Average of 20 years (1940–59).
Bolshaya—5_2. Average of 2 years (1929, 1932).

The above data are taken from the following sources: Karluk River (Rounsefell, 1958a); Naknek—Kvichak, Egegik, Ugashik, Nushagak (Eicher, MS, 1957); Kvichak, Wood River (F.R.I. 1963); Kamchatka, Paratunka, Ozernaya, Bolshaya (Krokhin and Krogius, 1937b); Ozernaya (Egorova et al., 1961).

The periods of residence of the sockeye in fresh water and in the ocean have a bearing on survival and on the time of return, as will be indicated in later sections of this Bulletin. These, in turn, have much significance in calculating the returns from known spawnings and in devising appropriate management programmes.

MIGRATION OF SOCKEYE SALMON FROM OCEAN TO RIVER

As sockeye move in from the ocean to the coastal rivers in which they will spawn, they become the object of an extensive and intensive commercial fishing effort. Until recent years this fishery took place in coastal areas, in the passages between islands and in the river estuaries themselves. It is important to know where the sockeye caught in each individual area are going, i.e., to which river they are bound, and through what waters they pass in getting there. This information makes known, on the one hand, the contribution which each river makes to the fishery and, on the other, the extent to which each river's spawning run is reduced by commercial exploitation. A study of the migratory patterns of the salmon, as they moved along the coast and into the rivers, was thus an early objective of investigation.

TAGGING METHODS

The first tagging experiment was conducted in 1918 (O'Malley and Rich, 1920) in Juan de Fuca Strait, through which sockeye salmon passed en route to the Fraser River and other smaller streams emptying into the Strait of Georgia and Puget Sound. A "bachelor button" type of tag was used, which was attached to the upper lobe of the caudal fin of sockeye taken alive from salmon traps at Sooke and elsewhere. Each tag bore a number. Thus, upon recovery of a tagged fish, the place and date of tagging could be determined and its route of migration and the time of passage ascertained.

In later taggings an aluminum strap tag (cattle tag) was used. This was affixed, by special pliers, to the upper lobe of the caudal fin, preferably in the area where the skin extends over the bases of the fin rays. This type of tag was readily procurable and easy to apply without appreciable effect on the fish. It was used for many years in Alaska (Gilbert, 1923; Gilbert and Rich, 1925; Rich, 1926, 1932; Rich and Suomela, 1927; Rich and Morton, 1929) and in British Columbia (Bolton, 1930; Williamson, 1927).

One disadvantage of the caudal strap tag was the fact that it was not very conspicuous on fish in the rivers, either on live or dead specimens. Furthermore, on the spawning grounds, where the caudal fin is used a great deal and is subject to considerable wearing away, the chances of the tag being torn off or lost were great. For these reasons a new tag was utilized when the International Pacific Salmon Fisheries Commission commenced, in 1938, its extensive and intensive study of the Fraser River. A "Petersen" disk tag was adopted. This tag was originally used by Petersen in 1894 on European plaice and consisted of two bone disks connected together by a silver wire. Over the years disks of various materials had been used—bone, brass, ebonite, celluloid—and of various colours and sizes. For the Commission's tagging a new type of disk was employed—of white celluloid, 13.5 mm in diam., and with a red spot on one side 7 mm in diam. When affixed to a fish the red spot was put on the outer side. These "bull's-eye" tags were quite conspicuous, both on the silvery, fresh fish and on mature individuals with dark or bright red colouring, and were easily seen on live and dead fish.

Petersen-type disk tags have since been used extensively along the Pacific coast of North America for many years. They have varied greatly in colour and in size. Recoveries have been very satisfactory. However, more recently a new tag has been tried in high-seas tagging, a "spaghetti-type" tube of plastic (polyethylene) which is threaded through the dorsal part of the fish in the vicinity of the dorsal fin and then knotted, or the ends sealed with a special clamp. In high-seas or open ocean tagging, many immature salmon are tagged and the tag must allow for 1 or more years' growth of the fish prior to recovery. This the spaghetti tag will permit much more readily than the Petersen disk tag.

In the western Pacific, tagging by the Japanese Fisheries Agency has been undertaken. Initially, a single tag was used consisting of a coloured celluloid round or oval plate attached to the fish by a fine silver or copper wire around its caudal peduncle. More recently, however, a new tag has been developed and tried out, a "pendant" tag. It consists of a coloured plastic disk attached to a short length (1–2 inches; 2–5 cm) of nylon thread. This, in turn, is attached to a barbed pin which can be thrust into the back of the fish behind or in front of the dorsal fin and held firmly by the bones at the base of the fin. The true effectiveness of these tags has not been clearly established since, in the high-seas tagging work to 1960, salmon caught in gill nets were used, fish whose subsequent survival cannot be assured because of the varying delayed effects of the gilling and threshing about in the nets for varying periods of time prior to release. Since 1960, sockeye caught by longline gear have been used for tagging, with much greater success.

MIGRATION ROUTES

Sockeye salmon are taken commercially chiefly by nets, either traps, seines or drift gill nets. They are but rarely caught by trollers since they do not often take artificial lures. Therefore, only fish from trap or seine catches have normally been used for tagging experiments. This has, in consequence, limited the tagging operations to coastal waters until recently and thus the earlier taggings indicated only the coastal and inshore movements of the fish.

The main findings of the various sockeye tagging experiments (see Fig. 2 for general location) are briefly reviewed to show the general movements of the fish from point of tagging to point of recapture:

1. In 1918 a tagging of 831 sockeye was conducted at the traps at Sooke, south end of Vancouver Island (O'Malley and Rich, 1920). A recovery of 147, or 17.7%, was obtained. A definite migration route eastward through the Juan de Fuca Strait to the Washington coast was indicated, then northward through Rosario Strait, past Point Roberts to the Fraser River. Three tagged fish were taken up the Fraser River.

2. In 1925, a tagging of 519 sockeye was conducted at Deep Water Bay, at the southern end of Johnstone Strait (Williamson, 1927, p. 298) of which 260 were normal fish, i.e., had not had their olfactory organs tampered with. From the recovery of 65, or 25%, it was found that 91% moved southward to the Fraser River.

3. In 1925, a tagging of 659 sockeye was undertaken at Haystack Island, near the entrance to Portland Inlet, in the northern British Columbia coastal area (Williamson, 1927, p. 286). The recovery of 135, or 20%, revealed that 65% proceeded on up Portland Inlet (most of them taken in the Nass River fishery), 10% moved southward to the Skeena River and 20% went northward to Alaskan areas.

4. In 1922 a tagging of 4000 sockeye was undertaken in waters along the southern coast of the Alaska Peninsula, from the Shumagin Islands to Ikatan Bay (Gilbert, 1923). The 709 recoveries (18% of the tagged fish) indicated that (a) a very limited number moved eastward, thus suggesting that a fishery here would have little effect on the salmon supply of the Chignik, Karluk, and Cook Inlet fisheries, (b) the vast majority of the fish belonged to a definite westward migration which was bound for the streams emptying along the Bering Sea shores of the Alaska Peninsula and in Bristol Bay, and (c) salmon tagged from the same trap at Unga Island scattered to more than 20 different streams, ranging from Cook Inlet on the south to the Kuskokwim and the mouth of the Yukon in the far north.

5. In 1923 a tagging on the southern side of the tip of the Alaska Peninsula, similar to that summarized in 4) above, was repeated, (Gilbert and Rich, 1925). Of 9122 fish tagged, a recovery of 3296, or 36.13%, was made. The results confirmed the findings of the previous tagging, thus indicating that the migration in 1922, a year when the Bristol Bay run was exceptionally heavy, was relatively typical for the areas studied.

6. In the years 1924, 1925, 1926, 1927, and 1928, tagging experiments were conducted in southeastern Alaska waters (Rich, 1926; Rich and Suomela, 1927;

Rich and Morton, 1929). These were designed to define the route of migration of the sockeye (Alaska red salmon) coming in from the ocean to the various east-west passages, and from thence through the coastal passages among the islands to the inlets and bays and the streams emptying into them. In general, (a) mixed populations of sockeye were found in the outer channels with a fair degree of to and fro movement, (b) in the inner channels migration could be to the north or south, with much to and fro movement within the inner channels, and (c) as the fish penetrated closer to the coastal inlets there was a greater segregation or coming together of the fish bound for particular river systems or streams.

7. For the Asiatic side of the North Pacific there are available to us only the results of Japanese tagging experiments. Of those conducted from 1917 to 1942, chiefly off the coast of Kamchatka, the results have been summarized by the Japanese Fisheries Agency (INPFC, 1955):

> "A scrutiny of some 250 returns of tagged fish liberated on the Kamchatka coast has indicated that the sockeye salmon which emerge from the east around Cape Kronotskii turn either north or south. . . . Generally speaking, the northerly course would be taken in the early half of the season from the end of May through June, whereas the southerly direction is followed in the latter half from July to the beginning of August. . . . A majority of the northern migrants proceed up to the Kamchatka rivers, the rest heading further north. The southern group, coasting down to the northern tip of the Kurile Islands, turns around to the Okhotsk shore of the peninsula, then ascends streams such as the Opala, Koshogochek, Yavina, Ozernaya, and Icha Rivers."

Taguchi and Nishikawa (1954), after further study of the taggings on the east coast (1936–41) and west coast (1937–38) of Kamchatka, have shown that on the east coast the movements of sockeye are mainly northward prior to mid-June and thereafter decline sharply while the southern migrations increase. On the west coast, however, the migrations are principally northward up the coast.

8. As part of the research program of the International North Pacific Fisheries Commission to reveal the high-seas distribution and migration of sockeye, tagging experiments were undertaken by both Japan and the United States.

In 1956 and 1957 there were tagged from Japanese vessels 627 and 621 sockeye, respectively. No returns from the 1956 tagging have been reported. Of the 1957 tagging, 11 recoveries were made, 6 of them on the high seas in Bering Sea and 5 in Bristol Bay. These latter, all tagged in areas north of the Aleutian Islands Chain (one at approximately 176°W, 52°30′N, 2 around 169°20′W, 55°15′N and 2 around 168°45′W, 55°45′N), indicated a northeasterly migration from the high seas to Bristol Bay coastal areas (INPFC, MS, 1957).

In 1955, from United States vessels there were tagged 298 sockeye, of which 47, or 15.8%, were recovered (INPFC, 1956, p. 59). The taggings were in coastal waters, just outside the fishing areas, and the recoveries were, in general, relatively local.

The results of the 1956 and 1957 taggings in the North Pacific may be tabulated as follows (from INPFC, Annual Report, 1958):

	1956	1957
Total no. tagged	3403	1949
No. of immatures	1572	1074
No. of mature fish	1830	875
No. of recoveries, 1956	100[a] or 5.5%	
No. of recoveries, 1957	29[b] or 1.8%	53[c] or 6.1%
Recoveries in high-seas fishery, 1956	1 or 0.05%	16 or 1.8%
Recoveries in high-seas fishery, 1957	16 or 1.0%	16 or 1.8%
Recoveries in American estuaries, 1956	99 or 5.4%	
Recoveries in American estuaries, 1957	13 or 0.8%	37 or 4.2%
Recoveries in Asian estuaries	Nil	Nil

[a] Based on matures tagged in 1956.

[b] Based on immatures tagged in 1956 and recovered in 1957.

[c] Based on matures tagged in 1957.

Tagging was conducted along the entire length of the Aleutian Chain and well offshore north and south, as well as in the Pribilof Island area. Most of the tagging was done east of the 180° International Date Line (all in 1956 and 58% in 1957). A comparison of the 2 years' findings indicates that, while in 1956 99% of the recoveries of mature fish were made in North American coastal areas, only 71% were made in these waters in 1957. This may have been due, in large part, to the fact that in 1957 the large body of westward-moving mature sockeye which, in 1956, was encountered off the southeast end of the Aleutian Chain (i.e., in the area south of Umnak and Unalaska islands) was practically nonexistent.

The purpose of this brief review of tagging experiments has been to try to connect up the movements of sockeye from high-seas or open-ocean feeding grounds to coastal areas, and thence to the rivers; and thus to dispel the idea held by earlier salmon authorities that, if salmon returned to the stream in which they had been bred, it was only because they did not, while in the ocean, go far from the river's mouth and not beyond its influence. This belief the data do not support. It is now clearly evident that not only do the sockeye go far, both in coastal waters and out to sea, from their natal river mouth but the stocks of salmon from many rivers intermingle in the oceanic pastures during much of their ocean life. Subsequently, as they approach maturity they return to coastal waters, many "races" or separate river populations travelling together, and there they disperse, each to seek out its particular parent stream.

This seems to be a reasonable hypothesis but there is required much more high-seas tagging to provide the proof, especially for sockeye from Canadian Pacific rivers. As the tagging operations for the solution of the International North Pacific Commission's problems are continued by the United States, Japan, and Canada, more pertinent data will become available. Quite irrespective of the Commission's requirements, however, this information should be extremely valuable for Canada and the Canadian salmon industry. With a fuller knowledge of the whereabouts of sockeye from Canadian rivers in the ocean during their several years' residence there, it may become possible, with appropriate oceanographical observations, to arrive at a better understanding of the feeding and growing conditions during the ocean period of the life cycle of the fish and thus be able to predict more closely the probable survival and return from known brood years.

THE PARENT STREAM THEORY

The return of Pacific salmon to spawn in the very same spot where they were hatched is one of the most striking features of its life history. It has been even thus expressed: "So powerful is the homing instinct of the salmon that it persists even in species which have been landlocked over the ages, and which have lost the habit of ever leaving fresh water for salt" (Shultz and Stern, 1948, p. 10).

The opposite view has also been supported. At one time Cloudesly Rutter (1903) emphatically stated that "it is incredible that the salmon remember their native stream during 2 to 3 years of ocean life and that they consciously seek it when they desire to return to fresh water." Even the eminent fisheries authority David Starr Jordan (1925, p. 306) remarked that "it is the prevailing impression that the salmon have some special instinct which leads them to return to spawn on the same spawning grounds where they were originally hatched. We fail to find any evidence of this in the case of the Pacific salmon and we do not believe it to be true."

Since then, many studies have been conducted and much evidence has been compiled. All of it substantiates that, for all species of Pacific salmon, there *is* a definite return of adult fish to the natal stream or, if the eggs be transferred to a different area for hatching and liberation, to the new locality.

EVIDENCE SUPPORTING THE THEORY

From his early studies of the sockeye runs to the Fraser and other major river systems of British Columbia, Dr Charles H. Gilbert (1914–25) had detected certain differences between the runs of sockeye to the various rivers—in age-classes, time of arrival each year, and scale pattern. These differences were so consistent year after year that to him they suggested the return of these populations to their own particular river. Furthermore, even within a river system, sockeye with distinctive characteristics appeared to occur. He states (1918, p. 37):

> "To one who watches pass before his eyes this procession of types possessing a certain uniformity, who detects, as it is so often possible, the advance skirmishes of the next invasion when they make their first appearance during a transition period, who watches the new type becoming the dominant one and the old form soon represented by only a few stragglers—to such an observer the connection seems inescapable that the run consists of a number of sub-races, each bound to its own spawning area within the Fraser basin. . . . If this theory be true, not only do sockeye salmon return to their own river-basin at maturity, they predominantly return to the particular part of the river-basin in which they were reared as fingerlings, in which case their homing instinct is far more rigid in its workings than heretofore has been accepted."

MARKING OF YOUNG SOCKEYE SALMON

Marking of salmon, by applying suitably distinctive marks to the young fish at or prior to the time of seaward migration, makes possible the identification of the fish wherever encountered in the sea or during the spawning migration. It makes possible the recognition of the adult fish when they return to the stream where they were marked and liberated.

Ideal and incontrovertible evidence of the movement of salmon from river to sea and return to the river again would be provided by (1) the capture of marked individuals at sea, (2) the tagging of them, and (3) their subsequent recapture in the coastal fishery, the river estuary or, preferably, on the spawning grounds. Unfortunately, the capture and tagging of a marked salmon at sea is a very rare occurrence, due to the very few marked salmon likely to be encountered during a tagging programme. It has never occurred for sockeye. It has been reported only once, in connection with a pink salmon tagging experiment in the Strait of Georgia–Puget Sound area (Pritchard, 1943, p. 9). Two marked adults came into taggers' hands as they migrated into coastal channels from the sea, were tagged and subsequently recovered in the natal stream. These recoveries served to confirm that pink salmon go to sea and return to the natal stream.

For sockeye, however, we can accept only indirect evidence. While Cobb (1917, 1921, 1930) has referred to early marking experiments as "a favourite recreation for quite a number of Pacific coast people" it has been actually a serious endeavour to elicit the facts.

One of the earliest, if not *the* earliest, sockeye marking experiments was conducted at the Fortmann Hatchery on the Naha River in Alaska in 1903 (Chamberlain, 1907, p. 66), when 1600 fry were marked by excising both ventral fins with fine, curved scissors. In 1906 two adult sockeye with ventral fins lacking appeared at the hatchery and in 1907 seven more. In addition between 50 and 100 adult sockeye with ventral fins missing were reported from the spawning beds of Yes Bay, some 10 miles further up Behm Canal than the Naha, but, according to Marsh and Cobb (1911, p 26), the authenticity of these, as properly marked individuals, is in question. The fact that 10 specimens having the 1903 mark were reported (Marsh and Cobb, 1911, p. 26) in 1910 from Yes Bay, which would place these specimens in their 8th year, casts doubt on the Yes Bay reports, especially since one of the fish when caught, a male, was only 20.5 inches in length. This obviously could not be an 8-year sockeye. Proper marking of sockeye fry is a very delicate operation and seldom resorted to because of the difficulties and the probable very high mortality due to handling. Nevertheless, if the nine marked adults reported by Chamberlain from the Fortmann Hatchery were authentic marked fish, which he believed, then the recovery does indicate a definite return to the parent stream.

Rather interesting marking experiments were also conducted on the Columbia River (Holmes, 1928, p. 646–648). These had to do with the importation, by the Oregon Fish Commission, of sockeye eggs from Alaska in an effort to build up the runs of Columbia River sockeye, or "bluebacks" as they are locally called. Importation of eggs, their incubation in Columbia River hatcheries, and liberation of the young fish commenced in 1910 and was carried on for a number of years. It was found, in due course, that no adult fish were returning to those tributary streams in which they had been released. The question, therefore arose: Did the marked fish, of Alaska origin, return to the Columbia but seek out other tributaries than those in which they had been planted, did they return to some other river system than the Columbia, or did they survive at all in the ocean?

In 1916 a release of 50,000 marked year-old sockeye of Alaska origin was made. Marked adults returned to the Columbia in 1918 and 1919 as 4- and 5-year fish. Subsequent experiments confirmed this. It was therefore concluded that: "there has been a distinct tendency on the part of the adult fish to return to the place of liberation. What straying has occurred has been mainly to the tributaries in the vicinity of the one in which the yearlings were liberated." This, it must be emphasized, had reference to sockeye eggs transferred from Alaska, the young fish being reared and released in tributaries of the Columbia.

In the Karluk River area of Kodiak Island, Alaska, several sockeye (Alaska Red) marking experiments were conducted in the period 1926–35 (Barnaby, 1944). These were initiated primarily to determine the survival rate of sockeye during ocean residence. They also, of course, substantiated the return of the marked fish to the natal stream after 2- or 3-years' residence in the sea. The grouped data for all of the experiments wherein the adipose and left, right, or both ventral fins had been removed gave a return of 17.4% for "3-freshwater" fish (those leaving the lake at the start of their third growing season) and 25.7% for "4-freshwater" individuals. No recoveries in any areas other than Karluk were reported. No information is available as to ocean recoveries which might indicate the marine feeding grounds of these fish, or the extent and direction of the return migration to the Karluk River.

With regard to the return of sockeye to the more or less precise area of incubation of eggs, hatch, and emergence of fry, reference may be made to experiments conducted by the Fisheries Research Board of Canada at Cultus Lake, British Columbia (Foerster, 1936b). Cultus Lake is a natural sockeye spawning area tributary to the lower Fraser River (Fig. 5 and 6) and for many years (1925–38) was used as a test area for sockeye salmon propagation studies. In the years 1930 and 1931 all the young sockeye migrating from the lake were marked by removal of both pelvic fins (in 1930) or both pelvic fins and the adipose (in 1931).

Recoveries of returning marked adults were expected in 1932, 1933, and 1934. In order to obtain a record of those taken by the extensive fishery, extending, as shown in Fig. 3, from the Swiftsure Banks in the open Pacific, through the Juan de Fuca Strait, the San Juan Archipelago, and the Strait of Georgia to the Fraser River, observers were stationed in each canning centre to scan all sockeye entering the canneries and to segregate the marked individuals. On the Fraser River, however, eight canneries were operating and, as it was not feasible to post an observer in each nor to have the local observer visit all canneries when sockeye were being landed, it became necessary to enlist the cooperation of fishermen and cannery employees to watch for and put aside marked fish for subsequent examination by the observer. Rewards were paid for each marked fish so set aside. In 1934, when only 5th-year marked sockeye were expected to return, observers were located only at certain "key" canneries. The proportions of marked fish to unmarked in the landings observed at these "key" canneries were accepted as an index of the probable total occurrence of marked sockeye throughout the fishing areas and the latter calculated on the basis of total landings.

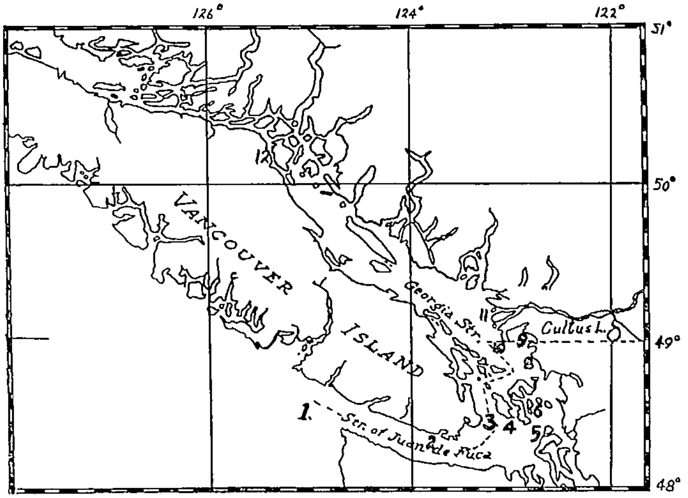

FIG. 3. Map of northwestern British Columbia and Washington showing the principal fishing grounds traversed by sockeye salmon migrating to the Fraser River. The numbered areas are: 1—Swiftsure Banks; 2—Sooke salmon traps; 3—Salmon Banks; 4—Iceberg Point; 5—local fishing banks off Whidby Island; 6—Rosario Strait; 7—Lummi Island; 8—Birch Bay; 9—Boundary Bay; 10—Point Roberts; 11—Fraser River and estuary; 12—Deepwater Bay, Johnstone Strait. (From Foerster, 1936a, p. 28.)

We are here interested primarily in the place of recovery of these marked Cultus Lake sockeye. From Table 2 wherein are set down the numbers of recoveries per week for 1932 and 1933 (as taken from Foerster, 1936b, p. 38,39) it will be seen that these fish were recaptured all the way from Swiftsure Banks to the Fraser River. In addition, 85 marked sockeye were taken in 1933 by cannery personnel from landings, at the Quathiaski Cove cannery, of salmon caught in Johnstone Strait, chiefly at Deepwater Bay. From as far out into the Pacific as the commercial sockeye fishery was conducted, Cultus Lake sockeye were taken, thus attesting to the fact that these fish were resident, during the marine period of their life cycle, in the ocean well beyond the influence of the water from Cultus Lake, if not from the Fraser River itself. On their return migration from the ocean they come in, along with many other populations of sockeye, bound for other tributaries of the Fraser and for certain streams in Puget Sound. There is as yet no definite proof that the Fraser River sockeye and those from Puget Sound streams, which go out to sea and return through the Juan de Fuca Strait, do not remain in the ocean water off the entrance

TABLE 2. Recoveries of 4_2 and 5_3 marked Cultus Lake sockeye during the 1932 and 1933 fishing seasons, arranged according to date and area of recovery (Fig. 3).

Date (week ending)	Fishing areas													
	(1) + (2) Swiftsure Banks Sooke Traps		(3) Salmon Banks		(4–6) Iceberg Pt. Whidby I. Bank Rosario Strait		(7 + 8) Lummi I. Birch Bay		(9 + 10) Boundary Bay Pt. Roberts		(11) Fraser River		Cultus Lake	
	1932	1933	1932	1933	1932	1933	1932	1933	1932	1933	1932	1933	1932	1933
July 16	–	1	–	5	–	–	–	–	–	1	–	0	–	–
July 23	–	3	–	1	–	–	–	–	–	0	–	3	–	–
July 30	12	5	4	11	1	–	–	–	1	0	–	0	–	–
Aug. 6	21	29	46	9	5	9	20	4	44	6	–	2	–	–
Aug. 13	18	149	44	73	8	23	17	81	46	23	–	10	–	–
Aug. 20	48	290	124	477	22	125	67	177	39	119	18	23	–	–
Aug. 27	57	294	43	514	16	297	41	202	117	468	52	34	–	–
Sept. 3	58	869	39	938	13	217	89	130	36	35	70	84	–	–
Sept. 10	13	177	–	900	2	137	14	26	6	256	88	255	–	–
Sept. 17	1	20	–	64	–	–	–	–	–	32	129	319	–	–
Sept. 24	1	18	–	0	–	–	–	–	–	27	244	169	–	–
Oct. 1	–	9	–	7	–	–	–	–	–	5	166	288	–	8
Oct. 8	–	–	–	10	–	–	–	–	–	–	26	160	–	72
Oct. 15	–	–	–	–	–	–	–	–	–	–	3	96	–	75
Oct. 22	–	–	–	–	–	–	–	–	–	–	1	129	–	306
Oct. 29	–	–	–	–	–	–	–	–	–	–	2	55	5	610
Nov. 5	–	–	–	–	–	–	–	–	–	–	13	40	20	254
Nov. 12	–	–	–	–	–	–	–	–	–	–	5	6	78	216
Nov. 19	–	–	–	–	–	–	–	–	–	–	1	–	113	443
Nov. 26	–	–	–	–	–	–	–	–	–	–	1	–	260	679
Dec. 3	–	–	–	–	–	–	–	–	–	–	–	–	394	105
Dec. 10	–	–	–	–	–	–	–	–	–	–	–	–	396	73
Dec. 17	–	–	–	–	–	–	–	–	–	–	–	–	301	10
Dec. 24	–	–	–	–	–	–	–	–	–	–	–	–	123	5
Dec. 31	–	–	–	–	–	–	–	–	–	–	–	–	58	–
Jan. 21	–	–	–	–	–	–	–	–	–	–	–	–	17	–
Total:	229	1864	298	3009	67	808	248	620	289	972	819	1673	1765	2856

to the Strait. The general opinion is, however, that these fish, after entering the Pacific Ocean, proceed northwestward and mingle with sockeye from many other North American river systems in a vast, general feeding ground in the Gulf of Alaska and south of the Aleutian Islands. This is discussed more fully in the section on "distribution of sockeye in the sea," (p. 329). We must await further tagging operations in the high-seas areas of the North Pacific, however, to provide the necessary evidence on where the sockeye spend their 1 to 3, rarely 4, years of ocean residence feeding, growing, and maturing.

The general results of the experiment are tabulated in summarized form below:

	First experiment 1930–33	Second experiment 1931–33
No. of seaward migrants marked	104,061 (in 1930)	365,265 (in 1931)
Total adults returning to Cultus Lake	2,511	3,471
Adults marked	1,827	2,864
Adults unmarked	684	607

In 1932 the unmarked adults, if of Cultus Lake origin, would have to be of the 5-year age-group, i.e., spawned in 1927 and migrating to sea in 1929, unmarked. Determination of age from the scales was difficult because of absorption of the outer part of the scales as maturity approached but studies of the length frequencies of the small numbers whose scales could be read for age indicated that most, if not all, of the unmarked individuals were of this age-group, hence probably of the 1927 Cultus Lake generation.

The unmarked adults of 1933, however, if of Cultus Lake origin, would belong to the 3-year age-group, which is generally conspicuous by its small size. These fish are, furthermore, chiefly males. Of the 607 unmarked fish in 1933, 538 were males and 69 were females. Of a sample of 426 actually measured, 409 obviously belonged to the 3-year age-group. The ages of the remaining 17, or 4%, were in doubt. They could have been strays from alien spawning areas or merely individuals which had escaped being marked. In any event the proportion, if representing genuine infiltrations from other areas, is very small. It may be added that a watch was kept at other lower Fraser areas where hatcheries were in operation—Pitt Lake, Harrison Lake, Pemberton Lake—for sockeye bearing the Cultus Lake marks. None was reported.

Again in 1936 all sockeye migrants leaving Cultus Lake—496,232 yearlings and 1366 2-year-olds—were marked by removal of both pelvic fins. In 1938 the adult run consisted of 13,342 fish, made up of:

1603 large males, marked:	7377 large females, marked
70 large males, unmarked:	66 large females, unmarked
3838 small males, unmarked:	388 small females, unmarked

The small unmarked adults were unquestionably 3-year fish which had migrated seaward in the spring of 1937 and were not marked. The large unmarked adults, 1.5% of the large fish, were most likely individuals which had escaped marking in 1936 or whose fins had regenerated.

A planting of "eyed" sockeye eggs in a small stream tributary to Cultus Lake produced most significant and illuminating evidence of the return of sockeye to the place of spawning, incubation, and hatch. In the spring of 1935 approximately 2.7 million "eyed" eggs were taken from the Cultus Lake hatchery and planted in prepared redds in Spring Creek, a small stream which meandered with fairly uniform flow through pasture lands at the head of the lake (Fig. 35). This planting represented 47% of the total egg plant in 1935. Spring Creek had never been to any extent frequented by spawning sockeye in previous years and the bed of the stream was composed of hard compacted shale (upper section) or fine, loose gravel (lower section). Most of the plantings were made in the upper section and it was only with much effort that the shale bottom could be dug up to make satisfactory planting areas.

In 1938, the year of return from those plantings, a total of 2696 adults returned to Spring Creek (Howard, 1948, p. 37, table 21). It was heavily populated, as compared with previous years, and contained 57% of the total lake spawning population. Preparation of redds by the spawning fish was very difficult in the once more hard, compacted shaly bottom. Many fish died unspawned, quite an unusual circumstance for Cultus Lake.

There is no record available of the fry migration from Spring Creek to Cultus Lake in 1939 but it must have been extremely low. It is known, however, that very few adult sockeye returned to Spring Creek in 1942. The stream had reverted again to a very indifferent spawning habitat as in all years but 1938. The evidence, therefore, of (1) a high return in 1938 from the planting of eggs in 1935, (2) the presence of but few spawners in 1939, 1940, and 1941, and (3) again a low population of adult sockeye in 1942 resulting from the poor spawning in 1938, indicated not only a parent stream return to the Cultus Lake area but, further, a tendency to return to the exact tributary stream or location where the fish had been hatched.

The results of these Cultus Lake experiments suffice to confirm the parent stream theory. It is not suggested that it applies rigidly, for inevitably in the biological world exceptions occur. It is sufficiently the rule, however, not only among sockeye but also among the other species of Pacific salmon (and indeed among trout and other species of fish), to be of prime significance in management of the fishery, as referred to elsewhere below.

Marking of sockeye in many other areas amply support the Cultus Lake findings. For example, in 1949 sockeye eggs artificially spawned from a few individuals of the native spawning population of the upper Horsefly River (tributary to Quesnel Lake in the upper Fraser River system, Fig. 6) were incubated, hatched, and reared to fingerling stage in the Quesnel Field Station on Horsefly Lake (IPSFC, 1954, p. 23). In November, 1950, the fingerlings, 94,000 in number, were transported by air to Quesnel Lake and released at the mouth of the Horsefly River. In order to identify these fish upon return as adults, 64,500 of the fingerlings had been marked by removal of adipose and right pelvic fins.

In 1952, 6829 3-year adult sockeye returned to the upper Horsefly River spawning grounds, the place of origin of the eggs taken to the Quesnel Field Station in the fall of 1949. Of this number 2228 were examined (IPSFC, 1954, p. 27) carefully for marks but no marked fish were found. During the same period, 13 3-year sockeye, 9 of which were marked, returned to the rearing-pond outlet in Horsefly Lake, where adult sockeye had never been observed before.

In 1953, 105,000 adult sockeye returned to the upper Horsefly River. Of 46,917 examined for marks, only one was a marked individual. On the other hand, 203 marked and 66 unmarked sockeye returned to the Quesnel Field Station rearing-pond outlet into Horsefly Lake, and 15 marked fish were recovered dead and spawned-out in that area of the Horsefly River lying just upstream from the confluence of the Little Horsefly River which drains Horsefly Lake. A definite return of adults to the place of hatching and early development is indicated, but not to the original spawning area, Upper Horsefly River, where the eggs were collected.

Other transfers of fingerlings, however, conducted by the International Pacific Salmon Fisheries Commission (IPSFC, 1954, p. 28) were not as successful. In one case, eggs collected in 1949 from Seymour Creek, which flows into the Seymour Arm section of Shuswap Lake, were transported by air to the Quesnel Field Station on Horsefly Lake, incubated and hatched, and the young fish reared to the fingerling stage, then flown south in November, 1950, for release (84,000 of them) in Adams Lake where the Upper Adams River enters. A goodly number (30,000) of the fish were marked but no recoveries were subsequently made either in the commercial fishery or in the Adams River system. Similarly a release in Anderson Lake at the head of the Seton Lake system of 193,000 fingerlings reared from eggs of the late Adams River spawning run in 1950 at the Quesnel Field Station failed to produce any returning adults (IPSFC, 1955, p. 34).

On the other hand, "eyed-egg" transplants involving the transfer of stocks from the same areas as above, but with the rearing in yet another watershed eliminated, proved successful (IPSFC, 1955, p. 36). In 1950 a planting of 667,000 sockeye eggs, collected in Seymour River and incubated there to the "eyed" stage, was made to the Upper Adams River. A return of 205 adults was observed in 1954. Though none of these fish was marked and so could not be identified positively, the fact that for many years no sockeye were found in this river strongly suggested that they had resulted from the 1950 planting. They returned, it is stated, to the "exact riffle where the eggs were planted." In 1950 eggs were collected from the Lower Adams River sockeye run and, after incubation to the "eyed" stage, around 300,000 were transferred to and planted in prepared redds in Portage Creek where it flows out of Anderson Lake, Seton-Anderson system. A return of 3505 adults in 1954 suggested that this planting had been successful. None of these adults could be associated positively with the planting but since there were but few native spawners in 1950 and since the returning fish spawned chiefly where the eggs had been planted, the good return, in spite of a heavy commercial fishery on the Fraser River, was believed to be attributable to the planting in 1950.

And, finally, it seems particularly pertinent to refer briefly to tests conducted on kokanee salmon, *Oncorhynchus nerka kennerlyi*, a variety of sockeye (*O. nerka*) which is popularly termed "land-locked." It normally remains in a lake throughout its life cycle, and is usually of very small size when mature, from 7 to 10 inches in length.

In an experiment conducted at Cultus Lake (Foerster, 1947), kokanee eggs collected from a Kootenay Lake spawning area in 1932 were transferred to the Cultus Lake hatchery for hatching and rearing. In the spring of 1934 the product, a total of 63,874 1-year fish, was marked by removal of both pelvic fins and released in the outlet stream of Cultus Lake below the smolt counting weir so that none of the liberated fish could get up into the lake. In 1936 a search for marked adults from this liberation was made in the commercial fishery and, of course, marked specimens were watched for at the Cultus Lake weir. None was recovered. In 1937, however, 25 marked adults were observed in that portion (approximately 34%) of the commercial fishery examined, or an estimated 74 returns in all. At Cultus Lake 17 individuals bearing the appropriate mark were taken.

In the Wenatchee Lake area of the Columbia River, landlocked blueback (sockeye) eggs were collected in the fall of 1944, and transferred, for hatching and rearing, to the Leavenworth Hatchery. This Hatchery is located near the mouth of Icicle Creek, which empties into the Wenatchee River about 20 miles downstream from Lake Wenatchee. In the fall of 1945 some of the reared fingerlings (60,128) were marked and returned to Lake Wenatchee. In the spring of 1946 the remainder (29,129), bearing a different mark, were returned to the lake and liberated. In 1948 recoveries of 302 marked adults from the commercial fishery and 62 from the spawning beds were made, all obviously of 4-year fish (Anon., 1949).

These experiments thus attest, again, to the existence and operation of a parent stream return under rather unusual conditions. Firstly, there was the transfer of eggs to a different area for partial or almost complete rearing and then return to the natal area prior to seaward migration. Secondly, there was the introduction of an entirely different pattern of behaviour, i.e., the migration of the young to the sea, a period of ocean residence and the return upriver to the parent spawning area.

GUIDING FACTORS

Although the ocean life of sockeye, as far as we know it, will be discussed in a later section, it may be appropriate here to consider just how the fish, when they reach the appropriate size or age, turn from their rich oceanic feeding areas and undertake the long trek "home." Only limited information is available concerning, on the one hand, where the fish are in the ocean and, on the other, how they react to whatever physical and chemical stimuli may serve as guides or sign posts during migration.

It has been said (Sumner, 1939, p. 245) that:

> "Unfortunately we are unable to put questions, or at least verbal ones, to our fishes, with any reasonable expectation of receiving replies. But the animals are none the less able to inform us, to a certain extent, regarding their sense impressions. . . . A fish's replies to our questions are given in physiological or behaviouristic terms. . . . It is common sense, rather than scientific experiment, which leads us to believe that the fish is not a mere unconscious mechanism."

At the present time, then, we can only piece together what knowledge we possess and endeavour to draw a picture of what takes place.

We know, for example, that the young sockeye migrate downriver during the spring and early summer. Travelling with the current but at a faster rate, i.e., actively swimming and not merely drifting like a cork, they enter the estuarial areas and from thence pass out to sea. Those from the Fraser River are believed to move (Fig. 3) primarily through the Juan de Fuca Strait, though some may proceed seaward through the northern passage of Johnstone Strait. Once in the coastal waters off Vancouver Island the young fish go with the currents and the drifting plankton food which move (Fig. 78) northeastward along the Pacific Coast (Doe, 1955, p. 21, fig. 12; Fleming, 1955, p 38, fig. 15). As they proceed along the coast they may be joined by other groups of migrants from other river systems, Rivers Inlet, the Skeena, the Nass, etc. Eventually they all end up in the rich feeding areas of the northeast Pacific, perhaps in the waters of the Alaska Gyral or further west (Fig. 4 and 78), south of the Aleutian Islands.

DISPERSAL FROM A COMMON OCEAN FEEDING GROUND

From tagging experiments in the Gulf of Alaska south of Kodiak Island in 1958 (FRI, 1959, p. 17) (see Fig. 2): 1 tagged sockeye was recovered in the Skeena River and 3 were recovered in the fishery which exploits chiefly salmon bound for the Fraser River. In 1959 (FRI, 1960, p. 12) 1 sockeye tagged as an immature in

TABLE 3. Returns reported through Mar. 31, 1963, of sockeye tagged in 1962 by the Fisheries Research Board of Canada in the Gulf of Alaska. Adapted from table 5, page 44, of the INPFC Annual Report for 1962 (published 1963).

	Tagging period						
	Apr. 9 to May 6	May 10 to May 24	May 28 to June 13	June 18 to June 30	July 3 to July 14	July 15 to July 27	Total
Total tagged	2331	1446	1238	826	308	111	6260
Recoveries							
Bristol Bay	39	16	17	–	–	–	72
Chignik Bay	13	3	5	3	–	–	24
Kodiak Island	18	11	24	10	–	–	63
Cook Inlet	19	13	9	6	1	–	48
Copper River	35	13	3	1	–	–	52
Southeast Alaska	15	9	6	5	6	–	41
Nass and Skeena rivers	32	5	11	5	16	3	72
Central British Columbia (South to Smith Inlet)	30	15	14	22	17	3	101
Fraser River Area	25	22	35	21	23	18	144
Others	11	8	12	2	13	0	46
Total:	237	115	136	75	76	24	663
Percentage:	10.2	8.0	11.0	9.1	24.7	21.6	10.6

1957 near Kiska (177°E) was retaken in Rivers Inlet, over 2000 miles distant. One sockeye, tagged south of Adak, was captured in Portland Inlet, Nass River estuary, approximately 2 months later (K.V. Aro, personal communication). These returns reveal a very definite eastward and southeastward migration.

Taggings conducted in the Gulf of Alaska in 1962 by the Fisheries Research Board of Canada have provided the data in Table 3. In addition to confirming the movement of maturing sockeye to the east and southeast, these returns revealed wide dispersion also to the west, northwest, north, and northeast, in other words, a fanning out of sockeye from a common congregating area.

The recoveries of tagged sockeye in 1963 corroborate the 1962 results and also, as reported by Neave et al. (1964), serve to emphasize the tendency of sockeye reared in streams emptying into the eastern North Pacific—and from Bristol Bay as well—to congregate in what might be considered a common marine feeding ground (Fig. 94) well within the Alaskan Gyral (Fig. 77 and 78).

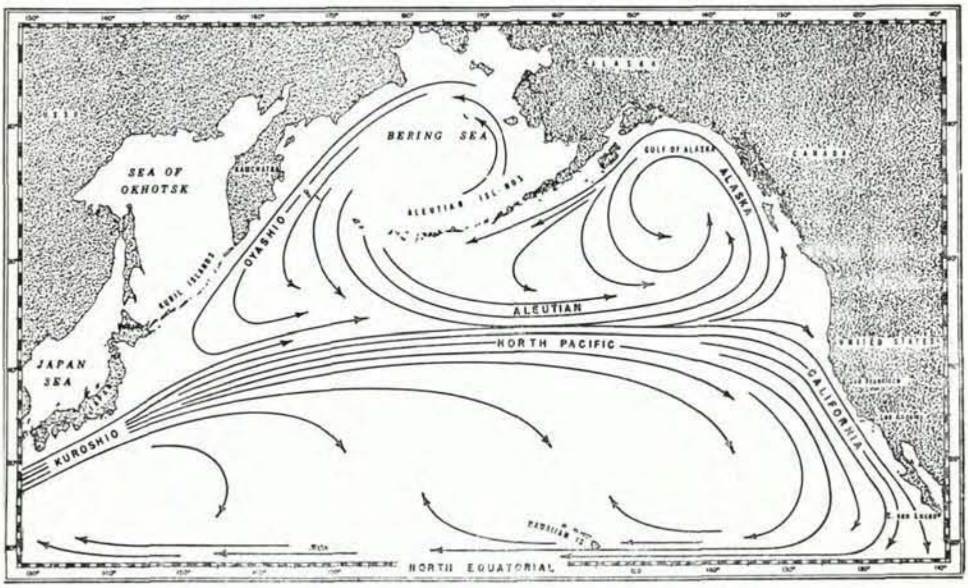

FIG. 4. Major North Pacific surface current patterns. (Taken from Clemens, 1961, p. 99.)

Were we to confine our consideration of sockeye salmon movement, from open ocean areas to coastal regions, only to the North American rivers south of the Alaskan Peninsula, it would be possible to visualize their return adult migration as just the reverse of their earlier route of travel as smolts. In other words, at some appropriate time, reacting to a specific physiological stimulus or urge, the sockeye change direction and, breasting the currents of the counterclockwise Alaska Gyral and the northwestward-moving coastal waters (Fig. 78) come eventually within the influence of their parent stream as its waters pour into and contribute to the northerly flow along the coast. The waters of the American Coastal Region are reported (Fleming, 1955) to have a northerly flow, north of about 50°N, with low salinities due to local precipitation and runoff and with relatively warm temperatures. In the Alaska Gyral the salinities are moderate and the temperatures relatively high. Thus, once in the Alaska Gyral or in the North American Coastal Region, as depicted in Fig. 4, the sockeye would follow a broad against-the-current pathway to whatever inshore area and coastal stream they may be bound.

For the return of sockeye to Kamchatka areas, a counter-current movement of the maturing adults may or may not also explain their return to that coast. According to Japanese investigators (Taguchi, 1956) the salmon moving westward from the open Pacific in the vicinity of the Aleutian Islands would migrate to the coast *with* the westward movement of the offshore water and thus come within the influence of the southward moving Oyashio Current. Those resident in the more southerly waters of the North Pacific region (Fig. 81) would, on the contrary, breast the south and southeast ocean current as they sought the coastal waters. This is in accord with the findings of USSR investigations (Birman, 1958) and is shown in Fig. 5.

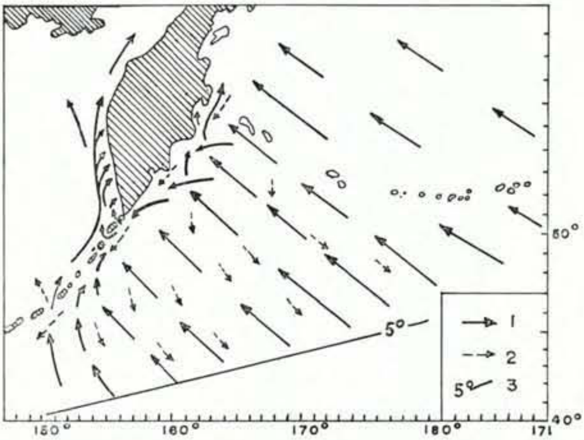

FIG. 5. A sketch of the migration paths of sockeye salmon in the western North Pacific. (Taken from Birman, 1958, p. 39.) 1—direction of migration; 2—direction of surface currents; 3—surface isotherm of 5 C in February.

But such simple, straightforward counter-current homing migration seems *not* to be the mechanism in the light of the tagged sockeye movements in the Canadian 1962 experiments tabulated above. On the contrary, the data suggest a quite general intermingling of sockeye in the Gulf of Alaska region and a subsequent sorting out and dispersion of the maturing fish to their natal spawning streams.

The same situation applies, more or less, in the mid-Pacific south of the Aleutian Island chain. Taggings conducted in 1956–58 indicated (Hartt, 1962, p. 56–57) a feeding concentration of sockeye of Asian and American origins in this region and a wide dispersion later of the maturing fish. Tag returns revealed a preponderance of

Bristol Bay, Alaska, sockeye as far west as 172°E long, while Asian sockeye were present at least as far east as 178°W long. In other words, there is evident here also a mass concentration of feeding fish and a subsequent dispersion of the maturing fish eastward, northward or westward to the spawning areas.

Under such conditions we must ascribe to the sockeye some faculty of knowing their general whereabouts and of being able to set a course, as it were, for their home spawning stream, or at least of knowing in which direction they must go in order to reach the coast where they originated. There must be present, therefore, some directional guiding system and some sensory-perception mechanism within the fish which accurately causes it to proceed in a certain direction until such time as it enters the coastal waters where olfactory or auditory senses and stimulations may take over and become more precise guiding agents.

Recently the sun has been suggested as a suitable celestial direction guide (Hasler, 1956; Hasler et al., 1958). Experiments in a lake with white bass showed that fish, taken from the spawning grounds in a bay on the northeast side of the lake and released again in the centre of the lake with light floats attached so that their movements underwater could be traced, usually set out in a northerly direction if the sun were shining. If it were an overcast day or if the fish had been fitted with opaque eye cups, the movement was random. Tests in experimental tanks, using two other species of freshwater fish, the pumpkinseed, *Lepomis gibbosus*, and the bluegill, *L. macrochirus*, indicated that these fish also have the ability to use the sun as a direction finder at any time of day.

Experiments of this kind on sun-orientation and homing of fish are being continued and may, it is hoped, be applied to Pacific salmon. One puzzling feature is that in the North Pacific, according to available field reports, dull, stormy weather or heavy fog may prevail for long periods. If the fish make use of the sun or other celestial body as a directional guide they should, at times, be considerably delayed in starting out or carrying forward, if once begun, their homeward journey. Yet it is well known that the salmon are remarkably regular in the time of appearance in the fishing areas and in migrating upstream.

A second problem arises in this acceptance of a relatively direct or "beeline-for-home" migration from open ocean to specific coastal region, such as would take place in following a celestial direction-oriented course. It is—how can the fish accommodate themselves to the sudden and abrupt changes in physicochemical properties of the various water masses which they must cut across during such migration? One would assume that the differences in physicochemical conditions must be appreciable in order to be distinctive and mark off the several water "domains" (Dodimead et al., 1963), Fig. 78, present in the North Pacific. "The concept of a domain contains the ideas of consistent properties, structures, behaviours (flow, heating and cooling, etc.), climatic locality and continuity" (Dodimead et al., 1963, p. 24).

It is generally surmized that movement of fish takes place along routes where conditions are similar or are subject to gradual change. At locations, however, where the physicochemical factors differ markedly, such as the interphases between two water masses, where fresh water meets salt water, or where a tributary stream empties into a larger one, there is present, normally, a zone of mixing or an estuarial region, through which the fish must pass and thus become accustomed gradually to the new conditions into which they are directed by the guiding forces. But in cutting across water masses and ocean currents, as envisaged above, such regions of mixed water do not occur, boundaries are abrupt and pronounced, according to the oceanographers. Is it possible, then, for the migrating sockeye to pass readily and without delay from one to another?

The purpose of this general discussion of ocean migration of sockeye is only to indicate the general relation of the migration to water-mass movements and to consider the guiding factors involved. In some cases the salmon appear to move *with* the current, in other areas they proceed *against* it. It is not clear how, in the open ocean, with no apparent reference points by which they may be guided, salmon can determine (if they do) whether they are moving with or against a slow and weak current. Therefore, it would seem that they must be guided to coastal areas by some inherent, genetically developed directional guiding stimulus. Further clarification of this problem must await: (1) more detailed knowledge of ocean water movements, (2) extensive tagging of salmon in high-seas areas and their subsequent recovery during or after migration to coastal waters, and, as well, (3) a fuller understanding of the physiology of salmon, particularly with regard to how small, delicate, or weak a change in current flow, water pressure, water density, or in illumination may influence behaviour.

SELECTION OF NATAL RIVER SYSTEM

The maturing sockeye, having proceeded from their oceanic feeding areas to coastal waters, must then seek out and enter the river system which they descended 2, 3, or 4 years earlier on their seaward migration from their nursery lake.

Just how they locate their natal stream has not been determined. To explore the possibility that the olfactory senses may be involved, experiments were undertaken in 1925. During a normal sockeye tagging operation at Deep Water Bay (Fig. 2, location 2) near the southern end of Johnstone Strait (Williamson, 1927, p. 298–302) a certain number (249 out of 513) had their olfactory nerves severed. A comparison was then made of the recoveries of the operated fish and of the normal individuals. They may be summarized as:

	Normal Fish	Operated Fish
Total recoveries	65	42
Recovered in Deep Water Bay	3	14
Recovered in Fraser River	59	23
Recovered in other streams	3	5

The carefully expressed conclusion of the investigator (Craigie, 1926, p. 223) was that "the elimination of olfactory sensibility appears definitely to interfere to some extent with the migration of the sockeye salmon, but whether by removing guiding impulses or in some less direct way is not clear." This statement seems, indeed, a very fair and sound one. It is only unfortunate that a further remark, namely that "the results do show, however, that farther and more extensive experiments of this kind upon both the olfactory and other senses may yield very interesting and valuable information and it is hoped that it will be possible to carry them out," has not been acted upon by Canadian investigators, particularly now (1959) with better techniques and a fuller understanding of the physiology and sensory perception of salmon and of their movement from ocean to river and to river tributaries. Hasler and associates, working at the University of Wisconsin, whose studies have been referred to already, seem to be the only ones investigating this fascinating problem.

From quite another angle, that of the chemical constitution of the water and its relation to the respiration of the fish, Powers, in a series of studies (Powers, 1939, 1940, 1941; Powers and Clark, 1943; Powers et al., 1932) has given consideration to the influence of the carbon dioxide tension in water as a guide to migration. The gist of his findings may be summarized as follows:

1. Carbon dioxide tension of the blood is known to have far-reaching effects upon the physiology of respiration of vertebrates including fishes.
2. In mammals the carbon dioxide tension of the blood is nicely regulated by the rate of ventilation of the lungs but fishes must, of necessity, depend more upon the carbon dioxide tension of the water to regulate the carbon dioxide tension of the blood.
3. The carbon dioxide holding capacity of a mixture of fresh water and of sea water is always greater than the sum of the carbon dioxide holding capacities of the two waters before they are mixed.
4. The increase in the carbon dioxide holding capacity of mixed fresh and sea water is greater in the higher freshwater–lower seawater mixtures than in the lower freshwater–higher seawater mixtures, thus resulting in a downhill gradient from that point out in the ocean where mixed sea water–fresh water occur toward the river mouth.
5. Researchers have indicated that fishes (brook trout, *Salvelinus fontinalis* and rainbow trout, *Salmo gairdneri irideus*, were tested) do respond to a carbon dioxide tension gradient.
6. As salmon mature there is an increase in the protein metabolism, i.e., a tendency toward "acidosis" or a lowering of the alkali level of the blood, which, in turn, brings about a response to a lower carbon dioxide tension of the water.
7. A salmon with a low alkali reserve blood would find low carbon dioxide tension water more advantageous.
8. Tagging experiments in Alaskan waters have shown that the red salmon migrate to the spawning grounds along paths of salinity gradients.
9. Rivers draining lakes have carbon dioxide tensions more nearly in equilibrium with the carbon dioxide partial pressure of the air than do spring-fed rivers, i.e., a lower carbon dioxide tension (Powers and Hickman, 1928).

"To summarize," states Powers (1939, p. 82), "in order that there be a directive response there must of necessity be a gradient of the stimulating factor or factors. . . . There are two possible gradients, a fresh-salt water gradient and a carbon dioxide tension gradient. Time will tell which of the two gradients dominates the spawning migratory movements of the salmon from the sea to the freshwater. At the present time the evidence seems to favour the carbon dioxide tension gradient. . . . The physiological evidences favouring the carbon dioxide tension gradients are (1) the presence of receptors in the morphological regions of the gills among vertebrates sensitive to carbon dioxide tension as such and (2) the special type of metabolism necessary for the ripening of the germ cells."

While the suggestions put forward by Powers may have some bearing in guiding salmon in from the ocean to a river mouth, as do also the ideas presented by Fon-

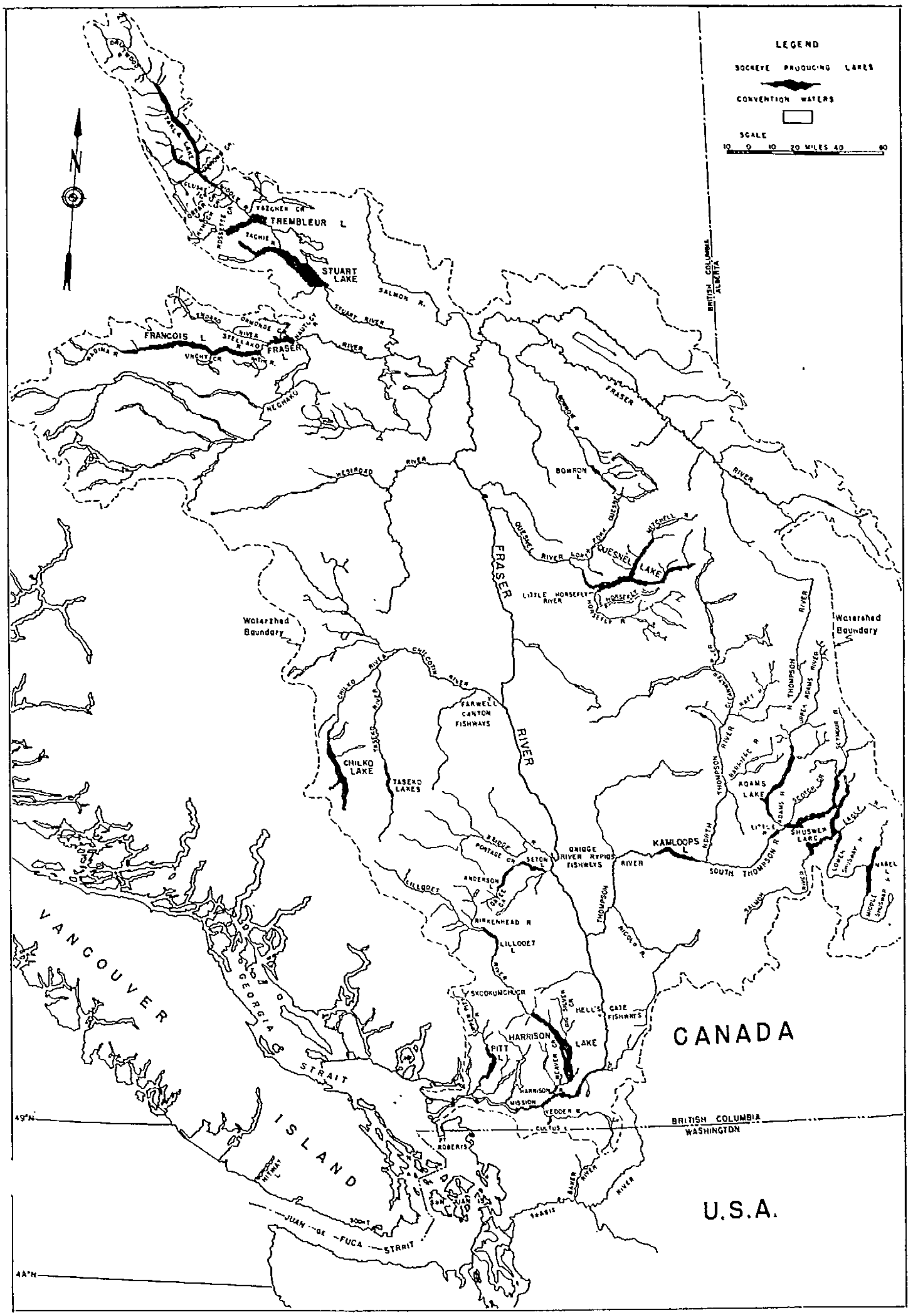

FIG. 6. The Fraser River system, showing important lake areas.

taine and Vibert (1952) for a salinity gradient in attracting Atlantic salmon to European streams, they do not explain how salmon coming in from the ocean and swimming along the coast *select* certain "home" streams as their ultimate destination. Were the salmon to come in directly from ocean areas lying off the river mouths, thus moving in to within (if not always resident within) the influence of the "home" stream alone, the guiding effect of a salinity or carbon dioxide tension gradient might be recognized; but where the fish, moving along the coast, must pass through waters from many rivers there must surely be some more selective guiding attraction at work.

For example, at Baker Lake, the source of the Baker River, a tributary of the Skagit River in the State of Washington (Fig. 6) there is a native race of sockeye which has been in existence since time immemorial. These sockeye, in order to reach the Skagit, must come in from the ocean through the Juan de Fuca Strait along with the hordes of sockeye bound for the Fraser River and its many tributaries. In the ocean off Juan de Fuca Strait and in the Strait itself any characteristic gradient, either of salinity or of carbon dioxide tension, must be predominantly due to the outpouring of Fraser River water, affecting Fraser River and Baker River sockeye alike. Where, then, and reacting to what guiding stimulus, do the Baker River sockeye break off, in their on-to-the-Baker journey, from the hordes of sockeye going to the Fraser? It seems extremely unlikely that any physicochemical gradients could be sufficiently selective. No sufficiently precise and definite receptor mechanism within the fish has, as yet at least, been discovered.

We come back then, to the viewpoint that odour of some kind must be the directive guide for selection of the "home" stream. Hasler and associates have investigated this problem (Hasler and Wisby, 1951). Hasler (1956, p. 204) takes the view that:

> ". . . there is, in rivers and creek waters, some characteristic odour to which young salmon become conditioned while in the stream and which they recognize and to which they orient upon reaching the parent stream as mature migrants. This theory embodies the principle that a salmon returning to its parent stream reacts differently to the odour of that stream than to that of any other. In order for a salmon to return to its home stream there must be some possibility of a differential reaction, not a single response to a repellent or an attractant. This guiding odour must remain constant from year to year and have meaning only for those salmon which were conditioned to it during their freshwater sojourn.
>
> This theory presents three distinct problems:
>
> 1) Do streams have characteristic odours to which fish can react? If so, what is the nature of the odour?
> 2) Can salmon detect and discriminate between such odours if they do exist?
> 3) Can salmon retain odour impressions from youth to maturity?"

Promising but not wholly conclusive affirmative answers were obtained experimentally for all three questions. The problem is whether such odours, of a very mixed nature for a large river, such as the Fraser, Skeena, Columbia, with many sockeye-producing tributary systems, can be detected individually by the returning salmon. Conditioned, let us assume, to the odours of their birth place and nursery area during the relatively short period of residence there, can they detect these specific odours from all others in the estuary or in the mixed fresh–salt water out-

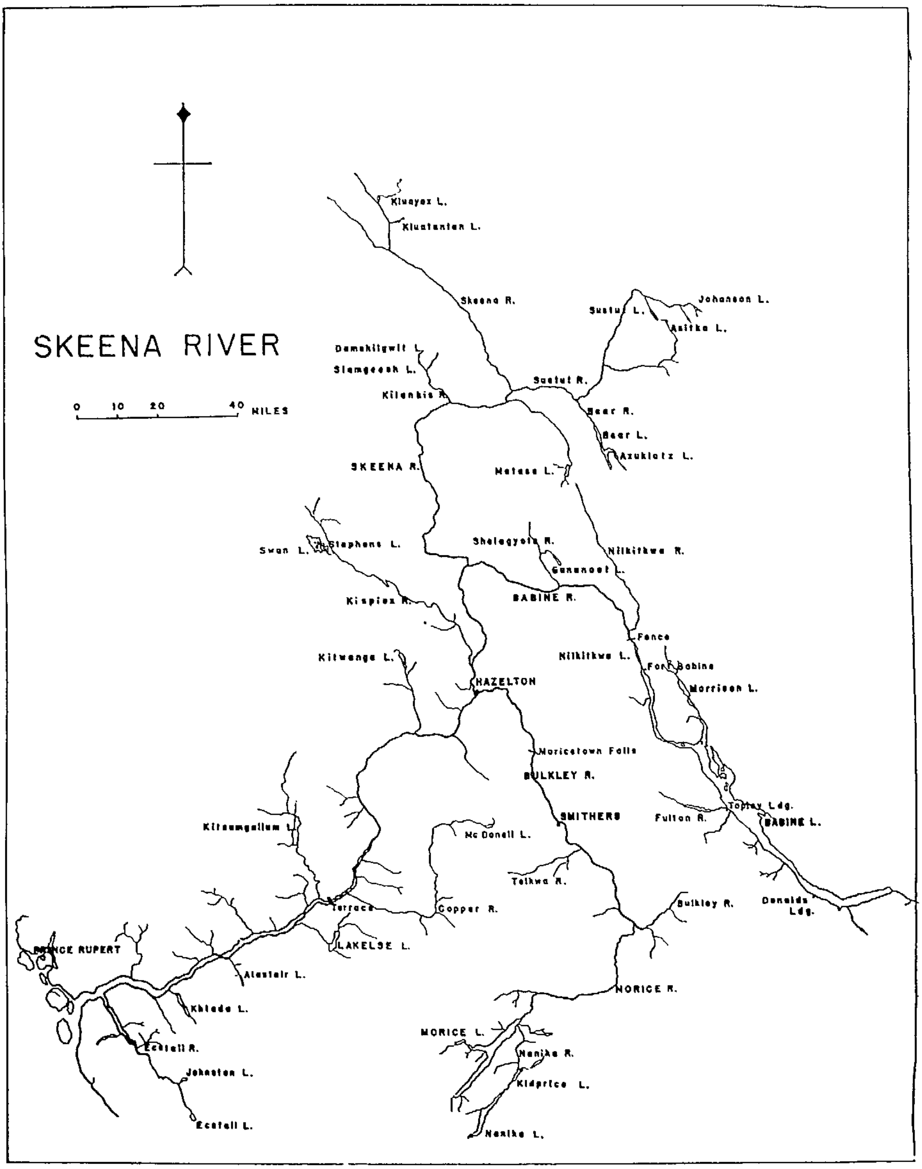

FIG. 7. The Skeena River system, showing important lake areas.

pouring into the sea or do they, as they migrate seaward down the large rivers, become further conditioned to the mixed river water as a whole and respond primarily to it?

SELECTION OF NATAL STREAM

Equally as remarkable and intriguing as the "homing" of salmon to the coastal stream or river system is the selection of that particular "home" tributary of a complex river system such as the Fraser or Skeena (Fig. 6 and 7) where the fish were originally hatched and reared. That the current influence stimulates their upstream ascent is a well-recognized fact. What guiding factors, though, cause them to turn off from the main river into certain tributaries and seek out specific spawning areas in the streams feeding the lakes or along the lake shores where seepage flow occurs?

It is noteworthy that although all investigators of salmon migration have freely admitted that many factors may play a part in directing salmon upstream to their natal spawning areas, and although many have recognized that water quality, as detected by the olfactory organs, may be of great significance, yet in field observations attention has been directed primarily to certain physical and chemical factors in the water whose selective-guiding properties are decidedly debatable.

Shelford (1914, p. 28) remarks that:

> "fishes recognize exceedingly minute quantities of numerous substances and not only turn back upon encountering them but are able to recognize and orient their bodies with reference to increases and decreases of such substances often present in water."

Ward (1930, p. 33) states that:

> "the third environmental stimulus which I believe affects the movements of the salmon is the quality of the water. . . . Their olfactory organs, by which the quality of the water can be tested, are very well developed—especially the nerve centres, with which the terminal organs are connected directly—are of a size and complexity that is conspicuous among all vertebrates and beyond the size reached by these organs in most members of that group. It is legitimate to correlate activity of function with degree of structural development. Furthermore, there are some indications that this function is actively concerned in determining the movements of the salmon."

The temperature of the water of streams was one of the first factors investigated. From observations carried on in Alaska in the early years of the present century (1903–05), Chamberlain (1907) came to the conclusion that the sockeye select those streams whose waters "are somewhat warmer than the surface in the adjacent salt water at the time of the run, i.e., that the fish leave the colder for the warmer water." Also, "it may be postulated that streams with lakes at levels accessible to salmon possess a higher summer temperature than streams of similar volume without lakes." Yet he proceeds to say that:

> "There is a class of streams, however, such as that at Bartlett Bay, where the lake outlet furnishes only a small part of the volume of the main stream. In the Bartlett Bay stream a temperature of 46° at the mouth June 26 decreased to 39° before the lake in which the sockeyes spawn was reached. The main volume of the stream is glacial water, and there is nothing at the mouth

to intimate to human intelligence the existence of lakes and suitable spawning beds in its course. With even this temperature, however, the river was probably warmer than the surrounding salt water, in which ice was then drifting."

These early observations of Chamberlain are dealt with at some length because their substance, namely, that sockeye proceed in the direction of an increase in temperature, has been both confirmed and contradicted by other investigators elsewhere, while a preliminary study in the lower Fraser River tends to question the whole directive effect of purely physical-chemical factors.

The confirmatory evidence comes from studies on a sockeye salmon river in Kamchatka, the Paratunka, where two runs of sockeye occur, one going to Lake Blizhnee, the other to Lake Dalnee. The water flowing from Lake Dalnee passes down the Dalnyaya River into the Little Bystraya and thence to the Paratunka. Lake Blizhnee empties into Blizhnyaya River which flows directly into the Paratunka a few miles below the Little Bystraya (see sketch, Fig. 8). As explained by Krogius and Krokhin (1957), in Kamchatka in early summer an extensive melting of the snow at high elevations takes place during the day, appreciably lowering the stream water temperatures. An upstream gradient of colder water thus occurs. However, this prevails mainly during the daytime. Thus, there are waves or pulsations of cold snow water moving down the streams. As the investigators put it: "in the river every 24 hours a wave of cold water moves down the river; upstream from the crest of this wave there exists a positive temperature gradient, below it—a negative one."

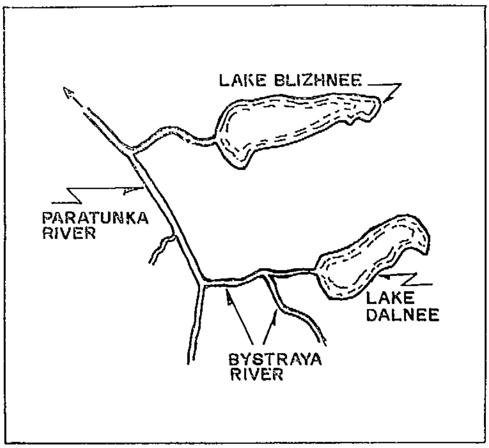

FIG. 8. Plan of location of lakes Dalnee and Blizhnee, tributary to the Paratunka River, east coast of Kamchatka.

During June 9–10, 1953, and July 9–10, 1955, series of temperature readings were taken every 2 hr at two points on the Paratunka River during the time of the early run of sockeye to Lake Dalnee to determine whether a negative or positive temperature gradient occurred above the lower tributary, the Blizhnyaya and below the upper one, the Little Bystraya. It so happened that during the winter of 1952–53 an exceptionally light snowfall had occurred whereas in the winter of 1954–55 there had been a very heavy accumulation. Therefore, in spite of the month's difference in time of observation, the series of temperature readings in both years coincided with the peak of the spring-summer flood.

A comparison of the temperature readings at the two locations revealed that at the lower station the daily rise in temperatures occurred some 2–3 hr later than at the upper point. As a result between 15–17 and 23 hr each day the temperature in the Paratunka between the mouths of the Blizhnyaya and the Little Bystraya rose. Precisely during this period a movement of sockeye upriver took place. Thus, the sockeye appeared to be stimulated to proceed up the Paratunka above the junction with the Blizhnyaya River tributary because of the positive (rising) temperature gradient. The investigators do add, however, that this interpretation is only a working hypothesis and that further studies are required, particularly of the salt content of the waters whereby the origin of the water masses passing through specific cross-sections of the river at different periods of the 24 hr may be identified.

The contradictory evidence comes from the studies of Ward. As a result of observations on the Copper River, Alaska (Ward, 1920, 1921), and on the Skagit River, Washington (Ward, 1930, 1939), it was found that:

> "in a considerable series of cases where the branches of a stream differ in water temperature, the salmon universally choose the one which has the lower temperature. . . . In some cases the migrating salmon show equal definiteness of choice at junctions where no appreciable or constant difference in the temperature of the two streams could be demonstrated. Such a choice is evidently conditioned by some yet undetermined factor. Thus far no instance has been found in which the migrating salmon at a stream junction have chosen the branch exhibiting at the time of choice a higher temperature than the branch which was not followed" (Ward, 1939, p. 6).

That sockeye salmon proceeding up a river system with many tributaries in which they are known to spawn, such as the Fraser (Fig. 6) or Skeena (Fig. 7), turn off into their natal tributary because the water temperature of the tributary is warmer or colder than the main river at the time they arrive at the junction seems really rather incredible. Surely the run of sockeye bound for, say, Stuart Lake (Fig. 6) at the northern end of the Fraser River system, must pass, during ascent of the Fraser, many inflowing streams with temperatures lower than the Fraser itself. There must be a great variety of temperature differences at stream junctions along the main river's course and it is difficult to believe that, whether the sockeye be an early-running or a late-running strain, at only one junction would the temperature relations be appropriate for that particular group to be attracted into its natal stream.

During the early years of a study of the sockeye runs to Cultus Lake, a spawning area of the lower Fraser River system, this matter attracted attention. Cultus Lake, a relatively small, warm lake, empties into Sweltzer Creek, which, about 2 miles downstream, flows into the Chilliwack River (Fig. 6). The Chilliwack River, draining Chilliwack Lake 20–25 miles east of Cultus Lake and a quite rugged, mountainous watershed of 450 square miles, joins the Fraser River some 5–6 miles below where the Sweltzer Creek enters. Both Cultus Lake and Chilliwack Lake have sockeye salmon runs, the run to Chilliwack Lake occurring in August; that to Cultus is later—late September and October.

As revealed by several series of temperatures taken during the summer of 1926 (Foerster, 1929a) the Chilliwack River was consistently colder than Sweltzer Creek. The early running sockeye, bound for Chilliwack Lake, turned from the Fraser into the Chilliwack (earlier called the Sumas River in its lower reaches) which in early August was somewhat warmer (19.8 C as compared with 17 C for the Fraser) but slightly cooler (15.5 C as compared with 16.0 C for the Fraser) in late August, and then proceeded on up the Chilliwack, passing right by the much warmer Sweltzer Creek. A few stragglers were observed in Sweltzer Creek.

One month later the sockeye run to Cultus Lake appeared. These fish, according to the temperature readings available, selected the cooler water of the Chilliwack River, at its junction with the Fraser. However, at the junction of the Chilliwack and Sweltzer Creek, several miles above, they turned into the latter, into water substantially warmer.

The conclusion arrived at from these observations was that "temperature cannot, broadly speaking, be a prominent directing influence." No evidence has since been presented to modify or alter this viewpoint, though it must be admitted that very little attention has been given to the problem by workers in the field.

Reference has already been made to the findings of Krogius and Krokhin in Kamchatka which indicated that, on their upriver spawning migration, sockeye follow a positive gradient of temperature, i.e., when a choice has to be made at stream junction they always select the warmer water.

These investigators had earlier, however, undertaken a much more extensive study of upstream migration. This involved not only temperature but also the chemical quality of the water as affected by hydrogen ion (*p*H) content and the content of the dissolved gases, oxygen, and carbon dioxide. Having regard to the fact that, as the salmon mature, profound changes take place in the metabolic processes of the fish, which, in turn, affect the respiratory exchange (the uptake of oxygen and release of carbon dioxide by the blood through the gills) it seemed to them that the factors influencing migration from ocean to river and thence to a specific tributary would lie in the relation between the movement of the fish and the variations in those environmental conditions which are most important for respiration, namely, temperature, *p*H, dissolved oxygen, and dissolved carbon dioxide or carbon dioxide tension.

Observations made on the Paratunka, already referred to (p. 37), showed (Krogius, 1954) that the sockeye moving up the Paratunka, into the tributary streams and lakes Dalnee and Blizhnee (Fig. 8) gradually pass into waters with higher temperatures and *p*H and lower dissolved oxygen and free carbon dioxide content. It was further noted that the runs of sockeye occurred in those hours when the differences in temperatures, *p*H, and dissolved gases were least pronounced. While the conditions favouring the upstream ascent of sockeye chiefly occur in the early morning or late evening hours, they vary considerably. Under certain peculiar weather conditions the favourable conditions for ascent may not be present in certain parts of the river for as long as 24 hr or more. Until they do occur the sockeye remain in pools in the river channel and below the mouths of the tributary streams into which they will go. The fact that the migrations seem to be closely related to the temperature, *p*H, and content of dissolved gases and may take place during the night or in bright daylight suggests to Dr Krogius that the intensity of light does not have a direct influence but is of only incidental significance.

One factor which universally has a pronounced effect on upriver movement of salmon is that of a freshet or flood, normally caused by heavy rainstorms in the river's watershed. The sudden rise in flow markedly stimulates upstream ascent. Whether it is due primarily to the increase in current or to the rush of fresher water has not been determined. Foerster (1929b) shows that at such periods the maximum and minimum temperatures more closely approximate each other by reason of a rapid drop in the former. This is in line with Krogius' inference that the fish proceed when changes in water temperatures and other characteristics are least.

SUMMARY

By way of summarizing the factors which bring about the return of salmon from the high seas to the "parent stream" or natal rearing area, a phenomenon which now is generally accepted, we may note the following:

1. Sockeye, responding to some physiological inner stimulus associated with the onset of maturity, turn from the ocean feeding areas and proceed to coastal waters.
2. Where the fish are congregated in the ocean, whether freely intermingling or in more or less separate geographical areas according to the coastal region from which they came, is only now being made known.
3. Presently available evidence indicates that from the ocean feeding grounds the Kamchatka Peninsula sockeye move westward, those from Bristol Bay and northern Alaska proceed north or northeast, while a third segment travels generally eastward or southeasterly.
4. Whether in this coastward migration they (a) follow a course directed by some sun-oriented mechanism, (b) merely follow back along a current gradient, even though a weak one, detected by lateral line sensory organs or other means, or (c) react to a particular respiratory organ stimulus associated with the changing metabolism of the maturing fish (the carbon dioxide tension of Powers), remains yet to be decided.
5. Once returned to coastal waters, where the inflow of fresh water from adjacent river systems and coastal streams is a prominent factor, the selection of the parent river results from a physicochemical characteristic of the water which influences respiration (according to Powers) or which stimulates the olfactory organ (according to Hasler). Volume of outflow appears to be an incentive to entrance into a river but it can have no selective guiding influence. Temperature difference has been suggested, the fish, according to Chamberlain, selecting streams with water warmer than the sea, these being allegedly characteristic of streams with lakes at their head.

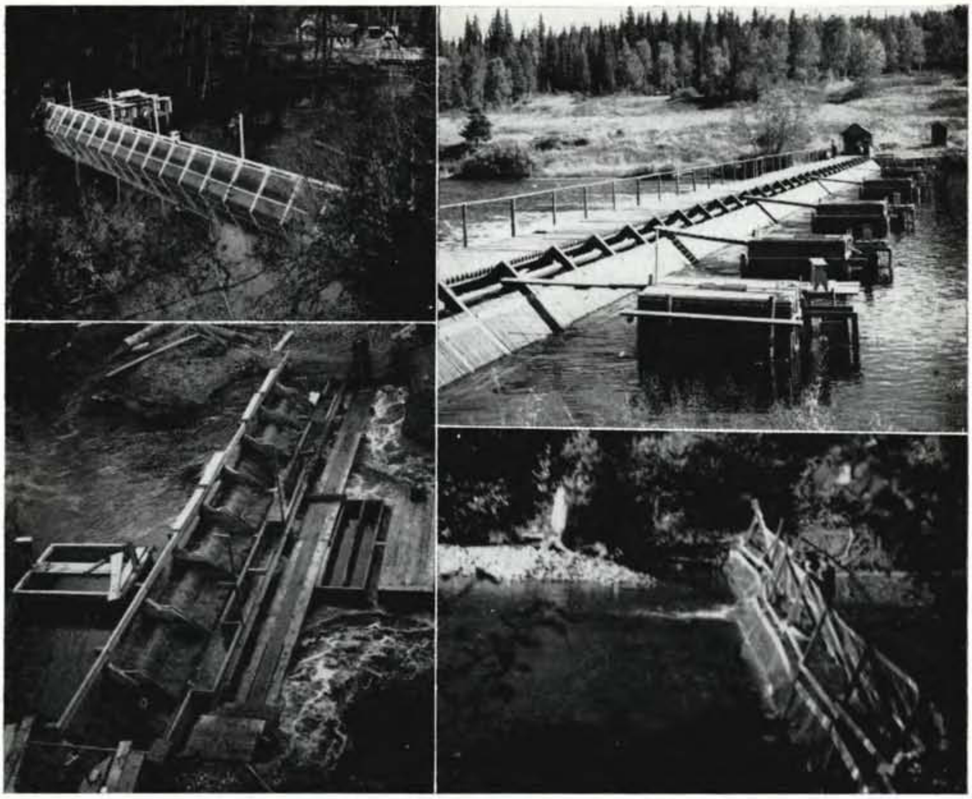

PLATE III. Salmon weirs.

Upper left: Fine-mesh, heavy wire screen smolt weir, Sweltzer Creek, outlet of Cultus Lake. Weir is set at an angle to the stream flow and smolts are collected, for counting, etc., in the six traps at the downstream end. Weir and traps rest on a fish-tight plank flooring, sealed on either side with 2-inch sheet piling.

Upper right: Adult salmon counting weir, Babine River. River completely blocked by panels of wooden pickets placed between "A" frames resting on a solid floor of 2-inch planking. Scouring of gravel beneath the flooring is guarded against by driving 2-inch sheet piling along both upstream and downstream edges of the floor. Watertight bulkheads of planking, well anchored and braced with heavy rock, prevent scouring at either end of the weir. Ascending salmon pass through tunnels into the several traps above the weir from which, in turn, small tunnels in the upstream side allow the fish to escape over a white board for counting and species identification.

Bottom left: Inclined-plane wire screen fry weir at Six Mile Creek, Babine Lake, similar to the structure at Port John as described in Plate VII. Dammed-up water drops onto the sloping screens through which the water escapes leaving the fry to proceed down to a collecting trough from which they swim to the more quiet waters in the recessed sections provided at the downstream edge of the weir.

Bottom right: A temporary light wire mesh weir constructed in a salmon stream to prevent the ascent of salmon during a period of very low water when there was danger of the fish being stranded in pools or left high and dry on the riffles.

6. En route upriver, selection of a particular tributary or a series of tributaries in the same branch secondary system is made. Chamberlain and Krokhin and Krogius suggest that selection is made of the warmer water at a junction point. Ward states that colder water is chosen. Foerster is of the opinion that temperature is not a selective influence.

7. Krogius and Powers suggest that, because of the metabolic changes which take place within the fish as they mature, there is a need to seek out that type of water which will facilitate respiratory exchange of dissolved gases (uptake of oxygen by the gills and blood; release of carbon dioxide). Powers points out that as the sockeye matures—and also undergoes a period of fasting—acidosis of the blood tends to occur and the alkali reserve of the blood is reduced. Under such conditions a salmon would find low carbon dioxide tension water more advantageous. Hence, it would continue to seek progressively lower carbon dioxide tension water as it proceeded upstream. Thus, carbon dioxide tension is the guiding influence. Krogius merely shows, from certain observations, that migrating sockeye select, at stream junctions, those waters with higher temperatures and alkalinity (*p*H) and a lower oxygen and carbon dioxide content.

We may conclude by stating that, though the subject of the parent stream return has been of interest for half a century, and though its existence is now generally accepted, little progress has been made in determining the controlling or directing factors. The initial stimulus appears to be physiological, associated with the onset of maturity, and, as maturity proceeds, the migration to the spawning grounds overrides all distractions and interferences within the capabilities of the fish.

The salmon may be guided from the high seas to coastal areas by a system of sun navigation. They may, on the other hand, return along a gradient of carbon dioxide tension, led on by changes in water quality most closely meeting the changing physicochemical changes in the fish themselves. However, in the selection of specific rivers and tributaries of rivers, such qualities as carbon dioxide tension can have no particular selecting effect. They remain a stimulus to migration but not a guiding factor. Guidance to a specific "home stream" can only be provided by a particular attribute of that "home stream," presumably one of smell or odour, the guiding senses of the fish being their olfactory organs. Such it must be, unless we can postulate an automatic "memory track" within the fish whereby it somehow records the route of its seaward journey as a young smolt (or a small fry in the case of the pinks and chums) and merely reverses its course when it matures 2, 3, or several years later. This seems highly unlikely.

Chapter 2. The sockeye salmon fishery

HISTORY OF UTILIZATION

That characteristic of the salmon's life history which brings the fish back to the rivers, after a certain period of growing and fattening in the ocean, thus making them readily available to the various catching devices, has contributed greatly to man's utilization of this great natural resource. In all lands bordering the North Pacific the history of the salmon fishery has been much the same.

Firstly, aboriginal populations residing along the coast and along the numerous river systems, some of them penetrating far inland, e.g. the Fraser (Fig. 6), found the annual runs of salmon a welcome source of food. Salmon were used either fresh or in smoked or dried form (Plate IV). They constituted also a staple food for the dogs. One authority has described the situation on the Fraser River as follows:

> "In favourable years the number of schools of ascending fish and the mass of individuals composing them, baffle calculation; eye witnesses say that when the schools arrive at the narrower or shallower parts of the rivers the fish actually push each other out of the water; or that a stone thrown into the midst of a school could not sink to the bottom without touching several fish. In such localities, the native population reaps a rich and, to them, a most important harvest as these roughly-cured fish are their only means of subsistence during the winter when other sources of food have failed or are exhausted."

Fishing was conducted in very primitive fashion; with handmade nets or hook and line in salt water;* with spears, dipnets, and weirs in the rivers.

With the arrival of traders and settlers on the North American Pacific coast in the early 1800s, interest in the commercial utilization of the salmon began. Salting of salmon was the first undertaking. "In August, 1829, at Fort Langley . . . . 7544 salmon were obtained from the natives at a cost of £13.17s.2d in goods. The trade increased; in 1835 and for many years thereafter 3000 or 4000 barrels of salt salmon were exported, principally to the Hawaiian Islands" (Howay, 1914).

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* On the rather gradually sloping beach at the head of Port John Bay on King Island, about 30 miles north of Rivers Inlet (Fig. 2), may be seen the remains of old Indian salmon traps. These consisted of piles of rocks or boulders arranged in a semicircle or wide horseshoe along the beach, open at the shallow beach end, the walls some 2 ft high at the outer edge, some 40 ft across. They were constructed so that two lay on either side of the mouth of Hooknose Creek. Thus, as the salmon came into the bay and at high tide gathered at or off the mouth of the creek they would, as the tide fell, become trapped in the enclosures and eventually be left high and dry for ready capture. It is even said that, as the waters fell, the women stood on the walls and strove to keep the fish within the trap until the water level was below the top of the wall.

TABLE 4. Commercial packs of sockeye salmon in North Pacific areas, 1905–61,[a] in thousands of 48-lb cases (1 case = 70 lb raw fish approximately).

Year	Eastern USSR[b]	Japan[c] High Seas	Western Alaska	Central Alaska	Southeast Alaska	Northern British Columbia	Fraser River[d]	Columbia River
1905	–	–	1021	346	207	243	1675	8
1906	–	–	799	452	251	277	365	8
1907	–	–	658	483	177	254	157	6
1908	–	–	1087	377	198	298	1245	9
1909	–	–	1075	358	281	292	1684	28
1910	6	–	825	365	282	433	398	6
1911	15	–	669	413	239	325	186	6
1912	44	–	1228	422	255	336	309	8
1913	103	–	1419	364	191	288	2393	11
1914	85	–	1512	395	295	351	533	35
1915	155	–	1192	500	230	387	156	5
1916	178	–	1365	572	182	187	117	4
1917	275	–	1556	726	203	116	551	8
1918	297	1.6	1730	663	226	260	70	38
1919	377	1.3	527	437	240	340	103	7
1920	362	1.6	743	533	200	307	111	3
1921	433	0.6	1058	596	105	128	143	6
1922	539	2.6	1386	568	122	251	100	31
1923	585	3.0	1258	422	179	305	79	38
1924	547	0.5	814	443	193	333	109	7
1925	386	1.2	549	365	151	361	147	6
1926	540	4.6	1353	631	174	253	130	22
1927	589	43.7	885	320	116	251	159	7
1928	939	3.8	1405	432	107	177	90	5
1929	747	4.6	1075	456	162	221	173	10
1930	779	10.7	362	270	217	370	456	10
1931	621	37.3	1108	440	148	237	128	4
1932	559	85.8	1305	660	140	201	147	3
1933	397	197.0	1615	487	81	205	181	7
1934	597	507.6	1814	708	104	232	492	7
1935	229	213.0	273	391	160	274	117	1
1936	442	458	1424	839	220	249	244	10
1937	337	668	1477	459	165	223	161	8
1938	440	643	1849	485	190	261	322	14
1939	280	582	1118	657	196	197	98	5
1940	107	–	444	384	125	280	163	24
1941	145	–	613	414	138	306	282	33
1942	161	–	438	352	121	248	710	23
1943	246	–	1315	582	85	92	51	3
1944	296	–	987	462	132	140	126	1
1945	378	–	609	435	130	206	133	0

(Continued.)

TABLE 4. (Concluded.)

Year	Eastern USSR[b]	Japan[c] High Seas	Western Alaska	Central Alaska	Southeast Alaska	Northern British Columbia	Fraser River[d]	Columbia River
1946	416	–	656	351	59	161	611	10
1947	321	–	1350	470	56	195	41	15
1948	195	–	1278	319	39	177	155	3
1949	278	–	530	391	39	144	177	7
1950	293	–	590	514	49	169	225	4
1951	241	–	340	363	70	168	263	5
1952	290	–	730	377	75	236	249	10
1953	161	–	530	331	121	334	369	3
1954	126	186[e]	393	299	113	194	998	8
1955	98	624	373	233	55	150	181	3
1956	180	520	577	357	81	320	168	19
1957	110	1061	492	189	82	127	219	8
1958	32	607	278	131	80	659	860	30
1959	126	518	361	161	62	133	257	17
1960	126	826	890	243	44	130	195	9
1961	247	1075	954	275	36	282	235	4

[a] Records taken principally from Pacific Fisherman Yearbooks.

[b] Includes Soviet and Japanese cannery packs prior to 1937; 1937–39 includes only the Japanese pack in Kamchatka. Figures from 1940 onward are from INPFC, 1962, table 24; here they are converted to cases at 1 m ton = 31.5 cases.

[c] Packs of sockeye in Japan, including Japanese floating canneries in the North Pacific Ocean and Okhotsk Sea.

[d] Includes both Canadian and United States Puget Sound packs.

[e] Segregation by species not available prior to 1954 during the post-war period, but the packs then were preponderantly pink salmon.

The first salmon canning on the Pacific coast was undertaken (Cobb, 1930) in 1864, in California, using techniques already found satisfactory on the Atlantic coast. In June, 1870, the first salmon cannery in British Columbia began operation on the Fraser River near New Westminster, under Messrs Alexander Loggie, Alexander Ewen, James Wise, and David S. Hennessy. Mr Wise was an experienced fisherman; Messrs Loggie and Hennessy had had experience in the canneries of New Brunswick. In this same year Captain Stamp set up a cannery at Sapperton, New Westminster. In succeeding years salmon canning developed along the coast: Skeena River, 1877; Nass River, 1881; Rivers Inlet, 1881; Southeastern Alaska, 1878; Bristol Bay, 1884.

From the Fraser River northward, with the exception of southeastern Alaska where the pink salmon is the most abundant species, the sockeye was and continued to be the species principally canned. The report of the Inspector of Fisheries for British Columbia for the year of 1876 states (Canadian Department of Marine Fisheries, 1877, p. 343 of Fisheries Appendices) that "the *suck-kai* of the lower Fraser, though a smaller and not as rich a fish as the *kase* [chinook], may be regarded, at present, as the staple product of the Fraser River fishery. The weight of this fish is about eight lbs, or more, and it is canned in large quantities for exportation."

Interest in the canning of salmon was keen. Rapid expansion in the industry took place. A statement which appeared in "A guide to the Province of British Columbia" for 1877–78—"there would appear to be no limit to the catch of salmon but the question of markets must always be considered"—would seem to typify the general situation along the whole coast. That suitable markets must have been readily found would seem to be indicated by the trend in records of sockeye salmon catches from 1905 on (Table 4), for all North Pacific areas where the sockeye salmon resources were exploited commercially. The data are as authoritative as it has been possible to make them from available sources of information, but are probably low for the USSR, since many sockeye there are marketed in salted and frozen condition.

It is not to be inferred, of course, that the sockeye salmon was the main species exploited everywhere along the coast. In California, which represents the southern limit of distribution of the Pacific salmon along the North American coast, the chinook or quinnat salmon is the principal species, particularly in the Sacramento and San Joaquin rivers; it is taken by drift nets or haul seines in San Francisco Bay and the river estuaries. Immediately after establishment of the first transcontinental railway line, the shipment east of fresh frozen fish became an important feature of the fishing industry. In Northern Californian waters the coho or "silver" salmon also occurred and contributed to the commercial fishery.

Along the Oregon coast the coastal stream fisheries initially caught chinook, coho, and chum salmon, chiefly by means of drift gill nets. About 1912, commercial trolling in the ocean off the coast began, firstly off the Columbia River, subsequently spreading to other coastal areas.

The Columbia River, which, according to Cobb (1930, p. 428), is the largest river of the Pacific coast and has produced more salmon than any other river in the world, has greatly dominated the fisheries of Oregon and Washington, principally by the canning of chinooks but with moderate packs of coho and a minor pack of chums. Sockeye (blueback) were first canned in 1899 and have constituted a minor but nevertheless important fishery. The highest catches were made in 1892 and 1898; the fishery is now smaller, less than one-sixth of its earlier extent, but quite appreciable in value. Cleaver (1951) states that "the blueback salmon or sockeye has suffered the greatest harm from dam development on the Columbia since their spawning grounds are primarily located far upstream . . . . The decline in the landings represents a real decline in the abundance of this species of salmon . . . . Recent runs have shown a significant increase, which demonstrates that this valuable species can be developed by proper management."

In the State of Washington all five species of salmon are of appreciable importance. In numbers of fish the mean yearly landings (all districts) for the period 1935–55 amounted to: chinook—574,371; chum—829,447; pink—5,254,770 (based on odd or "big" years only); coho—1,133,765; sockeye—1,448,276. Practically all of the sockeye were taken from the Fraser River runs. There are a few streams in Puget Sound which have relatively small runs of sockeye while one coastal stream, the Quinault River, supports a moderate fishery.

In British Columbia, while from the inception of the industry the sockeye continued to be the most valuable species, the catches of pink and chum salmon became important. In years subsequent to 1916 they exceeded the catches of sockeye (Fig. 9). Sockeye propagate chiefly in the large river systems, the Fraser, Rivers Inlet, Skeena, and Nass but the pinks and chums spawn not only in the lower tributaries of the major river systems but also in most of the thousand or more coastal streams. The fishery, by drift gill net and seine, is conducted along the whole coast.

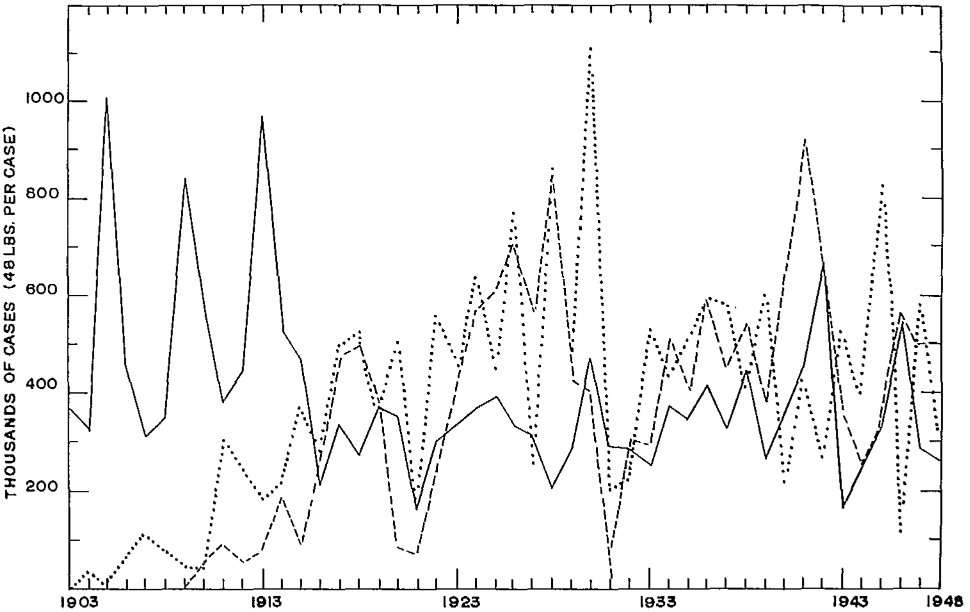

FIG. 9. Pack of British Columbia salmon, 1903–48, in thousands of 48-lb cases: sockeye: ————; pink: ....; chum: ----------. (Taken from Pacific Fisherman, 1959, p. 116.)

The very extensive coastline of Alaska may be conveniently divided into three regions—southeast, central, and western. To indicate the relative importance of sockeye in them we use the fishery statistics, as provided by the Pacific Fisherman Yearbook. The average packs (in cases) of each area during the 1949–58 period (Pacific Fisherman Yearbook, 1959, p. 94) were

Pack of Alaska canned salmon, by districts

Area	Sockeye	Pink	Chum	Coho	Chinook
Southeast Alaska	76,669	754,305	381,820	100,990	1,475
Central Alaska	318,615	565,735	313,846	54,310	31,610
Western Alaska	483,317	7,744	36,105	6,197	21,357

The Central Alaska area includes the well-known and once heavily producing sockeye streams, the Karluk, Chignik, and Copper rivers; Western Alaska includes all of Bristol Bay.

In the USSR far east, the east and west coasts of the Kamchatka Peninsula are the main sockeye-producing regions, with a few streams along the northern coast of the Okhotsk Sea making small contributions. Nevertheless, here too the sockeye are by no means the dominant species. According to available catch records (Baievsky, 1926), the fishery in 1920 in the three coastal areas mentioned above caught the following numbers of salmon:

Area	Sockeye	Pink	Chum	Coho
Okhotsk Sea	38,704	3,553,627	5,061,424	27,810
West Kamchatka	5,140,304	6,616,818	34,151,040	485,245
East Kamchatka	2,005,531	4,232,519	21,849,480	999,917

Since 1920 the pink salmon have become exceedingly important. Alperovich (1957) quotes the USSR Far Eastern catch in 1956 as follows:

sockeye — 58,200 centners or 128,300 cwt
chum — 772,600 " " 1,703,300 "
pink — 721,600 " " 1,590,800 "
chinook — 10,208 " " 22,500 "
coho — 41,900 " " 92,400 "

The sockeye have thus dropped to a poor third in the Kamchatka salmon fishery. According to Krogius and Krokhin (1954):

> "a significant decrease in the size of the salmon runs has been noted in most areas of Kamchatka. Since 1948 there has been a sharp reduction in the runs of sockeye to the Kamchatka River and to other east coast streams. Also, for many years now the important sockeye runs to the Palani River have been lost to the fishery industry. In comparison with 1929 the whole catch of Kamchatka sockeye has been reduced to approximately one-third of its former abundance."

Moiseev (1955) reports that "at the present time the catches of sockeye have greatly declined as a result of the severe decline in numbers of sockeye in the Kamchatka River runs and a marked deterioration in conditions for return of sockeye to the Ozernaya River due to the very intensive high-seas fishery."

By way of summarizing the relative importance of sockeye, in comparison with other species of Pacific salmon, we present, in Fig. 10, a block diagram showing the total catches of each of the three dominant species in the North Pacific area for 1952–57. These include the high-seas catches by the Japanese fleet of motherships and catcher boats in the North Pacific. The following become readily apparent:

1. The comparative high abundance of pink salmon in all areas, but particularly in the USSR in the odd numbered years up to 1957.
2. The relative importance of the United States (chiefly Alaska) sockeye catches, although in 1955 and 1957 they were exceeded by the high-seas fishery.

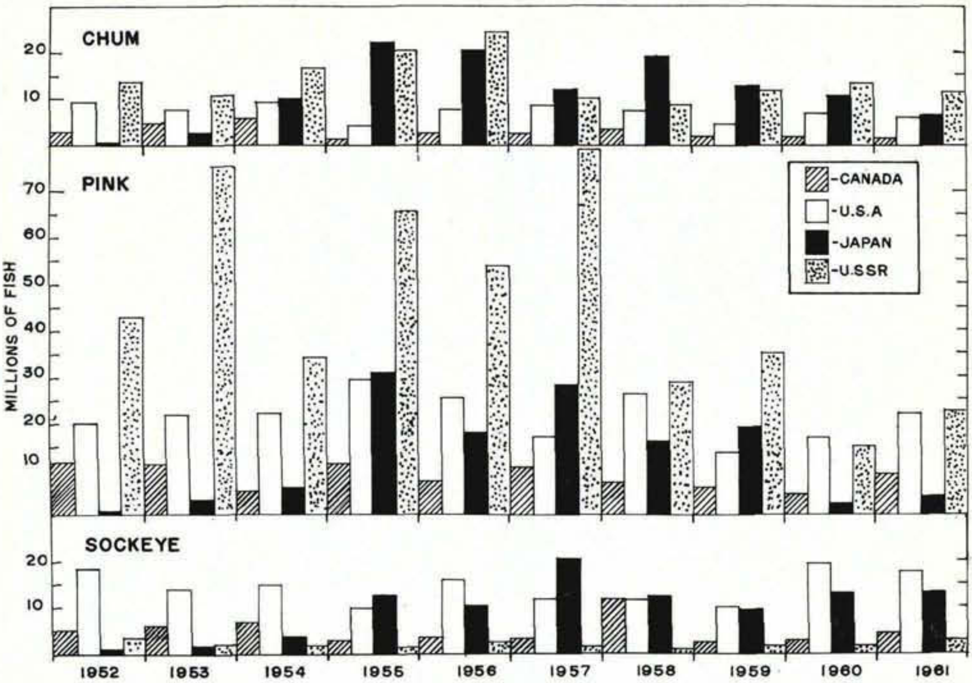

FIG. 10. The relative catches of sockeye, pink, and chum salmon in the North Pacific Ocean by Canada, the United States (Alaska and Washington), Japan (mothership and North Kurile fisheries), and the USSR, 1952–61. (From INPFC Bull. No. 12, Part I, 1963: "Catch statistics for North Pacific salmon" by Hiroshi Kasahara.)

TRENDS IN COMMERCIAL EXPLOITATION

It is not the purpose of this Bulletin to discuss in detail the history of the commercial fisheries for sockeye salmon over the years since commercial exploitation began. It is necessary, however, to consider broadly the general trend throughout the period of reliable recording, since the declines in the catches in many areas have brought about (1) a need for a thorough scientific investigation of the life history and natural propagation of the species, and (2) an attempt to develop "management policies" for the commercial exploitation of the sockeye populations on a "sustained yield" basis, that is, so that the populations may be continued at a high level of production each year.

It will suffice simply to draw attention to the downward trends in the sockeye catches, as revealed by Table 4, for the major North Pacific areas. The declines are readily apparent even without taking into consideration the changes in (1) the numbers of fishermen and their increasing efficiency and in (2) the marked increase in effectiveness of the fishing gear. Both of these factors should have led to a gradual rise in the annual commercial catch, other things being equal. The fact that, in spite of them, the annual pack of sockeye fell off serves to accentuate the genuineness of the decline.

The data for the Japanese high-seas fishing fleet do not, of course, conform to the general decline trend. The reasons are clear. In the first place the fishery is a far-flung one, exploitating sockeye populations from many producing areas—Bristol Bay, Alaska, to the north and east, and Kamchatka to the northwest and west. Secondly, the fishery is a relatively newly developed one, subject to unusual geographical restrictions and quota limits. It thus is not comparable with that of other areas.

The important point is that the commercial fishery has become an extremely extensive one, highly mechanized and highly mobile. It is capable of taking a high proportion of the salmon population, especially in the river estuaries. The extent to which a high-seas or open ocean fishery develops will be of much significance. Obviously whatever stocks of sockeye are there exploited will be reduced; the inshore or estuarial fishery for these stocks will be adversely affected accordingly.

Chapter 3. The significance of the spawning escapement

Causes of the downward trend in abundance of sockeye, as revealed by the catch statistics, Table 4 and Fig. 9 and 10, have been sought but clear evidence of the responsible factors is difficult to obtain. The decline has presumably been the result of (1) overfishing and a consequently too low escapement to the spawning grounds, 2) a reduced rate of production of the young in the freshwater rearing areas because of adverse changes in the spawning grounds or in the environmental conditions for the young fish or (3) a combination of both (1) and (2). Studies are in progress in British Columbia, Alaska, and Kamchatka, as outlined below, to elicit the facts. It is agreed, meanwhile, that the declines in commercial catches *are* indicative of *real* reductions in the sockeye stocks, however caused. How to halt the decline and reverse the trend are the prime objectives at the present time. Whether they can be achieved without cutting down the commercial fishery too drastically has to be determined. Stringent measures must be adopted, however. The resource is too valuable to exploit uneconomically; it is potentially too important not to develop to the fullest extent, i.e., to so "manage" that the highest yield sustainable year after year may be enjoyed.

THE SPAWNING ESCAPEMENT

It has been long recognized, in a general way, that the maintenance of salmon runs depends primarily on the numbers of maturing adults that reach the spawning grounds and on the progeny successfully produced therefrom. The exact number, however, of adults actually required to maintain the population of a river or of a river system at a high level of abundance has never been made known.

This release or passage of fish to the upriver spawning areas is termed the "spawning escapement." A run of sockeye, therefore, coming into a river or river system from the ocean is, when it reaches the fishing areas, divided conveniently into two parts: the "catch," representing those fish taken by the commercial fishery, and the "escapement," made up of those fish which (a) either escape the fishing gear during the time that it is operating, or (b) pass through before or after the fishing season or during weekly "closed" periods when fishing is prohibited.

The number of fish required to constitute a good or an adequate spawning escapement is not yet clearly known, as already intimated and as will be made evident in the discussion below. Nor has it been satisfactorily determined whether the spawning escapement should constitute a relatively definite percentage of the total population returning to the river or be a fixed number of fish, closely related to the capacity of the spawning grounds or the nursery areas. It is becoming clear, however, that the spawning escapement should bear some close relationship to the incoming total population with regard to timing. That is to say, as the run of sockeye coming into an area starts with a small number of fish, rises to a peak and then declines as the season wanes, so should the spawning escapement proceed. The assumption is that the fish arriving at mid-season, at the peak, are likely to find conditions on the spawning grounds most favourable, hence the bulk of the escapement should consist of these fish.

But before entering upon a consideration of catch-to-escapement relationships let us consider, as a background picture, the situation existing before commercial fishing began.

THE SITUATION PRIOR TO COMMERCIAL FISHING

Under natural, primeval conditions one would assume that, in general, sockeye populations would be large and would be limited only by the capacity of (1) the spawning grounds to accommodate and incubate successfully the eggs deposited or (2) the nursery lakes to rear the young fish. With each female fish containing around 4000 eggs, a survival of only 2 (or 0.05%) of these eggs through to the adult stage would be required to maintain the population, that is, to replace each pair of parent fish with 2 successors in the next generation. Nature has thus allowed for tremendous mortality during the life cycle—99.95%. While losses during incubation, early residence in the lakes, seaward migration, and life in the sea, are undoubtedly heavy, it is suspected that the greatest loss takes place right on the spawning grounds because of overcrowding and overseeding.

Fluctuations in survival are bound to occur at all stages of the life cycle as the environmental factors governing the well-being of the fish are good or bad. These fluctuations vary about some general average value which might be taken to represent the mean survival. For the most part the factors bringing about loss of fish during the life cycle will be ones which may be considered *compensatory*. That is, as losses occur and as the population as a whole is thereby reduced, conditions for the remainder are improved and there will be a better chance of their surviving.

On the other hand, environmental conditions may, in some years, be unusually favourable, resulting in a below-normal average mortality. Rich stores of food may abound, there may be a diminution in predators, and so forth—all of which will greatly enhance survival. As a result there may be an overtaxing of the later occupied feeding grounds; a greater incidence of disease or parasitism may then occur. There will follow, therefore, an increase in mortality.

Some workers believe that *noncompensatory* factors of mortality can exist. Ricker (1954) reports that "no sharp line can be drawn between the kinds of mortality which are compensatory and those which are not, although Nicholson, Smith, and others have felt that as a rule biological factors tend to predominate among the former, and physical agents among the latter, for insects at least." Reference is made to such physical agents as extremes of water temperatures, drought and floods but even in such cases a compensatory reaction in subsequent survival may result. There would seem to be exceedingly few cases, barring almost total extermination of a run of sockeye, where a completely noncompensatory factor would exist.

Occasions may develop where, through the operation of some factor which has reduced a sockeye population to a very low level, the compensatory increase in survival has little or no noticeable effect. For sockeye this would apply, chiefly, during the time of their residence in a lake(1 or 2 yr, or for some lakes of Alaska and Kamchatka, 3 yr) and also during the time of their ocean residence. The situation would be this:

1. The lake (or sea) community is made up of a number of populations of fish in a lake—salmon, trout, char, squawfish, suckers, dace, sticklebacks, etc.—each occupying a separate, though perhaps overlapping, niche, or sphere of influence in the lake. Within its niche each population concerned strives to increase but is limited in numbers primarily by the pressures applied by the other populations with respect to available food supplies, available space in which to live, attack and consumption by predators and so forth.

2. When, through some circumstance, any one of these populations, say "X", becomes reduced in numbers or influence and does not fully occupy its niche there is an immediate reaction. The species "X", now reduced, will strive, through faster growth and lessened mortality, to fill the niche; other species, normally held back by species "X" will expand and increase. It thus becomes a battle of the species to see which occupies the new territory and thus increases its sphere. The most versatile species, of course, will succeed, the one which can most quickly take advantage of the opportunities.

3. Whenever, in this dynamic situation, a niche of one species has been occupied by one or more competing species it becomes a question as to how long and how securely the successful occupants can hold their expanded territory, "maintain their new front," as it were. The species "X" which vacated the niche, through forces beyond its control, would obviously be the one best equipped to occupy it. The new occupant would be required to marshal all its presumably less efficient talents and facilities to hold its ground and retain the new area.

4. Once the factor limiting the production of "X", whether it be a flood, a severe winter, a drought, a blockade of upstream-migratory spawners, is removed and production becomes normal again, a "battle royal" in the lake begins. The young of population "X" appear in quantity only to find their preserves occupied by other species. Can they regain old territory? The extent to which they can and the speed with which it is accomplished depend primarily on the relative strengths of the competing species, with the odds favouring the species originally occupying the niche. The reoccupation process may be quick, with heavy losses to the retreating species; it may be slow, with obviously heavy loss to the species striving to retrieve its position.

To what extent this matter has been given consideration by salmon management experts is not clear from the literature. From experience it would appear that in many respects the sockeye occupy a niche which is not too clearly occupied by other fishes nor do they overlap greatly on the niches of other groups. Therefore, for sockeye the conditions would appear to be such that loss of biological niche may not follow a serious or sudden drop in population. Consequently, quick recovery may take place when the factor responsible for the decline is removed.

THE SITUATION AS COMMERCIAL FISHING EXPANDED

Once commercial fishing began, at first quite limited but rapidly expanding year after year, the principal effect was to reduce the number of adult fish returning to the spawning grounds. This meant a reduction in the number of ascending females, hence in the total number of sockeye eggs available for deposition. Yet the females so removed might actually be looked upon as those which normally would be forced to spawn in poor ground, in marginal areas where conditions were unfavourable. Thus, by reducing the total number of fish in the run, the fishing merely reduced competition for the best ground. The effect of the fishing was to remove the surplus fish, those likely to produce least effectively. Furthermore, with a reduced spawning escapement, there would be not only less competition for good spawning areas, but less crowding of redds, less superimposition, a smaller hatch and hence less crowding of fry in the feeding areas. In short, better conditions for fry growth and well-being would result. Survival would be higher, hence a higher production would be achieved from fewer eggs than prior to commercial fishing. The removals by the commercial fishery would be followed by a reduced but more effective spawning, or better production and survival throughout the early phases of the life cycle.

In the final analysis a commercial fishery may be looked upon essentially as the utilization of that part of a highly productive natural resource which is in excess over that required to maintain the resource. It not only removes the surplus adults, thus reducing the spawning escapement to the productive capacity of the beds, but goes even further. It thereby brings into play the compensatory mechanism of the organism and thus achieves a higher rate of productivity than before.

WHAT CONSTITUTES A PROPER CATCH:ESCAPEMENT RATIO?

The point or level at which removal of fish by commercial fishing should cease is the vital question. What proportion of the total population can be removed safely without jeopardizing the maintenance of the stock? What catch to escapement ratio provides the best production?

Forty years ago this matter came to the fore in the case of Alaska reds (sockeye) where the stock had appeared to have reached a serious state of depletion. Gilbert and Rich (1927, p. 2) report:

> "It remains, then, to apply the remedy, and the question at once has arisen of how extensive a spawning reserve must be provided to check depletion and increase the size of the colony. . . . It is a generally accepted motto that we limit our spawning reserves to the lowest numbers consistent with safety, sparing every fish that can be spared for the world markets and for human consumption. . . .

> "It had been realized, however . . . that our ignorance concerning the size of an optimum spawning reserve constituted a serious handicap in the administration of the salmon runs, and a program of investigation had been adopted in 1921 with the purpose of obtaining the desired knowledge. As the essential part of the problem is to ascertain the complete return from spawning colonies of known size, the streams selected for investigation must be so situated and of such character that both the portion of the run taken for commercial purposes and the portion that escapes to the spawning grounds can be accurately enumerated year after year."

The situation facing the Far Eastern salmon fishery of the USSR is much the same though the occurrence of fluctuations in abundance due to natural causes, exclusive of the removal of fish by the commercial fishery, is duly recognized. One authority (Semko, 1953) reports that:

> "After 50 to 60 years' experience in the salmon fisheries we know that sharp fluctuations in the size of the salmon runs occurred not only at the very start of the industry, when exploitation was extremely light, but also later during the years of a highly developed fishery. This suggests that the intensity of exploitation is not the major factor determining the condition and annual variation in the salmon stocks. Nevertheless, it would be a mistake to consider that the size of the commercial catch and the intensity of commercial exploitation of stocks has no influence whatever on the extent of salmon reproduction and, hence, on the state of the stocks in later years. The actual commercial catch of adult salmon migrating to the rivers for spawning will undoubtedly have an effect on the reproduction of stocks because of the reduced number of spawners. . . .
>
> "During the last 5-year period the condition of the pink and sockeye salmon stocks in Kamchatka has grown much worse. . . . The Kamchatka River—the largest one on the peninsula—used to have abundant runs of salmon. In 1926–28 up to 8 million were taken here. Since then the number of local sockeye runs has undergone wave-like fluctuations, the stocks have constantly decreased and the catches have dropped to 1.5% of their former size. . . .
>
> "The unfavourable changes in salmon stocks are the result of two inter-related processes: (1) annual and often sharp fluctuations in the number of fish and (2) slow changes in the stocks due to the disturbance of normal propagation conditions or resulting from systematic over-exploitation. . . .
>
> "In order to reach an understanding of these problems and their solutions, great importance attaches to the development of methods of estimating the size of the stocks, the possibility of controlling or modifying the conditions and fluctuations, and the carrying on of an extensive study of the biology of salmon."

This problem of what must be done to assure a successful fishery arises wherever a sockeye fishery exists and where careful management in order to ensure a maximum utilization of the resource year after year is the goal. That is why the quotations above, succinctly outlining the problem, have been given in full. That is why the developments carried out in different areas are reviewed below.

STUDIES IN ALASKA

Two areas, which met the necessary conditions outlined above, were selected for intensive, long-term study. They were the Karluk River on Kodiak Island, where a counting weir was installed in 1921 for the enumeration of the spawning escapement, and the Chignik River, on the south coast of the Alaska Peninsula near its outer end, where a weir was built in 1922.

TABLE 5. Catches and escapements of sockeye salmon, Karluk River, Alaska, 1921–36 (Barnaby, 1944).

Year	No. of fish Catch	 Escapement	Ratio Catch:escapement
1921	1,643,000	1,500,000[a]	1:0.91
1922	658,000	400,000[a]	1:0.61
1923	730,000	695,000	1:0.95
1924	891,000	1,109,000[a]	1:1.2
1925	1,323,000	1,621,000	1:1.2
1926	2,386,000	2,533,000	1:1.1
1927	715,000	873,000	1:1.2
1928	1,001,000	1,094,000	1:1.1
1929	227,000	900,000	1:4.0
1930	167,000	1,097,000	1:6.6
1931	752,000	873,000	1:1.2
1932	674,000	738,000	1:1.1
1933	845,000	987,000	1:1.2
1934	919,000	1,146,000[a]	1:1.3
1935	655,000	876,000	1:1.3
1936	1,078,000	1,376,000	1:1.3

[a] Estimated.

According to Barnaby (1944, p. 238) "The White Act (43 Stat., 464–467; June 6, 1924) provided that there should be a 50% escapement of all salmon populations." Presumably this percentage had been selected as a suitable one or a reasonable one on the basis of previous experience or earlier observations. The data of catches and escapements to Karluk in 1921, 1922, and 1923 (Table 5) suggest this. However, as Barnaby goes on to relate (see Table 5):

> "Subsequent to the passage of that act, commercial fishing in the Karluk area has been so regulated that the catch of red salmon for a season has never exceeded the escapement. Unfortunately, this restriction of the commercial catch has not increased the size of the runs of red salmon in the river to the level of abundance that existed during the early years of the fishery. Factors other than the total numbers of salmon spawning in the river system each season have played an important role in the abundance of the runs."

In substantiation of this statement, Barnaby shows that while the runs for the 16 years from 1920 to 1936 averaged slightly over 2 million fish per year, the catches alone in the 7-year period of 1888–94 averaged over 3 million fish per year.

The 50:50 ratio between commercial catch and spawning escapement could be maintained only in those river systems of Alaska where counting weirs were operated to enumerate the sockeye proceeding upstream. Since such weirs were present in only scattered localities and did not operate every year it was virtually impossible to achieve the 50:50 division of the sockeye runs except in very special instances. One was Karluk (Table 5), as noted above. Here, even with a seemingly very high

TABLE 6. Catches and escapements of sockeye salmon, Naknek-Kvichak River systems, Alaska, in millions of fish (Eicher, 1957).

Year	Catch	Escapement	Ratio
1921	9.7	4.5	1:0.46
1922	15.6	4.2	1:0.27
1923	14.4	0.8	1:0.06
1924	6.8	1.8	1:0.27
1925	3.4	1.0	1:0.30
1926	12.7	4.1	1:0.32
1927	8.9	3.3	1:0.37
1928	11.5	2.8	1:0.24
1929	5.9	2.4	1:0.47
1930	2.5	1.3	1:0.52
1931	10.3	4.7	1:0.47
1932	10.9	6.5	1:0.60
1933	16.9	4.5	1:0.27
1934	14.4	4.5	1:0.31
1935	1.7	2.2	1:1.30
1936	17.7	4.5	1:0.25
1937	13.9	4.2	1:0.30
1938	21.0	4.5	1:0.21
1939	6.9	1.4	1:0.20
1940	3.0	1.8	1:0.60
1941	5.2	1.6	1:0.31
1942	3.2	5.0	1:1.56
1943	12.8	3.0	1:0.23
1944	6.5	1.3	1:0.20
1945	4.3	2.0	1:0.50
1946	5.1	2.6	1:0.51
1947	14.0	3.6	1:0.26
1948	9.1	3.1	1:0.34

escapement ratio, the runs deteriorated with a variability almost as great as in the Naknek-Kvichak river systems (Table 6) where no 50:50 ratio of catch to escapement prevailed, but rather one closer to 1:0.33 or with an escapement of one-quarter of the total runs.

The proposed 50:50 ratio of commercial catch to spawning escapement, even though it provided a relatively very liberal spawning population, did not prove as effective as had been anticipated. Actually, using Karluk Lake as an example, the runs were not maintained, let alone increased, and declined as much as in areas where such a rigorous escapement ratio did not occur. In other words, the total number of spawning salmon is not the only factor to be considered in the maintenance of sockeye stocks at high level. It may not be even the major factor, though it is obviously of some consequence—up to the optimum capacity of the spawning beds, as will be discussed in later sections.

Up until relatively recently there has not been available, in British Columbia sockeye salmon rivers, any means of measuring or even estimating the size of the spawning escapement in relation to the commercial catch. In the silt laden murky water of the lower reaches of the principal rivers the fish cannot be seen; several weeks elapse before the fish reach the spawning areas where their numbers can be estimated. It is thus remarkable that the Department of Fisheries inspectors, charged with the responsibility of ensuring, each year, an adequate spawning escapement in order that there be a good seeding of the spawning areas, have been successful,

TABLE 7. Fraser River sockeye data.[a]

	Catch made by					
Year	Commercial fishery	Upstream Indian fishermen	Spawning escapement	Total run	Commercial catch:escapement[b]	Total catch:spawning escapement[c]
1938	3,308,900	40,000[d]	839,800	4,118,700	1:0.27	1:0.25
1939	1,121,100	25,000[d]	133,500	1,279,600	1:0.14	1:0.12
1940	1,690,000	40,000[d]	467,600	2,197,600	1:0.30	1:0.27
1941	3,677,200	52,900	427,900	4,105,100	1:0.13	1:0.11
1942	7,969,400	46,700	2,809,800	10,825,900	1:0.36	1:0.35
1943	591,800	27,000	113,000	731,800	1:0.24	1:0.18
1944	1,440,000	42,800	431,800	1,914,600	1:0.33	1:0.29
1945	1,686,100	44,000	482,200	2,212,300	1:0.31	1:0.28
1946	7,791,400	50,100	2,875,500	10,717,000	1:0.37	1:0.37
1947	443,300	42,300	609,100	1,094,700	1:1.47	1:1.25
1948	1,841,000	86,400	998,000	2,925,400	1:0.59	1:0.52
1949	2,077,600	69,400	1,116,100	3,263,100	1:0.59	1:0.52
1950	2,115,400	70,800	1,756,900	3,943,100	1:0.86	1:0.80
1951	2,425,000	78,300	617,600	3,120,900	1:0.29	1:0.25
1952	2,267,900	84,500	851,900	3,204,300	1:0.41	1:0.36
1953	4,025,000	168,100	1,274,300	5,407,400	1:0.34	1:0.31
1954	9,528,700	94,500	2,487,100	12,108,300	1:0.27	1:0.26
1955	2,114,700	65,600	379,200	2,539,500	1:0.21	1:0.17
1956	1,801,700	62,200	879,000	2,742,900	1:0.52	1:0.47
1957	3,050,000	96,500	1,663,000	4,809,800	1:0.58	1:0.53
1958	10,498,900	82,400	3,815,800	14,397,100	1:0.37	1:0.36
1959	3,392,600	65,000	946,900	4,404,500	1:0.30	1:0.27
1960	2,454,200	86,500	620,000	3,160,700	1:0.29	1:0.24

[a] Data taken from the Annual Reports of the International Pacific Salmon fisheries Commission, 1938–60.

[b] Numbers of fish taken in commercial fishery in relation to upriver escapement. Commercial fishery:upstream Indian fishermen plus spawning escapement.

[c] Total fish taken by commercial and upriver Indian food fishery in relation to numbers of fish arriving on spawning grounds. Commercial fishery plus upstream Indian fishermen: spawning escapement.

[d] Our estimate.

over a long period, in regulating the commercial catches so that sockeye populations have been maintained. The inspectors have been guided to some extent by the size of the daily catches, by comparisons with previous cycle year experiences, sometimes by test-netting in the fishery areas to ascertain what numbers of fish are passing during periods when commercial fishing has been prohibited in order to allow free passage of fish, and by observations at upriver sites where numbers of passing fish can be observed. When, in their opinion, the commercial catch has been too heavy and the spawning escapement too light, the fishery has been stopped for a certain period to allow a greater escapement. If it has been anticipated that the run of sockeye coming in from the ocean in any year is likely to be a very small one, particular attention is paid to the amount of fishing effort arrayed against it and regulations are set up to curtail the commercial catch in order to assure a reasonably good spawning escapement.

However, from studies conducted on the Fraser River since 1938 by the International Pacific Salmon Fisheries Commission and on the Skeena River since 1944 by the Fisheries Research Board of Canada, it has been possible to ascertain the ratio each year of commercial catch to upriver escapement, i.e., what percentage of the sockeye coming in from the ocean to the river are caught by the commercial gear and what percentage are not caught.

For the Fraser River, Table 7, the catch:escapement ratio has varied exceedingly over the years indicated. In the early period, 1938–45, the escapement averaged 26% of the commercial catch—range, 13–36%. During the period 1946–50, when the Commission had instituted additional restrictions on commercial fishing in order to increase the escapement, the latter averaged 76% of the commercial catch. During the last 10 years, with a relaxation of restrictive measures, escapement has again averaged 36% of the catch. On the basis of those years in which fishing may be considered "normal" for the Fraser River (1941–45; 1951–55), i.e., when no special restrictive regulations were applied, the commercial catch represented, on the average, 77% of the total run and the escapement through the fishery and to the upriver areas, 23%.

TABLE 8. Skeena River. Estimates of numbers of sockeye in the commercial catch, Indian catch and escapement, in thousands (from Brett, 1952a, p. 463).

	Year						
	1944	1945	1946	1947	1948	Average	Per cent
Commercial	810	1200	620	390	1200	840	45
Indian	90	150	75	70	150	110	6
Escapement	620	1400	680	690	1200	920	49

For the Skeena River, on the other hand, the situation is a bit different. The commercial catch for the years 1944–48 amounted to 45% of the total run and the escapement through and past the fishery areas, 55% (Table 8). In other words, the

TABLE 9. Catch and escapement of Columbia River sockeye (bluebacks), in numbers of fish. Data for 1938–50 are from table I of Gangmark and Fulton (1952); those for 1951–56 were kindly supplied by Mr George A. Harry of the Oregon Fish Commission.

Year	Catch	Escapement above Bonneville	Catch:escapement	Rock Island count	Total run
1938	128,818	38,596	1:0.30	17,123	167,414
1939	80,756	40,010	1:0.50	19,591	120,766
1940	109,636	76,141	1:0.70	26,894	185,777
1941	153,091	18,365	1:0.12	949	171,456
1942	58,303	34,959	1:0.60	16,282	93,262
1943	43,727	29,930	1:0.68	17,665	73,657
1944	15,534	7,174	1:0.46	4,932	22,708
1945	2,529	8,068	1:3.24	7,142	10,597
1946	40,759	61,319	1:1.50	45,029	102,078
1947	219,182	119,166	1:0.54	79,833	338,348
1948	29,028	109,934	1:3.80	84,626	140,452
1949	7,259	46,407	1:6.40	18,601	53,666
1950	51,262	58,683	1:1.14	50,047	109,945
1951	48,627	155,742	1:3.20	101,782	204,369
1952	180,177	140,184	1:0.77	113,694	320,361
1953	59,777	200,302	1:3.55	151,747	260,079
1954	74,172	104,409	1:1.41	91,234	178,581
1955	45,000	197,768	1:4.40	155,000	242,768
1956	81,597	120,955	1:1.48	92,443	202,552

catch:escapement ratio was 1:1.23, thus allowing a much greater proportion of the run to pass upriver than prevailed in the Fraser. The significance of this difference in ratio will be discussed below.

STUDIES ON THE COLUMBIA RIVER

The sockeye salmon (or "blueback," as they are called there) situation on the Columbia River is of particular interest. Not only is there a long series of comparable statistics available but also the reaction of the stocks or runs to a reported reduction in area of spawning grounds can be traced.

The catch:escapement data from 1938 to 1956 are given in Table 9. In 1938 there became available (1) daily records of the commercial salmon catches and (2) counts of the salmon passing Bonneville Dam. The trend of the stocks can thus be fairly closely followed.

For the period prior to 1938 the picture is not so clear. Rich (1940a, 1940b) reviewed the blueback fishery from 1892 to 1938 and reported (1940b, p. 39) that "the blueback runs were greatly reduced as long ago as 1900, since which time there has been no marked change in the size of the catch. This depletion of the blueback was probably due chiefly to the reduced spawning area available" (that is, to the utilization of the water resources of the Columbia basin for other purposes). On the basis of the data available, Rich (1942, p. 136) calculated the catch:escapement ratio of 1938 to be approximately 1:0.30, giving an escapement of around 23% of the total run.

From 1938 on, with the exception of 1941, the commercial catches, in relation to escapement, declined, as did indeed the total sockeye run. A low was reached in 1945, after which the population increased gradually, with considerable fluctuation from year to year. At the same time, 1945–56, the catches amounted to less, generally, than the escapements, frequently to much less. At the present time the catch: escapement ratio is quite different from that of 1938 and earlier years.

As reported by Gangmark and Fulton (1952, p. 7), "since the low of 1945, the runs have shown signs of recovery . . . . Of particular interest is the marked increase of bluebacks passing Rock Island Dam. The count there probably represents the best measure of the spawning escapement, because no commercial fishery takes place beyond it, and because there is no evidence that the fish unaccounted for between Bonneville Dam and Rock Island Dam spawn successfully."

EFFECTIVENESS OF CATCH:ESCAPEMENT RATIO FINDINGS

The catch:escapement ratios for different areas have thus differed greatly. In Alaska the ratio of 50:50 (or 1:1) established by the White Act in 1924 applied only to a few streams on which counting weirs were operated. Here, using the Karluk River as an example, the adherence to the 50:50 ratio did not lead to an improvement in sockeye production. For two sockeye rivers in British Columbia, the Skeena and the Fraser, catch:escapement ratios of approximately 1:1.23 (or 45:55) and 1:0.3 (or 77:23), respectively, prevailed. For the Columbia, while the ratio for 1938—and probably earlier years also—was estimated as 1:0.3 (or 77:23) it has, in recent years, changed greatly and for the past 9 years, 1948–56, has had a mean of 1:1.8 (or 36:64).

While it is important that there be, each season, a suitable division between the commercial catch and the escapement in the run of sockeye to a river system it is equally important that this division applies throughout the season (see also p. 52), so that all sections of the run be represented in the escapement upriver. Reports from Alaska indicate that, in many areas, in order to achieve the 50:50 catch:escapement ratio, fishing was curtailed in the early and later periods of the season but that during the peak period the fishing was very intensive. Even though a 36-hr closed period each week was mandatory throughout the season, the escapement during the peak of the run was most inadequate. Hence, the bulk of the spawning population consisted of early- or late-running sockeye. Environmental conditions may, at early and late periods of the spawning season, be less favourable to effective spawning and survival of eggs.

It has been found for the Fraser River, which possesses many separate tributary lake systems, that the runs of sockeye to these several areas are quite distinct, not only in morphological characteristics, but also in time of migration. They enter the river at specific times and constitute a succession of runs within a run. Many of them overlap in time of occurrence; some of them may occur at the same time. In any event, it is important, for the maintenance of these runs and for optimum production in all areas, that each individual run be given adequate protection. Hence, throughout the season there must be not only an overall adequate catch:escapement ratio but each individual run or "race" must have the protection of a suitable catch:escapement ratio. An excellent report on the timing of Fraser River sockeye salmon runs is given by Killick (1955) and on the basis of this information, Royal (1953) states that "in 1951 the exploitation of all races was allowed for the first time since 1945. Restricted fishing was permitted on all races at a level which, calculated on previously indicated productivity levels from escapements which had passed through the fish-ways, *would allow for some catch while still permitting any needed increase in escapements*" [author's italics]. Evidence is presented to show the effectiveness of this individual treatment applied to each race.

For the Skeena River also, the sockeye run has been found to be a complex of several individual runs, each going to different lake tributaries. There is this difference however. The Skeena system contains only one extensive lake tributary, the Babine, and here, as indicated by Brett (1952a), around 70% of the Skeena sockeye are produced. This does not mean, however, that other areas are not important, nor that they may not be built up to a higher production.

A particular study has been made of Babine Lake by the Fisheries Research Board of Canada and it has been found that within this lake, some 100 miles in length, and in the upper part of the out flowing Babine River, there are distinct early- and late-running spawning runs or "races," each of which requires separate management, even at as early a period as their entrance into the Skeena River and into the estuarial fishery, if optimum production is to be assured.

As, through research, knowledge of sockeye salmon behaviour and propagation increases, effective management practices must be further refined. They must provide not only adequate spawning fish to the river as a whole but to individual areas and to the important sections of those areas. To this end it is necessary to know *when* each individual "race" or population enters the river, and *in what quantity*, and to provide for each a proper division between catch and escapement.

Chapter 4. Variability of reproductive success

It is now common knowledge that when predictions of the number of sockeye that will return to a river in a certain year are made on the basis of the size of the escapement (number of spawners) in the preceding cycle year, these predictions are often quite at variance with the actual return. Good evidence of the extent of the fluctuations that may occur are available from the quite precise records obtained at Karluk Lake, Alaska (Rounsefell, 1958a, p. 95) for the years 1921–48 (Table 10).

TABLE 10. Numbers of sockeye spawners and the resulting runs, Karluk Lake, Alaska, 1921–48 (from Rounsefell, 1958).

Year of spawning	Escapement (no. of spawners) (1×10^3)	Returns (progeny) (1×10^3)	Return per spawner
1921	1500	4494	3.00
1922	400	2282	5.71
1923	695	1990	2.86
1924	1065	809	.76
1925	1621	1607	.99
1926	2534	1461	.58
1927	872	1618	1.86
1928	1094	2630	2.40
1929	901	1587	1.76
1930	1087	1172	1.08
1931	873	2578	2.95
1932	738	2538	3.44
1933	968	2186	2.26
1934	1450	1261	.87
1935	876	1250	1.43
1936	1375	1353	.98
1937	1265	1334	1.05
1938	1230	1587	1.29
1939	706	1831	2.59
1940	876	858	1.05
1941	932	575	.62
1942	629	687	.97
1943	921	1495	1.62
1944	769	1141	1.48
1945	659	1263	1.92
1946	442	822	1.86
1947	485	774	1.60
1948	754	811	1.08

No matter what level of escapement we compare, whether it be relatively high:

1924 — 1,063,000 spawners; return per spawner — 0.76
1928 — 1,094,000 spawners; return per spawner — 2.40
1930 — 1,087,000 spawners; return per spawner — 1.08

or relatively low:

1923 — 695,000 spawners; return per spawner — 2.86
1942 — 629,000 spawners; return per spawner — 0.92
1945 — 659,000 spawners; return per spawner — 1.92

the variations in production, as indicated by the number of adult fish returning, are quite marked.

This has been demonstrated quite clearly also in Kamchatka where, at Lake Dalnee, the runs of sockeye have been examined over many years (Krogius and Krokhin, 1954). In Fig. 11 are shown the returns from known spawnings from 1935 to 1947, in thousands of fish. The extent of the fluctuations and the lack of correlation between the numbers of spawners and the numbers of returning adults is readily apparent.

For the Fraser River, which has been called the world's best sockeye-producing river, the overall fluctuations in production, as indicated in Table 11, have also been quite appreciable. They have varied all the way from 2.2X in 1946 to 15.1X in

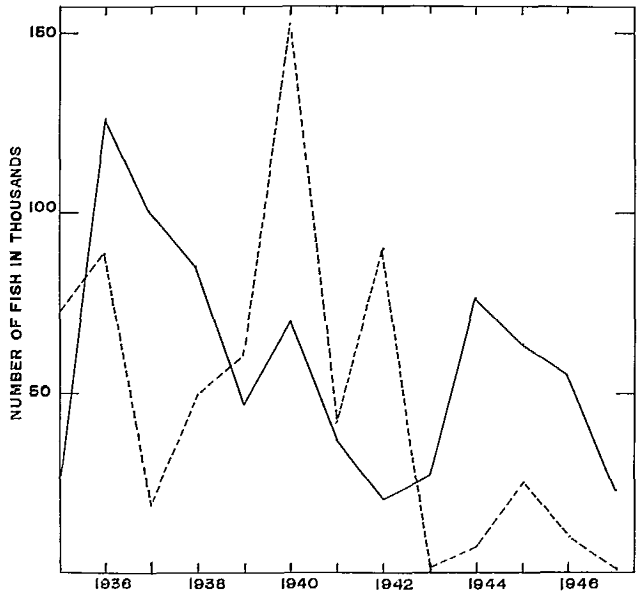

FIG. 11. Relation of numbers of adult sockeye in the spawning escapement each year (solid line) and numbers of adults returning from the sea in brood years (broken line) for Lake Dalnee, Kamchatka. (Taken from Krogius, 1951, table 3; 1953, p. 12.)

1943. Prior to the disastrous rock slide in the Fraser River canyon at Hell's Gate in 1913, heavy runs of sockeye returned to all the large upriver spawning areas in the same cycle year, e.g., in 1901, 1905, 1909, 1913, thus producing a really "big" run every 4 years and a very large catch. After 1913, this big run disappeared everywhere, and when big populations began to reappear, starting with Adams River in 1926, some of them had their dominant lines in other sequences of years. Spawning escapement estimates for recent years, reported by the International Pacific Salmon Fisheries Commission, reveal that the "big" or dominant runs to the Stuart and Quesnel regions are still in the 1901 cycle (1953, 1957, 1961), the Shuswap Lake or Adams River "big" run is in the 1902 cycle, the Stellako River (Fraser Lake) runs have been largest in the 1902 and 1903 cycles, while the largest Chilko run has

TABLE 11. Numbers of spawners and resulting runs (catch plus escapement) for the Fraser River, B.C., 1938–54. The return of adult fish per spawning female is also indicated.[a]

Year of spawning	Escapement (total spawners) (1×10^2)	Returns (progeny) (1×10^2)	Returns per spawner	Return per spawning female
1938	8,398	108,259	13.0	–
1939	1,135	7,318	5.5	–
1940	4,676	19,146	4.1	–
1941	4,279	22,123	5.2	7.0
1942	28,098	107,170	3.8	8.5
1943	1,130	10.947	9.7	15.1
1944	4,318	29,254	6.8	13.8
1945	4,822	32,630	6.8	13.4
1946	28,755	39,431	1.4	2.2
1947	6,091	31,209	5.1	9.1
1948	9,980	32,043	3.2	5.5
1949	11,161	54,074	4.8	8.4
1950	17,569	121,083	6.9	14.4
1951	6,176	25,595	4.1	7.9
1952	8,521	27,429	3.2	6.4
1953	12,743	48,098	3.8	8.6
1954	24,851	143,971	5.8	9.2

[a] Data on numbers of sockeye are taken from Annual Reports of the International Pacific Salmon Fisheries Commission. Sockeye are all considered as of 4_2 age-group. In the Commission's reports, separation is made, in the escapement records, between the 3_2 age-class and the $4_2 + 5_2$ age-groups, but no differentiation is made in the catch records. In the years 1945, 1949, 1953, the sockeye runs to the Adams–Shuswap area (in the years preceding the dominant "big" run) were chiefly (around 80–90%) 3_2 males, hence contributed little to production in the area. Full consideration of the significance of the 3_2 males with respect to production does not greatly change the returns as tabulated. Without data on the 3_2 fish in the catches, more precise calculations do not seem warranted.

been in the 1904 cycle, although recently (1963) the 1903 cycle year has taken first place, perhaps only temporarily.

Hence, with different spawning areas dominating the Fraser runs in different years one might anticipate a fluctuation in production each year according to the production conditions and the production capacity of each major area. This does occur, as already observed. Nevertheless, a marked variation in production is found between those years when only one major area is the chief contributor or producer. Thus, for the 1902 cycle, when the Adams River run is the major one, the production of adults returning 4 years later per spawning female has varied in the following manner: 1942—8.5; 1946—2.2; 1950—14.4; 1954—9.2. For the 1901 cycle, when the Chilko run is the dominant one, the production factor varied as: 1941—7.0; 1945—13.4; 1949—8.4; 1953—8.6.

Much of this fluctuation is due to variations in survival of the young in fresh water, either during the egg or fry stage or during the period of residence in the lake. This is clearly indicated by data from Lake Dalnee, Kamchatka, where there is a close relationship between numbers of seaward migrating young sockeye and the number of adults returning from the sea (Fig. 12). It is quite in contrast to Fig. 11 where no good correlation was found between the number of spawning fish in the escapement and the subsequent return of adults in the next brood year. It is thus

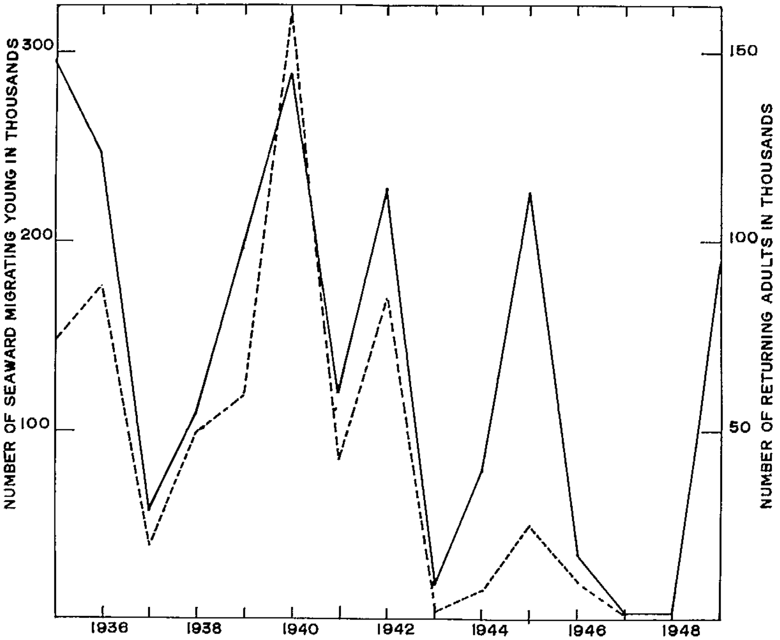

FIG. 12. Relation of number of seaward migrating sockeye (solid line) to number of adult fish returning (broken line), Lake Dalnee, Kamchatka. (Taken from Krogius, 1951, table 3; 1953, p. 12.) Year dates are those of time of spawning, i.e., of the brood years.

indicated that most of the variability in production occurs during the freshwater developmental stages.

To know, then, the extent of the losses in fresh water, when they occur and how they are caused, becomes of paramount importance. With this knowledge one can determine the efficiency of natural propagation which is fundamental to an understanding of what escapement of spawners is required for best production in an area; one can also assess the feasibility of eliminating or appreciably reducing the losses and thus materially building up production.

HYPOTHETICAL MORTALITY TABLE

Let us, for general discussion purposes, set up a hypothetical tabulation of the mortalities estimated to occur at each life-history stage of the sockeye's life cycle, i.e., from the time the fish, after escaping through the coastal, estuarial, and river commercial fishery areas, and eluding the Indian fishermen, proceed upstream to the spawning grounds, to the time—3, 4, 5, or 6 years later—when the offspring adults return again from the sea. Let us assume that we are dealing with a run of 1000 fish, with the sexes equally represented, i.e., there are 500 females, each of which carries 4000 eggs. The egg content of the run thus amounts to 2 million eggs.

Let us assume the following losses:

During upriver migration—5% or 100,000 eggs; remainder—1,900,000 eggs.
During spawning and incubation—50% or 950,000; remainder—950,000 alevins.
During emergence from the redds and migration into the lake—75% or 712,500 fry; remainder—237,500 fry.
During residence in the lake—92% or 218,500 fry; remainder—19,000 seaward migrants.

The resulting seaward migration of young sockeye (19,000) constitutes an overall survival during the freshwater period of 0.95% of the original egg content of the spawning escapement, or, roughly, 1%.

In order to maintain the populations of sockeye under natural conditions, i.e., prior to any commercial fishery, each pair of fish has merely to assure the production of one pair of sockeye in the offspring generation. Assuming 4000 eggs per female this would involve a total survival—egg to adult—of 0.05%. In other words, in order to maintain the sockeye population at a stable level, the overall percentage survival would fluctuate around a level of 0.05, or one-twentieth of 1%.

In the hypothetical mortality table given above, we have established a survival to the seaward migrant stage of 0.95%, i.e., 19,000 migrants. If we further assume a 90% mortality in the ocean or a 10% survival from ocean residence, which one experiment on the Fraser River (Foerster, 1936b) revealed, the 1900 adults returning from the ocean would represent a return of almost twice as many adults as spawned originally. This is, roughly, 0.1% of total original eggs. If, on the other hand, we assume a 20% ocean survival as was found for Karluk Lake, Alaska (Barnaby, 1944), 3800 adults will return, overall survival being 0.19%; if there is 33% survival, as found in Lake Dalnee, Kamchatka (Krogius, 1951), then

6270 adults return and survival is 0.31%. For the Fraser River and the Columbia it has been indicated that the ratio of catch to escapement is in the neighbourhood of 4:1, i.e., that 5 fish return for every spawner. In such case the overall survival amounts to 0.25%.

All of these instances, in which more than two adults return for each one that spawns, require that a freshwater survival appropriately greater than our hypothetical 0.95% must occur or that ocean mortality be less than 90%. During some stage or stages of life the survival must be greater than in our hypothetical table. This matter is discussed elsewhere below.

All factors of the environment, physical, chemical, and biological, have an effect on sockeye survival and abundance. Every spawning ground, every rearing area, and each stream channel through which they pass will differ appreciably in many of these environmental features. Therefore, as the young sockeye pass through one stage of development to the next, their fate will be determined by the conditions to which they are subjected. If throughout their freshwater cycle all the series of stages are favourable, production will be high. If, however, at any one or more stages the conditions be unfavourable, mortalities will occur, representing one or more limiting factors to overall high survival. The old saying that "a chain is as strong as its weakest link" aptly applies.

Depending on the particular conditions prevailing in a sockeye-producing area the stocks may have a high rate of reproduction, making possible a high catch in relation to the spawning escapement required to maintain the population at a high level, or a low reproduction rate which will require a much higher spawning escapement and permit only a relatively low commercial catch. There may be areas in which the whole returning ocean run is required to spawn to maintain the stock.

It would be quite remarkable actually if any area could be found to which the hypothetical table, given above, would apply, since it is a composite of data compiled from many areas. Nor is it likely that any other table, prepared for a specific area for a certain year, would be found to meet the conditions in any other area or in the same area in other years. We are dealing with a highly dynamic situation and to hope to arrive at a useful average state or set of data seems highly unlikely. We may, however, achieve an understanding of the ranges of variation in production of young and acquire some insight into the major limiting factors applying in specific areas; we may, for particular rivers or certain tributary spawning-nursery regions of river systems, establish a particular range of production which will give the best possible sockeye fishery.

For this purpose we bring together the results obtained, so far as they are available, for all areas in which studies of natural propagation have been conducted. Certain phases of the life cycle may have been investigated in only one or perhaps two regions, and hence, the application of the results to other areas may be debatable. Nevertheless, they are contributions to knowledge and obviously have specific usefulness.

Although our natural production tabulation is based largely on the research which has been done under the auspices of the Fisheries Research Board of Canada, full use has been made of similar work done by other investigators and agencies on the Columbia, the Fraser, on Alaska streams, and in Kamchatka. In some cases, only certain phases of the life cycle have been studied by other investigators. The data obtained have been incorporated, however. It becomes abundantly clear that the greater the amount of pertinent scientific data that can be made available, by scientific publication, on salmon production in any life-history stage, the more accurate will be the overall understanding of what does occur in nature and what remedies must be applied to achieve maximum or optimal production.

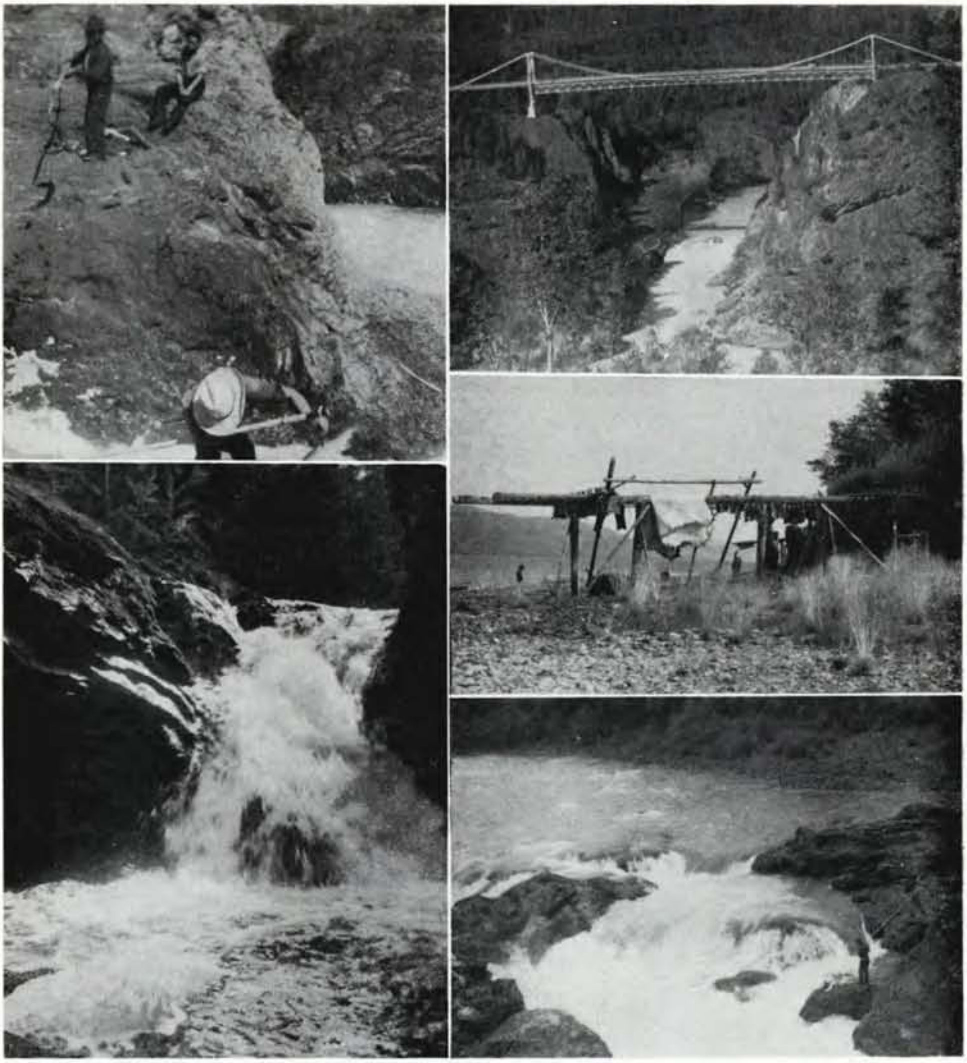

PLATE IV.

Upper right: Hagwilget Canyon, Bulkley River, near Hazelton, B.C. A narrow, turbulent, fast-flowing section of the river which, at certain water levels, blocks the ascent of salmon. Not far upstream is Moricetown Falls where (see text p. 90) Indians catch, by gaffing with long pole and large, sharp hook, their fish food supplies for the winter (*left top and right bottom*).

Right centre: Sockeye carcasses, cleaned and split by the Indians, hung up to dry and cure in the sun. Usually a small wood fire is kept going under the racks to provide some degree of "smoking."

Lower left: A small falls or cascade of water in Fifteen Mile Creek, Babine Lake, about a mile upstream from the lake. This forms an effective block to further upstream migration for spawning. A survey indicated that extensive good spawning areas lay above this falls and a larger one, Quartet Falls, a short distance further upstream and in the same rocky canyon. Construction of a fishway to allow salmon to surmount these falls was at one time considered but abandoned by the Department of Fisheries of Canada.

Chapter 5. Migration of sockeye to their spawning grounds

UPSTREAM ASCENT OF THE ADULTS

Once past the commercial fishing grounds, normally located in the lower parts of a river or in its estuarial areas and where from around 50 to 85% of the run is removed, the sockeye embark upon their upstream ascent to the far-flung spawning grounds, persisting against all obstacles to reach their destination—the natal stream.

Two factors have a major influence on the achievement of that mission—(1) the condition of the fish and (2) the rigours and hazards to be faced and overcome.

Sockeye, in common with other Pacific salmon species, do not feed once they enter fresh water. Therefore, for sustenance during the several months of fasting, for development of the sex products, and for energy to make the long and gruelling stream ascent, they must rely on the reserves of fats and proteins stored up within the body during the period of ocean residence. The general view is that, in its evolution, each stock of salmon has inherited the capacity and ability to store up sufficient energy reserves to enable it, under normal conditions, to get back to its natal spawning area and to reproduce. This becomes of prime significance in the case of long river systems, perhaps outstandingly represented by the Fraser River, where the natural spawning areas in tributary river systems occur all the way from some 50 miles from the Fraser mouth (Pitt River) to some 700 miles farther upriver (upper Stuart River system) (see Fig. 13).

The matter came to the fore in connection with consideration of the lack of returns to one upriver Fraser area (Eagle River in the Shuswap Lake system) from quite large planting of eggs from lower Fraser spawning grounds (Birkenhead River and Cultus Lake) made by the Federal Department of Fisheries in the 1920s. It was suggested that the lack of success might have been due to the fact that the lower Fraser stocks, which had, normally, a much shorter and less hazardous migration route, would not have the physical capacity, i.e., the energy reserves, required to accomplish the much longer and rougher migration to the Shuswap region. Assuming these transplanted fish, which were transferred as eyed eggs, had successfully hatched out, migrated to sea and returned from the ocean, they might have either (1) perished somewhere in the Fraser in a vain effort to reach their goal, (2) returned to their parental spawning ground, or (3) sought suitable spawning beds in intermediately located streams.

In order to obtain evidence in this regard, series of experiments were undertaken (Foerster, 1946). Eggs were collected from (1) a lower Fraser area, Cultus

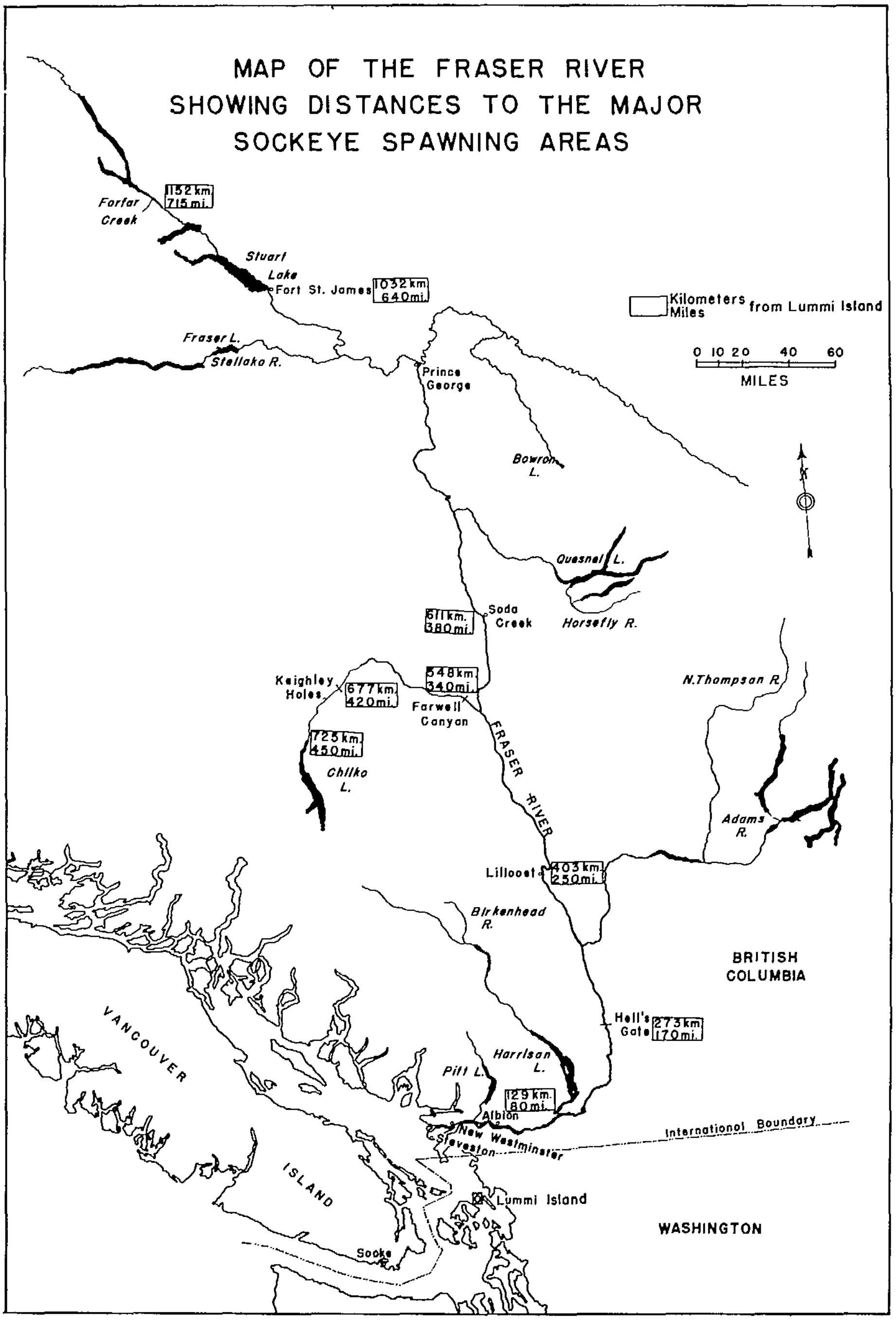

FIG. 13. Map of the Fraser River showing distances to the major sockeye spawning areas. (From Idler and Clemens, 1959, fig. 1.)

Lake, in 1928 and 1931 and from (2) an upriver area, Adams River (which is within the Shuswap Lake watershed and fairly close to Eagle River) in 1929 and 1930. They were transferred to a small hatchery at Eagle River, hatched, reared in ponds for 6 months, then marked and released. It was anticipated that the returning adults arriving at a weir, constructed in the lower reaches of Eagle River, would indicate whether the particular characteristics of the stock, i.e., lower Fraser or upper Fraser, had any influence on the return and on the ability to make a much longer upriver journey.

From the first Cultus Lake transplant (1928 brood year) 12 marked adults were recovered in the 1932 commercial fishery but none returned to Eagle River. From the second test (1931 brood) no returns were reported from anywhere, although the extensive recovery campaign throughout the fishing area conducted in 1932, 1933, and 1934 was not undertaken in 1935. It seemed reasonable to suppose, however, that had any considerable number of marked sockeye been encountered by a fisherman or cannery attendant some would have been noted and reported.

From the first Adams River transplant (1929 brood) 104 marked adults were recovered in the commercial fishery and 3 at the Eagle River weir. From the second test (1930 brood) 43 marked adults were taken in the fishery and 7 at the weir.

The experiments thus were rather inconclusive in indicating the significance of distance of spawning ground from the sea when planning the restocking of depleted sockeye areas by transfer of eggs from other areas. Both types of transplants were ineffective in producing a substantial return of adults. A few Adams fish did return to Eagle River. To what extent other factors involved in the tests affected the results is unknown. The autumn release of the marked fingerlings may have been detrimental (it would have been too costly to hold the young fish in ponds in the area over the winter); many of the released fingerlings may have remained in Shuswap Lake or may have been consumed by predators. Suffice it to say that a quite independent planting of some 16 million sockeye eggs from Cultus Lake in the spring of 1929 (brood year 1928) resulted in no increase in the small number of unmarked sockeye returning to Eagle River in 1932.

Other agencies also have given consideration to the importance of distance of spawning area from the sea and thus extent of migration as a racial characteristic of importance. In its 1958 Annual Report (p. 17) the International Pacific Salmon Fisheries Commission reveals that eyed-egg transplants, made with special consideration given to the location of the stream from which the eggs were taken, were sometimes quite successful. At Portage Creek between Seton and Anderson lakes "a run of sockeye has been created which is capable of a rate of natural reproduction apparently equal to that of the original stock in its native freshwater environment."

Thus, the extent to which the returning adult is nutritionally equipped to return to its spawning area and reproduce successfully is of prime importance. How much reserve energy the fish possesses is not clearly established but it is obvious that every unusual hazard with which it has to contend, whether it be a flood and fast water, a drought and low water, a natural obstruction in the river or a hydroelectric dam, and which causes delay or extra exertion, will deplete its surplus reserves and possibly prove detrimental. It seems but natural that some reserve to meet emergencies will be provided by nature, but the question is—how much?

ENERGY EXPENDITURES OF ASCENDING ADULTS

In 1956 the International Pacific Salmon Fisheries Commission commenced a study of the energy expenditures of Fraser River sockeye during upstream migration (Idler and Clemens, 1959). Two stocks or populations were investigated, one going to the Stuart Lake system, the most northerly spawning area of the Fraser and some 700 miles from the river mouth, the other proceeding to Chilko Lake, about 450 miles (see Fig. 13). Specimens of each stock were collected at several intermediate points along the Fraser, separation being made on the basis of time of running and scale pattern.

For each fish in each sample, analyses were made of the water, fat, and protein contents of (1) the eviscerated fish, (2) the viscera, (3) the gonads or sex organs. Fat and protein content were subsequently converted into caloric value, taking 1 g of fat as equal to 9.3 cal (kilogram-calories) and 1 g of protein as equivalent to 4.1 cal.

TOTAL EXPENDITURE OF ENERGY

From the time of entrance into the Fraser until the completion of spawning the utilization of energy reserves was found to be:

Race of sockeye	Distance travelled		Elevation of spawning ground		Days out	Fat		Protein	
						♂	♀	♂	♀
	(miles)	*(km)*	*(ft)*	*(m)*		(%)	(%)	(%)	(%)
Stuart	715	1152	2270	693	34	91	96	31	53
Chilko	450	725	3840	1170	36	78	91	42	61

The total energy expended by a standard Stuart Lake male in travelling from Albion (80 miles from the river mouth but well within the limits of tidal influence) to the spawning grounds (fish examined at time of death) in Forfar Creek, tributary of the upper Stuart River, a distance of 635 miles (1023 km) and at an elevation of 2270 ft, was 1398 cal for the maintenance of 1 kg of live fish, or 1.01 cal per kg per km of travel. For females the corresponding value was 1644 cal, or 1.16 cal per kg per km. For the Chilko run, a distance of 370 miles (596 km) and at an elevation of 3840 ft, the energy expended was 1293 cal for males and 1903 cal for females.

With regard to the energy reserves of the body diverted into the development of the gonads it was found that the weight of the male testes increased only from 2.36% of the live weight of the fish to 3.12%, whereas in the females the ovaries increased from 3.59 to 15.7%. Further tests in 1957 revealed that the energy used up in development of ovaries was 339 cal (22.5 g of fat and 31.9 g of protein) more than for the male testes, or roughly 10% of the energy reserve of the female fish.

The energy utilized by the upstream migrating fish during various stages of the upriver ascent is of interest particularly where the migration is long and varies in ruggedness. Table 12 gives the pertinent data for the Stuart Lake sockeye run as it proceeded upriver in 1956 (Idler and Clemens, 1959). Similar data for the Chilko run are less reliable due to the small and seemingly unrepresentative samples obtained at Farwell Canyon. Commenting on these findings the authors state:

TABLE 12. Utilization of body energy reserves of a standard male and female sockeye while migrating up the Fraser River to the Stuart Lake spawning grounds in 1956. F = fat; P = protein. (Energy reserves in kilocalories (kcal) at Lummi Island at the start of the run were: for males 3395F + 2000 P = 5395 total; for females 3136 F + 1814 P = 4950 total) (from Idler and Clemens, 1959).

Section of river	Distance *miles(km)*	Difference in elevation *ft(m)*	Days out	Energy utilized					
				Percentage of original					
				Males		Females		Males	Females
				F	P	F	P	*kcal*	*km*
Lummi I. to Hell's Gate	170(274)	280(85)	7	23.3	0.96	21.2	3.82	2.80	2.68
Hell's Gate to Lillooet	80(129)	384(117)	3	14.1	11.5	9.1	4.5	5.46	2.84
Lillooet to Soda Creek	130(208)	657(200)	4	13.2	2.79	20.2	7.41	2.42	3.67
Soda Creek to Fort St. James	260(421)	904(275)	9	22.5	1.78	26.2	8.52	1.89	2.32
Fort St. James to Forfar Creek	75(120)	45(14)	4	–	–	–	–	–	–
Forfar Creek (spent fish)	– –	– –	7	15.6	15.2	16.4	16.6	–	–
Forfar Creek (dead fish)	– –	– –	5	2.6	1.2	2.6	11.8	–	–
Total:	715(1152)	2270(691)	39	91.3	33.4	95.7	52.6		

"In travelling between Lummi Island and Hell's Gate the body of the standard female used 2.68 Cal/km of fat and protein; over the same route 2.80 Cal/km were expended from the body of the standard male. . . . The increased energy consumption for males between Hell's Gate and Lillooet, as compared with the interval between Lummi Island and Hell's Gate is apparent. The females used 2.84 Cal/km compared with 2.73 Cal/km while the males used 5.46 Cal/km as compared with 2.80 Cal/km. . . . An increase would be anticipated because the elevation of the river shows an average increase of only 0.312 m/km between Lummi Island and Hell's Gate whereas a rise of 0.908 m/km exists between Hell's Gate and Lillooet. Further, the temperature of the river would also result in increased energy consumption between Hell's Gate and Lillooet (62°F) as compared with Lummi Island to Hell's Gate (58°F). It would

> appear that the increased energy consumption is either too great for the males or too small for the females since such significant differences would not be anticipated between sexes. Apparently the consumption found for the males between Hell's Gate and Lillooet is too high, i.e., the average male taken at Lillooet had greater reserves than the average of the run. This conclusion is strengthened by the low energy consumption for males between Lillooet and Soda Creek, 2.42 Cal/km as compared with 5.46 Cal/km between Hell's Gate and Lillooet. This would not be anticipated as the change in elevation of the river between Lillooet and Soda Creek is 0.957 m per km, as compared with 0.907 m per km between Hell's Gate and Lillooet and the water temperatures were very similar, 62.5°F as compared with 62°F. The females reflect the trend that would be anticipated and show an energy consumption between Lillooet and Soda Creek of 3.67 Cal/km as compared with 2.84 Cal/km between Hell's Gate and Lillooet. . . .
>
> "From Soda Creek to Fort St. James it would be anticipated that the energy consumption would be less than between Hell's Gate and Soda Creek because the change in altitude in metres per kilometre is 0.907 between Hell's Gate and Lillooet, 0.957 between Lillooet and Soda Creek and only 0.660 between Soda Creek and Fort St. James. The data support this reasoning. The standard female used 2.32 Cal/km while the standard male used 1.89 Cal/km between Soda Creek and Fort St. James. . . .
>
> "The energy expended by the sexes from Fort St. James until the time the fish spawned at Forfar Creek was 73.9 Cal/day for the females and 75.6 Cal/day for the males. When these data are re-calculated and expressed as the body energy required to maintain the life processes of a kilogram of live fish they become 35.7 Cal/day/kg for females and 30.1 Cal/day/kg for males.
>
> "The energy expenditure by the female from spawning until death was very much greater than that expended by the male. The female expended 58.8 Cal/day as compared with only 22.7 Cal/day for the male."

The data obtained for the two Fraser River runs apply to only 1 year's sampling. Further work was done in 1957 and still more is contemplated. A better understanding will be available when further evidence is obtained. The present findings agree well, it may be noted, with similar studies on chum salmon of the Amur River (Pentegov, Mentov, and Kurnaev, 1928). The two sexes of Amur chums appeared to draw nearly equally on their body reserves of energy, whereas the present data indicate that, in sockeye, the females utilize more than the males. The Chilko sockeye used up more body protein energy than the longer-run Stuart Lake individuals, which, in turn, relied more on the fat reserves.

CHANGES IN SWIMMING ABILITY DURING UPRIVER MIGRATION

Closely allied to the studies on energy reserves and energy consumption are tests conducted on the Columbia River (Paulik and DeLacy, 1958) in 1956 and 1957 of the swimming ability of sockeye (bluebacks) as determined at several localities (Fig. 14) on the upriver migration route. The swimming ability was determined by the length of time the fish would continue to swim against currents of known velocity.

The 1956 experiments were largely exploratory and preliminary. They involved the collection of adult sockeye at five locations (Table 13) and their removal to the laboratory at the College of Fisheries, Seattle, where tests of their swimming

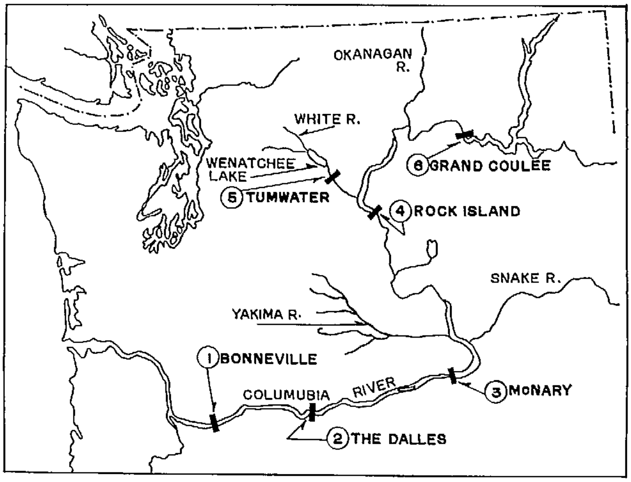

FIG. 14. Sketch of lower Columbia River system to show the location of dam sites referred to in the text and of the Okanagan, Wenatchee, and Snake rivers. 1—Bonneville Dam; 2—The Dalles; 3—McNary; 4—Rock Island; 5—Tumwater; 6—Grand Coulee.

ability were made in an annular tank of water caused to revolve at a speed which produced a current velocity of 4.3 ft/sec (2.93 miles/hr or 1.31 m/sec). Elaborate precautions were taken in capturing the fish, transferring them to the laboratory and handling them prior to testing but, despite the care and attention given, the results of the tests made were reported to be inconclusive in showing clearly any change in swimming ability at the various locations.

TABLE 13. Mean lengths of swimming time (in seconds) in water flows of stated velocities (in feet per second) at various locations in the Columbia and Wenatchee rivers (see Fig. 14). (Figures in the 4.3 ft/sec column are average swimming time on first three test days of the 1956 study. The data in the next three columns pertain to tests made in 1957 (see text). Underlined records are considered significantly different (from Paulik and DeLacy, 1958).

Location	Distance from mouth		Elevation		Water velocity (*ft/sec*)			
					4.3	5.3	6.6	9.4
	(*miles*)	(*km*)	(*ft*)	(*m*)				
Bonneville Dam	150	240	70	21	355	–	–	–
McNary Dam	290	470	335	102	347	–	196.4	64.9
Rock Island Dam	450	720	600	183	524	292	173.8	62.4
Tumwater Dam	500	800	1500	460	278	215	153.7	59.2
White River	535	860	1900	580	152			

The Rock Island samples showed throughout a greater swimming ability than lower-river individuals (Bonneville and McNary). However, this was found to be due partly to the inclusion in the test sample from Rock Island of a number of smaller-sized fish (some evidence was obtained of an inverse relationship between size of fish and the length of time it was able to swim in the annular tank), and partly to a better adaptation of Rock Island fish to the holding conditions at the laboratory. While the mean swimming time of the Rock Island sample was consistently greater than those from McNary and Bonneville dams, it was not significantly greater in all cases. However, a definite decline in swimming power was demonstrated after fish had passed through Lake Wenatchee and entered the White River to spawn. The sockeye from Tumwater Dam, below Lake Wenatchee, swam for 278 sec before exhaustion in a current of 4.3 ft/sec, whereas samples from the White River swam for only 152 sec (Table 13).

The 1957 experiments were conducted only on McNary, Rock Island, and Tumwater Dam samples. They were carried out in a 25-ft (7.6 m) flume set up on a floating barge which was moved to McNary and Rock Island Dam sites to avoid the long tank-truck haul to the Seattle Laboratory. Three water velocities were used. The first averaged 1.62 m/sec or 5.3 ft/sec (varying from 4.9 ft/sec at the head of the flume to 5.6 ft/sec at the downstream end of the 20-ft section); the second was 2.01 m/sec or 6.6 ft/sec (6.4–6.8); and the third was 2.87 m/sec or 9.4 ft/sec (8.9–9.9). Swimming time was represented by the number of seconds that elapsed between the time the fish was placed in the test flume and the time it drifted down through a barrier 5 ft above the lower end of the 25-ft flume, i.e., was no longer able to maintain its position in the current. The entire 20-ft testing secion of the flume was darkened by means of a canvas cover.

The results of the 1956 (water velocity test at 4.3 ft/sec) and 1957 experiments are summarized in Table 13. Only those swimming times which have been underlined were considered significantly different statistically to denote changes in swimming ability as the sockeye moved upriver, becoming less the further upstream the fish were tested. The differences in swimming time at different water velocities in 1957 are also quite apparent, as would be expected.

Some consideration was given throughout the 2 years' experiments to the ability of the weakest fish, rather than the average for the sample, to meet the conditions set up by the different water velocities. The lowest 10% of the combined samples tested at each location was studied. It was felt that the ability of the weakest segment of a run to negotiate a rapid stretch of water would be of greater significance than determining what an average individual might do. However, for the three locations examined—McNary, Rock Island, and Tumwater—and at water velocities of both 6.6 ft/sec and 9.4 ft/sec, no clearcut differences were found.

To illustrate the variations between individual fish in a run, with respect to swimming ability, the swimming performances of 406 sockeye tested in the straight flume at McNary and Rock Island dams at 9.4 ft/sec were compared. Since no differences in swimming ability were found between locations tested, it seemed permissible to pool the results. Fig. 15, taken from Paulik and Delacy (1958), shows the variations occurring in swimming performance. While the strongest were able to swim at 9.4 ft/sec for 112 sec, the weakest gave up after only 22 sec. Furthermore, while a sockeye may swim at a high speed for a short time, it becomes exhausted quickly if forced to sustain such activity for very long. No fish among the 406 tested was able to maintain its position in the 9.4 ft/sec flow for as long as 2 min.

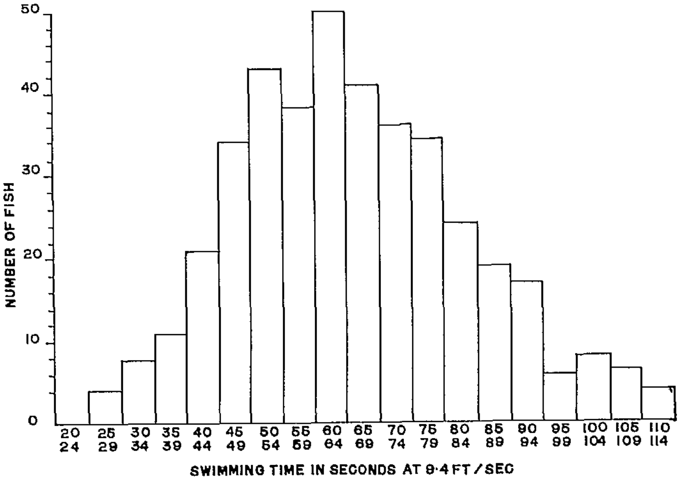

FIG. 15. Distribution of swimming performance times for 406 adult sockeye salmon at a water velocity of 9.4 ft/sec. These observations were taken in the Columbia River in the straight flume during 1957 from McNary, Rock Island, and Tumwater Dam. (Paulik and DeLacy, 1958.)

Two conclusions of general interest which resulted from the swimming ability tests on the Columbia River were that:

1. a comparison of the total amount of work which a sockeye might do at different stages of maturity depends upon the rate at which the work is done;
2. a certain amount of delay and exertion may be more harmful at one location in the river than at another.

A third conclusion, resulting from the Fraser River energy reserve utilization studies, referred to above, might be that the amount of work done in negotiating obstructions or fast water during upstream ascent eats into the store of energy available to the fish and may lead to a serious depletion or total utilization of the energy resources before the fish reaches the natal spawning bed or completes its spawning.

Recently there has become available pertinent information concerning the *in situ* swimming speeds of Alaska sockeye (Becker, 1962) as observed in the Kvichak River, Bristol Bay. Here, where, at 6 inches (15 cm) from the bottom of the river current, velocities ranged from 1.55 to 2.13 ft/sec (0.47–0.65 m/sec) (Becker, 1962, p. 357) the adult salmon were found to be passing upriver "at an average relative speed of 1.52 ft a second against the bottom currents," or slightly over 1 mph.

The swimming speeds for the Kvichak River are appreciably lower than those used in the Columbia River tests. They were, of course, obtained under strictly natural conditions but whether during early phases of the spawning run or just when, is not recorded. The degree of maturity seems to have a significant bearing on the rate of upstream movement, the later-running and more mature individuals proceeding more speedily. Nevertheless, the overall rate of swimming, i.e., 1.52 + 1.84 (mean current flow) or 3.36 ft/sec (1.05 m/sec or 2.3 mph) is a valuable record.

FATIGUE IN SALMON

Intimately associated with studies of energy reserves, energy utilization, and swimming activities, and with the success of sockeye in completing migration and spawning, is their reaction or response, firstly, to the normal and sometimes lengthy journey upstream, and secondly, to the more difficult and exacting situations and conditions which face them. We know (and it has been adequately demonstrated) that salmon are endowed by nature with the strength or energy to return them normally to their home spawning area. How they accomplish this feat is not yet clear. Do they continually swim upstream or is their ascent a succession of periods of travel and rest? Even while resting they must, in many rivers, remain active in order to hold position in the prevailing current flow.

It is a common sight to see salmon congregated in back eddies of a stream or quietly holding position below the junction of two streams or below a counting weir. Are they resting there, "girding their loins," for a further struggle upstream, much as a mountain climber from time to time stops for a rest? Or is their congregating at such places attributable to quite different factors?

TABLE 14. Blood levels of lactic acid of young trout and young sockeye salmon prior to and after vigorous exercise for 15 min (from Black, 1957a, b, c).

	Blood level of lactic acid (*mg/100 g*)			
Species	Before exercise	after exercise	2 hr after	Recovery
Yearling Kamloops trout (age 1+)	16	100	170	Returned to 100 after 6-hr rest Returned to normal after 16-hr rest
Young lake trout	13.7	91.9	177	Returned to 100 after 6-hr rest Returned to 13.3 after 24-hr rest
Fingerling sockeye (age 0+)	11.9	112	211	Returned to resting level after 6-hr rest
2nd yr sockeye (age 1+)	19.5	103	172	

Extremely interesting studies have revealed that after a period of relatively vigorous exercise or activity, recovery of fish and return to the normal resting state is remarkably slow. In fact the effects of exercise (as measured by the blood level of lactic acid which results from body metabolism during muscular activity) were found to increase for some hours *after* exercise had ceased. Actual recovery, or diminution of the blood lactic acid, did not commence immediately the fish was returned to quiet water, but rather not until some time later.

Working first with young Kamloops trout, *Salmo gairdneri* (Black, 1957a), and young lake trout, *Salvelinus namaycush* (Black, 1957b), Dr E. C. Black showed that when the experimental fish were exercised vigorously for a period of 15 min the blood level of lactic acid increased sevenfold *and continued to increase* during the first 2 hr after being returned to quiet water with no exercise. The lactic acid level declined rapidly between the 2nd and 6th hr of rest but did not return to the initial low unexercised level until after 24 hr rest (Table 14).

Tests with young sockeye salmon fingerlings (age 0+) in fresh water and 1-year-olds (age 1+) in salt water gave similar results (Black, 1957c). They again showed a marked increase in the blood level of lactic acid during exercise and for some 2 hr *after* exercise had stopped, followed by a slow decrease to the former pre-exercise state.

The explanation offered for the significant increase of lactic acid in the blood above the relatively high level immediately following vigorous exercise is this: that the lactic acid, produced during activity as a result of chemical changes in glycogen stored in the muscles, diffuses slowly from the muscles to the blood, due to the lower temperature coefficient. The lactic acid thus continues to flood the circulating body fluid for a long time. Ultimately the lactic acid is removed from the blood by the liver and other organs and tissues which utilize or excrete it, but these may not function very rapidly, again because of the lowered diffusion rate. It is also suggested that the rate of circulation in general may be seriously reduced because of the effect of the lactic acid upon the heart. Whatever the cause may be of the prolonged presence of lactic acid in the blood of salmon after a relatively short period of sustained and vigorous activity it seems obvious that the continued buildup of lactic acid and its much delayed removal must limit appreciably the subsequent activities of the fish.

From this evidence obtained from young trout and salmon, one is likely to get the impression that upstream progress of salmon must be essentially a succession of spurts of vigorous activity and periods of rest and recovery. But does this prevail for adult maturing sockeye?

Swimming ability tests with adult coho salmon, *O. kisutch* (Paulik, DeLacy, and Stacy, 1957) have shown that, after an exhaustive swimming effort in a rotating annular tank with a flow velocity of 3.4 ft/sec (1.04 m/sec), one-third returned to normal after a 1-hr rest, less than half recovered after a 2-hr rest, and two-thirds recovered after 3 hr. All fish recovered completely after 18–24 hr of rest. Water temperatures were 48–50 F (9–10 C). Adult steelhead trout, *S. gairdneri*, similarly tested to exhaustion at water velocity flows of 4–10 ft/sec (1.22–3.05 m/sec) were completely recovered after a 6-hr rest (Paulik and DeLacy, 1957). These coho salmon and steelhead were taken during the spawning migration and were in various stages of maturity. Some of the coho males shed milt when they were being handled. One is bound to wonder, therefore, whether, as the salmon mature, physiological changes may not take place whereby the circulation of blood is speeded up and the exchange of gases—release of carbon dioxide and uptake of oxygen—is facilitated. Experiments on adult fish, similar to those already made on the young, are required.

EXTENT OF MORTALITY AMONG UPSTREAM-MIGRATING SOCKEYE

To what extent migrating sockeye die during the course of their upriver spawning migration, as a result of severe muscular activity and exhaustion, is not really known. There is abundant evidence that heavy mortality may occur where ascent of a river is blocked because of a rock slide, as at Hell's Gate on the Fraser in 1913 (Babcock, 1914) and at Babine River in 1951 (Godfrey et al., 1954). What losses may occur annually, however, under normally varying river flow conditions, have not as yet been determined.

In the tests on the effect of vigorous activity for 15 min on 2-year-old sockeye salmon (Black, 1957c), 3 fish out of 19 tested died during the first hour's recovery period and 2 more expired within the second hour. These tests were carried out in sea water. Since the blood levels of lactic acid of these 5 fish which died were not significantly different from those of the fish which remained alive, other factors must have contributed to death. Black (1957c) states, however, that "recently A. C. DeLacy and G. J. Paulik (personal communication) found that mortalities occurred in adult sockeye salmon following severe muscular exercise. The exercise was induced after the fish had been held in fresh water for a month."

It had been hoped that perhaps the counts of Columbia River bluebacks passing over the several dams—Bonneville, McNary, Rock Island—might give some indication of the losses among the fish as they proceeded up the river, even though some of the loss might be abnormal and due to delay in finding and ascending the fishways, etc. This is the only river in which counts at various points would give the information desired. The pertinent records are given in Table 15, taken from the Annual Statistical Reports of the Washington State Fisheries Department and the Oregon Fish

TABLE 15. Counts of sockeye at four dams on the lower Columbia River. A—percentage of the count at the dam immediately downstream; B—percentage of the count at Bonneville.

Year	Bonneville (no. of fish)	The Dalles		McNary		Rock Island		
		No.	A	No.	A	No.	A	B
1954	104,409	–	–	108,185	–	91,184	84.3	87.3
1955	197,768	–	–	173,758	88.0	155,782	89.6	78.8
1956	120,955	–	–	102,136	84.4	92,209	90.3	76.2
1957	90,608	90,201	99.6	85,460	94.3	71,267	83.4	78.7

Commission, and from the Annual Fish Passage Report for the Bonneville, the Dalles, and McNary dams, Columbia River, prepared by the United States Army Corps of Engineers, Portland, Oregon. Except for 1954 when some confusion arose at the counting stations over the identification of young bluebacks, as distinct from young chinooks, the several dam counts show a progressive decline.

Between Bonneville and McNary dams, a distance of 140 miles (225 km) which includes the impounded reservoir above Bonneville Dam, from 5.7 to 15.6% of the sockeye disappeared. There are reported to be no natural sockeye spawning streams tributary to this section of the Columbia. Between McNary Dam and Rock Island Dam, a distance of 160 miles (257 km) of which 61 miles consists of the reservoir above McNary Dam, from 9.7 to 16.6% of the sockeye disappeared. Between these dam sites, however, the Snake River enters. At one time a good run of sockeye ascended the Snake to the Wallowa, Payette, and Redfish lakes systems (Gangmark and Fulton, 1952) but these runs had been destroyed by dam installation. The Redfish Lakes are now accessible but "surveys in the area during the 1946 and 1947 seasons revealed only six blueback." It is possible, then, that some of the differences between the McNary and Rock Island Dam counts mights be due to a migration of the fish up the Snake River. The recent construction of the Ice Harbour Dam on the lower Snake should reveal the relative extent of such runs.

For our present purpose the various dam counts of sockeye merely reveal the possible upper limit of "falling by the wayside" of sockeye ascending a major river system. The limits, as computed from the Bonneville Dam counts, would be from 23.8 to 12.7%, or on the basis of the 4 years' data, an average of 20%, for 300 miles of river travel.

MORTALITY DUE TO PREDATION

Information concerning the losses from predation among adult sockeye during upstream migration is scanty. The consensus seems to be, however, that such loss is of little significance in general though in certain localities it may be appreciable. The predators are principally harbour seals in lower river areas and bears in the more remote spawning tributaries, plus, of course, man's activities, which may be legal or illegal.

SEALS

The Pacific harbour seal (*Phoca vitulina richardi*) occurs commonly in the coastal waters of British Columbia and Alaska, penetrating up many of the larger rivers to the upper limit of tidal influence and frequently some distance beyond, i.e., to Hazelton on the Skeena River, about 200 miles from salt water (Fisher, 1952), Harrison Lake on the Fraser, 100 miles from the sea (Scheffer and Slipp, 1944). It is suggested (Fisher, 1952) that the upriver distribution may be slowly increasing because of the cessation of up-country hunting effort by the Indians. A pertinent comment by the Chief of the Kitselas Indians of the Skeena River, reported by Fisher (1952, p. 21), reveals that only within the last 40–50 years have seals become numerous in the Skeena above the mouth of the Lakelse River, 70 miles from the sea. Before this time tribes of Indians lived along the Lakelse River and the Kispiox River, etc., and for them the seal was an important factor in their welfare. Only since these Indian tribes have disbanded have the seals become more plentiful and more widely dispersed.

The upriver migration of seals coincides with the annual upstream movement of the salmon. Though the early phase of this migration also coincides with the pupping season there seems to be no doubt but that the presence of a good food supply also attracts the seals upriver. They are to be found chiefly where the salmon are abundant and their numbers appear to vary according to the size of the salmon population.

The numbers of seals present in any river system, the numbers of salmon killed by each for food, and, thus, the extent of predation, remain unknown.

For the Skeena, Fisher (1952) estimated there were 450 seals in the lower river area, not including pups, and "several hundred more distributed along the Skeena River up to and possibly above Hazelton." He calculated that if there were 1000 seals in the entire river system, each eating 10 lb of salmon per day for 6 months, a considerable quantity of salmon would be consumed. If the salmon consumed were sockeye the loss would amount to some 36,500 fish but of course other species may also be involved, particularly chums and pinks which congregate in the lower river in much greater numbers and would be more readily captured.

For one Alaskan river, the Copper, studies indicated (Imler and Sarkar, 1947) that a population of at least 6000 seals was present in the entire delta area. Observations were confined only to the estuarial region and the gillnet fishery. The loss through seals robbing the gill nets was estimated as $15,000 for 1945 or only 2% of the total sockeye catch. It was concluded that "the harbour seal is an insignificant factor in the conservation of the salmon runs, though a costly nuisance to the salmon fishermen using gill nets."

For Rivers Inlet and the Owikeno Lake area, Foskett (1958) reports merely that "harbour seals follow the run and are observed in the lake off the mouths of the spawning streams. The numbers of seals and the number of salmon taken by each is not known."

BEARS

Any predation on salmon by bears that might be considered at all significant takes place right in the spawning streams themselves rather than in the main rivers. Much bear activity has been observed in all areas where these animals are present but the question arises as to whether the fish taken by the bears are fresh, unspawned individuals or partly spawned and "spent" ones which are much more easily captured and have already partly or fully accomplished their mission.

On the one hand are the observations made on one stream, Moraine Creek, tributary to Karluk Lake, Alaska, by Shuman (1950) where, of 14,826 sockeye counted through a weir, subsequently 4640 (31.3%) unspawned individuals were killed by bears and a further 5916 spawned-out individuals were taken also. It is suggested by Shuman (1950, p. 5) that:

> "in streams, such as those at Karluk, where the streams are clear and shallow, where few hiding places occur, and where the fish are relatively abundant and easy to catch, the bear tend to eat only bright, unspawned fish. Therefore, the use of 31.3 percent as applied to the entire escapement is conservative. . . ."

Shuman goes on to calculate that if the ratios found at the Moraine Creek weir are applied to the 300,699 sockeye that were presumed to have spawned in the rivers tributary to Karluk Lake in 1947 (lake-spawning fish have been deducted from the total) a *minimum* of 94,119 salmon were killed by bear before having had a chance to spawn. Therefore:

> "it can be stated categorically that when a salmon population is so depleted as the Karluk red salmon population, the loss of 94,000 potential spawners from the escapement is a serious matter. . . . Elimination or extermination of the bear need not and should not be attempted, but some control of the population urgently is needed."

On the other hand, the observations of Foskett (1958) in the Rivers Inlet area, a good grizzly bear region, indicate that the bears there:

> "appear to wholly consume those salmon which they obtain at the beginning of the run. As the run progresses, the spawned-out salmon are much easier to catch, and being presumably less tasty, the bear is more inclined to take one or two bites or perhaps scorn the fish entirely after having caught it. Toward the end of the run, the bears apparently become fascinated by the sport of catching the fish, often making piles of salmon near favorite fishing spots. . . . I have examined large numbers of these salmon, and incompletely spawned fish are seldom found in the piles; nearly all are spawned out. This abundant evidence of bear predation is thus deceptive in that it is relatively harmless, while those salmon consumed green are usually marked by only a few opercular plates on a trail in the bush, and are very apt to be completely overlooked."

Destruction of salmon by bears has also been reported from Kamchatka salmon areas. There, too, the extent of predation varies greatly but nowhere is it indicated that it is excessive.

Therefore, while the conclusion reached by Hubbs (1941, p. 161), after a survey of the situation in Alaska, that: "there is no reason to suppose that any really significant percentage of the salmon in any locality is destroyed by the bears. Consequently, no bear control can seemingly be justified on the basis of the depletion of salmon," may be generally accepted, there may be situations where, with greatly depleted sockeye runs, the loss of potential spawners by marauding bears may be an important consideration and some measure of local control may be profitable.

GULLS

It is a well-known fact that the presence of flocks of sea gulls is almost as characteristic of a good spawning area as is the presence of spawning salmon. In general they have been observed feeding primarily on dead carcasses with a strong predilection apparently for the eyes of the fish. Carcasses with gaping eye sockets are quite common in all spawning areas.

However, Mathisen (MS, 1955, p. 256) reports for one area in the Wood River system of Bristol Bay, Hansen Creek, that gulls were actually attacking live sockeye.

> "Large flocks of seagulls lingered around the creek mouth and along its banks, attacking any fish which, in its struggle to pass a shallow ripple, took a rest and exposed its body to the predatory birds. The pattern of attack was the same in every case. The eyes were first picked out by a few cuts with the bill, and when the exhausted fish fell on its side the same sharp bill opened the abdominal cavity behind the cleithrum and pulled out the soft viscera which was devoured immediately.
>
> "Usually the fish was left at this stage if salmon were plentiful. Within a few days the proteolytic enzymes would soften the meat and make it more available to the juvenile birds which hardly dared attack a live salmon. . . . Older birds seldom ate the carcasses before the run tapered off and the supply of fresh fish became scarce."

In Hansen Creek, out of a total of 107 male and 97 female sockeye tagged, 56 males and 43 females were found dead within 4 days. Gulls were deemed responsible. It is indicated that a kill of such magnitude by sea gulls is not typical of Bristol Bay streams, even where salmon are equally as vulnerable. Nevertheless, without maligning the gulls too harshly it would appear that they may contribute a fair share to sockeye losses prior to spawning and play a part in the hypothetical 5% loss attributed (p. 67) to mortality during the spawning migration.

MAN

Consideration is given here only to the illegal catching or poaching of salmon which undoubtedly goes on in all remote areas where conditions are advantageous and food scarce or difficult to obtain.

I recall many years ago, while on a visit to the Thompson River area, being impressed by the activities of a Fisheries Guardian in the area in watching out for, locating, and prosecuting local inhabitants of the area who were poaching salmon on or below the spawning grounds. The numbers of sockeye in the streams were low. Therefore, every fish removed was a serious loss to the rehabilitation of the runs.

I recall also the activities of Fisheries Officers in the lower Fraser River area trying to stamp out a quite well-organized plan to catch sockeye in the Fraser River, well above the commercial fishery boundary and often in the easily fished back eddies of the Fraser Canyon below Hell's Gate, and transport them to the canneries for sale. In many instances the catching of the fish, by Indians, under permit to net fish for food purposes, was quite legal and only the sale and transport to the canneries unlawful. Therefore, operators had to be caught while illegally transporting the salmon. Herein lay the problem since all types of subterfuges were utilized, such as camouflaged gasoline trucks, trucks loaded with bales of hay but with quantities of salmon packed away beneath, ordinary motor cars with compartments under and behind the rear seat for fish. On one occasion, it is reported, a funeral hearse was used, suitably equipped. However, in spite of the ingenuity and daring of the illegal operators, the efforts of the enforcement officers made such poaching practices an expensive and risky business. Hence, it has been appreciably curbed, if not entirely stamped out.

In the valley of the Kamchatka River, as well as in other areas, the removal of sockeye by settlers for food purposes is referred to (Semko, 1953) as a factor impeding the restoration of runs to badly depleted streams. No indication of the extent of these operations is given.

In general, the extent of such poaching or illegal removal of sockeye en route to the spawning grounds is probably of minor significance. It is included here merely as one of the factors causing some loss of migrating fish. It is a fact, however, that wherever poaching or illegal fishing is practised, its detrimental effect in reducing the number of spawners and hence cutting down the seeding and subsequent crop becomes greater in years of poor runs than of abundant ones. Though the catch by poachers may be less, it becomes of greater significance to the spawning and seeding as a whole. Thus, its importance is much greater in "poor" years than in "big" ones.

OBSTRUCTIONS TO UPSTREAM MIGRATION

HELL'S GATE ROCK SLIDE

The dire effect of a rock slide in blocking the upriver movement of salmon has been most dramatically revealed by the now-famous Hell's Gate disaster on the Fraser in 1913. In this canyon, approximately 140 miles from the mouth of the river, where

> "at three points the force of the water is such that the ascending salmon are called upon to exert all their strength and skill to make the ascent" (Babcock, 1914, p. 20–21)

and where

> "in years of a big run the major portion of the salmon have always been delayed . . . but have eventually all reached the slower waters above and thence passed on to the lake sections of the river's watershed . . . this year the greater portion of the sockeye which reached the canyon in August and September were unable to pass through, the natural difficulties having been increased by the great amount of rocks thrown into the river during the construction of the Canadian Northern Pacific Railroad. . . . The rock displaced by these operations, and the great slides incidental thereto, was tumbled into the river, further narrowing the passage-way for salmon, and so increasing the difficulties that at times the channel was rendered impassable" (Babcock, 1914).

Some of the early running fish successfully negotiated the canyon when the water level was high but

> "all through August, September and early October the major portion of the run could be seen in the eddies below Hell's Gate, extending downstream for over ten miles" (Babcock, 1914).

Suffice it to say that the spawning runs to the major highly productive sockeye areas of the Fraser suffered a devastating blow. This became very evident in 1917 when the adults produced from the greatly reduced 1913 spawning escapement returned to provide a catch only one-quarter of that of 1913 (IPSFC, 1958, p. 23).

Unfortunately, while plans were being completed to remove the masses of rock in the canyon during the period of winter low water, and to clear the river for the 1914 upriver salmon runs, another extensive slide from the cliff immediately above Hell's Gate occurred, much more severe than that of the previous year. It was estimated that 100,000 yd^3 of rock fell into the river which produced a fall of 13 ft in a distance of 300 yards (4 m in 270 m). Plans for clearing the river had, therefore, to be radically revised. For 6 weeks during the subsequent low water period, day and night operations to remove the rock were carried on. The river bed through the canyon above Hell's Gate itself was returned to as close to normal conditions as was possible but the obstrucions at Hell's Gate iself "were so extensive that they could not be removed in time for this year's [i.e. 1914's] run of fish" (Babcock, 1915, p. 16). Temporary measures to get the salmon over the obstruction were made with some success but undoubtedly much of the spawning escapement was lost. Babcock (1915) reported "fewer sockeye reached the spawning grounds of the Fraser this season [1914] than in any other with which I am familiar" and the commercial catch in 1918 was only 13% of that in 1914.

Further rock removal was undertaken during the winter low water period of 1914–15. It was reported that "the result of this work has been to practically fully restore the river to its former channel. . . At no time this season was there a noticeable number of sockeye assembled in any of the eddies in the river, except those immediately below the Gate, and it is believed that all eventually reached the waters above" (Babcock, 1916, p. 17). It may be noted that the commercial catch in 1919 was approximately 66% of that in 1915.

It is clearly evident that the slides which occurred in the narrow canyon of the Fraser in 1913 and 1914 substantially reduced the spawning runs and the subsequent cycle years' return of adult fish. Removal of the fallen rock and return of the river, in the canyon area, to its former channel should have led to the restoration, in large part at least, of its former productivity if appropriate measures had been taken to restrict the commercial fishery and thus ensure a greater spawning escapement. More eggs on the spawning beds would have led to more adult fish in subsequent years.

Fraser River salmon, when migrating from the open ocean to the river mouth, must pass through United States waters. Here they were subject to a heavy fishery, the catch of which much exceeded that in Canadian waters. Over this fishery, however, Canada had no control and, despite efforts over many years to negotiate a system of joint international regulation, no suitable agreement could be reached at that time. Hence, an exceedingly heavy fishing drain in 1917 on the remnant of the once "big" run kept the stock at a new low level.

Observations at Hell's Gate, made at various times during the 1920s and 1930s, revealed accumulations of sockeye in the eddies of the canyon areas at certain water levels. Taggings conducted by the International Pacific Salmon Fisheries Commission from 1938 on showed that many of these fish did not pass the Gate. Different opinions have been expressed concerning the significance and seriousness of this in the overall picture (Thompson, 1945; Ricker, 1947). However, it was generally agreed that obstruction to upriver migration was occurring, that losses were taking place, and that correction was desirable, if not imperative. This was accomplished in 1945–46 when fishways were constructed in the canyon area (IPSFC, 1946, 1947).

Whatever the real cause of the depressed condition of the Fraser River from 1917 to 1947—which Thompson (1945) had computed conservatively as a loss of $279 million resulting from the nonrecurrence of the "big" years alone—it is encouraging to note that current measures for the restoration of the fishery, now under international control through a formal Treaty enactment, emphasize the importance of a suitable spawning escapement to all of the major producing regions of the vast river-system. In order to assure it, commercial fishing throughout the whole of the estuarial and marine fishing grounds has had to be restricted.

BABINE RIVER ROCK SLIDE

In 1951 a rock slide occurred in the Babine River, in northern British Columbia, up which sockeye proceed to the extensive spawning areas of Babine Lake. These spawning grounds are reported to produce around 70% of the sockeye of the Skeena River system. First evidence of the existence of the slide was provided by (1) the occurrence of dead and injured fish drifting down the lower Skeena River and (2) by the late arrival and poor condition of fish passing through a counting weir in the river below Babine Lake.

Exact location of the slide area was not determined until too late in the 1951 season to effect any remedial measures for fish passage. Only about one-third (150,000 fish) of the sockeye run successfully negotiated the obstruction. Due to the remoteness of the area in which the slide occurred, a road had first to be constructed through difficult terrain over which the necessary equipment, required for removal of the rock and return of the river to its former condition, could be transported. This occupied all of the summer of 1952. Such temporary expedients as were possible were undertaken to ease the passage of the blocked salmon over the obstruction in 1952. Complete clearing of the river channel was accomplished during the winter of 1952–53. However, it was estimated that, again, about one-third (350,000 fish) of the 1952 run passed the slide.

The whole situation has been well-documented (Godfrey et al., 1954; Godfrey, Hourston, and Withler, 1956) and requires no further elaboration except, perhaps, to point out that measures for the restoration of the Babine sockeye runs were at once instituted. They consisted primarily in a careful control and regulation of the commercial fishery in order to ensure a normal return of spawners to the Babine Lake spawning grounds.

MINOR OBSTACLES AND DELAY-CREATING IMPEDIMENTS

When a severe, sudden, and spectacular obstruction, such as just related, occurs with its obvious devastating effect clearly apparent, something is *done immediately.*

If earnest considerations were to be given also to the possible effect of smaller, sometimes only temporary, often probably permanent, obstacles to the speedy and easy ascent of rivers, it is quite likely that many places would be found where upstream migration is impeded, resulting in delay and exertion of extra energy. One good instance of this is provided at Moricetown Falls (Plate IV), on the Bulkley River, a tributary of the Skeena River (Fig. 7). Here, as reported by Milne (1950), a "twenty foot drop of fast cascades at the upper entrance to a deep, narrow canyon which constricts the river channel for about one-quarter of a mile" caused appreciable delay in ascent of the river. The amount of delay was dependent on the prevailing stage of water level, being greater at low water. From tagging experiments conducted over three seasons the delay for sockeye migration was found to be 5.8 days.

Just how serious a delay of this duration may be for the races of sockeye involved is not known. From observations on the Fraser River, Thompson (1945, p. 143) has presented evidence to show that "after a long delay fish are less able to traverse the distance remaining to the spawning grounds and where delay is too great, fish do not pass Hell's Gate." This seems entirely reasonable but there must be wide latitude in the length of delay which can occur without serious effect on further migration and on ability to reach the natal spawning grounds at the right time, if at all. Much will depend (1) on the condition of the fish, (2) on the rigors of the further ascent, and (3) on the number of similar delays encountered by the fish earlier and later. It seems idle to speculate further on the matter since pertinent conclusive data are lacking. It seems sufficient to record here the possible overall detrimental effect of minor obsructions, impediments or hazards to upstream migration, be they falls, turbulent stretches of fast water, temporarily obstructing slides or stream-bank cave-ins. Their impeding influence will vary with the condition of the migrating fish but it seems reasonable to assume that to some degree, perhaps generally a small one, mortality occurs to reduce the spawning escapement ultimately reaching the natal spawning ground.

PHYSICAL, CHEMICAL, AND BIOLOGICAL HAZARDS

WATER TEMPERATURES

High-water temperatures in rivers up which sockeye are migrating and in streams in which they spawn may, at times, cause appreciable mortality of unspawned individuals. For example, it is reported (Anon., 1951, p. 58) that:

> "in 1942 considerable numbers of sockeye were found dead in the Fraser River and in the Nechako River in the vicinity of Prince George when temperatures were approximately 68° Fahrenheit and higher. Temperatures were recorded as high as 72.5°F in the Nechako River and during this period of high temperatures numerous dead adult sockeye were observed. . . . Water temperatures at or near 60°F over any of the spawning grounds of the Fraser River are considered to be abnormal for spawning sockeye."

In 1958 a relatively heavy loss of mature sockeye occurred in two streams flowing into Babine Lake. It was attributed (Skeena Salmon Management Committee, 1959, p. 6) to "a prolonged hot dry spell, which lowered and warmed some of the early-run spawning streams to levels lethal to salmon."

CARBON DIOXIDE CONTENT

A similar mass mortality of pink salmon occurred in a small coastal stream of southeast Alaska in 1931 and has been admirably described by Davidson (1933). The cause of death in this case was attributed, not to a high-water temperature though this no doubt was a contributing factor, but to the presence of a high carbon dioxide content "which caused a drastic change in the respiratory function of the fish." The mass mortality took place in a quiet stretch of the river where the fish had congregated in large numbers. The day had been hot. As the sun sank behind the adjacent mountain range and its penetrating rays left the creek, the air became very still and suddenly cool. It seemed as if "the sudden stillness of the air formed a temporary blanket over the quiet stretch of water where the school of 80,000 salmon slowly milled about. . . . This blanketing effect of the still air apparently caused a sudden rise in the carbon dioxide content of the water. This rise was sufficient to bring about the asphyxiation of the salmon and other fish. . ."

INJURY AND DISEASE

To what extent deterioration in the physical condition of migrating adult sockeye during upriver ascent contributes to mortality is but little known. That the fish can, at times, suffer wounds and abrasions, by being thrown against rocks, fallen trees, etc., is well-known. They may, in many instances, be injured in the gills and at the bases of the fins by being caught up in gillnet webbing and then escaping. Peterson (1954, p. 62) reports that at Hell's Gate on the Fraser River "when the fishery [in the estuarial and marine fishing areas] was in operation, the escaping fish were small and heavily net-marked. When fishing closures were in effect, the escapement was composed of larger fish containing fewer net-marks." In a graph of per cent of net-marked sockeye observed at Hell's Gate in 1946, during the fishing periods, from 40–70% of the fish observed carried net marks in comparison with less than 10% prior to commencement of fishery and around 20% during calculated weekly "closed" periods (Peterson, 1954, fig. 21, p. 61).

For the Babine run of sockeye, examined at a counting weir several miles below Babine Lake, it was found that in 1955 6.1% of a sample examined (22% of the total sockeye run) had net marks while 6.7% bore other injuries (SSMC, 1956, p. 12); in 1958, 13.9% of the sample examined were net-marked and 2.6% had other injuries (SSMC, 1958, p. 25).

In addition to the deleterious effect of loss of blood and body fluids from the cuts and abrasions, these wounds permit the penetration into the flesh of fungus spores, bacteria, and micro-organisms which, in developing and spreading, cause further damage and limit the activity of the fish.

The most wide spread infection among salmon is the common fish fungus, *Saprolegnia parasitica* (Coker), a saprophitic organism which builds up into a quite conspicuous grayish-white, furry mass on the fish. It is very prevalent on the spawning grounds, most of the spawned-out and decomposing carcasses becoming covered with it, but it occurs also among migrating fish. To what extent it actually causes death prior to spawning is unknown. Salmon have been observed carrying on normal spawning operations even though masses of fungus completely cover the head and eyes, but how effective the spawning is has not apparently been determined.

Columnaris disease, caused by infection by the myxobacterium, *Chondrococcus columnaris* (Davis), and very appropriately termed "high temperature disease," has been found to be particularly lethal to sockeye salmon in the Columbia River during periods of unusually high water temperatures. According to Fish (1948, p. 285) "below 60°F, columnaris disease is of little consequence, but between 60° and 70°, *C. columnaris* invades the inevitable cuts and abrasions on fish, quickly establishing a secondary infection that may prove lethal. Above 70°F, *C. columnaris* becomes a pathogen in its own right and needs no mechanical injuries to open a door through the protecting mucous coating of the skin and gills. In the high sixties, a degree or two difference in temperature spells a great difference in the severity of columnaris disease." For the Columbia River it is suggested that *C. columnaris* affects the runs to some degree each year but in 1941 it was particularly serious because of the high water temperatures. Of some 25,000 sockeye estimated to have escaped the commercial fishery in that year, only 949 appeared at the Rock Island Dam. Between June 15 and August 31, 1941, the water temperature in the Columbia, normally averaging around 66 F, averaged 68.5 F, with a high temperature, on July 20, of 74.5 F. To what extent columnaris disease may affect adult sockeye in more northern and normally colder streams is not known.

The occurrence of tuberculosis in salmonids is a fairly recent discovery. It was observed first in 1952 among adult chinook salmon (*O. tshawytscha*) in the Columbia River. An excellent account of its study is given by Wood and Ordal (1958). It is suggested that the development of the disease has been greatly aided by the hatchery rearing of Pacific salmon on the Columbia and that the widespread use of frozen salmon viscera as food for the pond-reared young fish may have contributed greatly. There was clear evidence that incidence of the disease in some of the hatchery-reared fish, whose length of pond rearing was known, was proportional to the period of hatchery rearing.

Only one tuberculous sockeye was found, a fully-developed female but only 11 inches in length, thus clearly one that had not gone to sea. Having been caught in a stream near the hatchery it is assumed that this individual was a hatchery-reared specimen that had escaped from a hatchery pond where experiments were being conducted. An adult sockeye taken near the mouth of the Columbia exhibited symptoms similar to tuberculosis but the causative agent was observed to be not the typical acid-fast bacillus but a slightly different organism.

As a result of their studies Wood and Ordal remark that while the evidence indicates that the tuberculous fish were mainly of hatchery origin "the possibility must be considered that the disease may become established in natural populations as a result of upstream migration and spawning of tuberculous adult salmon originally reared in hatcheries." Furthermore, "more comprehensive studies must be made of known stocks of naturally-propagated salmonoid fishes before the conclusion can be drawn that wild fish are essentially free from tuberculosis."

No data are available concerning any mortality that may have arisen because of the tuberculous condition of the fish. The disease was first observed in sexually-underdeveloped salmon, possessing small gonads with immature eggs or sperm. They were bright and silvery externally and had not developed the secondary sexual features of normal salmon after spawning time. However, most of the tuberculous fish exhibited perfectly normal characteristics and showed no external indication of the disease.

Within recent years also, a "virus" disease afflicting only sockeye salmon has been encountered (Rucker et al., 1953; Guenther, Watson, and Rucker, 1959). Its detrimental effect has been demonstrated only in the case of the hatchery rearing of young sockeye, the virus being introduced via diseased adult sockeye salmon viscera fed to the young fish. However, since it has been established that adult sockeye may act as "carriers" of the virus, there remains the question whether during their normal life cycle some of these individuals may succumb to the disease or infect other individuals. Most certainly, "carrier" adults returning to their natal spawning areas may prove a focus for subsequent mortality of naturally reared salmon.

Furunculosis, a bacterial disease caused by *Aeromonas salmonicida*, has for many years been known to occur in Atlantic salmon and trout in Europe and among trout reared in hatcheries. Davis (1946, p. 55) reports that "the disease affects chiefly the various species of salmonid fishes although a large number of freshwater and marine fishes have been infected experimentally. It is probable, however, that few of these fishes would contract the disease in nature and it apparently occurs in epidemic form only among the Salmonidae." And further (p. 57), "furunculosis was originally thought to be confined to hatcheries and fish farms but a number of epidemics have been reported in wild fish during recent years, especially salmon in streams of Great Britain. In this country serious outbreaks of the disease have been confined to trout in hatcheries and rearing ponds."

So far as is known at the present time no occurrences of furunculosis have been found among wild Pacific salmon in British Columbia. One instance is reported for British Columbia, at the Smith Falls hatchery rearing ponds, Cultus Lake, where artificially produced hybrids were being retained to maturity (Duff and Stewart, 1933). At the same place and during the same period sockeye salmon fry were examined. The characteristic pigment-producing bacterium was not recovered from any of them. In the Columbia River, however, Wood (1959) reports the diagnosis of furunculosis in adult spring chinook salmon returning to the Willamette River in 1958. Characteristic furunculosis lesions were also observed on fish of the same species present on the spawning grounds of the Snake River in Idaho. Wood states that "losses from furunculosis in these instances are of unknown magnitudes."

On the other hand, as a result of a quite thorough review of the furunculosis situation in fish, McCraw (1952, p. 43) reports that:

> "it is difficult to conceive the propagation of furunculosis among salmon or other fish in the sea as it has been shown that the specific organism survives for only a short time in sea water. Field observations and experiments have shown that active spread of furunculosis does not occur to any extent where the volume of water for single fish is great. Again, temperature conditions in the sea would generally be unfavourable to the development and spread of the disease. There is no proof of the existence of the disease among salmon caught by nets in the sea water even in infected districts or of its occurrence in sea fish."

Thus, it would seem that, if furunculosis were to occur among sockeye salmon, infection would take place only after the adults had entered fresh water. For Atlantic salmon the Furunculosis Committee in Great Britain reports, according to McCraw (1952), that salmon entering a river may contract the disease in from 4 days to 2 weeks. However, it is indicated that though the disease is spread by water and by food (particularly in hatchery rearing), high temperatures (55–66 F) and low water levels favour its prevalence. Organic pollution may favour its development. No doubt overcrowding may lead to more rapid occurrence of the disease, if temperatures are right, but so far no incidence in sockeye salmon areas has been noted.

A number of other diseases of Pacific salmon are recorded in the literature but their occurrence is associated with pond rearing at hatcheries. Here the unnatural conditions prevailing, such as confinement in ponds, artificial feeding, a varying degree of crowding, undoubtedly facilitate the development and spread of epidemics whose causative agents are introduced by contaminated food or are present in the water supply. To what extent these diseases may be present among, and cause mortality in, natural populations of sockeye in the nursery lakes or during seaward migration will be referred to in a later section (p. 308). At the moment, however, we are considering specifically mortalities among returning adult fish. Except for the possible occurrence, when conditions are ideal, of an explosive and devastating flare-up of columnaris disease and of the slow, maiming and weakening effect of *Saprolegnia*, developing as a secondary infection from an open wound or abrasion and spreading over the head or body, mortality among adult wild fish appears to be low and of little consequence. Yet, in certain situations it may be quite appreciable.

PARASITES

Sockeye salmon carry parasites of many kinds and types. They may be found attached externally, such as some of the parasitic copepods, they may be confined largely to the alimentary tract, they may be within the body cavity or well dispersed throughout the flesh. Some are of freshwater origin and may be lost when the young smolts reach and enter the sea; some are of ocean origin and may or may not die when the fish return to the rivers.

Early studies by Wardle (1932a, 1933) and Kuitunen-Ekbaum (1933) on internal cestode and nematode parasites, respectively, found in sockeye caught in the coastal commercial fishing areas, were primarily of academic interest only. Bangham and Adams (1954), in the course of a study of the parasites of freshwater fishes of British Columbia, listed, for adult sockeye taken in the lower Skeena River Drainage area, a total of 8 internal (3 cestodes, 3 nematodes, 1 trematode, 1 protozoan) and

1 (copepod) external parasites. For young sockeye smolts, migrating seaward from Lakelse Lake (Skeena River system) and Port John Lake (central coastal region), 9 internal (3 cestodes, 3 nematodes, 2 trematodes, 1 acanthocephalan) and 1 external (copepod) parasites were found. In the case of one of the nematodes, *Philonema oncorhynchi,* immature forms were found in the young sockeye while in the adults returning from the sea the parasites were mature.

Similar studies have been made on the parasites of Pacific salmon occurring in Kamchatka (Zschokke and Heitz, 1914; Akhmerov, 1954) and Hokkaido, Japan (Fujita, 1932, 1939), but the most complete investigation has been made by Dr Leo Margolis in connection with the possible use of parasites as an indicator of area of origin of sockeye caught on the high seas. The results of his researches have been reported in the Annual Reports of the International North Pacific Fisheries Commission for 1955, 1956, 1957, 1958, with a comprehensive summarization in 1961 (Margolis, 1963). In the report for 1956 (INPFC, MS, 1957, p. 39) it is stated that "forty-two identified species were found parasitic in sockeyes, of which 16 were acquired in fresh water and 24 in the sea. The origin of 2 species found in salmon taken in the sea is unknown. Of the known fresh water species, 4 were found to persist throughout the life of the fish." Japanese parasitologists are conducting similar studies in Japan. The results are also reported in the Annual Reports of the International North Pacific Fisheries Commission.

With regard to the effect of parasitism of sockeye on their survival, either in the young freshwater stages or subsequently in the ocean, the only information available is of an indirect nature.

From studies of sockeye smolts migrating out of Babine Lake, Skeena River system, Dombroski (1955, p. 94) found that those individuals infected with cestodes were smaller in size than uninfected ones. In 2 yr the size differences noted are shown in Table 16.

TABLE 16. Incidence of infection of sockeye yearling seaward migrants at Babine Lake, B.C., by cestodes and nematodes, and the average size of the fish of each type (from Dombroski, 1958).

	1952	1953
No. of migrants uninfected	909 (55%)	630 (51%)
Avg fork length (*mm*)	81.5±6.9	88.2±6.0
Avg weight (*g*)	5.1±1.3	6.7±1.5
No. infected with cestodes only	441 (27%)	380 (31%)
Avg fork length (*mm*)	77.3±5.4	82.3±5.5
Avg weight (*g*)	4.2±1.0	5.3±1.2
No. infected with nematodes only	202 (12%)	137 (11%)
Avg fork length (*mm*)	83.7±4.9	89.1±5.8
Avg weight (*g*)	5.5±0.9	6.8±1.3
No. infected with both parasites	102 (6%)	87 (7%)
Avg fork length (*mm*)	78.9±5.6	82.2±4.8
Avg weight (*g*)	4.5±1.1	5.2±1.0

Approximately half of the smolts examined in each of the 2 yr were parasitized either by the cestode *Eubothrium salvelini* or the nematode *Philonema oncorhynchi*, or both. Those containing the cestode—1–5 specimens, usually confined to the pyloric caecae—and those containing both parasites were significantly smaller in size than the uninfected smolts. Those carrying only the nematode were somewhat larger than the uninfected ones, this being attributed to the fact that they were feeding most likely more heavily on the available plankton, possibly in warmer areas of the lake where nematode-carrying plankton would be more common. The smaller size of the cestode-infected smolts is of particular interest since, as will be indicated later (p. 399), smaller-sized smolts suffer heavier mortality in the ocean than the larger individuals; this suggests that cestode-infected individuals may have a lower survival than those uninfected.

From studies of young sockeye in the Wood River system, Bristol Bay, Burgner (MS, 1958) found that in samples taken each season from 1948 to 1957, 71% of the smolts were parasitized by the cestode *Triaenophorus crassus.* Due to the activity of the plerocercoid (larval) stage of this parasite, considerable tissue was destroyed, which was assumed to have some deleterious effect on the growth and well-being of the young fish. It was suggested also that slow-growing young sockeye in the lakes, many of them remaining over for a second season, would be subject to greater parasitism.

To what extent actual mortality from parasite infestation may occur remains to be determined. For the cestode, *E. salvelini,* found occurring in Babine Lake, Wardle (1932a, p. 16) reports that in the Spray Lakes, Alberta, the intensity of infection in char, *Salvelinus alpinus malma,* "was very heavy and appeared to be responsible for an epidemic mortality among the young fishes." Heavy parasitism, then, may perhaps cause not only mortality among young sockeye during lake residence but, by adversely affecting the growth rate, subsequently may bring about greater losses in the ocean.

ASSESSMENT OF LOSSES DURING UPRIVER MIGRATION

Consideration has been given to the mortality assumed to occur during the passage of sockeye from above the fishing areas to the spawning grounds. This period embraces not only the time the sockeye are ascending the river but also the time spent in the lake prior to moving on to the actual spawning areas, a period which may embrace from 1 to 4 months. The mortality may result from (1) an inability of the fish to contend with and surmount the ordinary physical hazards during migration because of their weakened condition due to disease or parasitism, injuries suffered in escaping through the fishing gear, and delays during upriver ascent, or (2) the development of unusual situations in the upstream migratory path, such as rock slides, fast water, low water levels, unfavourable temperature conditions and so forth. Death may occur in the river or during the long period of lake residence.

There is very little information available regarding the actual losses in lakes, unfortunately. In Lakelse Lake (Fig. 7) where observations were made, (FRBC, 1954, p. 78) the mortality appeared to be related to injuries caused, in some unknown and undetectable way, by operation of the counting weir in Lakelse River below the lake.

Thus, the hypothetical 5% mortality of our mortality tabulation (p. 67) remains largely conjectural. The only comparable estimate available is a statement for the Fraser River for 1958 (IPSFC, 1959, p. 15) in which it is remarked that "this leaves a total of 322,588 fish which is a reasonable figure for those fish that escaped the fishery but failed to reach the spawning grounds." The 322,588 missing-and-presumed-dead sockeye represent 7.9% of the estimated total Fraser River run not caught by the commercial and upriver Indian food fisheries. The interesting feature is that this is considered a "reasonable" figure but the basis for its "reasonableness" is not indicated. It is indeed substantially higher than our hypothetical 5%, but its accuracy seems no more soundly based.

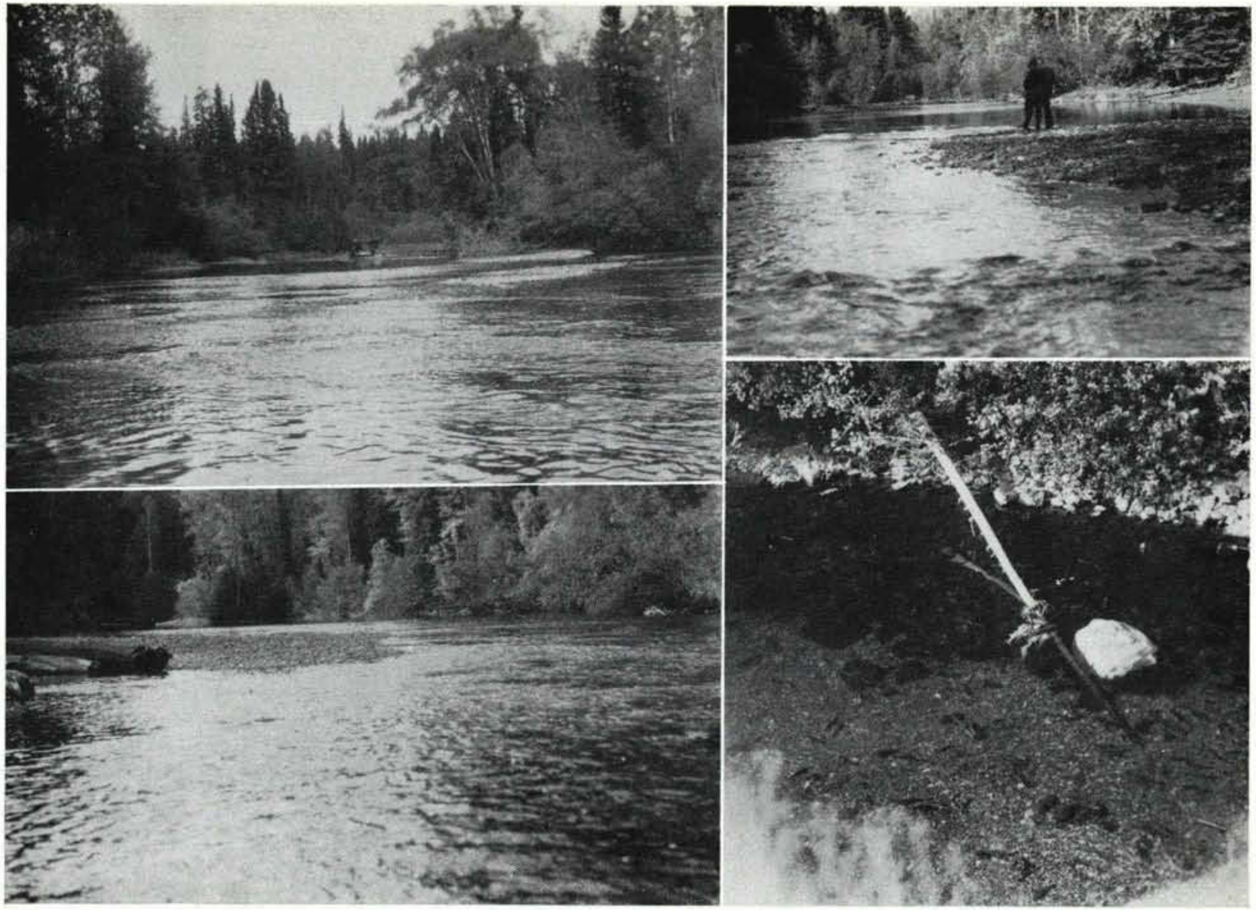

PLATE V.

Sockeye spawning areas: Fulton River (*left and right top*) and Fifteen Mile Creek (*lower right*), Babine Lake. Note the excellent gravel bottom and moderately shallow water, also gravel bars, exposed at low water, which will, under normal conditions, be well submerged at spawning time (after autumnal rains) and during the winter egg-incubation period. When severe frost or ice conditions coincide with periods of unusually low water, and but light or no snowfall, extensive mortality, due to freezing of the eggs in the gravel, may occur.

Chapter 6. Sockeye spawning grounds and spawning success

TYPES OF SPAWNING AREAS

Sockeye salmon usually select and occupy spawning areas which are closely associated with lakes, to which the fry, upon reaching the free-swimming stage, repair for one or more years of residence. These areas may be:

1. in the streams flowing into the lake,
2. in the upper sections of the outlet river,
3. along the shores of the lake where "springs" or seepage outflows occur.

Exceptions to this general characteristic lake-associated spawning of sockeye do occur. The outstanding ones are (a) the spawnings in the Harrison River Rapids area (Gilbert, 1917, p. 50; 1918, p. 29), and (b) the spawnings in "springs" in Kamchatka, particularly in the Kamchatka and Bolshaya rivers (Fig. 2).

Along the North American Pacific coast the order of importance is, in general, as listed above. Variations do, of course, occur according to the specific area. On the Fraser River, for example, most of the sockeye in the Chilko Lake area spawn in the relatively shallow outlet river; the Stellako River spawnings occur mostly below François Lake; the spawning in Little River, which drains Shuswap Lake, represents a significant fraction, roughly 25%, of that of the Shuswap system (IPSFC, 1939, p. 30). For the Skeena (Brett, 1952a), the spawnings in the Babine River, the outlet stream from Babine Lake, are estimated, for a 4-year period, to average around 10% of the total spawning in the Babine system. Later observations suggest that the average should be much higher. Lakeshore spawning, however, plays a very minor role, at least so far as observations have indicated. On the Fraser River, practically all of the spawning in the Cultus Lake area takes place along the beaches where seepage occurs but it represents a very small component of the total Fraser system spawning. For the Skeena River most of the spawnings in some of the small headwater lakes, Bear, Sustut, etc., are along the lake margins adjacent to inflowing streams. These, too, in total, are of minor significance.

For Alaskan waters, a review of available evidence indicates that, in general, while stream spawning is still the most important, lake-beach spawning increases in extent and significance. At Karluk Lake, on Kodiak Island, it is reported (Nelson and Edmondson, 1955) that about 75% of the spawning occurs in the streams, the remaining 25% on the lake beaches. For Bristol Bay and its highly productive sockeye areas there appears to be a transition in importance of specific types of spawning ground. In the eastern part, stream spawning ranks as the most important. For the Naknek and Kvichak River systems, Eicher (MS, 1957) states that "these each have a number of smaller lakes auxiliary to the main lake. Salmon spawn in streams tributary to these lakes as well as in streams connecting them to the main lake . . . the spawning in both systems is confined to stream bed areas rather than beaches." Further west, however, in the Nushagak River system which comprises 10 major lakes, the sockeye "spawn principally in the rivers between lakes and along lake shore beaches, although there are also a few important tributary streams" (Royce and Mathisen, 1960).

In the Kamchatka Peninsula (Fig. 2), lakeshore spawning appears to be the most important and most general. For the Ozernaya River system, at the present time the most productive region in Kamchatka, the spawning ground areas, as reported by Krokhin and Krogius (1937b, p. 86) are tabulated as:

Spawning grounds	Area (m^2)	Percentage
In the lake	202,000	63
In the lake outlet	70,000	21.6
In the springs	25,000	7.7
In the tributary streams	25,000	7.7
Total:	322,000	100.0

In the Bolshaya River system, one of the most extensive water arteries of the Kamchatka Peninsula and formed by the confluence of three large rivers—the Bystraya, Plotnikova, and Golzovka—plus the Udosk River which joins the Bolshaya near the mouth of the latter, much of the sockeye spawning occurs in spring-fed creeks and pools. Lakes are scarce but in one, Nachikinsky Lake, there is an important run of sockeye which utilizes chiefly the lakeshores. Of the 120,000 m² (143,520 yd² or 29.7 acres) of spawning area, the lake spawning grounds constitute 73% and those in the springs but 27% (Krokhin and Krogius, 1937a, p. 101). In a second lake area, the Sokoch, spawning occurs in the upper Sokoch River above the lake and in springs which drain into the upper river and the lake itself, as well as into Little Sokoch Lake which is located above the main lake.

For the Kamchatka River system, the most extensive and the principal river along the east coast of the Kamchatka Peninsula, pertinent data are scarce. Kuznetsov (1928) lists 90 tributaries to the 550-km-long (340-mile) river, of which 80 are frequented by sockeye. Of these, 35 are classified as rivers, 6 as creeks, 31 as springs, and 8 as lakes. Seven of the lakes are located in the lower section of the river, within 133 km (82 miles) of the river mouth; one of the most important, Nerpiche Lake, connected with the Kamchatka River by a short outlet, 5–6 km (3–4 miles) long, is well within tidal influence. Some 20 streams and springs drain into it and have abundant sockeye runs. A second lake, Azabache, located some 40 km (25 miles) upstream and about 10–12 km (6–7 miles) from the river, also is an important spawning area. It is surrounded on three sides by high mountains from which around 12 rivers and springs drain into the lake. Kuznetsov reports that "of all the streams draining into Azabache Lake, the most important is the Bushueva River, which is about 60 km long. Next in importance come five swift rivers about 7–8 km long and the rest are creeks. Springs have a slow current and are situated mostly near the shores of the lake." Spawning occurs in the rivers, creeks, springs, and along the lakeshore.

According to Kuznetsov "vast numbers of sockeye run up to the upper reaches of the Kamchatka River." The majority of these must spawn in the rivers, creeks and springs since no lakes are listed in the upper two-thirds of the river system. This brings us, therefore, to a consideration of what are termed "springs" [kliuchi] in Kamchatka and their general characteristics.

"Springs" are essentially out-pourings of ground water or subterranean flows which may occur (1) along the shores of a lake or (2) adjacent to the main stream or its tributaries into which they drain. The "springs" may take the form of short small creeks with relatively low flow or of lake-like pools. For example, it is reported (Kuznetsov, 1928, p. 16) that at the mouth of each spring in the Soldatskaya River which flows, in turn, into Nerpiche Lake, "there is formed a fairly wide but shallow and quiet level area (with outlets of numerous springs) which serves as the main spawning ground for sockeye and coho salmon. The spawning area of just two such level places reaches 15,000 m^2 [18,000 yd^2]."

Semko (1954a, p. 33) refers to the geological development of salmon spawning grounds. He places the river-type spawning areas as the earliest, geologically, associated with the formation of mountainous areas and their gradual erosion. Somewhat younger, but yet in existence over a long geological period, are the lake spawning areas, formed during the period of active mountain development, volcano activity, and glacial action. In course of time many of the lakes disappeared, due to the accumulation within them of the products of erosion and the cutting away of the original outlet shelf or threshold. On the other hand, some lakes are of comparatively recent origin, the result of changes in the earth's crust, volcanic action, rock slides, etc. The spawning springs are the latest developments and are thought to be due, in part, to the blocking-up of the mountain streams high up in the mountains and the subterranean flow of the water to the valley below. It is pointed out that "the most important and most typical springs are formed along the margins of a valley where the dynamic pressure of the subterranean waters is higher." These subterranean ground-waters are appreciably warmer in winter than surface flowing streams and have a good, steady flow, highly desirable attributes for the incubation of salmon eggs.

One particularly interesting feature of the extensive utilization of springs in some of the river systems of Kamchatka, particularly the Bolshaya and Kamchatka rivers, is the subsequent history of the young sockeye hatching therein. In general, as explained earlier, young sockeye usually pass to a lake for a year's sojourn or more before migrating seaward. Yet in many cases the Kamchatka springs are not associated with a lake. The question therefore arises: Do these young sockeye spend their 1st year in the springs or do they migrate to sea as fry?

Reference to a study of the age-classes among sockeye returning to the Bolshaya River (Semko, 1954a, p. 29, table 14) shows that, from age determinations made for samples of populations for the years 1935–47, 4.8% had had no appreciable freshwater residence and had returned after 3 years in the sea, while 2.8%

had returned after 4 years in the ocean, i.e., 7.6% in all. Whether this represents reasonably accurately the relative proportion of the Bolshaya River stock that returns to and utilizes the "spring" spawning areas is not known, but Semko (1954a, Table 24) indicates that the young sockeye (presumably from the small creeks and springs) "live principally in the springs, shallow channels, flood pools, old backwaters, and in the shallow sections of the main channels. They winter, apparently, in the non-freezing springs and creeks. Many of the young of the year remain in pools formed by wind-fallen trees and accumulated brush," i.e., above log-jams. Dr F. V. Krogius, on the other hand, states (personal communication), in regard to spring-reared sockeye of the Kamchatka and Paratunka River systems, that it is difficult to decide actually whether the sockeye which migrate seaward within the first summer are few in number or whether those that have done so have a lower survival in the sea. Probably both conditions prevail. Nowhere has there been observed a large-scale seaward migration of fingerlings or under-yearlings, and the numbers of adult fish which have not had a full year in fresh water are also very low.

A somewhat similar exceptional condition applies in one locality on the Fraser River. Here, at Harrison Rapids, on the Harrison River and within a few miles of its junction with the Fraser, a "sea-type" race of sockeye appears to occur (Gilbert, 1918, p. 50) i.e., the fry migrate to sea as soon as they are free swimming and before their scales have developed. Returning in their 4th year the adults "use gravel-bars in a shallow backwater region of the river, where they have no genuine lake conditions at their disposal, nor any lake into which the young can drop back after hatching" (Gilbert, 1919, p. 29). All of the 200 adult specimens of Harrison Rapids spawners examined in 1918 were of the sea-type. No investigation has ever been made of the propagation of these fish, the number of fry produced and the percentage return from the sea. No information is available, therefore, as to whether these tiny-fry seaward migrants suffer heavier mortality in the early life-history stages than yearling or older migrant. The run has persisted, however, representative of the unique (for Fraser River sockeye) migrating-to-sea-as-fry race. Specimens have been noted in other North American rivers but in small numbers only, although for the Karluk River (Rounsefell, 1958a, p. 156) in 1925, a total of 12,824 fish in their 3rd year and 3710 in their 4th year (in a total run of 2,944,000 sockeye) were of the sea-type.

CHARACTER OF SPAWNING GROUNDS

As indicated above, it is characteristic of sockeye normally to spawn in areas adjacent to lakes, either in tributary streams, in the outlet river, or along the lake beaches. As suitable sites for their nests or redds, they select areas of the gravel bottom where there is a good flow of water through the gravel, sufficient to provide oxygen to the developing eggs and embryos and to carry away the waste products of metabolism.

In view of the many different types of bottom utilized by sockeye, i.e., river, stream, lakeshore, spring, it seems unnecessary to describe in detail the characteristics of bottom selected, except to note that, in general, medium to small sized gravel with a limited amount of coarse sand, through which a good flow of water can be maintained, appears to be most suitable. Where small amounts of silt, detritus, and fine sand overlie or are interspersed with the coarser gravel, these will be removed by the fish in the process of excavating the redd.

In a study of the spawning grounds of "blueback" sockeye in the Wenatchee and Okanagan Lake areas of the Columbia, Burner (1951) found typical redds to be excavated where from 89 to 94% of the bottom material consisted of medium to small (6 inches or less) gravel with the small gravel (about the size of a golf ball) predominating, the remainder consisting of mud, silt, and sand.

On the other hand, the author has observed sockeye spawning in a stream connecting two lakes at the headwaters of the Kispiox River, Skeena River system, where the bottom was composed of large boulders, thickly matted with a heavy blackish-green growth of algae. The sockeye were paired off and actively spawning in this area, the eggs dropping down into the crevasses between the stones. It seemed a most unusual and extraordinary type of spawning area, though much the same was noted in 1938 on Adams River (Shuswap Lake section of the Fraser River system) when a dense spawning occurred and when many possibly marginal areas were populated by spawning sockeye. The eggs would be safe enough but one wonders about the success of fertilization. Probably as the eggs settled in among the boulders they could be fertilized by the simultaneously settling spermatozoa. No close observations of the spawning activities and behaviour of the males at the time of egg release by the females were possible at the time. Yet the fact that the heavy boulder area above Stephens Lake on the Kispiox appeared to be a regular spawning area for the sockeye there, suggests that this stock of fish must be maintaining itself in that location.

In general, then, in any area frequented by spawning sockeye, the fish will select, as suitable redd sites, any part of the bottom (a) where there is adequate flow of water for incubation of the eggs and (b) where the size and quality of the gravel bottom material are such that redds can be dug to the proper depth to assure adequate cover for protection of the eggs against subsequent scouring out by winter or spring floods, dessication if the water level of the area drops, movement or jarring during the incubation period, and light penetration. Rearing in the dark seems to be essential for successful incubation and, as will be explained later (p. 149), developing salmon eggs are, at certain stages, very sensitive to agitation or jarring.

We do not know, of course, how salmon select their spawning sites, i.e., in what way they are able to detect suitable places in which to excavate their redds. In lake and spring spawning areas Krogius and Krokhin (1956a, p. 8) report that the sockeye "select as locations for their redds those places with the strongest current of ground water. Experiments at Lake Dalnee have shown that sockeye, placed in penned-off areas where there is no flow of ground water, do not deposit their eggs and die."

HYDROCHEMICAL CHARACTERISTICS OF THE WATER AT SPAWNING SITES

Precise information on the quality of the water flowing through those areas selected by the spawning fish as suitable redd sites is quite limited. In Kamchatka where most of the sockeye spawn along lakeshores and in springs, where underground waterflows emerge, it has been observed that, while these chosen locations have a strong outflow, the water is found to have a lower oxygen content and a lower *p*H than elsewhere.

For Kurile Lake spawning areas, studies made by Krokhin and Krogius (1937b, p. 106, 107, 111) in the autumn of 1932 showed the following averages:

Type of spawning ground	Temperature	Oxygen		*p*H
	(*C*)	(*mg/litre*)	(*%*)	
Lakeshore areas	4.44	11.68	89.21	7.2
Streams	3.05	12.50	92.14	7.1
Springs	3.97	10.22	77.05	6.7
Mean for above areas	3.82	11.47	86.13	7.0
Mean for areas where *no* spawning took place	—	13.05	98.40	7.6

Quite similar conditions were found by Semko (1954a, p. 60) on the spawning grounds at Karymai Spring, Bolshaya River system, in August–September of 4 yr, 1945–46 to 1948–49. The averages for the 4 yr findings are:

A "sandbank" area—temperature, 6.7 C; O_2, 10.76 mg/litre; 89.4% saturation.

A "reach"* area—temperature, 6.8 C; O_2, 10.46 mg/litre; 84.4% saturation.

Smirnov (1958, p. 372) records that, while sockeye are primarily lake spawners, they spawn also in springs where the flow of water is moderate, usually not exceeding 0.1–0.2 m/sec or 0.33–0.66 ft/sec or 0.45 mph. Here there is found a reduction in the oxygen content (down to 3.55 mg/litre), an increase in CO_2 and a low *p*H (6.7).

SIGNIFICANCE OF COLOUR CHANGES IN MATURING SOCKEYE

Since sockeye, as observed in Kamchatka, select, for spawning purposes, lake and spring areas with a slower water flow and a reduced oxygen content, this peculiar behaviour has been associated with the distinctive bright red colouration of the skin (Plate VI) of mature fish. Smirnov (1958, 1959a) has related this specific colour manifestation to the presence of a high concentration of carotinoid and lipoid pigments in muscle and skin tissue. These pigments are very active oxygen carriers

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* "reach"—a moderately deep to deep part of a stream between sandbars or riffles, with a relatively level bottom.

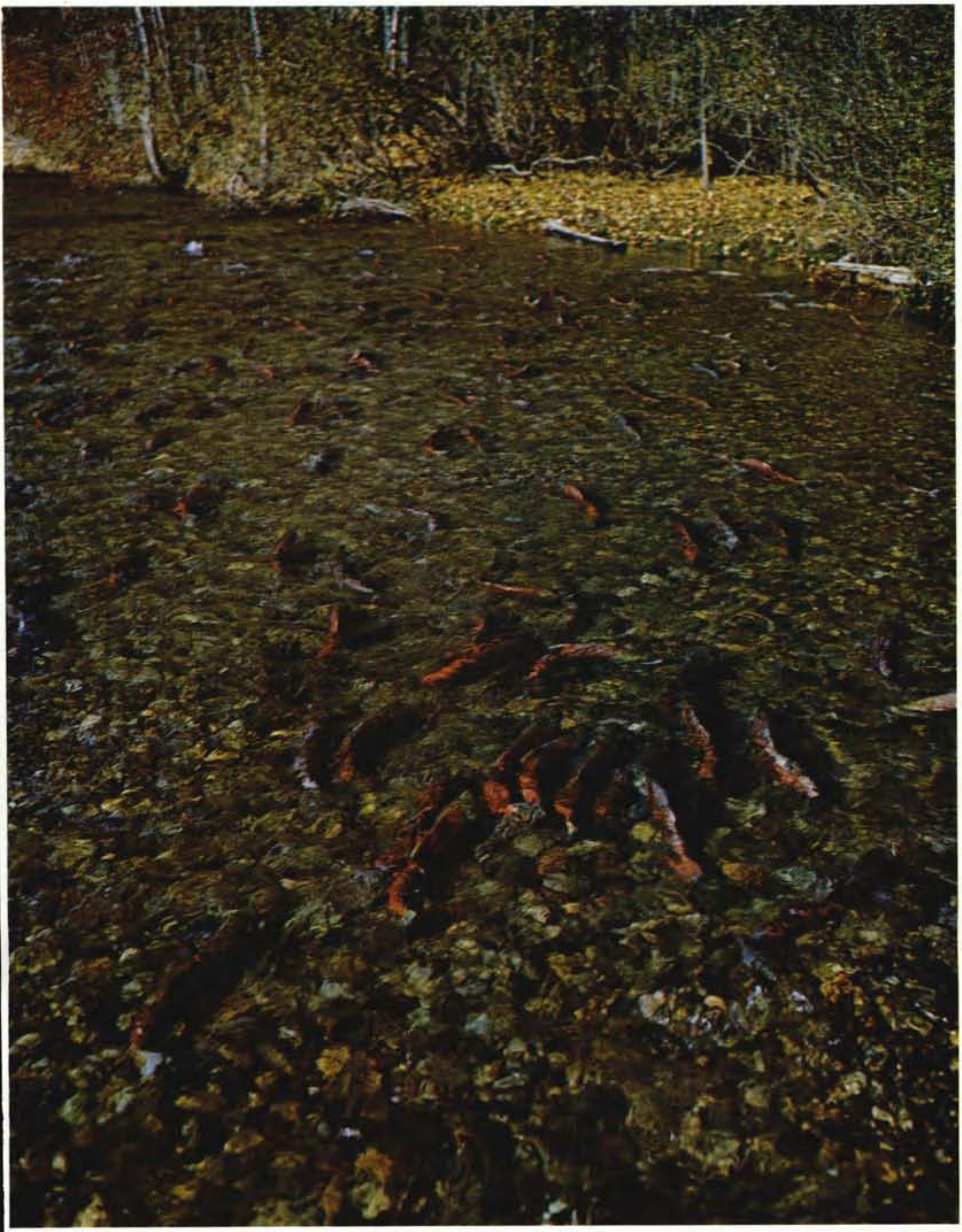

PLATE VI. Mature Sockeye paired for spawning—Adams River.

(Photo courtesy of Dr Loyd Royal, Director, International Pacific Salmon Fisheries Commission.)

as well as catalysts in the oxidation-reduction processes, thus making possible the more efficient uptake of oxygen from the external environment.

The remarkable changes which take place in salmonoid fishes and, in particular, the Pacific salmon, genus *Oncorhynchus*, are so great that were one not cognizant of the transformation which takes place, as the fish mature, one would not consider them the same species. These changes are: in the males—development of elongated jaws and hooked snout, large teeth, prominent hump on the back, and the body markedly compressed; in both sexes—a thickening of the skin, absorption of the scales and a striking change in colour from a bright silvery to one which varies according to the species, viz. pink salmon—slate gray on back and sides, creamy white on ventral surface; chum salmon—mottled gray and yellow on back and sides with prominent transverse dark markings on males and a long, conspicuous dark horizontal band along the side on females; chinook and coho salmon—dark red; sockeye—bright red with olive green on head in most areas (Plate VI) but in some regions (e.g., Cultus Lake) a most varied mottling of colours, particularly among the female fish. The significance of these pre-spawning changes has been considered by many investigators, from Charles Darwin on, and many hypotheses have been presented. They are reviewed by Smirnov (1959a). They include, for example, the suggestions that:

1. the huge teeth of the males serve as organs of combat in the fight for females while the bright colouration and hump on the back serve to attract females (Darwin, 1871);
2. the pre-spawning changes are (a) a pathological development (Barret Hamilton, 1900, 1902); (b) an atavistic feature without any purpose, injurious and burdensome, and not associated with sexual selection (Chernavin, 1918, 1921);
3. the colour changes are (a) for protection against enemies, having nothing to do with sexual selection (Abramov, 1953); (b) a means of species identification and of males finding their own females (Soin, 1956).

To all of these hypotheses serious objections have been raised. Smirnov, however, associates the pre-spawning changes in the skin with (1) a lower oxygen content in the water of the spawning grounds, (2) a reduced normal gill respiration, as revealed by a decrease in haemoglobin (to 11.9% for males and 18.5% for females of that found in fresh, silvery fish, and a decrease in erythrocytes (to 77.9% for males and 81.3% for females of that found in bright, silvery specimens) and (3) the necessity of maintaining, during maturation of the sex products and spawning, a normal degree of respiration. He concluded that:

> "the pre-spawning changes in the structure and the intensification of the carotinoid pigmentation in the skin of salmon should be appraised as morphological and biochemical prerequisites of the increased development of the respiratory function of the skin under conditions of a deficiency of oxygen in the environment and a reduction in the extent of gill respiration."

In substantiation of his hypothesis Smirnov points out that the order of intensity of spawning colouration, for three species for which data are available, is sockeye, chum, pink, and that the same order exists for oxygen content and current flow characteristics of their spawning areas, as follows:

Sockeye—3.5 mg/litre, current flow —0.1 m/sec or less
Chum —8–9 mg/litre, current flow—0.1–0.3 m/sec
Pink —10 mg/litre, current flow —0.3–0.6 m/sec

These are, of course, measurements of water flowing over and above the spawning ground. They may or may not be indicative of the flow of water through the gravel in which the eggs are laid, which depends to a large degree on the permeability of the gravel *in situ*. Wickett (1954) has found, from studies of water flow in a chum salmon spawning stream, that:

> "the supply of water to gravel one foot below the surface is derived from surface flow and from sub-surface flow of water (of lowered oxygen content) from the banks. . . . When the main stream rises, there is increased sub-surface flow from the water table on either side of the stream bed. The surface contribution will vary with the depth of the surface water and the permeability of the surface gravel. The permeability of the surface gravel varies with the presence or absence of silt and the degree of consolidation (porosity)."

CAPACITY OF SPAWNING GROUNDS

Great variations occur, from year to year, in the number of sockeye returning to specific spawning areas. These areas have, naturally, a limited amount of good spawning ground. Therefore, in any year the best redd sites will be the first ones occupied; later-arriving fish will have to resort to less suitable locations or, under crowded conditions, to marginal ground. This is one reason why calculations of fry production from spawning grounds reveal a lower per cent production from heavy spawning than from small or moderate ones. Many redds have been dug in inferior gravel areas.

Not only are the salmon, in years of heavy spawning, crowded out onto marginal or poor spawning territory, but the populations in good gravel areas tend to be greater. The redd areas become smaller in extent. For the sockeye of the Columbia, Burner (1951, p. 105) found a redd to have the following average size:

Area	No. of redds measured	Size	
		(yd²)	*(m²)*
White River	31	2.1	1.67
Okanogan River	37	2.1	1.76
Wenatchee River	31	1.8	1.50
Little Wenatchee River	42	2.4	2.00

Consideration was given also to the spacing of the redds or the amount of space between them. Burner states that "to arrive at a conservative figure for the number of pairs of salmon that can satisfactorily utilize a given area of gravel suitable for spawning, the area should be divided by four times the average size of the redds." Thus, a pair of spawners would require approximately 8 yd^2 (6.69 m^2).

Approximately the same estimate was obtained by Mathisen (MS, 1955, p. 128) from observations in Pick Creek, Wood River system, Bristol Bay, Alaska. By actual measurements the spawning density, defined as the average area available to each spawning female, seldom was less than 30 ft^2 (2.8 m^2). In pens large enough to eliminate any competition for space each female occupied an average of 75 ft^2 which was thus taken to represent "the maximum spacial requirements of a female in the absence of any interference." Under competition, however, each female usually managed to average only approximately 40 ft^2 (3.7 m^2) as spawning territory.

For the important and extensive Kurile Lake spawning grounds, Krokhin and Krogius (1937b, p. 90) have calculated that, on the basis of the numbers of sockeye spawning in different spawning areas, one pair of spawners or one female occupies, on the average:

Lake spawning grounds :	1.6 m^2
Lake outlet spawning grounds:	1.1 m^2
Spring spawning grounds :	1.0 m^2
Stream spawning grounds :	1.3 m^2

They remark that:

> "the amount of bottom used by one sockeye for a redd is around 150 cms in length and around 100–120 cms in width, i.e., 1.5–1.8 m^2, the pit itself is about 100 cms long and 50–70 cms wide, i.e., occupies 0.5–0.7 m^2 of bottom. Considering the space required for the separation of two neighbouring nests, one must conclude that for one female an area of about 2.5m^2 (3 sq yd) is necessary. Our colleague . . . A. S. Baranenkova . . . came to much the same conclusion from observations on the spawning of sockeye in Nachikinsky Lake. From her findings a redd in a spring area has a diameter of around 100–110 cms; including the space between redds the area required for the spawning of one female was calculated to be 3 m^2 (3.5 sq yd)."

These rather approximate measurements are confirmed by the recovery, when redds were dug up in the spring of the year following spawning, of an average of 2300 eggs/1 m^2. Kuznetsov reported for the Kamchatka River a recovery of 2500–3000 eggs per female, average egg content per female being estimated as 3763.

No actual data regarding sockeye redd dimensions are available from British Columbia waters. For the Skeena River, however, Brett (1952a), by calculating the total estimated sockeye escapement in relation to the total estimated areas of spawning ground available, arrived at 13.5 ft^2 (1.25 m^2) as the amount utilizable by each spawning pair. The variability ranged from 6.3 to 81.9 ft^2 (0.6–7.6 m^2). These calculations assumed, of course, that all the sockeye spawned at the same time. As will be discussed below, such is not the case. If, therefore, it be assumed that several successive waves of spawners came on to and utilized the spawning areas, the spawning territory available to each female or each pair of fish during its spawning period would be correspondingly greater.

Observations made on the natural spawning grounds in Williams Creek, Lakelse Lake (Fig. 7 and 37) in 1953 and 1954 (see p. 137) showed that density of spawners varied from 3.5 yd^2 (2.9 m^2) per pair of spawners to 6.3 yd^2 (5.3 m^2), depending on the concentration of fish in the area.

SUCCESSION OF SPAWNING RUNS

Adult sockeye, after migrating from the sea to their natal lake area, spend a varying length of time in the lake prior to final movement on to the spawning areas. During this sojourn in the lake, they, of course, continue to mature. Hence, when they move on to the spawning grounds they are more or less ready to spawn.

Within the population of spawners, however, bound for any specific spawning area, the rate of maturing varies. Not all of the spawners arrive on the spawning grounds at the same time. Throughout the spawning season, then, there is a cycle of changes. Early spawners arrive, complete their spawning operations, die and float downstream or collect in adjacent pools; others take their place and go through the same cycle.

In Kamchatka, where it was found that the sockeye spawning season may extend for as long as 3 months and that each sockeye spends approximately 15 days on the redd (Kuznetsov, 1928) it may be assumed that 6 shifts or groups of spawners will occur during the season. Krokhin and Krogius (1937b, p. 89) accepted this figure for lake spawning but reduced it to 4 shifts for spawning in the spring areas. From observations on the Okanogan River in 1947 Gangmark and Fulton (1952, p. 13) found the spawning period in the river to be 35 days and, from tagging experiments at Karluk Lake, Alaska, the stream life of a sockeye to be 7 days. Hence, there would be 5 shifts of spawners. They have used this figure in estimating the Columbia River sockeye runs, on the basis of the number of spawners seen at one time, i.e., on one spawning ground survey.

Observations in Hidden Creek, a tributary of Brooks Lake, Naknek River system, Alaska, indicated that, of 197 sockeye tagged as they entered the creek, 80% had settled and were spawning 3 days after tagging (Eicher, 1951). Comparison with untagged individuals showed that the tagging had, in no recognizable manner, altered the behaviour of the fish. Observations at Hansen Creek, Wood River system, Alaska, (Mathisen, MS, 1955, p. 119–121) revealed that within 24 hr of their release, after tagging, into the creek 87% of the females had selected redds and, further, that 78% had completed spawning and were dead within 1 day. In a subsequent experiment in Pick Creek (p. 118) where 10 male and 10 female ripe sockeye were placed in a pen it was found that, with one exception, egg deposition was completed within 3–5 days. For the Kvichak sockeye it is reported (Hartman, 1959, p. 48) that the female spawners remained on or over the redds for 7.75 days; three waves of spawners occurred.

THE SPAWNING ACT AND EGG DEPOSITION

Many observations have been made of the spawning of sockeye, which involves firstly the clearing of the redd area selected by the female for egg deposition and then the egg release itself, at which time the male fish is closely associated with the female and carries out his function.

It is generally agreed that the male takes little part in redd building. He is constantly in attendance within the redd area, presumably asserting his priority and driving off inquisitive invaders. The presence of the male, according to some observers, serves to stimulate the female in her redd construction activities. This is suggested by an experiment made by Mathisen (1955, p. 154–157) in which, in Pick Creek, two pens were prepared of approximately equal size, into one of which 10 ripe males and 10 ripe females were placed (Pen 3A), whereas in the other, there were only 10 females (Pen 3B). The progress of spawning was as follows:

	Pen 3A	Pen 3B
Experiment started	July 29	July 29
Spawning commenced	July 29	Aug. 11
Spawning completed	Aug. 14	Aug. 25
Average spawning period in days (Based only on those females which completed spawning)	5.1	10.7

The excavation of the spawning redd is thus the first duty of the female and to it she gives all her attention and effort. As quoted by Mathisen (MS, 1955, p. 260), the description of redd building, given by Jones and King (1950) for Atlantic salmon, is identical with that observed for Bristol Bay sockeye. Movies were taken of the redd digging in a specially-constructed tank and, from a study of the film, the following account is given:

> "In her cutting [i.e., digging] movements, the female starts from her normal position, i.e., head upstream, body on an even keel and almost parallel to the bed of the river. She then turns over on her side by firstly rotating her caudal fin so that it rests almost flat on or near the gravel, and follows this by a lesser rotation of the rest of her body which in this phase has its dorsoventral axis at about 45° to the bed of the river. . . . A bending of the body follows. In this phase the posterior half of the body is bent sharply downwards and the caudal fin rests fanned out on or near the gravel. The bending of the anterior part of the body is less pronounced, so that the head is often only slightly lower than the middle of the body. . . .
>
> "From this position, rapid straightening (the upstroke) and bending (the downstroke) of the body follow so that the posterior region of the body is thrust vigorously upwards and downwards from and to the gravel. This complete action of flexing and straightening occurs several times in quick succession and in the more vigorous cutting movements the anterior end of the body may be more bent. Throughout these movements, the pectoral, pelvic and dorsal fins are erect and the mouth is opened slightly.
>
> "It is suggested that the vigorous downstroke of the posterior half of the body thrusts the water against the gravel with sufficient force to loosen it, and that the upward flexion further assists the movement downstream of the displaced gravel by an upward suction" (Jones and King, 1950, p. 320–321).

Mathisen (1955, MS, p. 261–277) from very careful observation at Pick Creek has concisely described the subsequent activities of the spawning pair and we can do no better than quote directly from his excellent report, as follows:

> "Generally the female required one and one half seconds to complete one digging pass and this time seemed to be independent of the size of the fish. . . . Immediately after a set of suc-

cessive flections of the body, the fish swam forward a foot or so, almost as though to regain her balance before turning either to the left or right side. Digging on the right side was almost invariably followed by a turn to the left, and vice versa. . . .

"At intervals the female tested her redd during which she slowly swam over the excavation with her pectoral and pelvic fins close to, or even touching the gravel surface, seemingly to decide where additional digging was needed. At times one testing did not satisfy her and she repeated it. The subsequent digging took place in the same direction as the testing.

"The elliptical surface of the conical-shaped egg pocket at the time of completion measured about 20 by 30 inches. It was found that many stones 2½ to 3½ inches or over, could not be moved by the thrust of the fish tail on the spawning bed when there was no current to aid the transport of the loosened material. As the digging exposed such stones they fell inward and accumulated in the centre of the pocket. By the time this was completed the female had swept away all the silt and fine gravel lodged between the coarser gravel leaving crevices and hollows an inch or two deeper than the apparent bottom. . . .

"Of the 198 pockets examined in 1951, the distance from the gravel surface to the centre of the egg concentration was 3 to 5 inches in 22 instances, 6 to 9 inches in 149 pockets, and 10 to 12 inches in the remaining 27. . . .

"At irregular intervals the female circled her pocket two or three times and occasionally combined this with a trip outside the pocket giving the impression that she was watching for potential intruders or enemies. But in the majority of cases the male took upon himself to defend the redd.

"In addition to fighting and defense of the redd, the male behaviour in the pre-spawning period is characterized by his courtship. The pattern follows that described by Schultz for the landlocked sockeye salmon:

' . . . The male usually approaches her [the female] from behind a little to one side. He will just touch his head or snout to her body in the region between the adipose fin and the pectorals, gently move his body toward and against hers, at which moment he will vibrate or quiver vigorously for a second or two. He will partially erect his dorsal fin near the end of this act . . .' (Schultz, 1938, p. 371).

"On closer inspection these [the male's courtship activities] were not only a gentle touching of the female's side, but a vigorous act in which the whole body and head shook from a muscular spasm. It may be surmised that they have a dual effect in that they not only stimulate the female, but also prepare the milt for delivery by the convulsive and extensive muscular contractions. Furthermore, the male was also seen to repeat this procedure all by himself outside the redd.

"*Egg deposition.* About 70 spawning acts were observed in the pens in Pick Creek in 1951. With some exceptions, each of these was preceded by three to five extensive trial spawnings. During these the female assumed a normal spawning position and the male joined her over the pocket by approaching behind but the female usually left before the male got that far. In a few instances, the male succeeded and remained with the female for 2 or 3 sec without an extrusion of eggs or milt. In such cases a genuine spawning took place at the next trial or shortly thereafter.

"When the female placed herself over the pocket, the male followed a second or two later. Both fish regularly lowered their tails in order to bring the vents close together near the center of the pocket. This was accompanied by an outward tilting of the body, especially in the case of the male, and at the crest of this activity, his body usually formed a 10- to 15-degree angle with that of the female.

"When both the male and female were in position, their mouths gaped widely. In this respect, Greeley states:

'Experiments with a freshly-killed female prove that the open mouth was of aid in permitting the fish to stay in spawning position, since the mouth increased the current resistance of the normally streamlined body of the fish. The fins being spread, prevent downstream slipping so that the current-thrust which acts against the open mouth, wedges the fish into a firm position. This was duplicated with the dead specimen, which remained in position indefinitely, provided the mouth was wedged open' (Greeley, 1933, p. 243).

"This may well be true on spawning beds where there is considerable current but it had no importance as a stabilizing factor during the spawning in the upper part of Pick Creek. It was more reasonable to consider this gaping of the mouth to be coordinated with the quick and powerful contractions of the abdominal muscles as they forced out the eggs and milt. In addition the dorsal fins started undulating movements and the tail vibrated rapidly. All the eggs were extruded backwards and downwards into the pocket where the anal fin continuously fanned them. In this manner a system of localized currents was produced which mixed the eggs and sperm.

"The milt diffused into the water in big milky clouds, usually visible 4–5 ft downstream from the spawning fish before being diluted to the point of invisibility.

"The length of the spawning act, or more correctly, the time when male and female were in a copulating position, varied from 4 to 19 sec. Those instances in which the spawning act lasted only 4 to 6 sec were usually observed at the beginning of the pen experiments. In this creek the act was completed in 10–12 sec plus a second or two during which the female awaited the arrival of a male. At the end of this period the female closed her mouth and swam forward a foot or so and then turned either to the left or right, the male followed simultaneously, or slightly later, and turned in the opposite direction.

"*The post-spawning phase.* The manner of post-spawning digging was identical with that seen during the excavation of the pocket, except for a shift in position of 6–12 inches forward against the current.

"Immediately after spawning the digging frequency was noticeably accelerated as shown from observation of 13 females before and after spawning . . . the females before spawning averaged one dig per minute or less, at a fairly constant rate. Following this the speed increased to five per minute. But this varied with the individual fish, and a few females were observed digging eight to ten times per minute shortly after egg deposition. The frequency decreased during the first 30 min to one or two cuttings per minute and for the next half hour averaged one per minute, a speed maintained until the next pocket had been prepared. This increased digging is an infallible criterion of recently completed egg deposition.

"Depending upon the size of the fish, the time required to bury the eggs varied extensively. Normally, all, or a majority of the eggs, were buried after a minute or two of digging, while with particularly large females, they disappeared from the surface after two or three cuttings. The next stage, usually reached after 5–8 min, was a flattening of the ground as the pocket was filled with gravel."

Dr. Mathisen* and his associates of the Fisheries Research Institute at the University of Washington are to be warmly commended for this very excellent detailed account of sockeye spawning. It is clearly intimated that this description applies specifiically to an area where the water is relatively shallow and the current very slow, i.e., principally seepage or ground water from adjacent springs, the

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* A revised version of Dr Mathisen's thesis has been published in "Studies of Alaska Red Salmon" (University of Washington Publications in Fisheries, New Series, Volume I, University of Washington Press, Seattle, 1962, p. 469) entitled "The effect of altered sex ratios on the spawning of Red Salmon," p. 139–245.

source of Pick Creek. Variations in spawning behaviour and technique are bound to occur where the spawning ground conditions are different, particularly the degree of current flow, but in essence, however, the main behaviour is the same.

DESCRIPTION OF A REDD

The above description of the spawning act refers to the activity involved in preparing one "pocket" of a redd and the deposition of eggs therein. A salmon redd consists normally of several pockets since the female does not express all her eggs at one time. These pockets are usually located in an upstream direction. Thus, as successive pockets are dug, the gravel removed is directed downstream by the water current to cover over the eggs lying in the preceding pocket. A redd thus represents a trench in which will be found several "pockets" or "nests" of eggs.

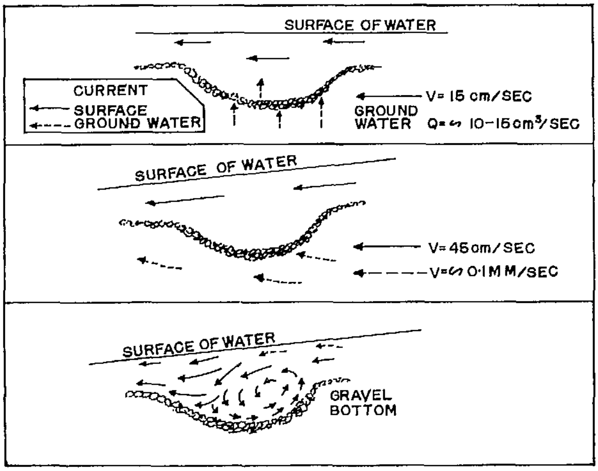

FIG. 16. Current-flow pattern in a pocket of a salmon redd. (From Semko, 1954a, fig. 6.) *Top*—in a "spring" or lakeshore area; *middle*—in a stream where the flow is greater; *bottom*—within the pocket itself.

From Semko (1954a, p. 38) we have reproduced in Fig. 16 profile sketches of a typical pocket or nest, showing the flow of water over and through the gravel depression under conditions prevailing in a spring-fed flat reach or on a lake shore (top sketch) and in a stream where the gradient is greater (middle sketch). The bottom sketch depicts the current pattern created within the pocket.

Kuznetsov (1928, p. 151) gives a sketch, reproduced in Fig. 17, of a series of three sockeye redds in the Okaiansky Spring, examined early in April. The first one observed, presumably the middle one of the three shown in the upper sketch, was

426 cm (approximately 14 ft) long and 71 cm (2¼ ft) wide and consisted of 5 pockets. The area of each mound or pocket covering was 70 × 70 cm^2 (approximately 5.3 ft^2). The second redd, with 6 pockets was 246 cm (8 ft) long and 71 cm (2¼ ft) wide, while for the third, containing also 6 pockets, no dimensions are given. In the first redd, fry were found at a depth of 17–26 cm (6.7–11.4 inches) in all pockets; in the second redd, no eggs or fry were found in any but the 4th pocket. Here, at a depth of 27 cm (10.6 inches) 40 dead eggs and 1 fry were noted. In the third redd the first 3 pockets contained fry 1½ months old; in the fourth only dead and decomposed eggs remained; in the fifth, 150 living fry and 70 eggs; in the sixth, 60 living fry. All of the dead eggs and fry were located in 9–10 cm of gravel and silt, this being the first time fry and eggs had been encountered at such a shallow depth, approximately 3½–4 inches.

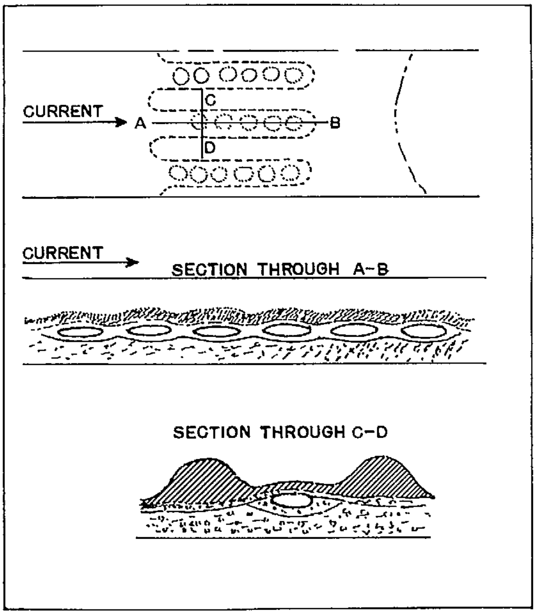

FIG. 17. Arrangement and location of pockets in a natural sockeye salmon redd in Okaiansky Spring. (From Kuznetsov, 1928, p. 1951.) See text for explanation.

By way of contrast, reference may be made to another type of sockeye redd described by Kuznetsov (1928, p. 148) from the Okaiansky Spring. This redd, more oval in shape (Fig. 18), 426 cm (approximately 14 ft) long and 132 cm (4.3 ft) wide,—approximate area 60 ft^2 or 5.6 m^2—contained a group of 7 pockets, all located in the downstream two-thirds of the redd area. Fry were found in all pockets at a depth of 21–29 cm (8–11½ inches). From this redd, a total of 2177 (98%) live fry was obtained. Dead eggs represented 1% and dead fry 0.4%. Assuming an average egg content per female to be 3763 for this area, the loss during the spawning and incubation period is computed to have been 42.2%.

Most interesting observations are reported by Mathisen (MS, 1955, p. 45–49) of the mean number of pockets excavated by a spawning sockeye female and the number of eggs deposited in each. The study was made in a penned-off area in Pick Creek in 1956. Within the pen, each of the 30 females had ample space to carry on activities without the disturbance normally occurring on natural spawning grounds. It was comparatively easy to separate most of the pockets. Furthermore, it was possible to dig up the entire pen, thus running no risk of overlooking any of the pockets.

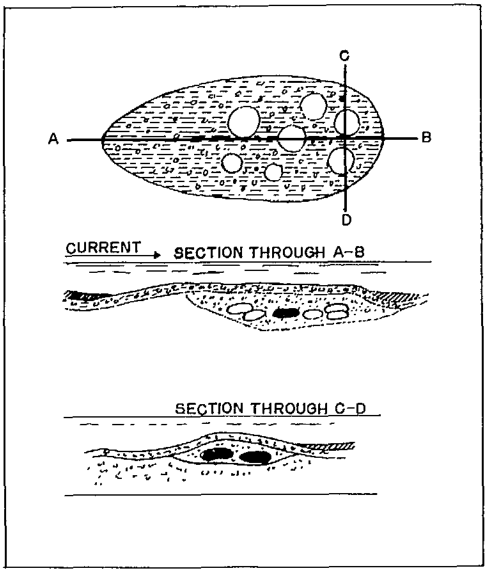

FIG. 18. Plan of excavations and location of natural sockeye salmon redd in Okaiansky Spring. (From Kuznetsov, 1928, p. 148.)

By plotting the numbers of eggs found in the pockets excavated, it was found that most of the pockets contained from 550 to 950 eggs, the average being 750. With an average egg content per female of 4000 eggs, it would be expected, then, that each female would prepare 5 pockets during the spawning act. That this was the case was confirmed by counting the number of pockets which could be definitely associated with a particular female. The findings were:

Number of pockets deposited by one female—3 4 5 6 7
Number of females observed —3 5 9 1 1

A distinct mode occurs at 5 pockets.

These data also suggest that the numbers of eggs deposited in each pocket of a redd vary appreciably. This was confirmed by examination of two instances in which the order of excavation and utilization of the pockets was known. From four pockets in the two redds numbers of eggs recovered were as follows:

Pocket number	1	2	3	4
Female 1	1087	1164	515	1000
Female 2	683	1618	402	262[a]

[a] An additional pocket with 743 eggs was also recovered, but the order of deposition is not known.

The information brought to light by Dr Mathisen's research in the small tributary streams of the Wood River system, Bristol Bay, Alaska, is most revealing. It gives us a much clearer understanding of the spawning behaviour and of egg deposition of sockeye in general. The areas where the observations were made were somewhat peculiar in that they were small, the current very quiet and low and the spawning fish not crowded for space. In other types of environment and under different water flow conditions, variations in number of pockets per redd, in shape of redd, and in digging activities are likely to occur, but to follow closely and precisely these features under less ideal conditions is extremely difficult.

Reference may be made to the results of observations made at Brooks River, Naknek Lake area of the Alaska Peninsula, as summarized by Hartman (1959, p. 48–49). The region studied was a spawning area 75 × 60 ft, gridded into 15-ft squares. Observations were made from a 40-ft aluminum scaffold at the river's edge over a period of 47 days.

> "A one-to-one male-female sex ratio was most common, but zero-to-one sex ratios increased throughout the period due to longer life of the females after completion of spawning . . . three separate waves of spawning occurred in the observation area, each succeeding wave being larger than the preceding one. There was no detectable relation between spawning waves and measured physical environmental factors. Females averaged 7.75 days on a redd site from selection through spawning to death and did not construct more than one redd."

FACTORS AFFECTING SUCCESS OF NATURAL SPAWNING

Sex Ratio of Spawners

In order to assure the fertilization of all eggs carried to the spawning grounds by the female fish it has, in the past, been commonly assumed that there should be present at least as many male fish as female, if not perhaps a slight surplus of males. Since the male and female fish pair off and proceed with their spawning activities together and since general observations had not revealed any specific polygamy among the females or polygyny among the males, it was but natural to regard an even sex ratio as most desirable. However, Gilbert (1914, p. 60) in the first of his very excellent annual "Contributions to the life-history of the Sockeye Salmon" in

TABLE 17. Estimated numbers of male and female sockeye returning to 7 Fraser and 1 Skeena spawning areas. (Data for Fraser River spawning areas taken from Annual Reports of IPSFC; data for Babine area taken from Investigators' Summary Reports of the Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C.)

	Fraser (*thousands of fish*)														Skeena (*per cent*)	
Year	Stuart Lake		Chilko Lake		Stellako River		Adams River		Birkenhead River		Weaver Creek		Cultus Lake		Babine Lake	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1958	24.0	23.2	49.6	70.5	50.3	61.9	930.7	796.4	9.0	6.1	14.1	21.8	5.8	7.5	39.	61.
1957	330.0	432.2	54.9	83.5	19.3	19.2	265.5[a]	1.3	7.0	7.5	8.9	11.4	7.2	13.1	49.	51.
1956	8.5	17.4	260.3	386.3	15.7	22.7	2.3	4.5	18.8	30.9	2.9	5.4	4.6	9.1	48.6	51.4
1955	4.8	4.9	46.1	71.7	20.3	31.7	17.9	36.1	5.1	18.4	7.8	13.5	8.0	17.9	47.2	52.8
1954	19.0	21.8	13.8	20.9	63.5	79.1	681.3	848.0	7.9	11.1	13.1	15.3	12.7[b]	11.1	39.7	60.3
1953	231.8	276.9	94.4	102.8	18.4	25.6	175.0[a]	2.3	30.0[b]	23.1	3.6	5.6	7.7[b]	5.3	44.0	56.0
1952	19.5[b]	13.1	231.4	255.6	19.9	20.5	4.9[b]	3.8	47.7	31.4	15.3	18.6	6.8[b]	12.1	41.	59.
1951	27.3	36.7	60.0[b]	58.1	41.3	54.8	54.3	80.7	23.5[b]	12.3	4.8	8.1	3.4	9.7	50.	50.
1950	26.3	28.2	17.9[b]	11.9	58.9	86.1	449.7	398.8	28.0[b]	44.5	13.7	16.8	10.7	19.9	–	–

[a] Spawning population consisted overwhelmingly of 3-year males.

[b] Three-year males present in fair numbers and included in male count.

which he dealt with the runs to the major river systems of British Columbia, refers to the "beneficial" effect of the gillnet fishery in catching more males than females since "one male can fertilize the eggs of several females."

That, in the ocean, the sexes of sockeye are equally represented is indicated by the examination of commercial salmon trap catch samples (Gilbert, 1914, p. 60; Clemens, 1938). This type of gear should not be selective as to sex of fish caught. Nevertheless, there may be exceptions to this general rule. Barnaby (1944, p. 277) reports, for 11 years data from the Karluk River, Alaska, an average return of 43.9% males and 56.1% females and concludes that, although a gillnet fishery is active to the north and south of the Karluk River which catches a great percentage of the larger fish, "it is not considered that the selective action by the gillnets accounts entirely for the discrepancy in the sex ratio. A differential mortality in favour of the females during the time spent in the ocean does not seem probable. A satisfactory explanation of the phenomenon is lacking at the present time."

Foerster (1954b), however, presents evidence which indicates, on the basis of numbers of marked adults returning from the ocean from certain releases of marked seaward-migrating young at Cultus Lake, Fraser River system, that there were appreciably fewer males than females taken by the trap and seine fishery, thus suggesting a possibly greater ocean mortality among males than females. Furthermore, the preponderance of females in the spawning run to Cultus Lake seemed to be much greater than could be caused by the selectivity for males of the gillnet fishery.

SELECTIVITY OF GILLNET FISHING GEAR

No matter whether the sex ratio in the ocean be 1:1 or be slightly in favour of the female fish, it is a well-substantiated fact that gill nets, which are a common form of fishing gear in coastal areas and river estuaries, are quite selective of males where and when the secondary sexual characters of humped back and hooked snout have commenced to develop. Many years ago, Gilbert (1914, p. 61) pointed out that in Bristol Bay, Alaska, from the catches of traps operated in the Wood River above a gillnet fishery, "it was universally recognized that the fish from these traps averaged smaller than those from the gillnets on the lower river and that they included a much larger percentage of females." More recently, studies on the Fraser River (Peterson, 1954) have indicated that in the late-run escapements the percentage of males was much lower than in the earlier escapements.

Examination of counts of sockeye approaching the spawning grounds and of estimates of the sex ratios of spawning individuals reveals that, in general, there is an excess of females. Appreciable variation occurs from year to year, as indicated in Table 17, where the estimated numbers of male and female sockeye are listed for several important spawning populations of the Fraser River system, as well as the weir counts for Babine River, Skeena River system. Only when a large return of precociously maturing 3-year males takes place is there a surplus of male fish.

It is of particular interest to consider the effect of a deficiency of males on the successful spawning and fertilization of eggs by the excess females. In a special study of this problem, Mathisen (MS, 1955) has provided most interesting information, though the actual findings and their real significance may have application primarily only to the type of spawning area in which he made his tests, namely, relatively shallow areas with very low and quiet current.

In Table 18 the results of Mathisen's experiments are summarized. The first remarkable fact is the extremely low mortality occurring not only in the natural spawning redds and those with a surplus of males but also in the pens where females predominated even to as high as 15 females to 1 male. Close study of the eggs in the separate pockets of the redds revealed that in a few cases a few pockets contained a great many unfertilized eggs. For example, the second pen in which 2 males spawned with 30 females, 3 pockets showed 87.1, 47.3, and 99.7% mortality, respectively, while all the others had a survival equal to that found in the naturally-spawned egg pockets. Presumably these unfertilized eggs were the result of the absence of the male at the time of deposition or of the male's temporary impotence. Observations had indicated that, after each spawning act, the male normally requires a certain rest period in which to recuperate.

TABLE 18. Summary of the Pen Experiments in Pick Creek—1948 and 1951.[a]

Sex ratio	No. of fish		No. of eggs			Per cent mortality
	♂	♀	Live	Dead	Total	
3:1	9	3	4,999	30	5,029	.60
2:1	4	2	2,628	7	2,635	.27
1:1	7	7	5,229	35	5,264	.66
Natural redds—1948			29,625	188	29,813	.63
Natural redds—1950			43,929	1,135	45,094	2.52
Natural redds—1951			17,066	231	17,297	1.34
Natural redds—all years			90,620	1,554	92,204	1.69
1:5	2	10	7,228	435	7,663	5.68
1:5	2	10	4,829	559	5,388	10.37
1:7.5	4	31	19,978	1,045	21,023	4.97
1:10	2	20	25,820	664	26,484	2.51
1:10	2	20	18,750	1,274	20,024	6.36
1:15	2	30	39,489	1,856	41,345	4.49
1:15	2	30	35,073	2,215	37,288	5.94
1:30	1	30	67,599	26,202	93,501	27.93

[a] Data taken from Mathisen, 1955, table 2, p. 41.

ACTIVITIES OF FEMALES

Referring again to the Mathisen experiment (see p. 108 above) in which in two adjacent pens there were retained (pen 3A) 10 males and 10 females and (pen 3B) only 10 females, the general activities of the females may be followed. As shown in Fig. 19, taken from Mathisen (MS, 1955, fig. 27, p. 124), it will be seen that:

"all of the females in pen 3A had selected redds the following day except for one fish (female 8) which roamed around eight days prior to selection of one, which she then continuously occupied. The other nine never left their redds during the entire period they were observed. . . . The unmated females in pen 3B commenced digging at the same time as their counterparts in pen 3A, but no comparable excavations resulted. The fish dug at irregular intervals without any methodical approach, in some places producing a general clearance of silt and fine gravel with only a central deeper spot, or what might be termed pockets in the initial stage. A total of ten such areas were observed but the female-redd association was of a highly unstable character. Two females (8 and 23) remained stationary during the entire observation period while 3 others (15, 19 and 20) made only a few short trips to other redds. The remaining five continuously milled from redd to redd and frequently engaged in fights with stationary females. When spawning finally commenced [see tabulation on p. 109 above] they settled more definitely on one of the unoccupied redds."

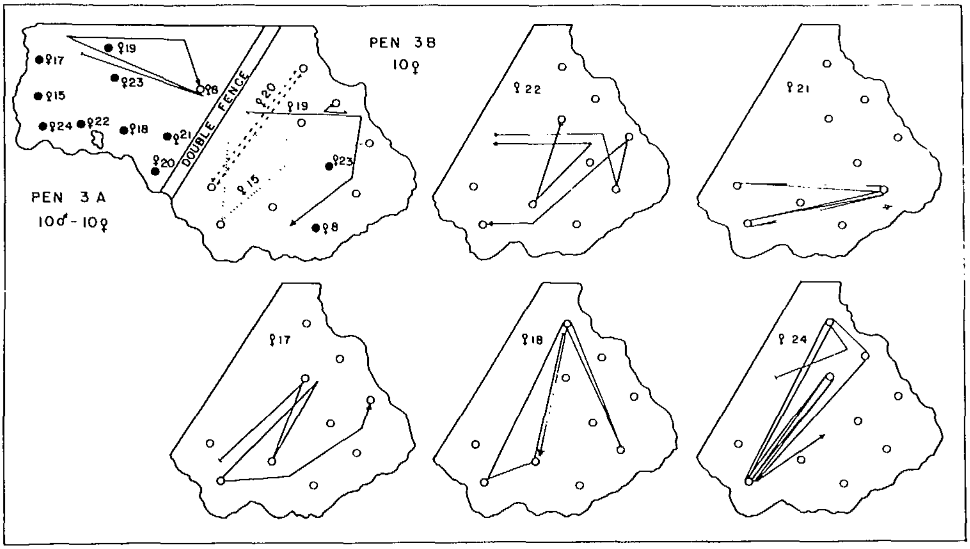

FIG. 19. Female redd association in pen 3A (10 males and 10 females) and in pen 3B (10 females only). Position of females in pen and activities of wanderers. Solid circle—female settled over one redd and remained there during the entire observation period (July 29–August 10, 1951). Open circle—roving female. Roaming behaviour indicated by arrows. (From Mathisen, MS, 1955, fig. 26.)

FERTILITY OF MALES

According to Smirnov (1959a, p. 371) the distinguishing feature of male sockeye appears to be the relatively small quantity of fluid milt produced. The amount ejected at one time may often be less than 1 cm^3; on the average it amounts to around 5 cm^3 and never exceeds 8.5 cm^3. In experiments where the males were completely stripped and then placed in tanks to recover it was found possible to obtain, within 1–2 days, a full amount of milt from one male up to 8 times. This thus confirms Mathisen's finding that a rest period is usually required by the male between spawnings.

From 10 to 11 million sperms (with a range of from 6.4 to 14.2 million) are contained, on the average, in 1 cm^3 of milt. Each sockeye male, then, produces around 50 million sperms per ejaculation. This may be compared with the much larger quantity found in coho males (Smirnov, 1960, p. 10), namely 250 million. Smirnov remarks that this difference reflects the character of the spawning ground of the two species. The sockeye in Kamchatka spawn chiefly in springs or along lake shores where the current is relatively slow and the spawners are quite densely aggregated. The cohos, on the other hand, spawn in more widely separated redds and usually in locations where the current is faster.

ACTIVITY OF MALES

The observations in pen 3A in Pick Creek of the movements of the males indicated (see Table 19) how these fish behaved under conditions of an even sex ratio, low current flow, and no disturbance from other schools of fish. Mathisen (MS, 1955, p. 30) reports that

> "in sharp contrast to the females, which maintained one and the same redd during the investigations, the males presented a diversified picture. Except for one (19), all the others attended from two to four females. Two males (15 and 24) were found associating with a female every day, while the remaining eight roamed inside the pen on one or several days apparently in search of partners. Nevertheless, the five males listed first in Table 19 were relatively stable

TABLE 19. Male-female association in Pen 3A, Pick Creek, July 27–Aug. 7, 1951. The numbers in the table refer to the code number of the females; asterisks (*) signify days in which the male was milling inside the pen without female or redd association (from table 23, p. 159, of Mathisen, MS, 1955).

<table>
<tr><th>Male</th><th colspan="3">July</th><th colspan="6">Aug.</th></tr>
<tr><th>No.</th><th>29</th><th>30</th><th>31</th><th>1</th><th>2</th><th>3</th><th>4</th><th>5</th><th>7</th></tr>
<tr><td>19</td><td colspan="7">♀22</td><td>*</td><td>♀22</td></tr>
<tr><td>15</td><td colspan="3">♀15</td><td>♀17</td><td colspan="5">♀15</td></tr>
<tr><td>8</td><td colspan="7">♀20</td><td>♀21</td><td>*</td></tr>
<tr><td>23</td><td>♀17</td><td colspan="6">♀19</td><td>*</td><td>♀19</td></tr>
<tr><td>20</td><td colspan="4">♀24</td><td>♀17</td><td>♀24</td><td></td><td>*</td><td>*</td></tr>
<tr><td>21</td><td>*</td><td>*</td><td>*</td><td colspan="3">♀18</td><td></td><td colspan="2">♀17</td></tr>
<tr><td>18</td><td>♀18</td><td>*</td><td>*</td><td>*</td><td colspan="2">♀23</td><td></td><td>*</td><td>♀23</td></tr>
<tr><td>24</td><td colspan="4">♀23</td><td colspan="2">♀21</td><td></td><td colspan="2">♀20</td></tr>
<tr><td>22</td><td colspan="4">♀21</td><td>*</td><td>*</td><td>*</td><td>♀22</td><td>♀24</td></tr>
<tr><td>17</td><td>♀19</td><td>♀17</td><td>♀18</td><td>*</td><td colspan="3">♀17</td><td>♀23</td><td>*</td></tr>
</table>

> and associated for long periods with the same female. . . . These data, although incomplete in some respects, nevertheless substantiate the conclusion drawn from studies of the natural spawning beds. In populations with an approximately even distribution of the sexes great stability is found, many males attending the same female during the greater part of the entire period involving actual egg deposition. But the male behaviour at the time of spawning was subject to great modification in the pens with a female surplus."

Just to show what happens in the case of a surplus of female fish, an experiment may be cited in which two males were released into a spawning pen containing 30 females (Mathisen, MS, 1955, p. 162). The activities of the two males were followed for 4 days for a total of 40 hr. Twenty-nine spawning acts were observed involving 15 different females. The general movements of the males from female to female are shown in Fig. 20. It is interesting to note firstly, that there was no suggestion of the two males establishing separate territories and attending to the females there and, secondly, that the two males, on occasion, spawned side by side with adjacent females or at opposite ends of the pen. However, it seemed that when one of the males spawned with a female, he continued to do so. Two instances were noted where the two males spawned with the same female, although these spawnings occurred on different days (females 18 and 15–21).

From Mathisen's excellent experiments and observations in the sockeye spawning streams of the Wood River system, it is apparent that polygamy is a natural

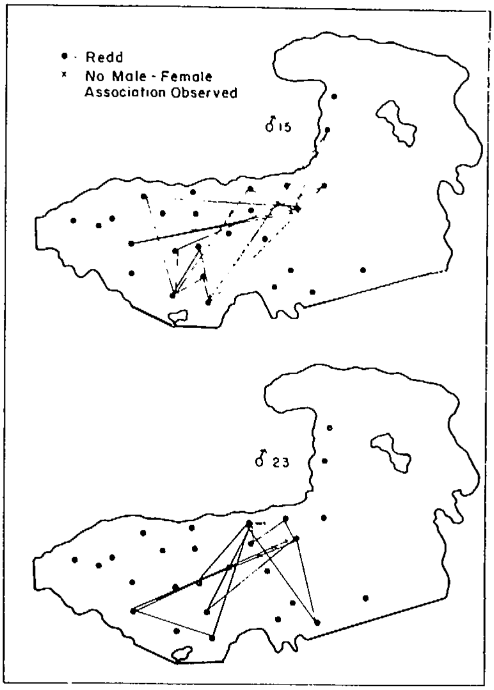

Fig. 20. Observed spawning acts in pen 4 (2 males:30 females) August 8–11, 1951. (From Mathisen, MS, 1955, fig. 32.)

phenomenon when there is a surplus of females. Furthermore, the eggs of the females when there is a superfluity of females, even to as high as 1 male to 15 females (see Table 18), appear to be relatively fully fertilized (average of 2 tests—5.2% mortality).

This finding has led to the suggestion that a more selective-for-males fishery might be developed thus utilizing a greater proportion of the male fish which seem to be not actually required on the spawning beds. Whether such a practice, even if beneficial for Bristol Bay areas—and this has not yet been generally established—would apply to other areas with different spawning grounds and quite different water-flow conditions remains to be tested thoroughly.

In contrast to the detailed description of sockeye salmon spawning in a small, quiet, spring-fed creek, (e.g. Pick Creek) observations conducted in 1953 and 1954 at Williams Creek, Lakelse Lake (Fig. 37) in the lower Skeena River system (Fig. 7) by Mr Dixon MacKinnon (personal communication) are of interest.

Williams Creek (see Pritchard and Brett, 1945, p. 4; Brett and Pritchard, 1946a, p. 14), originates in the Coast Mountains north of Lakelse Lake, and, before emptying into the lake, flows for several miles through a flat valley. It is a cold, moderately flowing stream. In summer and early autumn it carries a fair amount of glacial silt. The majority of the sockeye returning to the Lakelse Lake area spawn within the first 3–4 miles.

In 1953, a 360-yd^2 section of the creek was chosen for specific observations of sockeye spawning. At the peak of the spawning period 103 females and 109 males were present in the area, providing a density of one pair per 3.5 yd^2 (2.9 m^2). That this represented more or less full utilization of the spawning ground was suggested by the fact that "new unspawned fish attempting to start a redd were attacked by at least 2 and often 4 females. Males at this time took no active role in territory defence. . . ." MacKinnon notes that:

> ". . . A typical spawning unit consisted of one female and two males. One male was permanent and attended the female in the redd at most times while the other remained downstream from the redd and would dart into the redd with the spawning pair following a digging or quivering motion in the center of the redd. The 'substitute' male would also move into the redd with the female when the 'permanent' male was absent and would leave without being chased when the 'permanent' male returned. Competition between males was still vigorous yet this substitute male was accepted by both male and female in this role. . . . The activity occurred despite the 1:1 sex ratio in the area. The fact that all females were not in the same stage of spawning activity meant that some males were free to act as substitute males. In many cases where no free males were present, the male in the adjacent redd would leave its female and act as a substitute. In these cases it seemed necessary for the stimulus from a digging or quivering motion to bring the substitute male out of its own redd."

From a few observations at night, it was indicated that the behaviour pattern of the spawners might be somewhat different during that period. Territorial defence appeared to be less pronounced and the male and female seemed to be more closely associated within the redd depression. Digging seemed to be confined to the anterior portion of the redd and though no actual deposition of eggs or milt was observed "it was suspected that most spawning occurs at night."

Observations in 1954 confirmed, in general, those of the preceding year. Seventy spawning pairs occupied an area of 444 yd^2, thus providing 6.3 yd^2 (5.3 m^2) per redd, but in the most heavily populated sections each spawning pair occupied approximately 4 yd^2 (3.3 m^2). In 1954, there was much less substitute male activity and the typical spawning unit consisted of one male to one female.

FECUNDITY OF SOCKEYE

While, of course, the production to be achieved by any run of salmon depends primarily on the number of females available, the egg content of each female is also of some consequence. As one authority (Rounsefell, 1957, p. 451) has expressed it, "Fecundity is an especially interesting topic in the Salmonidae because the comparatively small number of large eggs suggests a demonstrable relation between the reproductive potential of the spawning stocks and the numbers of young surviving." Or, as Thompson (1959, p. 206) points out, "I regard . . . fecundity as an adaptation of the fish to its environment. The deeper such a fish penetrates into protected localities and the more perfect the mechanism of survival, the fewer eggs it needs." Semko (1954a, p. 45), in comparing the fecundity of the different species of Pacific salmon, notes that, "the fecundity is higher for those species of Pacific salmon the young of which spend a longer period of time in fresh water prior to seaward migration." He reports, for the Bolshaya River in Kamchatka, the following:

Pink salmon—1286 in 1944 to 1600 in 1946;
Chum " —2038 in 1949 to 2480 in 1948;
Sockeye " —4500 in 1943 to 5165 in 1947;
Coho " —2300 in 1943 to 5343 in 1946.

He concluded that "in our opinion these indices reflect more severe conditions for survival of the young salmon in fresh water than in the sea."

As revealed by many studies, the fecundity of salmon, as of other fishes too, is directly related to the size of the fish, the larger the female, the greater the number of eggs. An increase also in the size of the egg with increase in size of fish has been suggested by certain researches but because of the difficulty of collecting eggs in exactly the same stage of development or maturity for correlation with the length of the female fish producing them, investigations of this kind have been very few in number.

Robertson (1922a) measured sockeye eggs from three Fraser River stocks over the years 1914–20; the average diameters were very consistent from year to year, the 6-year means being: Morris Creek 6.09 mm, Harrison Rapids 6.60 mm, Cultus Lake 5.40 mm. For Cultus Lake sockeye in 1932 and 1933 average egg diameters of 5.77 and 5.29 mm, respectively, were obtained (Foerster, MS, 1934b). For Yes Bay, Alaska, Rounsefell (1957, p. 459) reports one measurement: 6.3 mm. He noted that "among the Pacific salmons, the smallest eggs are found in the sockeye, which normally spend the longest time in fresh water," thus corroborating Thomson and Semko, as quoted previously.

While the number of eggs per female varies directly with size of the fish, there is good evidence that this relationship is a racial characteristic and may vary quite appreciably from one stock or "race" of sockeye to another. In Fig. 21 are shown the regression lines for three populations of sockeye, the particulars of which are set out in Table 20. It will be noted that not only do the regression lines differ between the areas, thus revealing an inherited characteristic of egg content to size, but the relationships vary from year to year, undoubtedly partly due to the sampling procedures.

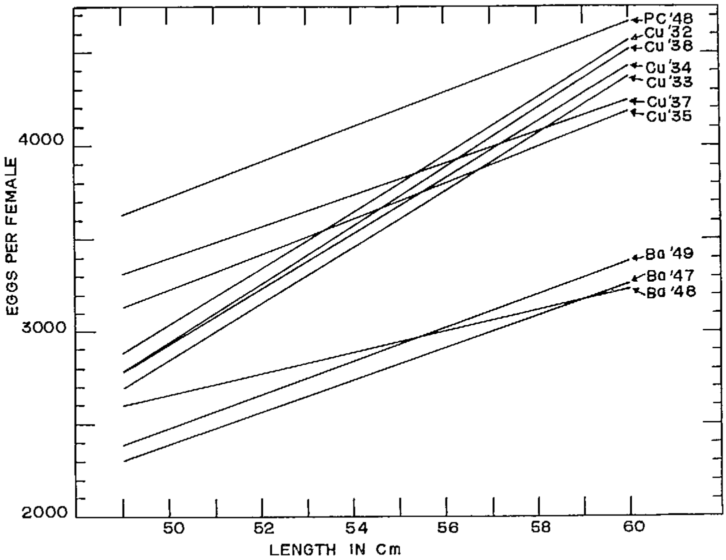

FIG. 21. Regression lines depicting the relationship of egg content (fecundity) of sockeye salmon to size of female for: (1) Cultus Lake, (2) Babine Lake, and (3) Pick Creek, Alaska, populations in the years indicated.

It is thus quite apparent that the number of eggs available for deposition by any run of sockeye will depend primarily on the number of female fish present but also on the sizes of the fish and their racial characteristic of egg content to size. The importance of the latter factor is shown in Fig. 22 where the reported fecundities from different sockeye areas (see Table 21) have been plotted in relation to size of the fish. For example, the sockeye returning to the Lake Dalnee and Lake Blizhnee spawning areas of the Paratunka River system (Fig. 8) in the southeastern part of the Kamchatka Peninsula, have a remarkably low egg content. They are of relatively small size and are not too dissimilar from the sockeye of Port John, a small coastal stream (Fig. 2) on the British Columbia coast. The length ranges of Lake Dalnee and Port John sockeye are quite similar to those of Pick Creek, Wood River system,

TABLE 20. Mean fork lengths of female sockeye sampled, mean numbers of eggs counted and regression equations of eggs on fork length, as reported for populations of sockeye from Cultus Lake (Foerster and Pritchard, 1941, p. 53), Babine Lake (Withler, 1950, p. 17), and Pick Creek, Alaska (Mathisen, MS, 1955).

Area	Year	No. of individuals	Mean length (*cm*)	Mean no. of eggs	Regression of no. of eggs (E) in length (L)
Cultus Lake	1932	46	58.5±0.30	4310±69	E = 152.0L–4565.3
	1933	47	56.5±0.19	3796±42	E = 152.66L–4786.6
	1934	75	59.0±0.18	4282±44	E = 149.6L–4548.3
	1935	55	59.0±0.22	4067±38	E = 95.6L–1552.2
	1937	35	56.0±0.28	3864±59	E = 76.5L–376.1
	1938	47	58.5±0.19	4246±54	E = 156.6L–4884.6
	Avg		57.9	4094	
Babine Lake	1946	59	60.9 (51.0–65.5)	3281 (2121–4466)	E = 57.0L–190
	1947	73	59.1 (49.5–67.5)	3187 (2157–4304)	E = 86.8L–1952
	1949	57	59.7 (50–66)	3353 (2161–4486)	E = 90.1L–2026
	Avg		59.9	3274	
Pick Creek, Alaska	1948	–	–	–	E = 4011 + 9.30(L–53.0)

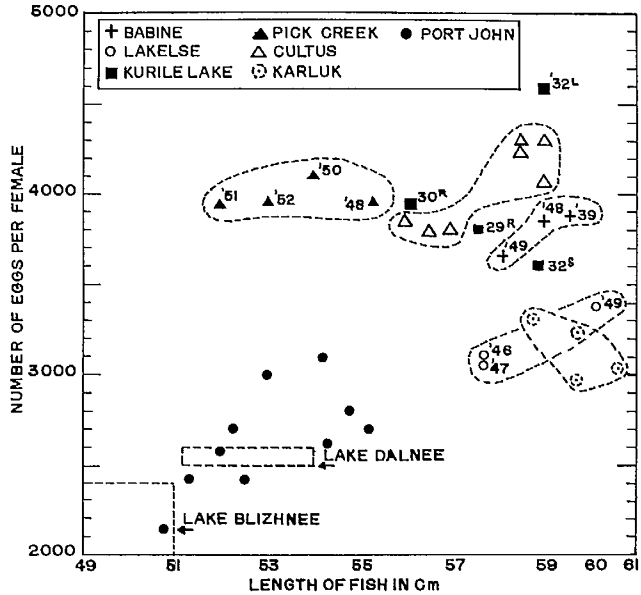

FIG. 22. The relationship of fecundity of sockeye salmon from various areas to length of females in centimetres.

Bristol Bay, Alaska (Fig. 2), yet their fecundity is only around two-thirds of the latter. On the other hand, the limited data for the Kurile Lake area, Ozernaya system, west Kamchatka, reveal that the sockeye are somewhat larger than those of Pick Creek but have almost the same egg content. The Karluk sockeye are roughly similar to those at Lakelse Lake but both have fewer eggs per female than Babine Lake individuals, which latter have a lower egg content:size relationship than the Cultus Lake sockeye.

TABLE 21. Fecundity of sockeye salmon in relation to size, as reported for various areas.

Area	Year	Mean length (*cm*)	Mean egg content	Authority
Babine Lake[a]	1946	60.9	3281	Withler (1950, p. 17)
	1947	59.1	3187	
	1949	59.7	3353	
Lakelse Lake[a]	1939	59.6	3888	Aro and Broadhead (1950, p. 18)
	1948	59.0	3860	
	1949	58.1	3699	
Pick Creek, Wood River[b]	1948	55.3	3968	Mathisen (MS, 1955)
	1950	53.8	4096	
	1951	52.0	3944	
	1952	51.7	3952	
Kurile Lake, Kamchatka[c]				
River spawners	1929	(57.6)	3790	Krokhin and Krogius (1937b, p. 96)
River spawners	1930	(56.1)	3895	
Stream spawners	1932	(58.9)	3600	
Lake spawners	1932	(59.0)	4585[d]	
Lake Dalnee, Kamchatka[e]	–	(51.2–54.0)	2500–2600	Krogius and Krokhin (1948, p. 4)
Lake Blizhnee, Kamchatka[e]	–	(49.0–51.0)	2000–2400	Krogius and Krokhin (1948, p. 4)
Port John, B.C.	1949(18)[f]	51.3	2425	Biological Station, Nanaimo, B.C.
	1950(9)	50.8	2157	
	1951(5)	54.3	2632	
	1952(7)	52.5	2436	
	1953(8)	54.8	2808	
	1954(9)	55.2	2711	
	1955(15)	52.0	2577	
	1956(15)	52.3	2694	
	1957(5)	54.2	3101	
	1958(14)	53.1	2998	
Karluk Lake, Alaska	1938–41(5_3)[g]	58.8	3306	Rounsefell (1958a, p. 466)
	1938–41(6_3)	60.6	3018	
	1938–40–41(6_4)	59.7	3238	
	1939, 1941(7_4)	59.7	2968	

(Continued.)

TABLE 21. (Concluded.)

Area	Year	Mean length (*cm*)	Mean egg content	Authority
Cultus Lake, B.C.	1932	58.5	4310	Foerster and Pritchard (1941, p. 53)
	1933	56.5	3796	
	1934	59.0	4282	
	1935	59.0	4067	
	1937	56.0	3864	
	1938	58.5	4246	

[a] No segregation according to age. Probably mostly 5_2 fish. According to Foskett (1956), Skeena River sockeye in these years were 70, 82, and 76% 5_2 fish, respectively.

[b] Both 4_2 and 5_2 fish involved.

[c] Egg counts not correlated directly with length of females. Hence, mean lengths of females, as recorded for the sockeye examined at the mouth of the Ozernaya River, are used. No age separation has been made.

[d] Only four individuals in the sample.

[e] Only ranges in length and egg content available. For lengths, males and females are combined. Neither for length nor egg content is there any segregation according to age. Several year-classes are involved.

[f] Figures in parentheses indicate the number of specimens.

[g] Figures in parentheses indicate the age of the fish on the Gilbert system.

What appear to be the greatest egg-producing sockeye are those of the Bolshaya River, as reported by Semko (1954a, p. 66, table 42) for the Karymai Springs. His records are as follows:

		Per cent age composition of the summer sockeye of the Bolshaya River			
Year	No. of eggs	3+	4+	5+	6+
1943	4500	–	–	–	–
1944	4668	11.1	73.4	15.5	–
1945	4552	34.1	58.0	7.9	–
1946	4834	7.2	83.6	9.2	–
1947	5165	–	95.4	4.6	–
1948	5136	2.6	65.0	32.4	–
1949	4829	2.2	63.25	34.5	0.05
1950	4633	31.0	31.5	37.5	–

In order to arrive at some explanation for the variations in egg content for females from year to year, we have added, on the right-hand side of the tabulation, data on the age composition of the Bolshaya River as given elsewhere by Semko (1954a, p. 29, table 15). According to North American terminology, the ages would be 1 year older, i.e., 4+, 5+, 6+, 7+. Whether the ages of the sockeye spawning in the Karymai Springs are identical with the age of sockeye sampled at the mouth of the Bolshaya River itself is not known, but they are probably indicative. If so, the high egg content prevailing in this region appears to be due to the high percentage 4+ fish (we would class them as 5+ year) in most years. In years when the egg content is lower, e.g., 1945 and 1950, the 3+ (4+ to us) age-class is more strongly represented.

Though it is apparent, in general, that within any race or geographical population of sockeye the larger females have a greater fecundity, consideration of age reveals that, *for sockeye of the same size*, those that spend a *shorter* time in the ocean have a higher fecundity than those that spend a longer period. Thus, Rounsefell (1957, p. 458) reports that younger ocean-age fish, e.g., 2 summers at sea, have a higher fecundity than older ocean-age individuals, e.g., 3 summers at sea, of the same size. Krogius (MS, 1949, p. 15) states that "for similar weights (within the limits of 1.4–2.1 kg) the fecundity decreased in the following sequence of ages: 3_1+, 4_1+, 4_2+, 5_2+," or, in our terminology, 4_2, 5_2, 5_3, 6_3. This is attributed to the faster-growing feature of the younger fish. It is further shown, by Rounsefell, that increase in period of freshwater residence has no consistent or significant effect on fecundity, but further data are required to settle this point. Since the differences in size between female sockeye spending an additional year in fresh water (i.e., between 4_2 and 5_3, or 5_2 and 6_3) are not too great and vary appreciably (Foskett, 1956, p. 34, 39), the lack of a clear egg content:fish size relation difference is understandable.

For species of Pacific salmon Rounsefell (1957, p. 461) has endeavoured to determine whether there is any relation between egg number and latitude. For four of the five species discussed, a suggestion of such relationship is apparent but further data are required.

In summary, fecundity is directly associated with the size of the female fish, the relationship itself being in the nature of a racial characteristic, hence varying from one population to another. For females of the same size within a racial population or stock, those which spend a shorter time in the ocean, thus presumably with a faster growth rate, have more eggs than those which remain a year longer in the sea. Fecundities vary all the way from 2000 eggs per female (Lake Blizhnee) to 5165 (Karymai Springs), according to size and age of the fish. Whether latitude, as having a bearing on growth of fish, is a factor in affecting fecundity remains a debatable point and requires further data for more precise evaluation.

BEHAVIOUR OF SOCKEYE FRY AFTER EMERGING FROM THE REDD

It is common knowledge that, once the young sockeye have hatched and have spent a few weeks in the alevin stage growing and absorbing the yolk sac, they wriggle up through the gravel to the bottom of the stream and commence to seek natural food. Those that have been propagated in streams flowing into lakes soon make their way directly to the lake; those that have been produced in the outlet stream of a lake swim up into the lake; those that result from eggs deposited in the gravel of lake beaches merely move off into the lake; those that are produced in springs, e.g., the Bolshaya River in Kamchatka (see p. 100), or in certain rivers, e.g., the Kamchatka (see p. 100), are reported (Semko, 1954a; Krokhin, 1960) to seek the deep pools or back-water channels and remain there for their 1st year.

The migration of the fry is not simply a case, however, of "popping up out of the gravel and away to the nearest nursery area." On the contrary it involves a definite series of behaviour reactions which are quite characteristic for the species. The various features of this behaviour pattern, to quote Hoar (1958, p. 394) who has made a most revealing study of them,

> "are normally set in motion by specific environmental situations (releasers) such as odours, visual pictures or mechanical stimuli. They are specific to each species and are inherited as a group of self-differentiating muscular movements, quite as characteristic of the species as any of its morphological features. These behaviour patterns are oriented in the world where the fish lives by gradients of light, temperature, current or the local geography. A characteristic internal [i.e., physiological condition or state] as well as external environment is essential to the expression of its instinctive behaviour."

When emerging from the gravel, sockeye fry are extremely light-conscious. During the daylight hours they remain at the bottom hiding under stones, etc. At dusk, however, they begin to move about more freely and at night rise up into the shallower more swiftly flowing water As reported for sockeye fry placed in troughs with running water where there were two areas of stones and gravel, and three equally-spaced pools (Hoar, 1958, p. 396), very few fry were seen during the day. Over a period of 3 weeks the maximum numbers observed in daylight (light intensities between 100 and 3000 ft-c) was 24% but usually fewer than 10% could be seen. Frequently none could be detected. In the evening, however, when the light intensity fell below 50 ft-c (more often below 10 ft-c) they emerged in large numbers and swam to and fro from one end of the trough to the other.

It is thus seen that for those young sockeye which hatch out in streams above lakes this behaviour would readily facilitate their downstream movement. Rising, at nightfall, into the faster-moving current they would be carried readily down the stream. Whether this is a purely drifting action or an active with-the-current, negative, rheotactic swimming has not yet been clearly established. This behaviour may likewise apply in those somewhat exceptional instances where the young sockeye fry go directly to sea, e.g., Harrison River (p. 102), Kamchatka streams (p. 100) and quite rarely in almost all sockeye areas, as evidenced by recovery of adults which had gone to sea as fry.

Where fry move upstream to the lakes, however, the situation is quite the opposite. Unless it be a case of the downstream-moving fry being displaced downstream by reason of their inability to fight the current whereas those fry which move upstream do so under stream-flow conditions against which they *can* readily and successfully contend, it becomes a case of distinctly contradictory and opposite reactions. Such fry can scarcely be considered "planktonic" (Hoar, 1958, p. 424). From observations of sockeye fry behaviour in troughs it was noted (Hoar, 1954, p. 95) that they undertook prolonged excursions, moved vigorously into turbulences of certain intensities and migrated upstream over rapids. It seemed quite conceivable that peculiar flow conditions might lead them for considerable distances upstream. However, their behaviour in currents being similar to that of chum salmon fry "it is hard to see how these responses will, in one case, result in downstream movement and, in another, movement in the reverse direction" (Hoar, 1954, p. 95). Elsewhere (Hoar, 1958, p. 412) it is reported, in commenting on the effect of temperature on salmon fry migrations, as revealed by certain experiments (Keenleyside and Hoar, 1954), that:

> "sockeye which are somewhat larger than recently-emerged fry become less sensitive to light, and, retaining their strong positive rheotaxis, may be stimulated by rising temperatures to swim more strongly against the current. This reaction might be caused by the direct acceleration of metabolic processes or temperature might be acting as a directing factor associated with rheotaxis."

From (a) casual observations on sockeye fry, found among the aquatic reeds, debris and under stones along the shore of Upper Babine River, fry which were presumably making their way up into Babine Lake, and from (b) a consideration of the situation on the Chilcotin River below Chilko Lake and on Little River below Shuswap Lake, where there are definite migrations of the fry up into the lakes, it would seem more correct to assume a behaviour pattern for sockeye fry in such areas quite different from that in others. One accepts, then, the existence of different behaviour characteristics for different stocks, the result of evolutionary development under quite different conditions of the environment in which they have been developed. Although Hoar (1958, p. 394) has remarked that "the salmon's repertoire of behaviour is limited and the same behaviour patterns will be seen wherever the fish are watched" he goes on to say that "an animal's behaviour is one of its most variable characteristics" and that "it is this same variability which enables the salmon to survive in a highly changeable environment and which permitted the genus *Oncorhynchus* to evolve its varied and efficient mechanisms of downstream migration."

It would seem that this same variability in reaction to certain conditions may apply *within* a species as *between* species and that between different stocks or geographical "races" of sockeye the behaviour patterns differ. This would explain, then, why some sockeye fry move downstream into a lake or, more rarely, into the sea while others move upstream to a lake. This would also explain why, in certain situations, the fry remain in the stream or in adjacent pools in back-water lagoons for a year subsisting, not on plankton, the common food of sockeye in lakes, but on the local bottom fauna. It is obvious that no one set of behaviour patterns can adequately account for the movements of the sockeye fry under the quite different environmental conditions known to occur. There seems to be no reason why the different stocks or "races" should not differ in behaviour reaction. Further study is required.

EFFICIENCY OF NATURAL PROPAGATION FROM EGG DEPOSITION TO ENTRANCE OF FRY INTO THE NURSERY LAKE

After considering the spawning sockeye on the spawning beds the next step is to determine how many free-swimming fry should result under so-called normal conditions. It is obvious that fry production will depend greatly on many factors, such as (1) the physical character of the spawning beds, (2) the water flow and water level conditions prevailing at spawning time and during incubation, (3) the size of the spawning population, whether less than or more than the capacity of the available suitable areas and (4) the presence of predators available to prey on and consume, firstly, the alevins emerging from the gravel and, then, the free-swimming fry as they migrate to the lake.

The most positive manner of determining how many fry are produced from a known egg deposition is to erect counting weirs in the streams and thus get a direct enumeration of the migrating fry. This means that only relatively small spawning streams can be studied. Though typical for many populations, they may or may not represent the situation in large river spawning areas or where lakeshore spawning occurs. In such instances, less precise methods must be used or approximations made on the basis of observations and other pertinent data.

Our plan is to discuss firstly the various stream studies where actual counts have been made in order to reveal the numbers of fry produced from the estimated egg deposition. These data give the percentage survival during this period. Then, by discussing the results of redd examinations and of predator activities on the spawning grounds and in the streams, we may be able to get an insight into just where the redd and stream losses occur, how extensive they are, and what the causes may be.

SCULLY CREEK FRY PRODUCTION

Scully Creek is a small sockeye spawning stream tributary to Lakelse Lake (Fig. 37), lower Skeena River system (Fig. 7). It has its origin in the mountain slope east of the lake and drains a low wooded area. The stream flow at spawning time is less than 20 ft^3/sec, but during the spring and fall rains it rises quickly and becomes a torrent.

The sockeye spawn during August and September from the mouth to 7300 ft upstream, digging their redds in the stream bottom gravel which varies from quite fine near the lake to very coarse in the upper spawning areas. Spawning activity is greatest in areas above riffles which are formed by sunken logs. Tightly packed gravel areas appear to be ignored by the fish. No area appears to be overcrowded and no superimposition of eggs by late spawners in redds used by early spawners was noted. From observations made in 1944–48 the annual sockeye spawning run consisted of from 1000 to 2000 fish, with a smaller and later run of coho.

The counting weir was constructed approximately 400 yards (366 m) from the creek mouth in such a way that sloping panels of pickets along the upstream face (Plate VII) could be installed to block off the ascent of adult fish and direct them,

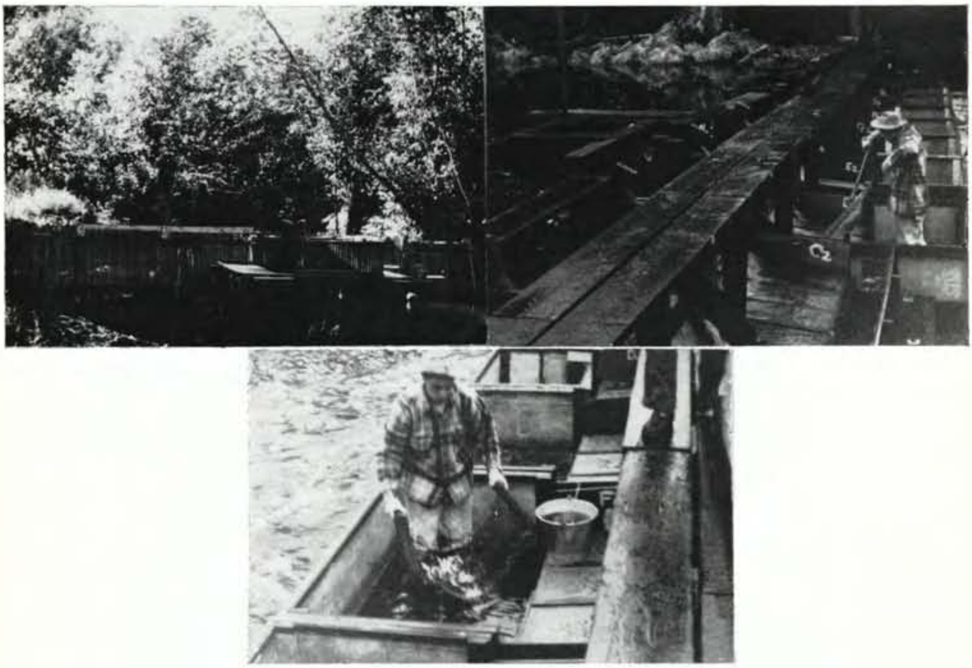

PLATE VII.

Dual-purpose counting weir for upstream-running adult salmon and downstream-migrating young.

Top left: Trap into which the adult fish proceed by means of a gradually narrowing tunnel is seen in centre of picture, also in left centre of central picture. Adult salmon may be dipped from trap and counted or released through a small gate in upper side-wall of trap.

Top right: Inclined-plane counting weir for downstream—migrating young. Stream is dammed up to suitable level by solid planking placed along upper face of weir. Stream then flows down over sloping screens through which most of the water drops while the fry or fingerlings proceed down the screen and drop into a trough of water.

Bottom: Fry being caught in hand seine and transferred to container for counting, marking, examination, etc.

Weir is built in sections for ready dismantling and removal when not in use, especially during the winter freshet periods. Weirs of this type, with certain modifications to meet local conditions, are in operation at Port John, Scully Creek at Lakelse Lake, and Six Mile Creek at Babine Lake.

through a wooden tunnel near the centre of the weir, into a slatted pen from which they could be counted. Sexes were determined at this time. In the spring a solid dam of 2 × 12 inch planks was placed across the "A" frames and the stream flow directed over a series of sloping wire-mesh screens, the mesh being sufficiently small to permit most of the water to flow through while the fry and other fish moved on down into a trough running the breadth of the creek. The trough in turn, emptied into a trap in the middle or at one end of the weir (Plate VII). From the trap the fish were removed and counted. In this way the young fish had a minimum of handling and suffered no injury.

Operations began in 1949 with the setting up of a camp at Scully Creek and the building of the adult weir for the first count of ascending spawners. The camp was operated from early spring to late autumn each season until 1955. In this year the fry counting weir was not used but the number of fry migrants was estimated by using a small conical trap-net on the creek, similar to those used in Williams Creek and described below. This device had been found, from earlier experiments, to capture migrants in proportion to the water strained. From the catch by the trap-net a close approximation could be made of the total fry escapement.

TABLE 22. Records pertaining to the spawning escapement, egg deposition, number of fry migrants and percentage fry production at Scully Creek, Lakelse Lake.

Year	Males		Females	Sex ratio[b]	Potential egg deposition	No. of fry migrants	Per cent production from eggs deposited
	Normal	"Jack"[a]					
1949–50	565	28	485	1:0.86	1,766,400	242,300	13.7
1950–51	195	146	121	1:0.62	377,800	35,100	9.3
1951–52	809	21	384	1:0.48	1,221,700	165,800	13.6
1952–53	556	40	507	1:0.91	2,053,400	249,900	12.2
1953–54	370	6	251	1:0.67	958,100	97,100	10.1
1954–55	263	7	394	1:1.5	1,693,800	233,200[c]	13.8[c]

[a] Precociously maturing small males.

[b] Males:females, but not including "Jack" males.

[c] Estimated from trap-net catch, as explained in text.

The complete records for the six seasons are given in Table 22.

One remarkable feature of the Scully Creek results is the relative constancy in the percentage fry production during the six test years. This is attributed in part to the stability of the stream conditions. Although much seasonal variation in stream flow occurred (minimum, 10 ft^3/sec; maximum, 400 ft^3/sec) there was no evidence of the water level being low enough to jeopardize the incubation, emergence, and migration of the fry, nor of the spring and autumn floods drastically altering the nature of the creek. Another stabilizing factor was the fact that more than sufficient suitable spawning gravel was always available each year. Thus, losses due to overcrowding of spawning beds or superimposition of redds were not appreciable.

It will be noted, however, that in the 2 years when egg deposition was lowest the percentage fry production was also low. These data serve to support the hypothesis that at low fry population levels the predators in the stream take a greater proportion of the fry than when the fry are more numerous.

SIX MILE CREEK, BABINE LAKE

An estimate of fry production at Babine Lake (Fig. 7), the main sockeye-producing area of the Skeena River (see Withler, McConnell, and McMahon, 1949, p. 6–10, for a description of Babine Lake and adjacent area), was undertaken in 1951 in order to give an indication of the effect of climate, etc., in this more northerly and interior lake area characteristic of the Central Plateau district of British Columbia. The sockeye stream selected for testing was a small one at the southern end of the lake and a counting weir, very similar to that at Scully Creek, was installed in 1950 in time to handle the spawning run of that year.

Unfortunately, conditions developed in Six Mile Creek which had been quite unanticipated and which had not been known to occur in earlier years when the stream was under observation. These were that:

1. in 1951 and 1952, because of an exceedingly low autumn rainfall, there was no flow of water through the lower section of the stream and into the lake. During August the stream water level dropped lower and lower and eventually ceased. Investigation in 1952 showed that, at approximately ¼ mile (0.4 km) above the weir site, the flow of water went underground, seeping through extensive gravel bars, presumably piled up by the extensive spring freshets of 1951 and 1952. The water did not, at a lower elevation, again enter the creek-bed and must have been diverted into some old channel which could not be detected despite much search. It is suggested that the upper gravel beds in 1952–53 must have become sealed-over and made more impervious to the flow of water through them, for in 1953 the stream returned to normal flow.

2. during the 1951 and 1953 spring seasons exceedingly frigid weather conditions prevailed which caused the water flowing through the screens to freeze. At such times the weir became inoperative for fry enumeration. Furthermore, excessive floods occurred. At times the flow was so great it scoured out some of the gravel areas to the extent that many alevins with yolk sac not yet fully absorbed were washed downstream.

Because of these conditions, and the high cost and difficulty in servicing such a remote field station in the spring of the year, the field stations was closed after the 1953 operation. The experiences at Six Mile were most disappointing for it had been envisaged that the observations there would be reasonably indicative of the other streams (and they are numerous) flowing into Babine Lake. It seems, nevertheless, that the Six Mile conditions may serve to demonstrate not only the way in which sockeye-producing streams may be adversely affected by prevailing climatic conditions but also the degree to which the productiveness of areas may fluctuate through the varying utilization of what might be considered marginal spawning areas.

Despite the periodic non-operation of the weir, what were considered good estimates of the fry migrations during these periods were obtained. Thus the data obtained in 1950–51 and 1953–54 may be considered a reasonable index of fry production in Six Mile Creek for the two seasons.

The pertinent records reported by Mr E. Dombroski, resident scientist, are as follows:

Year	Spawning escapement			Potential fry deposition	No. of fry migrants	No. of fry as percentage of eggs deposited
	Males	Females	Sex ratio[a]			
1950–51	691	546	1:0.79	1,625,700	188,000	12
1953–54	1,337	1,273	1:0.95	4,344,500	819,000	19[b]

[a] Male to female ratio. "Jack" salmon not included, of which 57 were reported in 1953.

[b] The investigators report the limits of error as 15–22%.

TALLY CREEK, PORT JOHN LAKE

On King Island, in the central coastal area of British Columbia (Fig. 2), there is a small lake and stream system which is visited by four species of Pacific salmon —sockeye, coho, pink, and chum. It had been selected in 1946 as an excellent site for studies of pink and chum production (Hunter, 1948, p. 105–106) but upon further investigation its possibilities in revealing the success of natural propagation of sockeye under such unusual conditions were recognized. Runs of sockeye to such small coastal lakes can never bulk very large individually but in aggregate they may be quite appreciable. In any event, from the scientific point of view they present sockeye production under quite a different set of conditions from other study areas.

Tally Creek is a small tributary of Port John Lake (Fig. 39), the largest of three known tributary streams, and flows from the surrounding high hills through a flat, well-wooded valley. It meanders through this valley for approximately 1 mile, never has a breadth greater than 10 ft and has, except in freshet time, a quite moderate and steady flow.

Weir operations began in the autumn of 1948 (Robertson, 1949). The records for the period of study (11 years) are given in Table 23.

The 11-year series of data for Tally Creek presents a wide fluctuation in fry production. The first year's extremely successful result might be looked upon with suspicion since it was the first year's weir operation, but, since the seaward migration of smolts resulting from the 1949 production of fry was not (as will be indicated later, p. 315) unusually high, this fact suggests that the fry count probably was not greatly in error. The low fry survival in the second test year (1.8%) is attributed to an extremely dry January (mean precipitation for month— 2.34 inches, as compared with 9.91 inches for the other 9 years, excluding 1953–54 when no records are available for the winter months, as measured at the Port John recording station), coupled with a very cold January (18 F) as recorded at Ocean Falls, in comparison with a 40-year mean air temeprature of 33 F. Extensive freezing of the gravel in

TABLE 23. Records of spawning escapement, potential egg deposition, and fry production at Tally Creek, Port John Lake, British Columbia, 1948–58.

Year	Spawning escapement				Potential egg deposition	No. of fry migrants	Per cent fry from eggs deposited
	Male		Female	Sex ratio[a]			
	Large	"Jack"					
1948–49	359[b]		149	–	387,400	74,900	19.3
1949–50	502	273	821	1:1.63	1,990,900	35,400	1.8
1950–51	257	198	197	1:0.77	424,900	21,800	5.1
1951–52	122	504	122	1:1.0	321,100	30,100	9.4
1952–53	136	430	164	1:1.2	399,504	19,100	4.8
1953–54	163	405	287	1:1.8	806,200	103,000	12.8
1954–55	128	500	244	1:1.9	661,500	64,200	9.7
1955–56	322	715	370	1:1.2	953,500	81,700	8.6
1956–57	132	256	500	1:3.8	1,313,500	75,200	5.7
1957–58	122	544	153	1:1.2	443,900	11,700	2.6
1958–59	173	184	360	1:2.1	1,079,300	140,600	13.0

[a] Male:female ratio, not including small "Jack" males.

[b] No differentiation between large and "Jack" males in this first year's records.

the creek was reported that year and redd inspection revealed a heavy mortality of developing eggs. In 1957–58, when fry production was again low (2.6%), precipitation, as measured at the Port John field station, was quite low during February and March (5.48 and 3.89 inches, as compared with a 10-year average of 8.39 and 9.25 inches) which may have hindered successful development of alevins.

CHILKO LAKE, UPPER FRASER RIVER SYSTEM

An interesting set of data on fry production in an important sockeye-producing area of the upper Fraser River (Fig. 6) is presented in the Annual Report for 1959 of the International Pacific Salmon Fisheries Commission. In this particular region the spawning takes place predominantly in the outlet river for some 4 miles downstream from Chilko Lake. The fry, after emergence from the redds, proceed upriver into the lake where they remain for a year or more.

In their movement to the lake the young sockeye fry are said to gather at the margins of the river where current is slower and to make their way upstream relatively close inshore. They form a narrow black band of steadily-moving fish. By methods, not as yet disclosed in report form, estimates of the abundance of these fry are made annually, and by relating these estimates to the estimated egg deposition each season, whose means of compilation have also not been reported in any detail, the egg-to-fry survival percentages have been calculated. In Table 24 are shown the spawning escapement records and the egg-to-fry survival rates as taken from the Commission's 1959 Annual Report (p. 14) and earlier reports.

Whatever the actual accuracy of these observations may be, if the methods used were the same year to year the percentage of fry production has been markedly

TABLE 24. Records of the spawning escapement and percentage fry production at Chilko Lake, upper Fraser River system, 1949–55.

Spawning year	Spawning escapement				Egg-to-fry survival
	Males				
	Large	"Jack"	Females	Sex ratio	
					%
1949	23,777	59	35,164	1:1.5	6.71
1950	9,223	8,677	11,900	1:1.3	6.49
1951	41,982	17,994	58,134	1:1.4	11.90
1952	231,364	2,544	235,565	1:1.1	6.04
1953	94,377	499	102,784	1:1.1	4.97
1954	13,818	1,820	20,896	1:1.5	9.50
1955	46,084	10,310	71,687	1:1.55	9.86

consistent, bearing in mind the many varying conditions that must have prevailed during spawning and egg incubation periods. There is no evidence of an appreciable drop in fry production as a result of spawning ground overcrowding. These findings pertain to a spawning area *below* a lake, where stream flow would be fairly stable and not subject to sudden and violent freshets nor to rapid and severe temperature changes.

WILLIAMS CREEK, LAKELSE LAKE, LOWER SKEENA RIVER SYSTEM

Fry production in the relatively small spawning stream, Scully Creek, flowing into Lakelse Lake, has already been discussed (p. 131). An attempt was also made to get an estimate of the fry produced in the major spawning river of the area, Williams Creek (Fig. 37). Here, because of the size of the river and the fact that it empties into Lakelse Lake through three channels with quite rapid water flow, operation of weirs for enumeration of fry was difficult and costly. Therefore, a sampling technique was tested whereby, by inserting long, conical traps in the river, the number of fry passing downstream through the volume of water strained by the traps could be determined. If the fry moved downstream relatively uniformly throughout the breadth of the river, and if the volume of river water strained by the net in proportion to the whole river flow were known, the trap catch should be an index of the total fry migration.

The trap, as finally designed for most effective use, consisted of a 14-ft (4.25 m) long straining funnel of fine-mesh galvanized hardware cloth attached to 2 × 2 inch (5 × 5 cm) wooden poles, with a 1 × 3 ft (30.5 × 91.5 cm) opening, tapering down to 2 × 4 inch (5.1 × 10.2 cm) at the downstream end. The funnel emptied into a plywood pen with a fine-mesh galvanized screen bottom, where the trapped fry congregated prior to removal. Cedar floats provided the necessary buoyancy and the trap was adequately staked along its length to prevent undue lateral swaying in the current. The total straining area was 55 ft^2 (5.11 m^2). Trial operation of three such traps in Williams Creek, which has a normal discharge of around 400 ft^3/sec (11.33 m^3/sec) and mean velocity of 1.7 ft/sec (0.52 m/sec), indicated that straining efficiency was quite constant unless the quantity of floating debris was heavy, and much of this could be removed by providing a suitable trash rack at the trap entrance.

In the spring of 1954 these traps were first used for fry enumeration. Three traps were placed across each of the three outlet channels of the rivers and strained a section of the water extending from the surface to the bottom. The traps were operated continuously, the fry being removed from the collecting pens each hour or as frequently as seemed necessary. The efficiency of each trap was examined and found to be good. The measured discharge strained equalled the calculated discharge strained. Known numbers of fry released upstream from the trap sites were recovered in correct proportion to the percentage of discharge strained.

Only counts for 3 years are available, the Williams Creek operation having been abandoned after 1955–56. The data are as follows:

Year	Egg deposition	Fry count	Percentage fry production
1953–54	17,765,000	1,378,000	7.8
1954–55	14,662,000	2,528,000	17.2
1955–56	6,300,000	998,000	16.5[a]

[a] In this year the fry traps were operated only every 3rd day and appropriate adjustment made in calculating total migration.

It will be noted that in 1954–55 percentage fry production was over twice that of the previous season. This highly satisfying development was attributed to extensive stream improvement work carried out by the Department of Fisheries. By blocking off an accessory diversion channel above the main spawning area, the flow conditions in the river were vastly improved in 1954. Much of the accumulated silt and algal growth was washed away and conditions for successful incubation of eggs enhanced. The effect of the improved conditions was evident again in 1955–56.

KARYMAI SPRINGS, BOLSHAYA RIVER SYSTEM, WEST KAMCHATKA (FIG. 2)

From a quite productive area of the Bolshaya River system where the sockeye spawn (as well as pinks, chums, and cohoes) in extensive "springs" (see page 101), where most of the water flow comes from underground seepage, weir counts have been made of sockeye spawning escapements and of the numbers of fry produced.

From a comprehensive report by Semko (1954a, table 42, p. 60) the records as shown in Table 25 have been taken. In the tabulation the losses in the redds and as a result of predation on the emerged fry are shown separately, which items will be considered further on. At the moment, however, we are interested particularly in the percentage fry production from eggs deposited, shown in the second from

TABLE 25. Results of the spawning of sockeye salmon (stream forms) in the Karymai Spring, 1943–50.

	Years							
	1943	1944	1945	1946	1947	1948	1949	1950
Spawning escapement: Males	1,500	590	570	1,526	3,967	930	384	124
Females	1,500	580	640	1,527	3,968	930	384	120
Total eggs for deposition:	6,750,000	2,713,800	2,853,600	7,416,600	18,882,000	4,776,500	1,854,300	556,000
Calculated fry emergence from redds	4,969,600	2,082,400	1,345,900	1,150,900	2,592,400	1,201,200	250,500	90,700
Calculated fry emergence from redds as per cent of total eggs	73.6	76.7[c]	47.2[f]	15.5	13.7	25.1	13.0	16.3
Fry consumed by predators	3,728,600	1,627,700	1,224,800	540,600	722,400	361,400	32,600	31,000
Consumption of emerging fry (per cent)	75.0[a]	78.2[d]	91.0	47.0	27.9	30.1	12.6[l]	34.2
Fry migrating	1,241,000	454,700	121,000[g]	610,300	1,870,000	839,800	217,900[m]	59,700
Fry migrating as per cent of total eggs	18.4	16.8	4.2[h]	8.2	9.9	17.6[j]	11.8	10.7
Fry migrating as per cent of emerging fry	25.0[b]	21.8[e]	9.0[i]	53.0	72.1	69.9[k]	87.0[n]	65.8

In the original table certain errors in arithmetic have been noted. These have been corrected as follows: [a] 71.0 to 75.0; [b] 29.0 to 25.0; [c] 76.5 to 76.7; [d] 77.4 to 78.2; [e] 22.6 to 21.8; [f] 47.0 to 47.2; [g] 186,100 to 121,000; [h] 2.5 to 4.2; [i] 13.8 to 9.0; [j] 18.7 to 17.6; [k] 74.4 to 69.9; [l] 13.0 to 12.6; [m] 218,900 to 217,900; [n] 87.3 to 87.0.

bottom line. They vary from 4.2% in 1945 to 18.4% in 1943, with an average value for the 8 years of 12.2%.

SUMMARY

In attempting to find a reasonable estimate of the production of fry from a sockeye spawning ground, that is, the numbers of fry that survive to reach the lake and form the basis for the new population, five separate series of data have been reviewed, each involving quite different conditions of climate, spawning grounds and size of spawning escapement or amount of seeding. These may be set down as:

Area	No. of years	Range of percentages	Mean percentage
Scully Creek, Lakelse Lake, Skeena River	6	9.3–13.8	12.1
Six Mile Creek, Babine Lake, Skeena River	2	12–19	15.5
Tally Creek, Port John	11	1.8–19.3	8.4
Chilko Lake, upper Fraser River	7	5.0–11.9	7.9
Williams Creek, Lakelse Lake, Skeena River	3	7.8–17.2	13.8
Karymai Spring, Bolshaya River, Kamchatka	8	4.2–18.4	12.2
	37		10.55

Wide variation occurs, ranging from 1.8 to 19.3%. The mean value for the 37 tests is 10.55%. In the hypothetical tabulation, page 67, fry production had been estimated as 12.5% (237,500 fry from 1,900,000 eggs deposited), thus proving to be slightly higher. Nevertheless, it is quite close.

BREAKDOWN OF LOSSES FROM SPAWNING TO ENTRANCE OF FRY INTO THE LAKE

It is of importance to determine at which stages the approximately 90% mortality prior to entrance of fry into the lake occurs, to ascertain where the heaviest losses take place and why. Since our calculations of efficiency of natural propagation are based on the total number of eggs carried to the spawning grounds by the females, i.e., total number of females multiplied by average fecundity per female, any factors which lead to a reduction in the numbers of eggs deposited are as significant as those factors which cause mortality of eggs and fry after spawning.

COMPLETENESS OF EGG DEPOSITION BY FEMALE SOCKEYE

Early in the investigations of the natural propagation of sockeye salmon at Cultus Lake in 1925, and again 10 years later in 1935, naturally spawning females were collected on the lakeshore spawning grounds to ascertain the number of eggs which had not been released but were still retained within the gonads of the females. These were found to be (Foerster, 1938a, p. 155):

Year	No. of eggs retained	0	1–20	21–50	51–100	101-300	301–600	601–1300
1925	No. of fish	22	21	3	3	2	2	1
1935	No. of fish	126	206	22	17	32	12	2

"Mean counts for the 54 samples of 1925 and the 417 of 1935 were 47.4±14.1 and 36.5±3.52, respectively. In both instances over 75% of the specimens examined contained 20 or fewer eggs per fish." On the basis of 4000 eggs per female, this extent of egg retention amounts to a mere 0.5%.

In general, these findings are in close agreement with those of other investigations. In 1949, Mr G. C. Broadhead reported that examination of 51 spawned-out female sockeye, in a total population of 485 at Scully Creek, showed that less than 2% of the eggs had been retained. Examination by Mr J. G. McDonald of 10% of the run of 507 spawning females in 1953 in the same area gave an egg retention of 1.1%. Two females had died unspawned and two had been killed by bears prior to egg deposition. At Six Mile Creek, Babine Lake, 75% of the 545 females were examined in 1950 and revealed an egg retention of 2.8%. In 1953, with a sockeye run twice the size of that in 1950, i.e., 2671 adults of which 1269 were females, 1.5% of the 1193 females examined, or 18, had died unspawned. The overall egg retention of the 1193 females amounted to 3.6% of the total probable egg deposition, or, excluding the unspawned individuals, an average retention of 2.1%

Elsewhere, other investigators obtained similar results. In Pick Creek, Bristol Bay, Mathisen (MS, 1955) reported 4–5 eggs retained per naturally spawning female; from experimental pens in which mature sockeye were being held for natural spawning at sex ratios varying from 1 ♂ : 1 ♀ to 1 ♂ : 15 ♀, but with adequate space available for redd preparation, the egg retention per female varied from 0.20 to 2.28% (see Table 26).

At Lake Dalnee, Kamchatka, Krogius and Krokhin (1948, p. 4) noted that "the quantity of 'lost' eggs varies from year to year, from 1% to 5% of total fecundity."

There appears to be a relationship between the total number of sockeye on a spawning ground and the completeness of egg expression. In addition to the spawned-out females at Cultus Lake referred to above, there were 3 females in 1925 and 99 in 1935 which had not spawned at all. Cause of death is unknown but in view of the fact that the numbers of female sockeye on the spawning grounds were 3883 in 1925 and 10,174 in 1935 it could be due to a greater competition for spawning ground. The same was suggested by Semko (1954a, p. 49), who reports the following eggs remaining in spawned-out sockeye in relation to the total number of sockeye on the spawning grounds:

312 eggs per female when spawning population is 7123
9 eggs per female when spawning population is 1859
24 eggs per female when spawning population is 768
7 eggs per female when spawning population is 219.

Among pen-retained sockeye in Pick Creek, Mathisen (MS, 1955) found that, where the fish were crowded, the egg release was not quite as complete (see Table 26, last two entries) suggesting an inverse relationship of egg deposition to available spawning area. Mathisen indicates, however, that the amount of loss in such instances will be of little consequence generally.

TABLE 26. Spawning density of experimental pens in Pick Creek and per cent egg retention, 1948 and 1951 (Mathisen, MS, 1955).

Pen No.	Area (ft^2)	Sex ratio male:female	No. of females	No. of females examined	Egg retention		Area per female (ft^2)
					No.	Per cent	
3	2512	1:15	30	29	377	0.31	84
4	7265	1:15	30	17	166	0.25	242
4	7265	1:10	20	20	239	0.28	363
5	2458	1:10	20	20	1896	2.28	123
1	9371	1:7.5	31	7	115	0.39	302
2	1998	1:5	10	10	88	0.21	200
6	2431	1:5	10	9	211	0.58	243
10	1500[a]	1:1	7	7	59	0.20	214
7	900[a]	1:1	5	5	162[c]	0.78[c]	180
11	500[a]	2:1	2	2	6	0.07	250
13	2000[a]	3:1	3	2	200	1.55	667
9[b]	378	1:1	30	30	14311	12.10	12.6
12[b]	400[a]	1:1	48	20	11494	13.81	8.3

[a] Approximate figure.

[b] Pens with excessive spawning density.

[c] One female in this pen died with 155 eggs. This number was included in computing the figure and percentage, although all five males were dead five days prior to her death. The egg retention in this case should properly be considered a result of the absence of males. The other four females contained only seven eggs.

By way of summary, it may be said, then, that during natural spawning practically all of the eggs (95–99%) are deposited by the females. However, when the runs are heavy and where competition for spawning ground is very keen the number of undeposited eggs in female fish and the number of females dying unspawned increases. No actual correlation factor has yet been obtained.

ASSESSMENT OF LOSSES DURING EGG DEPOSITION AND INCUBATION

During the spawning operations and the subsequent period of incubation of the embryos within the eggs, losses occurring because of unfavourable conditions may fluctuate exceedingly widely. They will depend, in large measure, on the abundance of fish on the spawning area, particularly if overcrowding occurs, and on the actual physical and physicochemical conditions prevailing in the gravel.

Without going into detail, at the moment, concerning the specific differences which are bound to prevail between spawning grounds of the major four types, i.e., stream bed, lakeshore, lake outlet river, and springs, and also between individual spawning grounds within each major type, it may be said that, in general, the greater the number of spawners the greater the total yield of fry *but* the lower the percentage yield or the yield per female spawner. This relationship has been shown quite clearly by Semko (1953) for sockeye spawning in the Bolshaya River basin and is represented in Fig. 23. It applies, in principle, to all salmon spawnings but the relative positions and slopes of the curves may differ for each spawning ground, depending on the conditions prevailing there.

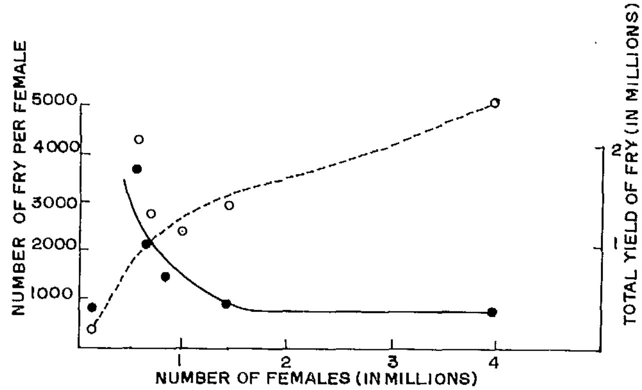

FIG. 23. The relation of surviving fry per female and the total yield of fry to the total number of spawning females. Broken line—total yield of fry; solid line—number of fry per female. (From Semko, 1953, fig. 1, for sockeye salmon in the Karymai Spring, Bolshaya River system, west coast of Kamchatka.)

Every spawning ground will be found to have a great variety of conditions. Some parts will be excellent for deposition and incubation of eggs, i.e., they will have good permeability and good water flow, and there will always be a sufficient depth of water so that no normal seasonal fluctuation in water level will cause them to become exposed, thereby resulting in the deposited eggs being subjected to drought or to freezing in winter. In such areas there will be little or no danger of floods or high water subsequently bringing down on to these areas quantities of mud and silt, which will tend to reduce permeability, cut the water flow and lead to poor aeration of the developing eggs and alevins. Other areas will differ in one or more of these features, culminating in what might be termed "marginal" grounds where the conditions are such that the chances are about equal that good or poor survival of eggs and hatch of fry will occur. In some years conditions may be favourable and excellent production of fry be obtained; in others, quite unfavourable conditions may prevail and mortality of eggs or alevins may be extremely heavy.

When adult sockeye return to the spawning grounds in limited numbers they generally occupy the best section. Where the runs are greater, not only do the good areas become crowded, with less area available to each spawning pair, but some of the fish are forced to occupy poorer areas. When very large runs occur, many spawners are forced to utilize marginal and submarginal areas where survival is questionable and depends primarily on the maintenance of favourable conditions throughout the incubation and hatching periods. It is true that, when runs are large, the spawners often dig up and clear off large expanses of gravel, thereby improving the quality of the potentially good spawning ground and extending the area of the beds. At the same time, however, the unsuitable crowding and the use of marginal and of submarginal ground leads to less effective burying of the eggs and the losses are greatly increased. Furthermore, when large successive runs of spawners, e.g., early and late runs, occupy the same spawning areas, extensive losses occur among already buried eggs which are dug up and scattered by the late spawners.

Data from Lake Dalnee, Kamchatka, serve to indicate the effects of heavy and crowded spawning, Table 27. These data have been taken from Krogius and Krokhin (1948, table 2, p. 6) and Krogius (1951, table 3, p. 11).

TABLE 27. Mortality of sockeye eggs on the spawning grounds of Lake Dalnee.

Year of spawning	No. of spawners (1×10^3) Total	No. of spawners (1×10^3) Females	Total eggs in all females (1×10^6)	No. of surviving eggs (1×10^6)	No. of surviving eggs Per cent
1936	141.9	73.1	166.9	1.7	1
1937	100.0	52.8	138.0	1.4	1
1938	84.9	47.3	125.8	14.0	11
1939	–	25.8	67.7	22.2	33
1940	–	34.3	86.0	15.1	18
1941	–	22.8	70.4	35.2	50
1942	20.3	9.3	22.0	15.4	72
1943	27.0	13.4	38.7	23.3	78
1944	76.0	38.0	111.0	87.7	79
1945	63.7	32.0	93.4	60.7	65
1946	55.0	27.5	57.7	28.8	49
1947	23.0	11.5	35.9	0.3	1

The extremely poor fry survivals in 1936 and 1937 are attributed by Krogius (1951, p. 12) to the digging up, by later spawners, of eggs deposited by earlier spawners when the run was large and the spawning period prolonged. The poor survivals in 1938 and 1947 have been attributed to freezing-over of the spawning grounds.

LOSSES DURING INCUBATION

During the period of egg incubation in the redds, the extent of survival of developing embryos varies greatly, depending on the type of gravel in which the eggs are laid, the permeability of the gravel, and the amount of water flow through it. It is generally considered that greatest losses occur either during the early developmental stages, when the embryos are quite delicate and highly susceptible to damage from agitation or jarring, or just prior to hatch when the demand for oxygen for the growing embryo is high. Losses can occur, however, at all stages, particularly in cases of severe water flow changes, due either to a severe drought and appreciable drop in water level or to a heavy flood with a consequent disturbance of the stream bed and the bringing down of large quantities of silt or fine mud.

Attempts have been made by various investigators to ascertain the extent of loss during incubation by digging up redds and noting the numbers of live and dead eggs therein. In some cases redds which had been clearly marked at the time of spawning were excavated in the belief that all eggs expressed by the female fish would be recovered; in others, areas of gravel where sockeye had spawned were dug up and the proportion of living and dead eggs determined.

During a survey of some of the sockeye streams in Kamchatka in 1926 and 1927, Kuznetsov (1928) made diggings in a number of spawning areas, particularly in the Kamchatka and Bolshaya River systems. A total of 175 redds were opened up. His findings may be summarized as follows:

Average fecundity per female–3763 eggs
Average egg content per redd–3079 eggs or 81.8% of fecundity
Average egg mortality per redd–497 eggs or 13.2% of fecundity or 16.2% of eggs in redd.

In other words, of the eggs contained in each female (3763), 18.2% were lost at time of spawning because of incomplete release of all eggs, ineffective deposition or subsequent digging up by later spawners, and 13.2% were either not fertilized or died during incubation. While the loss in the redds is reported as 16.2% (497 eggs out of 3079) Kuznetsov indicates that in many redds the mortality was quite low. If one omits from the tabulated data (Kuznetsov, 1928, p. 156) the four occasions when all eggs were dead, due obviously to exceptionally unfavourable conditions of some kind, the average loss in the remaining redds examined was 6.9%. In 130 of the 175 redds dug up the loss was 2.2% or less.

In Pick Creek, in the Wood River system, Alaska, Mathisen (MS, 1955, table 2) gives the following results of the examination, in late autumn, of areas where natural spawning had taken place:

Year	Live eggs	Dead eggs	Total	Percentage mortality
1948	29,625	188	29,813	0.63
1950	43,959	1,135	45,094	2.52
1951	17,066	231	17,297	1.34
Total for 3 years:	90,650	1,554	92,204	1.69

TABLE 28. Results of investigations of sockeye spawning grounds at Kurile Lake in the spring of 1933. Four types of spawning areas are included (from Krokhin and Krogius, 1937b).

Locality	Date	Type of ground	No. of eggs/m^2	Eggs		Fry		Total	Percentage	
				Live	Dead	Live	Dead		Live	Dead
Springs										
No. 1 pool, Hakyzin River near the bank of the brook outlet	May 1	Sand and pebbles	3422	–	7700	–	–	7700	–	100
Centre of same spring	May 2	Sand and pebbles	2700	1500	1100	–	100	2700	52	48
Same place	May 12	Sand and pebbles	4452	923	190	–	–	1113	83	17
Near centre of same spring	May 12	Sand and pebbles	–	–	–	–	–	–	10	90[a]
Near centre of same spring	May 12	Sand and pebbles	–	–	–	–	–	–	80	20
No. 3 pool, Hakyzin River	May 12	Fine sand or sand and gravel	–	–	–	–	–	–	10	90
No. 6 pool, Hakyzin River	May 12		3502	763	115	–	–	878	87	13
Same pool	May 12	Gravel and sand	–	–	–	–	–	–	95	5
No. 16 spring	May 13	Sand and pebbles	2006	860	140	3	–	1003	86	14
No. 15 spring	May 13	Sandy gravel	–	–	–	–	–	–	80	20
Kirushutk River	May 15	Sand and pebbles	3000	860	150	–	–	1010	85	15
Average:			3200						61	39
Inlet rivers										
Severnaya River 200 miles from mouth	May 6	Pebbles and gravel	1050	5	70	225	30	360	73	27
Etamynk River	May 10	Sand and pebbles	500	272	100	30	–	402	74	26
Lake										
North Bay at Cape Pulomynk	May 16	Pebbles and sand	2600	200	680	–	–	900	25	75
Same place	May 16	Pebbles and gravel	1340	25	150	145	–	320	50	50
Same place	May 26		2500	377	100	728	80	1285	86	14
Mouth of Etamynk River	May 18	Gravel and sand	800[b]	77	118	–	–	195	40	60
Same place	May 18		2820	682	5	155	5	847	99	1
Near the same place	May 18	Gravel and pebbles	–	–	–	–	–	–	95	5
Average:			2010						69.3	30.7
Outlet of Ozernaya River										
Near the bank	Apr. 26	Pebbles and sand	1220[c]	250	180	–	–	430	58	42
In same place	Apr. 28	Pebbles and sand	2160	662	78	–	–	740	90	10
Downstream from lake	Apr. 26	Gravel and sand	2900	310	320	–	68	698	44	56
Still further downstream	May 22	Sand and gravel	2500	67	435	–	–	502	13	87
In a small bay	May 23	Sand and gravel	2528	102	530	–	–	632	16	84
In a cove at mouth of creek	May 23	Sand and gravel	–	–	–	–	–	–	95	5
On south bank	May 25	Gravel and pebbles	–	–	–	–	–	–	90	10
On north bank	May 23	Gravel and sand	–	–	–	–	–	–	80	20
Average:			2458						63	37

[a] Complete count not made.
[b] Count not quite accurate since some alevins had been killed.
[c] Not a complete count as some eggs washed away in the current; these not used in computing the average.

In contrast to the above two sets of data we may consider the results obtained by Krokhin and Krogius (1937b) from an examination of sockeye redds in the four types of spawning grounds frequented by spawning sockeye in the important Kurile Lake area of the Ozernaya River system, namely, springs, lakeshore, lake outlet, and tributary streams flowing into the lake. The data are presented in Table 28, as taken from tables 29, 30, 31 of the original publication. The observations are repeated in some detail in order to emphasize the wide fluctuations that occur.

On the basis of the observations made at Kurile Lake, Krokhin and Krogius (1937b, p. 162) summarize their findings as follows:

> "The most crowded spawning occurs in the springs: on an average 3200 eggs are deposited per square metre; at the outlet of the Ozernaya River the average number is 2458; and on the spawning beds in the lake, 2010. The highest mortality is observed in the springs (39–40%): at the outlet of the Ozernaya River it is 37 per cent and in the lake 30.7 per cent. Average mortality is 36.7 per cent."

The higher losses in the springs are attributed to the greater crowding and to the more frequent occurrence of unfavourable conditions, such as shallow sand, muddy or grassy bottom, slow current and the great quantity of dead carcasses of spawned-out sockeye buried in the bottom. In the lake, where spawning is less dense, where the physical conditions are better and where dead carcasses are seldom found in the spawning areas, the mortality is lowest. The river outlet represents an intermediate condition.

For the Karymai Spring spawning areas (Semko, 1954a) it will be noted in Table 25 that, whereas in 1943 and 1944 the fry emergence was calculated as 73.6 and 76.7% of total eggs deposited, from 1946 to 1950 it amounted only to from 13.0 to 25.1%. The year 1945 appears intermediate, with 47.2%. In other words, for reasons not specified but presumed to be associated with conditions prevailing within the redds, mortality of developing eggs and alevins increased greatly, from around 25% of total eggs to 75% or greater.

Data from British Columbia spawning areas are very limited, principally due to the difficulty in marking off and subsequently digging up individual redds and in being certain that all eggs or alevins have been obtained. In many cases the dead eggs quickly decompose and cannot be recovered. However, some redd examinations have been made. The results are considered indicative, at least, of probable survival within a redd.

At Six Mile Creek, Babine Lake, six redds were carefully examined in the fall of 1950, October 24 and 25, and a total of 4700 eggs recovered. The eggs were then in pre-eyed stage of development. In April, 1951, four redds were opened. At this time all living eggs had hatched. As a result of these examinations the following mortalities were reported:

Eggs retained in females and not deposited	— 2.8%	of total eggs
Eggs dying in pre-eyed stage	— 7.4%	of total eggs
Eggs in eyed stage	—24.5%	of total eggs.

In addition, it was estimated that the loss in alevins prior to emergence was not less than 20% of the total eggs. In other words, the total loss during incubation and hatch amounted to around 50–60% of total eggs.

At Scully Creek, Lakelse Lake, sockeye redd examinations were also made in 3 years. Results are shown in Table 29. The counts of live and dead eggs and alevins indicate that in no case was a complete redd excavated since the egg deposition per female was in excess of 3000 in each of the years. It was believed that a count anywhere in the spawning area would be indicative of degree of survival, if eggs were found there. In the majority of cases the percentage survival of eggs or alevins was

TABLE 29. Results of redd examinations in Scully Creek, Lakelse Lake, 1949–52.

	No. of living			No. of dead		Per cent survival	
Date	Pre-eyed eggs	Eyed eggs	Alevins	Pre-eyed eggs	Eyed eggs and alevins	Eyed eggs	Alevins
1949–50							
Oct. 21	–	2063	11	7	12	97.5	–
Nov. 9	–	777	12	4	–	94.7	–
Nov. 9	–	1016	29	1	4	97.6	–
Nov. 10	–	236	0	111	48	58.3	–
Apr. 6	–	0	0	0	500	–	0
Apr. 6	–	0	816	0	0	–	100
Apr. 6	–	0	403	0	2	–	98.5
1950–51							
Sept. 13	43	–	–	95	–	32.2	–
Mar. 2	–	0	0	364	0	0	–
Mar. 8	–	5	68	0	0	–	100
Mar. 15	–	–	385	5	14	–	92.7
Mar. 16	–	–	97	0	0	–	100
Mar. 19	–	–	166	0	0	–	100
Mar. 19	–	–	0	0	0	–	–
Mar. 19	–	–	33	0	–[a]	–	?
1951–52							
Oct. 29	–	130	–	1	–	99.2	–
Oct. 30	–	1164	–	12	–[a]	?	–
Oct. 30	–	527	–	20	–[a]	?	–
Nov. 1	–	790	–	17	–[a]	?	–
Nov. 6	–	928	–	42	3	95.2	–
Nov. 6	–	766	–	6	0	99.2	–
Mar. 24	–	–	–	–	100	–	0
Mar. 24	–	–	156	–	–	–	100
Mar. 26	–	–	250	–	–	–	100
Mar. 26	–	–	322	–	–[a]	–	?
Mar. 26	–	–	–	76	225	–	0
Mar. 27	–	–	35	–	–	–	100

[a] Particles of dead eggs were recovered, but no count was obtained; hence the percentage loss could not be computed.

determined, but where only alevins were recovered there is no means of knowing how many eggs may have died in the redd and decomposed.

As evidence that these redd survival findings at Scully Creek are not reliable in general, it is noted in Table 35 that, when relating the estimated losses due to the actual fry migrant counts, allowance must be made for a redd mortality of from 41 to 62% of total eggs deposited.

FACTORS HAVING A BEARING ON SURVIVAL OF EMBRYOS AND ALEVINS IN THE REDDS

Mortality Due to Movement During Incubation

Reference has been made above to the losses which occur because of the digging up of already deposited eggs when late-arriving spawners prepare redds in areas which earlier spawners had already occupied. This digging-up generally leads to a scattering of the excavated eggs over the surface of the gravel downstream from the excavated redd. These eggs become (1) subject to damage by being exposed to the light, particularly sunlight, and (2) readily available for consumption by predator fishes and birds. Observations have been made, by many workers, on the activities of predatory fishes and birds on salmon spawning grounds (Kuznetsov, 1928, p. 177; Munro; 1923, 1924; Munro and Clemens, 1937) and, though heavy consumption of salmon eggs is apparent, the evidence suggests that the bulk of the eggs eaten were "waste" eggs, lying on the surface of the stream bottom or lake beach. Kuznetsov (1928) has remarked that, in this regard, the predaceous fish "are doing sanitary work."

When redds are dug up by later spawners and the developing eggs within these redds are dislodged to be moved downstream by the stream flow or by the current produced by the tail fin of the spawning female, some of the eggs may fall into crevices between rocks and become covered again with downstream-drifting gravel and sand. Many of those eggs could continue development and produce healthy fry were it not for the deleterious effect of the movement or jarring to which the eggs are subjected during dislodgement and resettlement. The extent of mortality due to such agitation depends greatly on the stage of development of the eggs.

As an example of the approximate extent of loss that can take place, in Table 30 we give the data, as reported by Smirnov (1960, p. 14), for coho, pink, and chum, salmon eggs when subjected to agitation (600 jolts or vibrations in 210 sec) in a mechanical vibrator. After deposition by the female and during the period of swelling with intake of water, the salmon egg is particularly sensitive to jarring. Thereafter, for a period of several hours, the eggs may be handled or moved with much less chance of loss. When cell division commences, sensitivity to movement again increases until eye pigmentation begins. From then on, sensitivity is minimal and it is generally accepted that transfer of eggs and a fair amount of rough handling or treatment can take place without appreciable loss. Data comparable to those

TABLE 30. Mortality of coho, pink, and chum salmon eggs under similar degrees of mechanical agitation at various stages of development (Smirnov, 1960, p. 14).

Stage of development of eggs	Loss of eggs after 600 jolts in a mechanical vibrator (%) Coho	Pink	Chum
15 min after expression	98.6	72.8	86.5
2 hr after fertilization	24.4	15.7	5.6
Beginning of cell division	30.0	20.0	13.7
16 blastomeres formed	40.1	24.3	13.2
Beginning of gastrulation	50.3	44.0	16.3
First somite formed	18.8	74.8[a]	17.8
Beginning of tail bud	23.9	36.9[a]	24.7
Beginning of blood circulation	5.1	29.5[a]	1.2
Beginning of eye pigmentation	9.4	0	0.5
Pelvic fins formed	4.2	0	0.4
1–3 days prior to hatch	2.1	0	0.6

[a] Pink salmon were found to be in an earlier morphological stage than the coho or chum embryos.

shown in Table 30 are not available for sockeye but, in general, are believed to conform. It would appear that digging up of already filled redds by later-arriving spawners can lead to serious mortality of the developing embryos, from around 75% immediately after deposition and while the eggs are swelling to around 20% while cell division and active development of the embryo is taking place, i.e., up to about 15 days. For a brief period, 8 hr, prior to active cell division and again after the eye spot becomes visible, sensitivity to jarring is minimal.

Studies in Kamchatka (Smirnov, 1958) have shown that sockeye have a much longer period of incubation than the other species of Pacific salmon. This seems not to be associated with an earlier time for spawning since early spawning chinook and masu salmon have also a short period of incubation. It seems to be related, rather, to the lower temperature of the water where the sockeye spawn. During their longer incubation period the sockeye embryos use up appreciably more of their yolk sac material (around 28%, which is twice as much as coho and chinook embryos), and at hatch they have a conspicuously smaller yolk sac. In consequence there is, according to Smirnov (p. 373) "a much reduced period of yolk sac feeding after hatch, a quicker adaptation to active search for food and thus an earlier complete reliance on external feeding. . . ."

RATE OF DEVELOPMENT OF SOCKEYE EMBRYOS

The rate at which salmon eggs develop within a redd depends primarily on the temperature of the water bathing the eggs; the colder the temperature, the slower the development. According to Smirnov (1958) Kamchatka sockeye eggs at Lake

Dalnee begin to hatch 55 days after fertilization, at a mean temperature of 11.4 C and after 148 days at a mean temperature of 4.6 C, while Semko (1954a) reports for Karymai Spring sockeye a hatch in 150 days at a temperature of 3.19 C.

A number of years ago data were collected at a number of sockeye hatcheries in British Columbia to determine the period of incubation according to prevailing temperatures. A "degree-day" unit was used, this being the mean daily temperature above 32 F. Thus, a mean temperature of 40 F for 1 day would be equivalent to 8 degree-day units. While too great reliance cannot be placed on the individual records because (1) the thermometers were not standardized and (2) only daily maximum and minimum readings were obtained, the records, as provided by the Fish Culture Branch, Department of Fisheries of Canada (personal communication of November 12, 1932, from Mr J. A. Rodd, Director of Fish Culture) are of interest. They are tabulated in Table 31.

Wide variation in the length of the incubation period would be expected in view of the quite different temperature conditions prevailing at the various hatcheries

TABLE 31. The length of incubation periods and the number of Fahrenheit "degree-day" units involved, for sockeye salmon reared in hatcheries in British Columbia (1 Fahrenheit degree-day = 5/9 Centigrade degree-day).

Location of hatchery	Year[a]	Date when first eggs taken	Date of first hatch	Period of incubation (days)	Degree days
Anderson Lake, west coast of Vancouver Island	1928–29	Oct. 25	Jan. 25[b]	92	1168
	1929–30	Oct. 19	Jan. 25	98	1291
Babine Lake (Skeena River)	1929–30	Sept. 9	Oct. 29	50	993.5
Lakelse Lake (Skeena River)	1928–29	Aug. 4	?	–	1220.5
	1928–29	Aug. 22	?	–	1231
	1929–30	July 28	Oct. 26	90	1333
Kennedy Lake, west coast of Vancouver Island	1928–29	Oct. 24	Feb. 7	106	822
	1928–29	Nov. 9	Feb. 27	110	707
(early run)	1929–30	Sept. 3	Nov. 16	74	1296
(late run)	1929–30	Oct. 29	Feb. 22	116	1040
Rivers Inlet, near the outlet of Owikeno Lake	1928–29	Sept. 30	Feb. 9	133	766
	1928–29	Oct. 1	Feb. 1	123	730
	1928–29	Oct. 9	Feb. 18	132	697
Pitt Lake (Fraser River)	1929–30	Sept. 2	Oct. 29	57	1085.5
Cultus Lake (Fraser River)	1928–29	Nov. 1	Apr. 6	156	623.5
	1929–30	Oct. 30	Apr. 19	171	1199.5
	1929–30[c]	Nov. 15	Apr. 5	141	1043.5
Pemberton (Fraser River)	1929–30	Sept. 9	Dec. 28	110	955.5
Stuart Lake (Fraser River)	1929–30	Aug. 28	Oct. 26	59	1098

[a] Year commenced July 1.

[b] Eggs "eyed" Nov. 29 after 519 units.

[c] These eggs were transferred to and reared in a subsidiary hatchery at Smith Falls.

but the mean for the 17 determinations, 107 days, corresponds reasonably closely with the findings for Kamchatka sockeye. There is also wide variation in the number of degree-day units required to hatch out the sockeye. This applies not only between different hatcheries but also between collections taken at the same hatchery at different times. Some of this variation may be due to the use of unstandardized thermometers, but much is due to the differences in temperature regime in the hatchery water supply. The mean number of units, 1069 degree-days (Fahrenheit) or 594 (Centigrade), corresponds, however, with records from Kamchatka (Semko, 1954a, p. 56; Krogius and Krokhin, 1956a, p. 8). As reported above, from Smirnov (1958), the sockeye have a relatively short alevin period and become free-swimming and actively feeding within 3–5 weeks after hatch, this period again depending on temperature. Semko (1954a) reports emergence of sockeye fry in Karymai Spring 5 months after fertilization of eggs.

OXYGEN CONSUMPTION OF SOCKEYE EGGS AND ALEVINS

In Kamchatka, sockeye select, for spawning, areas of lakeshore or creek bottom where there is a good flow of ground water or seepage (see p. 104). Here, too, are found (see p. 104) relatively low but uniform temperatures and a low oxygen content.

In association with the latter it is found that the small sockeye eggs (the smallest of all the Pacific salmon species) are heavily pigmented, the bright reddish-orange colour indicating a high carotinoid pigmentation which facilitates rapid transfer of oxygen from water to developing embryo. Furthermore, a very elaborate and dense network of capillaries covers the yolk sac which assists in the circulation of oxygen transfer by the blood. Together with a rapid and active movement of the embryo within the egg membrane which increases with rise in temperature (Smirnov, 1958, p. 373), these features assure adequate respiration in water of low oxygen content.

However, during the final period of incubation there is a reduction in the density of the capillary network surrounding the yolk and, consequently, a decrease in this very important embryonic organ of respiration. This, according to Smirnov, occurs just at a time when consumption of oxygen by the embryo is greater and this greater oxygen requirement by the developing embryo, just prior to hatch, is confirmed by tests conducted by Semko (1954a, p. 57–58) in an experimental incubating apparatus. In Fig. 24 are given the curves of oxygen consumption of four species of Pacific salmon reared under similar conditions. It is seen that the sockeye have a high consumption at around the 24th day, when the embryo undergoes rapid development (formation of eyes and initial growth of caudal peduncle), which is twice as great as that at 55 days when differentiation of organs, pigmentation of eyes and initial formation of the fins begins. Records for British Columbia sockeye embryos, provided by W. P. Wickett, indicate that at a temperature of 5.2 C, developing sockeye eggs, at the "eyed" stage, have an oxygen demand of 0.00296 mg per egg per hr or twice that indicated by Semko, above at the 55-day stage. In other words, the dip in the curve for sockeye in Fig. 24 is not confirmed by Wickett's data. Thereafter an increase in 0_2 consumption took place, continuing for around 80 days

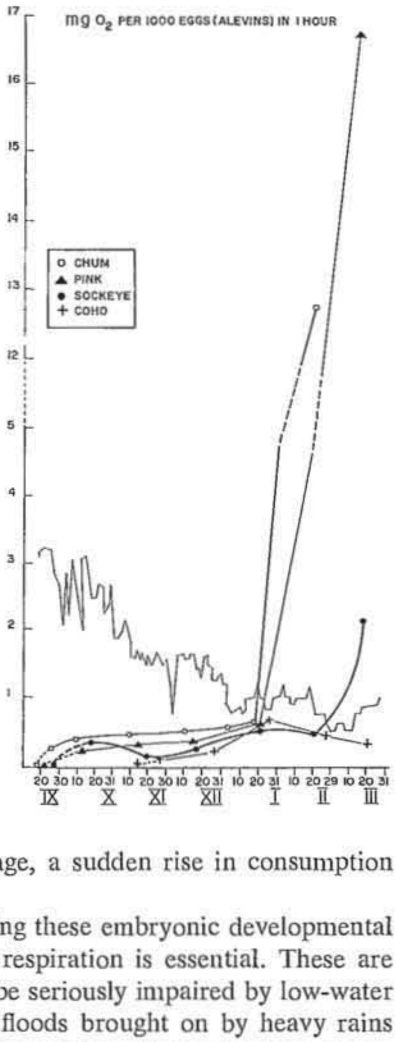

FIG. 24. Consumption of oxygen by salmon eggs and alevins in Karymaisky incubating apparatus (1947–49). Jagged light line across graph denotes the temperature of the water. (Taken from Semko, 1954a, fig. 10.)

until, with hatch and beginning of the alevin stage, a sudden rise in consumption again took place.

The point we wish to make here is that during these embryonic developmental stages, the provision of adequate conditions for respiration is essential. These are periods when water flow through the gravel may be seriously impaired by low-water winter conditions or by excessive silting due to floods brought on by heavy rains or temporary rapid snow-melt, so that proper metabolism of the young embryos may become seriously disrupted. At such times heavy loss may occur and conditions prevailing in the spawning-rearing areas may cause wide fluctuations in survival of eggs and alevins.

IMPORTANCE OF THE OXYGEN SUPPLY DURING EGG INCUBATION

Although Krogius and Krokhin (1956a) state that:

> "the successful development of eggs under conditions of a decrease in O_2 content and an increase of CO_2 content shows that (1) sockeye eggs are not as sensitive to scarcity of oxygen and a large amount of free carbon dioxide as was once assumed to be the case and (2) the role of ground water on the spawning-rearing grounds is primarily to assure the removal of waste products of metabolism from the sockeye redds,"

observations in British Columbia stream spawning areas suggest that an insufficient supply of oxygen to the developing eggs may be a very significant factor.

A special study of the flow of water through salmon spawning-rearing areas has been made by W. P. Wickett for the Fisheries Research Board of Canada. He has found in one chum salmon stream that, due to the activities of the spawning fish, the permeability of the gravel and the velocity of flow were high (20,000–50,000 cm/hr) at time of egg deposition, but that the situation deteriorated during winter and spring and the permeability and flow velocity decreased to quite low levels (1000–5000 cm/hr). Somewhat similar conditions undoubtedly apply also in sockeye stream spawning-rearing areas, with wide variation depending on the conditions in the streams during the winter-spring season.

A special ground-water sampler has been devised (Wickett, 1954; Terhune, 1958) to measure velocity of flow and oxygen content. By means of this instrument it was found (FRBC, 1959, p. 98) that at Williams Creek, Lakelse Lake, where a sockeye fry production of 17% was obtained, and at Scully Creek, with a mean fry survival of 12%, the survival rates were "proportional to the average permeability of their gravels." Further studies on sockeye spawning-rearing areas are desirable. Information of this kind is required if attempts are to be made to increase natural production of sockeye by improving natural spawning beds, constructing artificial spawning areas, etc. At the moment, we can only accept the general conclusion of Wickett (1957, p. 99) that "desirable standards for the gravel of salmon streams at present are those which will give an oxygen content of not less than 8 ppm 0_2 and a velocity of 50 cm/hr."

Reference has already been made to the possible deleterious effect of decaying carcasses of dead, spawned-out sockeye in Kamchatka sockeye areas, particularly on the lakeshore areas and in springs where they tend to accumulate in large numbers and where the underground seepage flows are low. In the decomposition process the oxygen demand is great and may readily reduce the residual oxygen supply to an extremely low level. Thus, eggs in adjacent sockeye redds may be substantially affected. To what degree this situation applies in stream spawning areas is not known but in regions where lake spawning prevails it may be an important factor.

Furthermore, the effect on egg respiration may be aggravated by the buildup of a high carbon dioxide content in the water bathing the eggs. Alderdice and Wickett (1958) show, from experiments with chum salmon eggs, that a high external carbon dioxide pressure may inhibit the diffusion of carbon dioxide from the eggs, particularly in those stages of early incubation prior to the development of the circulatory system and of blood pigments. The uptake of oxygen would be inhibited and a deceleration of the metabolic rate result, leading essentially to death, if the inhibiting influence is protracted.

PREDATION ON FRY

After the alevins have emerged from the redds and taken up free-swimming and active feeding activities prior to or in the course of migration to the adjacent lake, they are very vulnerable to attack and to consumption by predators, primarily other and larger fish species. Losses due to predation of this kind vary widely but are believed to be quite appreciable.

SCULLY CREEK, LAKELSE LAKE

For conditions prevailing in British Columbia streams, special studies at Scully Creek, Lakelse Lake (Fig. 37), were made by the Fisheries Research Board of Canada as part of the investigation of fry production (see p. 131). Newly emerged and free-swimming fry were collected at the fry-counting weir, anaesthetized in a dilute solution of chloretone, marked by inserting a light, double silk thread immediately in front of the dorsal fin, and released again into the creek at selected sites 500, 2000, and 4000 ft above the counting weir. Threads of different colours were used to designate the date and place of liberation. Recoveries were made both

TABLE 32. Percentage recovery of thread-marked sockeye fry at Scully Creek for 1950, 1951, and 1952, in relation to distance of release above the counting weir. The unmarked count at the weir on the night of release of marked fry is also indicated (from data of J. MacDonald).

Year and date	Percentage mark recovery when released above the counting weir at 500 ft (152 *m*)	2000 ft (610 *m*)	4000 ft (1220 *m*)	Unmarked fry count on night of release of marked fry
1950				
May 2	–	8.2	6.9	412
May 12	–	29.5	–	18,333
May 15	–	–	16.5	14,917
May 18	–	17.5	10.4	10,620
May 20	–	10.0	8.8	4,694
May 27	–	8.0	5.9	7,522
May 30	–	3.0	–	654
1951				
May 21	–	32.3	10.0	675
May 25	–	28.7	24.4	944
May 30	–	6.8	1.7	1,644
June 5	–	13.6	5.3	1,343
June 7	–	16.0	9.9	1,134
1952				
May 1	–	4.0	2.6	205
May 6	10.0	8.1	0.7	508
May 10	–	9.3	29.9	4,378
May 12	31.1	31.6	30.0	3,913
May 23	28.8	31.8	33.3	8,661
May 28	20.8	14.9	32.4	6,350
June 2	14.3	9.8	21.1	3,255
June 10	26.1	10.2	22.4	1,816

at the counting weir and in the stomachs of predaceous fish caught at the weir. Only those fry showing no obvious sign of distress due to the anaesthetic, the marking, or the handling were used in the experiments. Most of the recoveries of marked fry were made on the night of release, indicating an immediate downstream migration, but a small number were caught the following night. Only occasionally were marked individuals recovered at the weir three nights after release. The recoveries of marked fry were correlated with the total number of fry counted each night in order to take into account the extent of the fry population available to the predators present in the creek.

Mortality due to marking, as shown by retention in troughs with running water, was found to be negligible for the first 24 hr but increased rapidly thereafter. The greater susceptibility to predation because of the presence of the coloured threads and the loss of threads was tested only in comparison with fin-clipped fry (both pelvic fins removed) released at the same time. Recoveries at the weir (57% for thread-marked fry and 65% for fin-clipped) suggested a slightly greater loss among the thread-marked individuals, and recoveries from predator stomachs increased the overall returns to 64 and 68%, respectively. This close similarity in comparative returns indicated that loss of threads did not occur to any great extent.

The results of the tests in 1950, 1951, and 1952 are given in Table 32.

Wide variability in the returns for the 3 years is indicated but the recoveries in 1950 and 1951 show a lower recovery from those fry released furthest upstream which suggests a fairly random distribution of predators in the creek. In 1952, however, the recoveries from a release of marked fry at 2000 ft (610 m) above the weir were frequently substantially less than those released 4000 ft (1220 m) above and, on average, the recoveries from the latter closely approximated those recoveries from but 500 ft (152 m) above the weir. This suggests that in some years the predators may be more concentrated in certain areas. Water level conditions may have some bearing on predator distribution in this regard.

As would be expected, positive relationship is found between percentage recovery of marked fry and the total number of fry migrating on the same night. When the total population of migrating fry is greater, the chance of any marked individual being consumed is less. In 1951 this relationship was not apparent and may be attributed to the very small and scattered numbers of fry migrating that year.

TABLE 33. Minimum and maximum estimated survival of fry migrating at the same time as marked fry, Scully Creek, Lakelse Lake, B.C.

Year	Total no. of fry migrating on days of marked-fry recoveries	Estimated total hatch Minimum (No.)	Estimated total hatch Maximum (No.)	Per cent survival from hatch to weir count Minimum (%)	Per cent survival from hatch to weir count Maximum (%)
1950	57,152	122,000	413,000	14	47
1951	5,760	18,000	67,000	9	32
1952	29,086	43,000	136,000	21	68

Assuming that the survival of marked fry is a reasonable index of the survival of all those migrating, estimates of the survival of fry from the time of emergence from the gravel to arrival at the counting weir were made for that portion of the migration which descended with the marked fry, as shown in Table 33.

Since for 1951 the minimum survival rate is less than the survival established for the whole period from potential egg deposition to fry migration (Table 35) it is evident that this per cent return of marked fry is too low. Therefore, the actual survival rate for fry during the period of downstream migration will be somewhere between the minimum and maximum values presented.

A second estimate of fry loss due to predator fish was obtained by determining the numbers of predators in Scully Creek and the numbers of fry consumed by them. The principal predators in the stream were coho (*O. kisutch*) yearlings, cutthroat trout (*Salmo clarki clarki*), char (*Salvelinus malma*), and sculpins (*Cottus asper*). The numbers of each species present in Scully Creek each year were obtained from the counts at the weir, since practically all of them, with the possible exception of the sculpins, moved out of the creek into Lakelse Lake each season. The number of sockeye fry consumed per predator was found from a careful examination of predator stomach contents in 1951 and 1952 (Table 34).

In each of the 4 years 1950–53 the numbers of predators calculated to be present in the stream and actively preying on sockeye fry were as shown below; sculpins were estimated by mark and recovery, the salmonids by the weir count:

Year	Coho	Cutthroat and char	Sculpins
1950	1445	612	1197
1951	2179	423	705
1952	4146	292	1197
1953	9771	404	609

Tests indicated that, in young coho at water temperatures prevailing during the spring in Scully Creek, digestion of a sockeye fry was completed in approximately

TABLE 34. Numbers of sockeye fry observed in predator stomachs in 1951 and 1952 at Scully Creek.

	No. of predators sampled	No. of sockeye fry consumed	Mean no. of sockeye fry eaten per predator
1951			
Coho	123	386	3.14
Cutthroat and char	17	80	4.71
Sculpins	36	167	4.63
1952			
Coho	172	758	4.41
Cutthroat and char	15	161	10.74
Sculpins	46	249	5.41

48 hr. Using this figure for all predators, the percentage loss of sockeye fry by those predators calculated to be present in the stream was 1950—63, 1951—84, 1952—76, 1953—75. These percentages fall within the range of those calculated above from marked fry recoveries, and so are deemed reasonably indicative of the real and very heavy mortality caused by predation.

Accepting them, then, as close approximations to actual conditions and knowing the actual percentage migration from the potential egg deposition and the degree of egg retention by the female fish, the mortalities at the various stages of development may be computed. These are given in Table 35.

TABLE 35. Calculated losses from spawning to fry migration at Scully Creek, Lakelse Lake, during four test years, in percentage.

Year	Presumed egg deposition	Egg retention	Loss during incubation	Loss due to predation	Fry survival
1949–50	1,766,400	<2.0	62	63	13.7
1950–51	377,800	1.5[a]	41	84	9.3
1951–52	1,221,700	1.5[a]	42	76	13.6
1952–53	2,853,400	1.1	50	75	12.2

[a] No counts recorded; 1.5% taken as estimate.

The Scully Creek data may be considered as approximately representative of fry production in general, showing a mean mortality of eggs and alevins during incubation of around 50% and of mean mortality due to predation on emergent and migrating fry of 75%; all of which results in a mean fry production of 12.2% or slightly higher than the overall mean for all recorded tests of fry production (see p. 140) of 10.55%.

SIX MILE CREEK, BABINE LAKE

During the fry production studies of 1950–51 (see p. 134), release of thread-marked fry in the upper reaches of the creek was made to determine, by recovery at the counting weir, the extent of loss through predation. It had been previously observed that once the young sockeye fry had emerged from the gravel they were quickly displaced downstream and this behaviour was also noted in the thread-marked fry. Even though released as far as ¾ of a mile (1.2 km) above the weir they were almost invariably recaptured the same night down at the weir. Rainbow trout (*Salmo gairdneri*) were found to be the principal predator in the creek but no estimate of the population present was obtained.

Of 27 releases made at three different release points on Six Mile Creek above the counting weir and involving 1464 healthy thread-marked fry, only 35% were recovered at the weir, indicating that approximately two-thirds of the fry emerging from the gravel and proceeding downstream became the prey of predators.

PREDATOR ACTIVITIES IN KAMCHATKA AREAS

In his study of salmon production in the Karymai Springs area of the Bolshaya River, Semko (1954a,b) gave much consideration to the role of predator fishes, which consisted in that region of 1- and 2-year coho and 1- to 3-year and older char. Yearling sockeye also came into the picture though their cannibalistic tendencies are relatively minor. For example, the proportion of fish (chiefly young fry of various species) in the stomachs of older salmonids, in percentage of total weight of food contents, was found to be (Semko, 1954b, p. 127):

	Sockeye	Coho		Char	
Age	1+	1+	2+	1+	2+
April	10.0	35.0	48.0	53.0	58.0
May	17.5	70.5	90.0	70.0	80.0
June	2.0	56.0	80.0	36.0	82.0

The older the young predators the more intensely they preyed on the fry. Maximum consumption occurred in May when the fry are present in greatest numbers.

In the Karymai Springs pink, chum, and coho salmon as well as sockeye occur and during April, May, and June the young pink and chum fry, and to a lesser degree the coho, are also preyed upon by the predators. These fry serve as buffers, therefore, for sockeye fry and, when in abundance, appreciably relieve the pressure of consumption by predators on the young sockeye. The proportions which the fry

TABLE 36. Numbers of salmonid fry of different species migrating from Karymai Springs, 1943–51 (Semko, 1954a, p. 76).

Year		Pink	Chum	Sockeye	Coho	Char	Total
1943	No.	300,000	105,564	203,434	49,800	38,000	696,798
	%	43.5	15.3	29.4	6.3	5.5	100
1944	No.	229,000	2,070,000	1,241,000	1,197,000	57,000	4,794,000
	%	4.8	43.1	25.9	25.0	1.2	100
1945	No.	3,393	171,043	454,710	34,852	3,500	667,498
	%	0.5	25.6	68.2	5.2	0.5	100
1946	No.	30,700	133,479	186,142	27,665	1,361	379,347
	%	8.0	35.2	49.1	7.3	0.4	100
1947	No.	–	78,073	610,248	397,520	4,332	1,090,183
	%	–	7.2	56.0	36.4	0.4	100
1948	No.	49,801	2,219,156	1,869,951	627,181	75,457	4,841,546
	%	1.0	45.8	38.6	13.0	1.6	100
1949	No.	–	313,602	839,836	1,415	24,805	1,179,658
	%	–	26.6	71.2	0.1	2.1	100
1950	No.	15,856	93,712	218,914	87,150	35,965	451,597
	%	3.5	20.8	48.5	19.3	7.9	100
1951	No.	–	147,333	64,676	67,545	17,452	297,006
	%	–	49.6	21.8	22.7	5.9	100

of the various species represent of the whole fry population in the area vary widely from year to year, as shown in Table 36, and, so far as the sockeye are concerned, the loss due to predators will be quite different each year, depending not only on the quantities of fry of other species available to the predators but also on the numbers of predators present in the area, as shown in Table 37. For example, Semko (1954b, p, 129) records that:

> "the mass dissection of stomachs of young coho and char in one of the seasons indicated that in one period of the season on the average up to 0.5 fry were found in a yearling coho, up to 3 fry in a 2-year coho, while a 2-year-old char consumed up to 7 fry. Comparing these data, it might be concluded that since a 2-year-old coho consumed 6 times as many fry and a 2-year-old char 14 times as many fry as a yearling coho, they are the most destructive. In reality, this is not the case. Thirty-five thousand yearling coho were found in the basin which consumed per day 17,500 fry; there were 2000 2-year-old coho which devoured 6000 fry, and but 150 2-year-old char which consumed only 1050 fry per day. Consequently, in spite of their relatively low food ration, the most destructive predators were the yearling coho, on account of their much greater abundance."

TABLE 37. Fry of all species and sockeye fry consumed by the indicated numbers of predators (in thousands) in Karymai Springs, 1943–50 (Semko, 1954a, p. 66, 77).

Year of spawning	Total of all fry consumed by predators	Total sockeye fry consumed by predators	No. of predators (1×10^3)
	%	%	
1943	52.0	75.0	130
1944	73.1	78.2	222
1945	85.0	91.0	27
1946	38.8	47.0	14
1947	20.0	27.9	26
1948	34.4	30.1	24
1949	50.0	12.6	21
1950	66.6	34.2	74

It is quite apparent from the evidence submitted that consumption of fry by predators is a quite significant limiting factor. It will vary considerably according to the type of spawning area, whether in a creek, in a spring, or along the lakeshore, being probably least devastating in the last-named.

In our hypothetical production chart (see p. 67) we have set down the loss of fry in the streams due to predation at 75% of the fry emerging from the redds. This may be too high an estimate in view of the Karymai Spring data, but the circumstances there are somewhat unusual, particularly in regard to the buffering influence of pink and chum fry. For British Columbia sockeye areas, especially where the sockeye spawn in streams tributary to a lake, the fry losses due to predation undoubtedly are high and would seem to account for from 50 to 75% of the fry emerging and migrating to the lake.

Chapter 7. Lake residence of young sockeye

After emergence from the redd areas the young sockeye quickly migrate into the adjacent lake where they remain for 1 year, 2 years, of even for 3 years in some regions in Alaska. Exceptions are (1) those areas where the sockeye spawn along the lake beaches, in which case the fry merely seek the deeper waters of the lake and (2) those areas (chiefly in Kamchatka—the Bolshaya River, the Kamchatka River, etc.) where the sockeye spawn in springs (kliuchi) quite removed from any lakes, and the fry either migrate to sea or remain in the spring pools or the backwater lagoons of adjacent rivers for a year.

The fry enter the lake just prior to or at the onset of an increase in the plankton supply in the lake. In some lakes, for example Lake Dalnee in Kamchatka (Krogius and Krokhin, 1956a, p. 10), the young sockeye live for a month or so in the littoral part of the lake, feeding on small crustaceans, the larvae of insects which spend the early stages of life underwater, and terrestrial insects which fall on the lake surface. Then they pass to the main body of the lake where they live until they go to sea. During this period they feed on plankton Crustacea in the lake—the copepods (Cyclopidae and Diaptomidae) and the cladocerans (Daphnidae and Bosminidae). In the Wood River system, Bristol Bay area, Alaska, Burgner (MS, 1958, p. 14) reports that:

> "while the fry do leave the rivers between the lakes soon after emergence, downstream migration of fry in most of the tributary creeks is not completed for some time after breakup of the lake ice. In many of the creeks a portion of the fry population remains to feed and sometimes the fry acquire considerable growth before entering the lake.
>
> "Sockeye fry in the Wood River lakes are observed in abundance along the lake shores for at least a month after breakup of the lake ice. When the lake level is high early in the season they are to be found in droves in flooded grass along protected areas of the lake shore."

DISTRIBUTION OF YOUNG SOCKEYE IN A LAKE

VERTICAL DISTRIBUTION

Within a lake the sockeye are distributed within the upper strata. In Lake Dalnee, Kamchatka, their vertical distribution was found (Krogius and Krokhin, 1956a, p. 10) to be as shown in Fig. 25, that is, in the surface epilimmial strata during the summer, sinking to lower strata in the autumn. In the winter they occur at all depths but are more numerous in the upper levels. The vertical distribution of the plankton crustacean, *Cyclops*, the principal sockeye food form, and its seasonal changes in Lake Dalnee are indicated in Fig. 26. The drop in abundance in August is ascribed by Krogius (1953, p. 270) in large part to intensive consumption by the young sockeye.

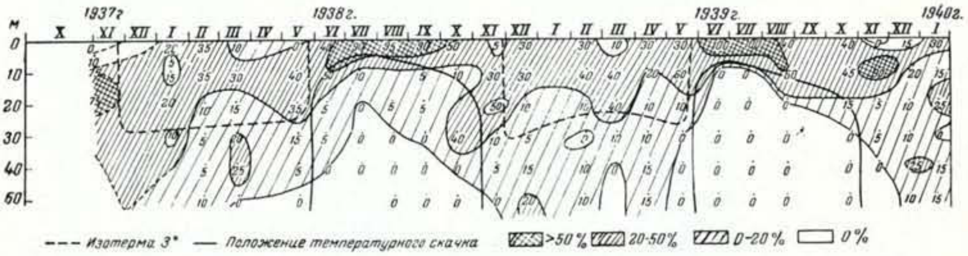

FIG. 25. Vertical distribution of young sockeye in Lake Dalnee (in per cent of all young, for each series taken), 1937–40. (From Krogius and Krokhin, 1956a, fig. 3.) Dotted line—3° isotherm; solid line—position of thermocline.

For northern British Columbia lakes a similar summer distribution is apparent, since Johnson (1956) reports that in both Babine and Lakelse lakes, Skeena River system, schools of young sockeye are observed active at the surface during daylight hours, restricted to offshore regions (depths greater than 2 m). Also, in the Wood River lakes, Alaska, near-surface tow-net operations from June to September were

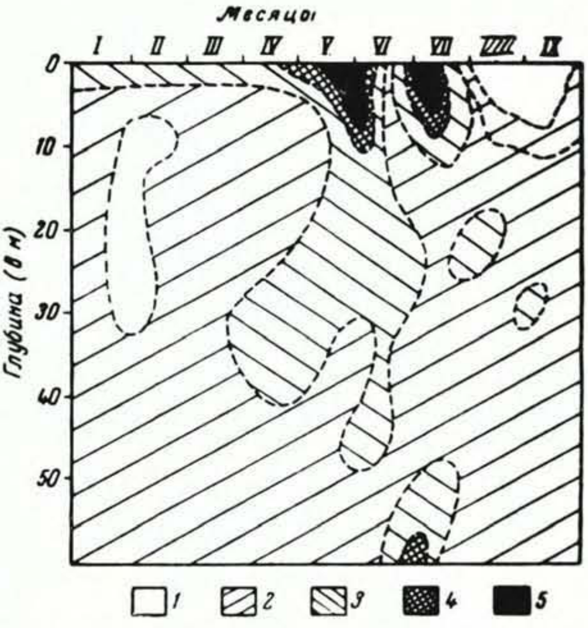

FIG. 26. Seasonal changes in the vertical distribution (in metres) of *Cyclops* in Lake Dalnee in 1938. 1—absence of *Cyclops*; 2—less than 5; 3—over 5; 4—over 10; 5—over 20 specimens per litre. (From Krogius, 1953, fig. 4.)

highly successful in capturing sockeye fingerlings, while deeper tows were not (Burgner, MS, 1958). It was found that here, too, in midsummer, the zooplankters on which the young salmon feed were abundant near the surface during the hours of reduced daylight, their dense concentrations thus favouring fish feeding near the surface at night.

In a more temperate area, such as at Cultus Lake, British Columbia, according to Ricker (1937b, p. 459), "it seems likely, therefore, that most of the summer feeding of sockeye fingerlings is done at levels higher than 20 metres, and probably between 15 metres and about 5 metres, which includes the whole of the thermocline, a narrow strip of hypolimmion and part of the epilimmion." Vertical distribution appears to be closely associated with the vertical movement of the plankton food supplies. Ricker (1937b, p. 459) suggests that, in lakes such as Cultus Lake, extensive feeding in the upper epilimmion, i.e., in the surface strata, seems to be barred by the scarcity of food there, unless the diurnal migrations of Crustacea into the surface strata are sufficient to add greatly to the food supply in early morning or late evening. The vertical distribution of important food forms in Cultus Lake by day during July, 1934, is shown in Fig. 27 (from Ricker, 1937b, p. 456).

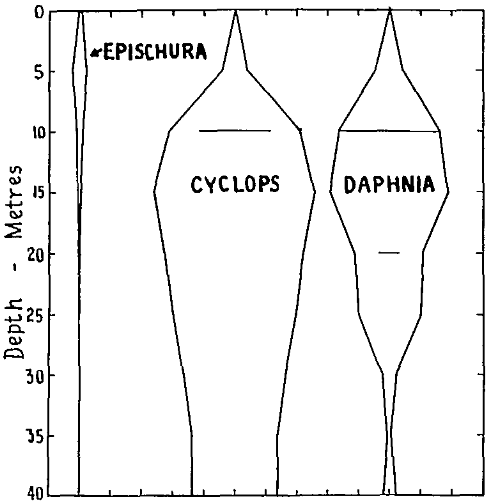

FIG. 27. Vertical distribution of Entomostraca, by day, in the pelagic region of Cultus Lake during July, 1934. Values indicated are the mean of three series of nine catches each, taken at the beginning, middle, and end of the month. Each division of the abscissal scale represents two organisms per litre. Horizontal lines at 10 and 20 m depth represent the relative number of each species eaten by sockeye which were held for 2 days at those depths on July 16–18, 1935. (From Ricker, 1937b, fig. 3.)

Horizontal Distribution

Evidence that young sockeye, upon taking up residence in a lake, do not become dispersed throughout the lake was first provided by studies at Babine Lake in 1955 by Johnson (1956). Previously, though many investigators had attempted to capture young sockeye in a lake, very little success had been achieved. However, with the introduction of fast and powerful outboard motors the problem became much less difficult.

The net devised by Johnson (Johnson, 1956, p. 696) is a cone-shaped bag (see Fig. 28) 9 ft (2.74 m) long with a mouth opening diam of 3 ft (92 cm), the open mouth end being given rigidity by means of a ring of $\frac{5}{16}$-inch (7.9-mm) stainless steel rod. The upper 6 ft of the net was made of $\frac{5}{8}$-inch (15.9-mm) stretched mesh nylon netting with the 3-ft bag end made of woven nylon material having openings of $\frac{5}{32}$-inch (4.0-mm). This net proved satisfactory for the capture of young sockeye, even of small, newly emerged fry. Towed by two boats running parallel 100 ft (30 m) apart and with 100-ft tow lines of $\frac{1}{4}$-inch (6.3-mm) nylon rope there was nothing directly in front of the net opening to drive the young fish away. Outboard motors of 15–25 hp were used and surface tows, fishing the upper 3 ft (1 m) of the lake, were made at a speed of approximately 7 mph (3 m/sec). Consecutive tows of 10–15 min duration were made for 1 hr in the evening, spanning the period of dusk and early darkness, and one such hour of towing comprised a unit of fishing effort. All tows were made in the pelagial zone of the lake at selected locations (see Plate VIII.)

Fig. 28. Diagram of tow net used to capture young sockeye in Babine Lake, showing the attachment of tow-lines when used from two boats. (From Johnson, 1956, p. 696.)

First tests on the equipment at Lakelse Lake (Fig. 37) in 1954 indicated that within a single-basin small lake (area 5.2 square miles, 13.5 km^2) a generally uni-

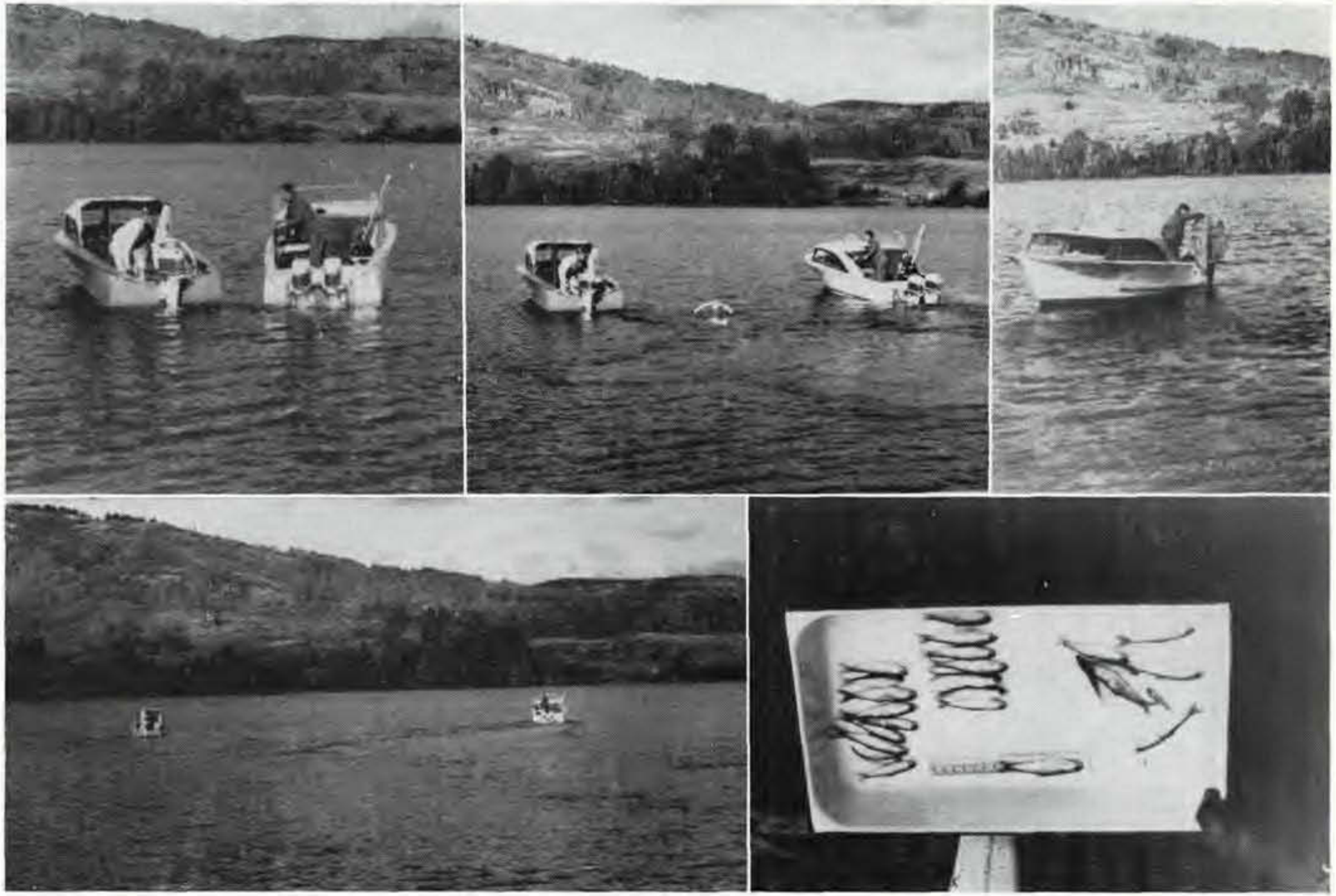

PLATE VIII.

Towing for fingerling sockeye, directly off shore from Halifax Narrows, Babine Lake, Sept. 1961. *Upper left*: two power boats preparing to commence the tow; *centre*: tow net in the water between the boats; *bottom left*: tow underway net being hauled just below the surface; *upper right*: tow completed, net being brought aboard; *bottom right*: catch laid out for measuring specimens, etc.

form offshore distribution prevailed. However, tows in the long, narrow, multibasin Babine Lake (Fig. 56) revealed a quite uneven dispersal of the young sockeye. These highly varying concentrations were found to be closely associated with the concentrations of parent spawners in adjacent spawning areas and suggested, therefore, a limited area of dispersal of the young fish from the point of entrance into the lake. From these findings Johnson (1956, p. 707) speculated that:

> "once having taken up a pelagic existence, whether they feed at random on plankton or seek out concentrations, they are subject to being carried along with their plankton food in the general circulation of the water mass. For this reason, it seems unlikely that they would chance to leave the circulating water mass of which they are a part, whether the water mass be one lake, or an independently-circulating water mass within one lake. Regarding multibasin lakes or extensively long, narrow basins, the movement of young sockeye from one region of circulation (water mass) to another is probably one of chance, dependent on the extent of intercirculation between adjacent regions of circulation."

The general significance of an unequal horizontal distribution in multibasin lakes is clear. If spawnings in different regions of the lake basin vary greatly in amount, the adjacent lake nursery areas, in the succeeding year, will have corresponding unequal quantities of fry to support. Assuming a uniform potential plankton productivity in all regions of the lake, those with the dense sockeye populations will be subject to heavy cropping. There will be less plankton available per fry and fingerling and hence a reduced growth. In those lake regions where spawning is light and the fry less numerous, food will be plentiful and growth much better. Whether survival rates are affected has yet to be ascertained, but the general belief is the better the growth, i.e., the larger the young sockeye, the greater the chances of survival.

THE NATURAL FOOD OF YOUNG SOCKEYE IN A LAKE

The well-being and growth of young sockeye depend primarily on (1) the abundance of the food organisms on which they subsist, (2) the numbers of young sockeye present, and (3) the numbers of other species of fish in the lake which compete with the sockeye for food.

FOODS CONSUMED

Planktonic Crustacea are, in all sockeye rearing areas, the most important food constituent. Early studies of the stomach contents of seaward-migrating young sockeye caught in the outlet of Cultus Lake (Foerster, 1925, p. 404, table 13) revealed that the copepods *Epischura nevadensis* and *Cyclops bicuspidatus* and the cladocerans *Daphnia pulex* and *Bosmina obtusirostris* were the main food organisms eaten at that time of year, April and May. From an examination of 65 specimens, collected during the seaward migration season, *Epischura* occurred only rarely while *Cyclops* constituted the main item of food, making up 85% of the total number of crustaceans consumed. *Daphnia* occupied second place or 12% while *Bosmina* was more rarely found, averaging 3% of total contents. Plankton studies in the lake had indicated that at this period of the year *Cyclops*, *Daphnia*, and *Bosmina* were the most abundant forms, the relative abundance being in the order given.

In order to get some understanding of the plankton forms consumed by young sockeye in the lake during the summer months, small groups of fry, ranging in length from 3.25 to 5.4 cm, and obtained from the hatchery retaining ponds, were suspended in a small wire cage in Cultus Lake at a depth of around 30 ft (9–10 m) in mid-July and mid-August. Lake water temperatures at this depth were 17–18 C. The weather was clear and warm. The food of these caged fingerlings varied appreciably but, in general, *Bosmina* was slightly more abundant in the stomachs than either *Cyclops* or *Daphnia* and the former formed the second most dominant food. *Epischura* was occasionally taken, also the rotifer, *Notholca longispina*.

During 1923, specimens of sockeye which had been planted in Hicks Lake, a small lake in the mountains on the east side of Harrison Lake, and which were migrating seaward were collected (1) above a waterfall a mile or so below the lake (where the migrants were stopped by a small weir and carried down below the falls by the Harrison Lake hatchery staff) and (2) at the outlet of Trout Lake, a small, plankton-rich lake which the migrants had to traverse en route down to Harrison Lake. Examination of stomach contents indicated that the food of yearling sockeye, when in a stream, was entirely different to that when in a lake. The alimentary tracts were practically empty, save for a few insect larvae (chironomid, caddisfly), a few crustaceans and some adult insect fragments. Those specimens from the outlet of Trout Lake showed very markedly the influence of the lake's rich feeding ground. There were present in the stomachs the copepods, *Cyclops*, *Diaptomus*, and *Epischura* and the cladocerans *Daphnia*, *Scapholeberis*, *Polyphemus*, and *Ceriodaphnia* in varying proportions. In short, all crustaceans had been used as food forms.

Through the kindness of Mr H. C. Crawford, Superintendent of the Dominion Government Hatchery at Stuart Lake, in the upper reaches of the Fraser River, 12 specimens of sockeye fingerlings from a natural retaining pond in the vicinity of the Stuart Lake hatchery were made available for examination of their stomach contents. The cladoceran *Alona affinis* was the only crustacean form found, but chironomid larvae and other insect fragments were common. This suggests again that the young sockeye will take for food whatever available crustacean forms are present in the plankton and will also make use of aquatic insect larvae and pupae, as well as whatever terrestrial insects fall into the water.

In Kamchatka lakes (Krogius and Krokhin, 1948, p. 8) the young fish in summer and winter (February-March) feed mainly on the copepod, *Cyclops*, but in the autumn and early winter, on the cladoceran, *Daphnia*. In Cultus Lake, however, (Ricker, 1937b, p. 454) *Cyclops* was found to be taken at all seasons, comprising 90% of the organisms consumed in winter and early spring but in summer only around 5%. *Daphnia* was the commonest food of summer and early autumn and was fairly common in the winter of 1932. *Bosmina* was taken most commonly by the small fingerlings in May and appeared again in good numbers in late autumn and to a lesser extent in winter. *Epischura* was never a common organism in the stomachs, usually representing around 1% of the total crustaceans. It appeared to be more intensively utilized in winter than in summer, compared to its abundance in the two seasons.

> "Stomach analyses of yearling sockeye taken from Lakelse Lake in 1944 show that their diets were made up of *Bosmina, Cyclops,* and *Epischura* in about equal proportions in July. In a portion of August the food utilized was predominantly *Epischura.* The 1948 results also show the stomach contents to be composed chiefly of this form throughout July. *Cyclops* was used to a lesser extent and toward the end of the month *Bosmina* was second in abundance to *Epischura*" (McMahon, MS, 1948b, p. 34).

In Fig. 29 the relative seasonal utilization of the important plankton crustacean forms in Cultus Lake is shown. Here the numbers of each species found in the stomachs of sockeye fingerlings during the year (as a percentage of the total number of Crustacea) are compared with the abundance of the four species in the lake at the same time, the latter values computed from the total vertical plankton net hauls. Ricker (1937b, p. 454) remarks that:

> "even making every allowance for the small size of some of the samples, it is evident that *Daphnia* is the organism most readily taken by the sockeye, except when the latter are very small (May and June). Next in order of utilization is *Bosmina,* which is also the form most often occurring in the youngest fish. The small *Cyclops,* although consumed in large quantities when Cladocera are scarce, does not command sufficient attention when they are commoner to be eaten in significant numbers."

From the evidence obtained Ricker (1937b, p. 454) observed that:

> "four factors can be postulated to account for the extent of predation of sockeye upon different plankters. *Abundance* of the plankton is naturally of prime importance. There exists for each species a lower limit of abundance beyond which it ceases to be of significant value. *Size* is important, as both with Cladocera and Copepoda the larger organism is taken more frequently than the smaller in relation to its abundance. *Habitat selection* appears the most probable explanation of the fact that *Epischura,* although as large as *Daphnia,* is much less intensively used in summer; at this time it inhabits the epilimmion principally, where the other crustaceans are relatively scarce [Fig. 27], and there is consequently little to attract foraging sockeye. A fourth factor must be postulated to account for the fact that *Bosmina* is more intensively exploited than *Cyclops,* although the two are of much the same size and occupy similar habitats. This might be because of a greater agility or lesser visibility on the part of *Cyclops,* different diurnal migrations, or simply a preference for *Bosmina* exhibited by the majority of the sockeye."

SELECTION OF FOOD BY YOUNG SOCKEYE

The evidence at hand indicates that young sockeye in fresh water feed primarily, if not almost exclusively, on crustacean plankton of the lake in which they are resident. It is not to be assumed, however, that they are merely passive feeders, consuming just whatever food organisms are filtered out of the water passing into the mouth and out through the gills and gill rakers, the latter being, in the sockeye, numerous, long and thin, in order to strain out plankton organisms more readily. On the contrary it is now generally conceded that an "act of capture," as Ricker (1937b, p. 460) has expressed it, is involved and that each plankter consumed is individually selected as a food item by the hungry fish.

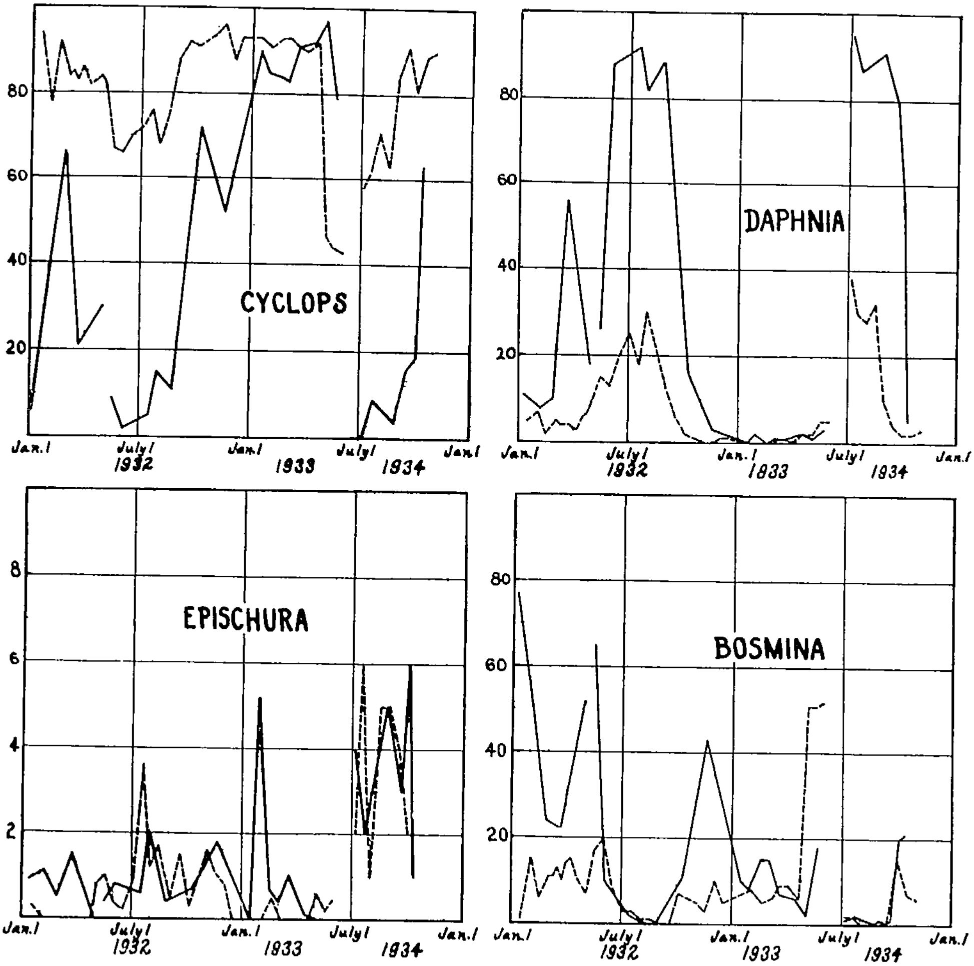

FIG. 29. Number of *Epischura, Cyclops, Bosmina,* and *Daphnia* in the stomachs of fingerling sockeye (solid line) and in the pelagic region of Cultus Lake (broken line), expressed as a percentage of the total number of adult crustacea present in each case. Note that the ordinate scale for *Epischura* is 10 times that of the others. (From Ricker, 1937b, p. 455.)

Whether, however, young sockeye are able to differentiate between different kinds of plankters and make a deliberate selection of a particular organism is still a somewhat debatable point. In the early sockeye food studies (Foerster, 1925) it had been expected that a relationship would be found between the size of young fish and size of plankters consumed, i.e., that the young free-feeding fry would feed on the smaller plankton forms—rotifers, copepod nauphii, *Bosmina,* etc.—and the larger fingerlings on the largest crustacean plankters. No such general relationship was observed. Nevertheless, the consumption of *Bosmina* by the small, caged fry (p. 167) in numbers greater than their representation naturally in the plankton, suggests a definite selection.

Ricker (1937b, p. 460) reports on a special study at Cultus Lake of the food preference among sockeye. The contents of the stomachs of 10 sockeye fingerlings, held in a cage at 10-m depth, were individually examined. The numbers of plankters observed were

	Stomach number									
	1	2	3	4	5	6	7	8	9	10
No. of *Daphnia*	132	26	61	97	33	8	70	72	80	69
No. of *Cyclops*	3	0	31	1	1	394	0	5	13	1

Ricker concludes that although:

> "the great preponderance, in most cases, of *Daphnia* over the equally abundant *Cyclops*, might possibly be explained on the basis of relative availability: the larger animal is doubtless more conspicuous, and might be less active and more easily caught, than the smaller. But for one sockeye to depart from such procedure so strikingly as did number 6, in selecting the smaller organism, calls for quite a different explanation. It is difficult to escape the conclusion that all the sockeye were well aware that two kinds of food were present, and that individual idiosyncrasy led one to prefer *Daphnia*, another to prefer *Cyclops*."

THE DAILY FOOD RATION OF YOUNG SOCKEYE

In his study of the food of young sockeye during their period of residence in Cultus Lake, Ricker (1937b) had to resort to the stomach contents of young sockeye found in the stomachs of predaceous fish which were caught in the lake by gill nets. In Fig. 30A the quantity of plankton in the stomachs of fingerling sockeye in Cultus Lake during 1932–33 is indicated graphically as the average net-weight of stomach contents per fish. Food consumption, low in May (0.3 mg), increased rapidly during the summer (31.1 mg in August), fell off in autumn and winter (21.6 mg in November to 6.1 mg in January) and, with the advent of spring, commenced to increase again (36 mg in April). The major fingerling growing season thus included July, August, and September. Growth, in the second season, commenced in April, just prior to or at the time of the usual seaward migration of the yearlings.

Consideration was given to the increasing size or bulk of the fish during the season, with which is associated greater food requirements and food capacity. Since the specimens examined were from predator stomachs they were seldom in condition to be weighed. Lengths could, however, often be taken, and since the weight of sockeye is roughly proportional to the cube of the length, the unit used was milligrams per cubic centimeter. The general trend is shown in Fig. 30B and indicates that the time of most active feeding, July–September, coincides with the season of most rapid growth, i.e., with higher water temperatures and greater food supply.

Stomach content measurements represent, of course, only the amount of food contained in the stomach at time of capture. If digestion of food is rapid there will be appreciably more organisms consumed during the 24-hr period. For Cultus Lake it is estimated (Ricker and Foerster, 1948, p. 200) that the food turnover, i.e., the ratio of the observed stomach contents to the daily ration, amounts, *most probably*,

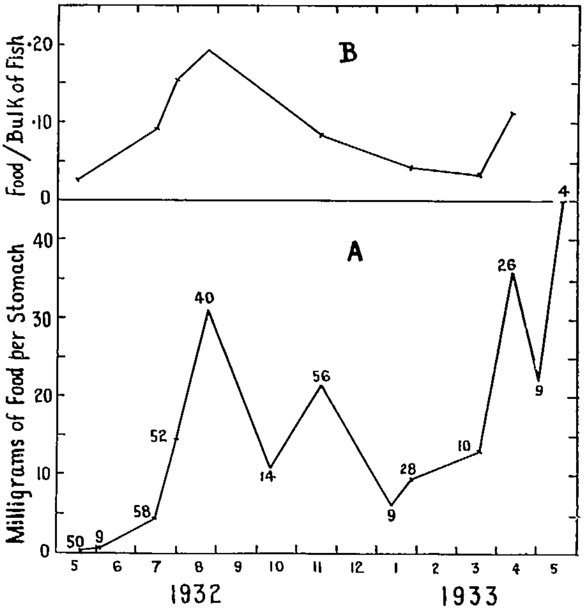

FIG. 30. A. Average quantity of food, in milligrams wet weight, found in stomachs of fingerling sockeye, 1932–33. Numbers indicate the number of stomachs examined. B. Quantity of food as above, divided by the cubes of the lengths of the fish, in milligrams per cubic centimetre. (From Ricker, 1937b, p. 453.)

to 4 times for the most active feeding period, May to September, 3 times for October and November, and 2 times for the winter months, November to March. With rising temperatures and greater activity of the fingerlings in the lake, the turnover will rise again in April to 3 times and to 4 times in May. Taking the turnover factor into consideration, the estimated daily ration of the young feeding sockeye rose from 1% of body weight in May to around 8% in late August and then declined gradually to 0.7% in February and March, increasing again as more active spring feeding of the fingerlings began. The overall yearly average daily ration approximated 3% of body weight.

For Kamchatka sockeye a quite comprehensive study was made of the daily ration of young sockeye resident in Lake Dalnee (Krogius and Krokhin, 1948; Krokhin, 1957b). Three methods were used:

1. Young sockeye in aquaria were fed known quantities of plankton organisms. After several hours the amount of plankton remaining unconsumed was determined. The difference between the quantity of plankton put in initially and the amount remaining uneaten represents the food ration at the temperatures prevailing in the aquaria. The daily (24-hr) ration per sockeye, according to size of fish or time of year, was then calculated.

2. By ascertaining, from stomach content analysis, the average amount of food found in the stomachs of young sockeye, and having knowledge of the rate of digestion of the food (see Fig. 31) at the prevailing temperatures, the daily consumption per sockeye could be computed. According to Bajkov (1936), the originator of this method,

> "if all the food passes from the stomach to intestine during a period of twenty-four hours and if it has been determined that the fish in question is feeding both day and night, the average stomach content will represent the daily consumption of fish. In the case of more rapid or slower digestion, the daily consumption could be calculated by means of the following formula:
>
> $$D = A \frac{24}{n}, \text{ where}$$
>
> D = the daily consumption during the time of the experiment
> A = the average amount of food in the stomach at the time of the experiment
> n = the number of hours necessary for passing all the food from stomach into intestine (rate of digestion).
>
> The exactness of such determination will depend on the number of specimens examined."

3. The oxygen consumed by the young fish in a unit time was calculated and this value was converted into its equivalent caloric quantity of food organisms. The rate of oxygen consumption is directly correlated with the temperature of the water in which the fish are held (Fig. 32). By ascertaining, then, the average temperature of the water in which the fish reside, the 0_2 consumption at such temperature, the caloric values of the plankton crustacea, *Cyclops* and *Daphnia*, upon which the young fish feed, and the curve of increase in weight of the young fish, the average daily ration at any time of year in the lake could be computed. The conversion factors adopted (see Krokhin, 1957b, p. 101) were: 1 g of oxygen absorbed = 3.38 cal; caloric value of 1 g dry wt of copepods = 4908 cal.

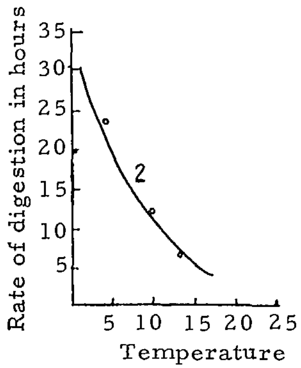

FIG. 31. Rate of digestion, in hours, in young sockeye at Lake Dalnee at different temperatures. (From Krogius and Krokhin, 1948, fig. 3.)

All three methods of determining the daily food ration gave similar results. The third method, termed the respiration method (Krokhin, 1957b, p. 109), was the preferred one. It required less material, involved less work, and gave more stable and reliable results. By using it, the average daily (24-hr) ration for Lake Dalnee sockeye was cumputed for each month of lake residence, expressed as the dry weight

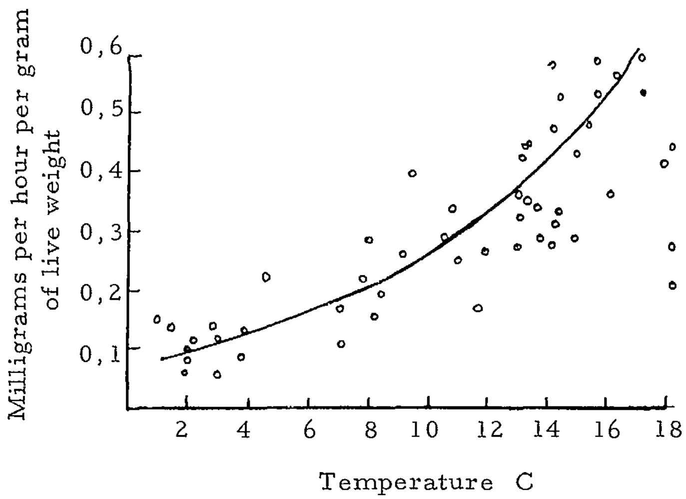

FIG. 32. Relationship of oxygen consumption by Lake Dalnee sockeye to temperature (milligrams per hour per one gram live weight). (From Krogius and Krokhin, 1948, fig. 4.)

of copepods and as a percentage of the body weight of the young fish, as given in Tables 38 and 39.

From the tabulated data and Fig. 33 it is seen that feeding of the young sockeye in Lake Dalnee commenced in May and continued through until May of the succeeding year, at which time they set out on their seaward migration either as yearlings or 2-year-olds. The most intensive period of feeding was midsummer (August–September) when the daily food ration was roughly 45 mg dry wt for fingerlings and 170 mg dry wt for fish in their 2nd year. During the winter the daily ration drops to 17–20 mg and 60–70 mg, respectively. The mean annual daily ration for fingerlings (23–25 mg) and for fish in their 2nd year (90 mg) constitutes 3% of the average annual weight of the young fish, assuming that the water content in copepods, for calculation of the wet weight of the ration, is 88% of the wet weight. As indicated in Fig. 34, the fingerlings—on the basis of percentage of body weight—fed much more intensively up to September than the young in their 2nd year. This is particularly apparent for the small fingerlings or advanced fry in May and June. From November on until migration time in the following April and May, food consumption is approximately similar for both age-groups. During the year in the lake the young sockeye consumed 8.5–9 times as much food, in weight, as their final weight.

To summarize, water temperature and size are important factors influencing the daily ration of young sockeye, so it is difficult to compare results obtained in different regions, i.e., Cultus Lake, British Columbia, and Lake Dalnee, Kamchatka. Nevertheless, on the basis of the food ration as a percentage of body weight, the correspondence in results is quite close, namely, from around 1% of the body weight in winter to 8–10% in midsummer or a mean daily ration over the year of 3% of

TABLE 38. The daily rations of fingerling sockeye during the first year in Lake Dalnee (from Krokhin, 1957b).

	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Avg for year
1937–38													
Avg wt (*g*)	0.4	0.9	2.3	4.3	6.3	8.3	9.5	9.9	10.0	10.0	10.0	10.0	6.83
Avg temp (*C*)	–	–	9.3	10.9	11.0	8.3	4.4	3.1	2.5	2.4	2.3	2.4	5.4
Daily ration (*mg dry wt of copepods*)	–	–	26.1	39.0	48.2	42.0	25.4	18.5	17.0	16.9	16.7	17.4	23.4
Daily ration (*% body wt of young*)	–	–	10.6	7.6	6.4	4.2	2.2	1.6	1.7	1.7	1.4	1.4	2.9
1938–39													
Avg temp (*C*)	2.6	5.6	11.0	13.7	11.2	7.5	4.3	3.1	3.1	3.1	3.1	3.1	5.96
Daily ration (*mg dry wt of copepods*)	3.1	9.9	28.8	45.6	48.8	39.5	26.5	19.6	18.6	18.6	18.6	20.0	24.9
Daily ration (*% body wt of young*)	6.4	9.2	10.4	11.3	6.5	4.0	2.1	1.7	1.5	1.5	1.5	1.7	3.0
1939													
Avg temp (*C*)	3.2	7.5	12.9	–	–	–	–	–	–	–	–	–	–
Daily ration (*mg dry wt of copepods*)	1.8	13.9	32.4	–	–	–	–	–	–	–	–	–	–
Daily ration (*% body wt of young*)	3.7	12.9	11.7	–	–	–	–	–	–	–	–	–	–
Consumption of food per month (*mg dry wt of copepods*)													
1937–38	–	–	810	1210	1450	1300	760	570	530	470	520	520	8530[a]
1938–39	90	300	890	1440	1470	1220	790	610	580	520	580	600	9090
1939	60	420	1000	–	–	–	–	–	–	–	–	–	–

[a] For the calculation of consumption in 1937–38 for May and June, the data of the second series (90 + 300) were used.

TABLE 39. The daily rations of young sockeye during the second year in Lake Dalnee (from Krokhin, 1957b).

	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Avg for year
1937–38													
Avg wt (*g*)	10.3	11.3	14.2	19.8	25.8	31.2	34.3	35.4	35.8	36.0	36.0	36.0	27.2
Avg temp (*C*)	–	–	9.3	10.9	11.0	8.3	4.4	3.1	2.5	2.4	2.3	2.4	5.4
Daily ration (*mg dry wt of copepods*)	–	–	96.0	143.5	175.5	130.0	87.8	72.5	62.5	60.8	59.8	59.9	86.2
Daily ration (*% body wt of young*)	–	–	5.6	6.0	5.7	4.0	2.1	1.7	1.5	1.4	1.4	1.4	2.7
1938–39													
Avg temp (*C*)	2.6	5.6	11.0	13.7	11.2	7.5	4.3	3.1	3.1	3.1	3.1	3.1	5.96
Daily ration (*mg dry wt of copepods*)	22.7	42.9	108.0	181.6	180.0	139.8	87.6	70.0	67.3	67.3	67.3	67.7	92.0
Daily ration (*% body wt of young*)	1.8	3.1	6.3	7.6	5.8	3.7	2.2	1.6	1.6	1.6	1.6	1.6	2.9
1939													
Avg temp (*C*)	3.2	7.5	12.9	–	–	–	–	–	–	–	–	–	–
Daily ration (*mg dry wt of copepods*)	23.3	58.7	130.7	–	–	–	–	–	–	–	–	–	–
Daily ration (*% body wt of young*)	1.9	4.3	7.7	–	–	–	–	–	–	–	–	–	–
Consumption of food per month (*mg dry wt of copepods*)													
1937–38	–	–	2970	4440	5260	4650	2640	2250	1940	1700	1860	1800	31500[a]
1938–39	700	1290	3350	5630	5400	4300	2630	2170	2080	1880	2080	2030	33540
1939	720	1760	4050	–	–	–	–	–	–	–	–	–	–

[a] For the calculation of consumption in 1937–38 for May and June, the data of the second series (700 + 1290) were utilized.

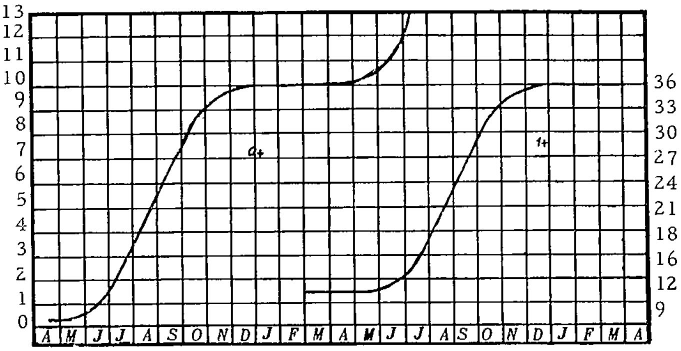

FIG. 33. Increase in weight (milligrams) of young sockeye in Lake Dalnee. The curve on the left is that of the growth of fingerlings, that on the right, of yearlings. The latter is related to the vertical scale on the right. Both curves are a graphic average presentation of the data for 1937–38. (From Krokhin, 1957b, fig. 3.)

body weight. It is also apparent that, when reduced to dry weight of Crustacea, the Cultus Lake young sockeye consumed roughly the same amount of crustacean food as the young sockeye in Lake Dalnee when the actual size of the fish is taken into account.

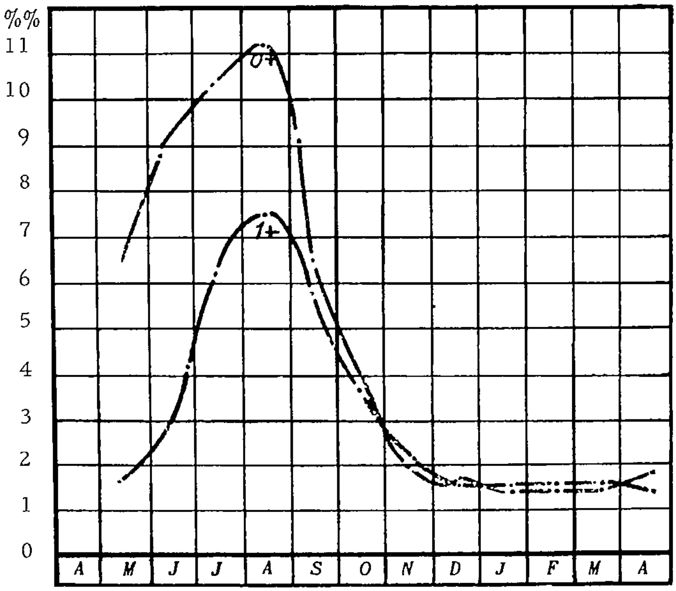

FIG. 34. The daily food rations of young sockeye in percentage of body weight, the upper curve representing the fingerlings, the lower one, the over-yearlings. (From Krokhin, 1957b, fig. 4.)

Chapter 8. Limnological and biological conditions in sockeye lakes

Since young sockeye generally spend 1 year—in some areas 2 or more—in a lake and since during this period mortality is greatest it is of interest to know what conditions—physical, chemical, biological—prevail in sockeye-producing lakes and how these affect the behaviour and the survival of the young fish.

Temperature conditions prevailing during the year determine to a certain degree where the young fish tend to congregate; they influence the production of plankton food; they are directly and intimately related to the growth and development of the fish.

Transparency of the water influences light penetration and photosynthesis and thus the development of phytoplankton in the water; it may affect the ability of young sockeye to see and capture their food organisms.

Chemical conditions play a varied role. As far as the dissolved oxygen and carbon dioxide content are concerned they may limit the penetration and dispersion of fish into the lower strata of deep lakes and, in rare cases, may affect the behaviour of young sockeye elsewhere; the amounts of nitrates, phosphates, and silicates have a direct influence on the production of plankton.

Plankton abundance is, of course, of paramount importance since the constituents of the plankton populations are the main food of the young fish. In addition to its actual quantity or biomass, the qualitative nature of the plankton may be of greater significance than generally recognized. The availability of the right organisms, chiefly in regard to their size, for the young fish, as they develop, may be extremely important.

TEMPERATURE CONDITIONS IN LAKES

ANNUAL TEMPERATURE REGIME

Generally speaking, in most lakes there is a definite pattern of seasonal changes during the year. As outlined by Ricker (1937a, p. 383) these are

1. Vernal circulation

(a) A complete circulation of water—sometimes referred to as the spring overturn—which lasts from the time that homothermy is established, at the end of the preceding winter's partial stagnation, to its end when a temperature gradient of at least 0.005 C per metre is produced by the warming of the upper waters.

(b) Partial circulation—from the end of homothermy to the time when an impenetrable stratified layer, so far as water movement upward is concerned, is established.

2. Summer stagnation

(a) Complete stagnation (i.e., no vertical upward or downward movement of water through the thermocline), accompanied by a warming of the epilimnion. It occurs from the time of establishment of thermal stratification sufficient to stop all circulation into the hypolimnion and continues until the epilimnial temperature reaches a maximum.

(b) Complete stagnation, accompanied by a cooling of the epilimnion. It lasts until there is some penetration of the thermocline by currents carrying warm water into the hypolimnion.

(c) Partial stagnation, which lasts until autumn homothermy is again established and circulation throughout the lake is complete.

3. Autumnal circulation

(a) Complete circulation of water, sometimes referred to as the fall or autumn overturn, which lasts for the duration of homothermy.

(b) Partial circulation, which extends from the end of homothermy to the formation of the ice cover.

4. Winter stagnation

(a) Complete stagnation, with falling temperature, lasting to and during the time of minimum temperature.

(b) Partial stagnation, with rising temperature, which extends from the beginning of warming (usually before the ice goes) to the establishment of homothermy (usually at the time of ice breakup or shortly afterward).

Thus, during the summer months stratification of the lake water occurs, represented by an upper and warm epilimnion, a deep and cold hypolimnion, and an intermediate thermocline in which the temperature change downward is rapid (defined as 1 C/m or more). During the winter, in areas where air temperatures are low and the lakes freeze over, a winter stratification may develop with the epilimnion cold and the hypolimnion warmer.

Summer epilimnial maximum temperatures, like winter minima, are a direct reflection of weather conditions and are accordingly quite variable. Summer hypolimnial temperatures, on the other hand, are, in large part, determined by the temperature prevailing in the lake when it was in the state of vernal homothermy and partial circulation, just prior to formation of the thermocline; the winter hypolimnial temperature is influenced by the temperature of the lake during autumn homothermy and subsequent partial circulation, i.e., the fall overturn.

TEMPERATURE CONDITIONS IN FIVE NORTH AMERICAN SOCKEYE LAKES

In order to depict the differences which occur in sockeye-producing lakes according to quite different climatic, morphological, and hydrological conditions, the

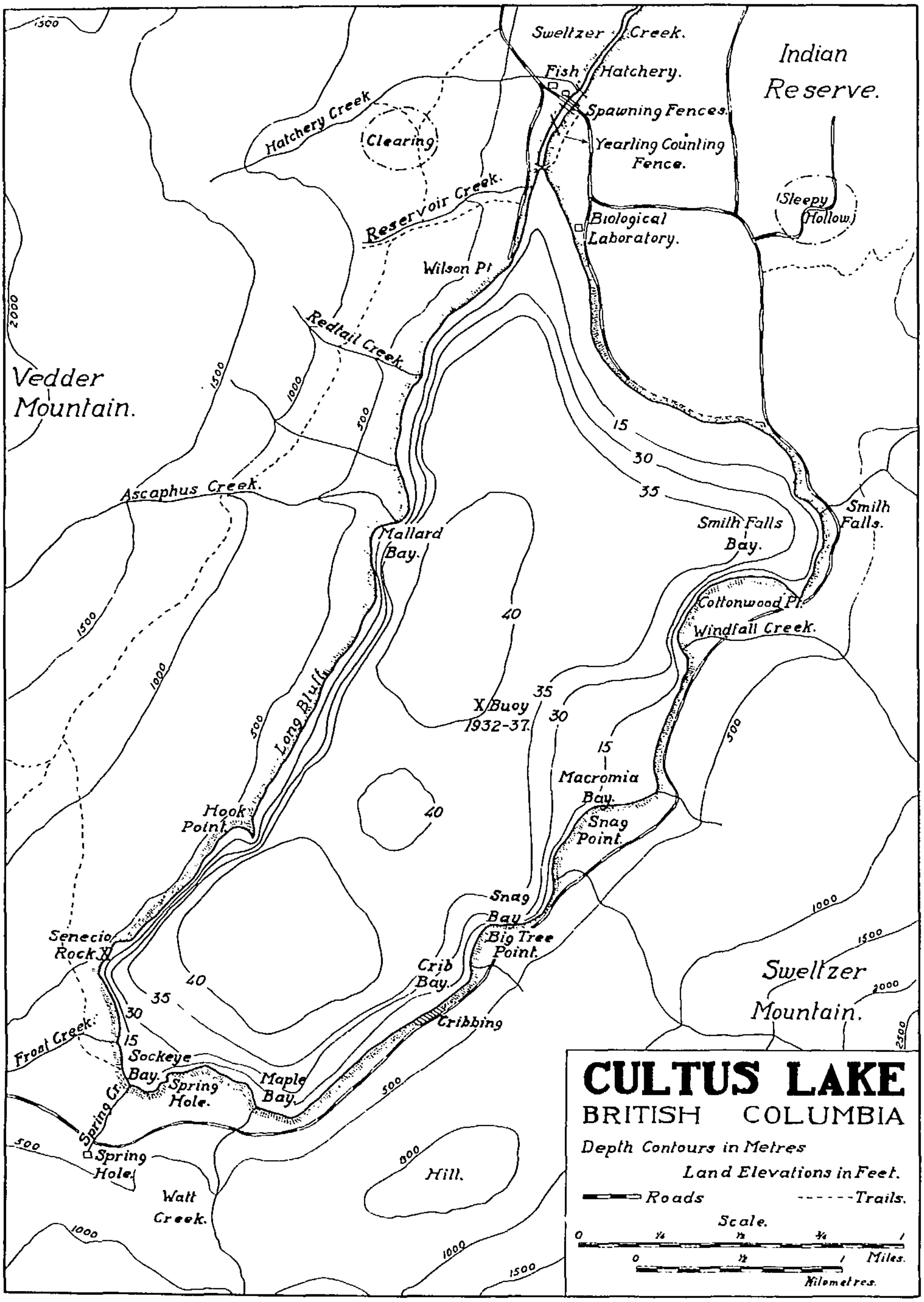

FIG. 35. Map of Cultus Lake, British Columbia. Depth contours in metres. X = central sampling station. Area—626 ha or 450 acres; vol—201 × 10^6 m^3; max depth—42 m. (From Ricker, 1937a, p. 365.)

situations with regard to stratification of water and the development of epilimnion, thermocline, and hypolimnion in four lakes in British Columbia and one in Alaska are briefly reviewed.

CULTUS LAKE

Cultus Lake (Fig. 35), tributary to the lower Fraser River (Fig. 6) approximately 70 miles inland from the coast, is situated in the southwestern part of British Columbia. The climate is mild and moist. In the winters, although periods of cold, freezing weather (the temperature dropping to as low as −15 C or +5 F), with strong north or northeast winds may occur on one or more occasions each year, the weather is usually calm, cloudy, and rainy. The lake rarely freezes over, although ice may occur around the margins. The mean rainfall is around 157 cm (62 inches), the greater part falling from October to February. During spring and autumn cloudy and clear periods alternate, the proportions varying from year to year. Summers, June–September, are usually rainless and warm, the temperatures on bright days occasionally reaching 38 C (100 F) but usually not exceeding 30 C (86 F).

The lake occupies a deep depression with maximum depth of 42 m, is oblong

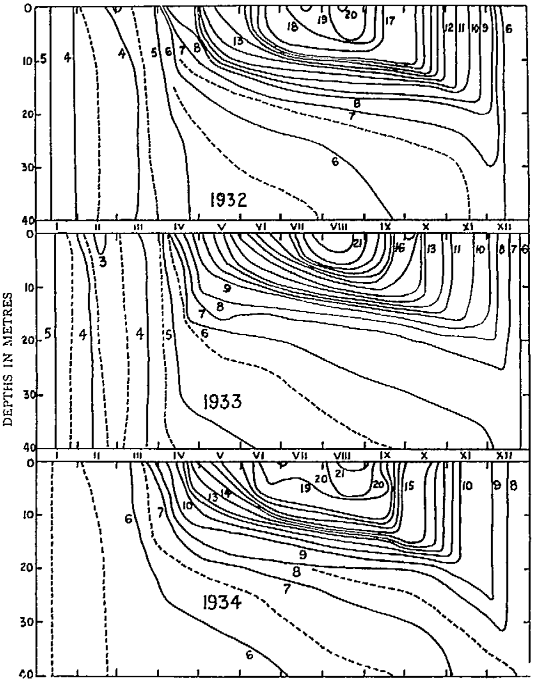

FIG. 36. Seasonal isotherms (degrees Centigrade) for Cultus Lake in 1932, 1933, and 1934, based upon temperatures taken at a central station, shown in Fig. 35. (From Ricker, 1937a, p. 369.)

in shape, 4.8 km long by 1.3 km wide (3 by $\frac{4}{5}$ mile), with a surface area of 626 ha (1550 acres) and volume of 201 million m^3 (163,000 acre-feet). There is a very limited amount of shallow water, mostly at the northern end. About three-quarters of the lake is 30 m (98 ft) deep or deeper. With a mean annual precipitation of 157 cm over a watershed of 83 km^2, a total of around 130 million m^3 of water must be removed anually by runoff and evaporation. The lake outflow varies from about $\frac{1}{2}$ m^3/sec in late summer to 25 under extreme flood conditions in winter or spring.

Lake temperature conditions for 1932, 1933, and 1934 (Ricker, 1937a) are shown in Fig. 36. Warming of the water and attendant temperature stratification commences in April, the point of maximum gradient being at first at a considerable depth (Krokhin, 1960b). By late May a thermocline in the strict sense (gradient more than 1 C/m) appears near the 10-m level, marking off the rapidly warming epilimnion from the deep-water hypolimnion. At first quite narrow in depth, this thermocline grows thicker throughout June and July, as the epilimnial waters increase in temperature, to extend from about 6 to 14 m. Not until the latter half of August, when the epilimnial temperature has passed its maximum of 20–22 C, does the thermocline begin to sink. By the end of September the epilimnion has reached the 10-m level, early in November the 15-m level and early in December it has dropped to 20 m and occupies roughly the upper half of the lake. By this time its temperature has decreased to within a few degrees of that of the bottom water and some mixing into the hypolimnion has begun; the first steady strong wind then causes a complete mixing of the lake water, the autumn overturn. During the winter complete circulation usually continues, minimum temperatures being 2.5–5.3 C; but in the more severe winters when the water has cooled below 3.5 C, one or more short periods of winter partial circulation may occur, marked by an inverse stratification, i.e., warmer at depths than at the surface. Winter stagnation occurs in the rare years when a complete turnover lasts for a week or more—as happened in March of 1937. Summer epilimnial temperatures become quite high, the temperatures at 5 m in 1932 being 19.4 C (66.9 F), in 1933—20.5 C (68.9 F), in 1934—20.9 C (70 F). In 1936, they rose to 21.4 C (70.5 F).

LAKELSE LAKE

At Lakelse Lake (Fig. 37), tributary to the lower Skeena (see Fig. 7) and approximately 70 miles from the coast, climatic conditions are quite different. Air temperatures (see Brett, 1950) range from around 38 C (100 F) in summer to around –18 C (0 F) in winter. The lake freezes over during the winter and snowfall is relatively heavy. Average precipitation per year is around 46.85 inches (119 cm), with an average of 2 inches (5.1 cm) per month from May to August and a peak in November of 7.48 inches (19.0 cm).

The lake, roughly 8.7 km (5.4 miles) in length by 1.1–2.4 km (0.7–1.5 miles) in width, has an area of 1347 ha or 3328 acres and a volume of 108 million m^3. Its maximum depth is 32.2 m (98 ft) near the northern end but the southern half is quite shallow, giving a mean overall depth of only 7.8 m (24 ft). Almost 80% of the lake is contained in the 0–10 m stratum.

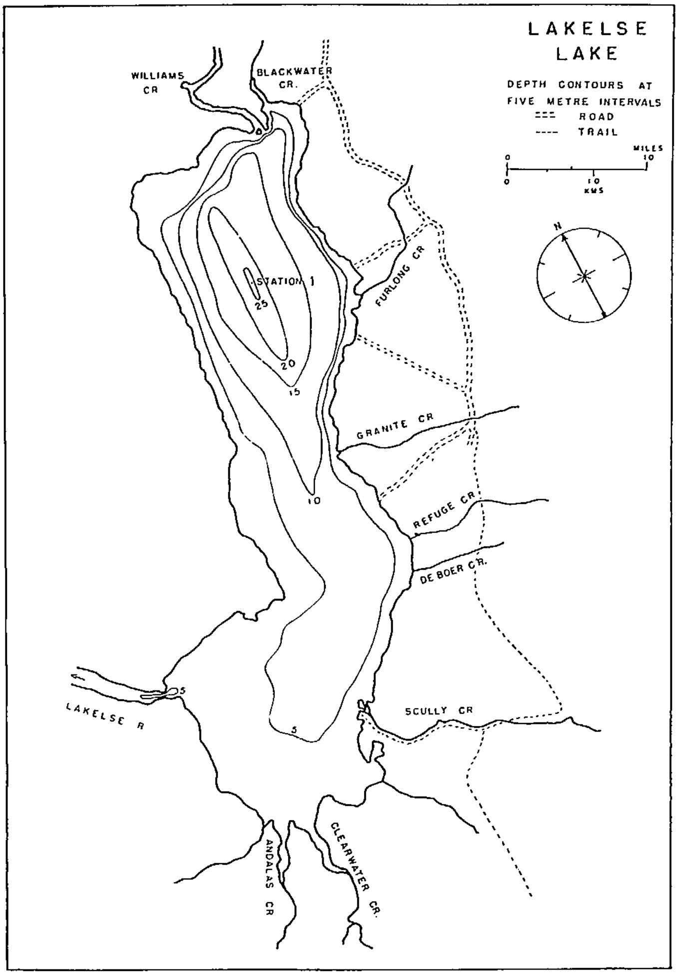

FIG. 37. Map of Lakelse Lake, British Columbia, showing bottom configuration. Area—1347 ha or 3328 acres; vol—108 × 10^6 m^3; max depth—32.2 m. (From Brett, 1950, p. 87.)

The temperature regime in Lakelse Lake for 2 years is indicated in Fig. 38, as revealed by temperature readings taken at 2-week intervals at a central station (Station 1, Fig. 37) with a standardized Negretti-Zambra deep-sea reversing thermometer. One unique feature (Brett, 1950, p. 90) is that:

> "during the summer intense winds, sweeping up the open Kitimat Arm of the coast and through the Lakelse lake valley, often disrupt the thermal layering of the lake resulting in marked fluctuations in the presence, absence or position of one or more true thermoclines. The very deepest portion of the lake, however, remains at least partially out of circulation. Lakelse lake . . . might be described best as a lake which undergoes thermal stratification of varying degrees, sometimes exceeding 1°C per metre, with an upper zone of water which tends to circulate

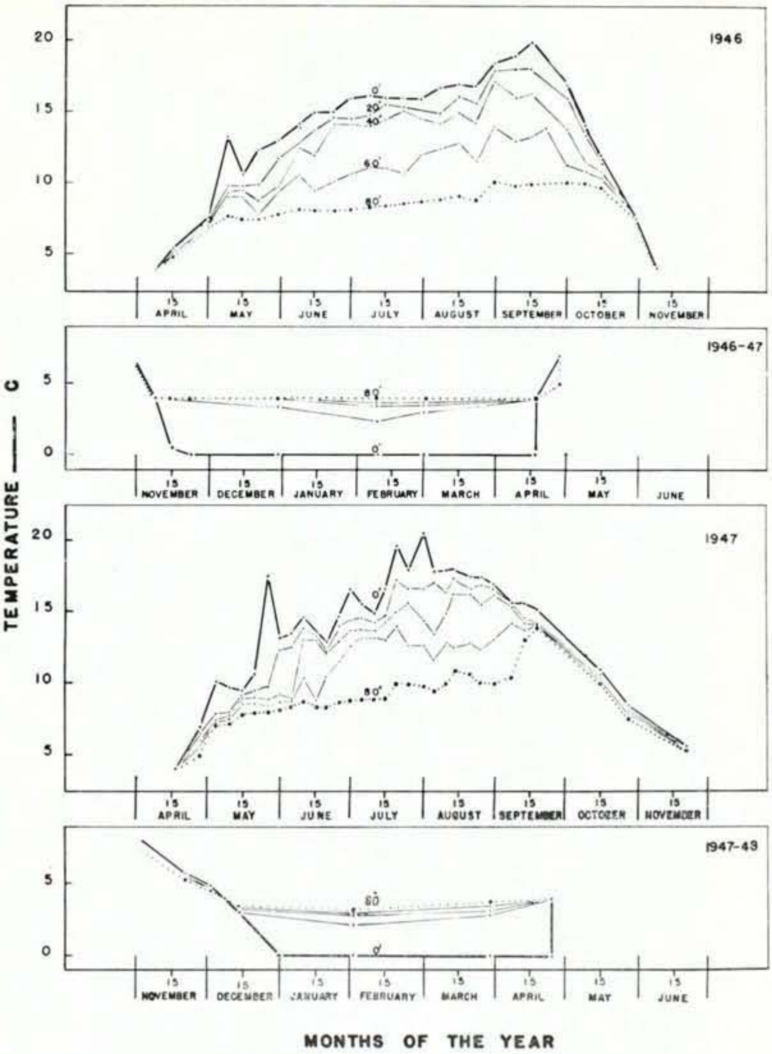

FIG. 38. Temperature variations, Lakelse Lake, at depths of 20-ft intervals, station 1, from April 1946 to April 1948. (From Brett, 1950, p. 92.)

as a separate body and which becomes more distinct as a maximum in water temperature is approached. This zone of water usually varies from 10 to 20 metres in depth and yet may be dispersed within a few hours by wind action."

Following a period of winter stagnation (late November or December to April) with inverse thermal stratification, the ice-cover breaks up and a spring overturn occurs. This may be of quite short duration, depending upon the extent of increase in air temperature and the amount of wind action. Thermal stratification develops early, its depth influenced by the intensity and duration of the winds. Temperatures throughout the whole lake rise as summer advances, reaching a maximum in August of around 20 C (68 F) at the surface and 11 C (52 F) at the bottom. During September the lake begins to cool and by around the end of October uniform temperatures prevail throughout and the autumn overturn commences. With the approach of winter an inverse stratification occurs culminating in the freezing of the lake when wind action can no longer induce any circulation.

A particular feature of Lakelse Lake is its extensive area of shallow water with temperatures rising to as high as 20 C (68 F). While restricting the inhabitable zone for young sockeye the presence of this vast littoral area promotes the growth of aquatic plants and plankton, resulting in a greater unit abundance of food and a greater capacity for supporting larger populations of young fish.

PORT JOHN LAKE

Port John Lake (Fig. 39) (see Robertson, 1954) is a small lake located on King Island on the central British Columbia coast (Fig. 2). Of small area (91 ha or 225 acres) it is relatively deep, 49 m or 160 ft, and has a volume of 22.8 × 10^6 m^3. Over 60% of the lake is 20 m or less in depth, however. Annual precipitation throughout the drainage basin of 3.6 square miles (9.3 sq km) is 116 inches (295.5 cm) and around 72% of the lake's water is replaced during the course of the

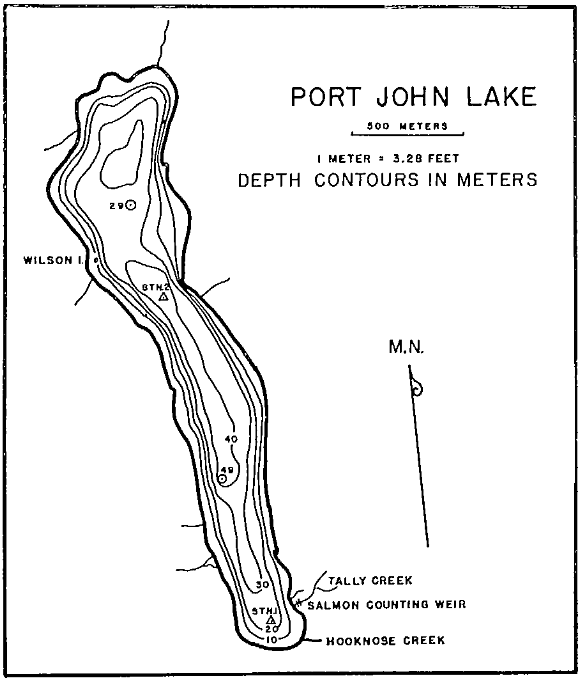

FIG. 39. Map of Port John Lake, British Columbia. Area—91 ha or 225 acres; vol—228.3 × 10^6 m^3; max depth—49.0 m. (From Robertson, 1954, fig. 2.)

year. Because of its location between high hills it is exposed to the sun for only a limited period of the day (about 8 hr in midsummer) and it is exposed to wind action from the north and south.

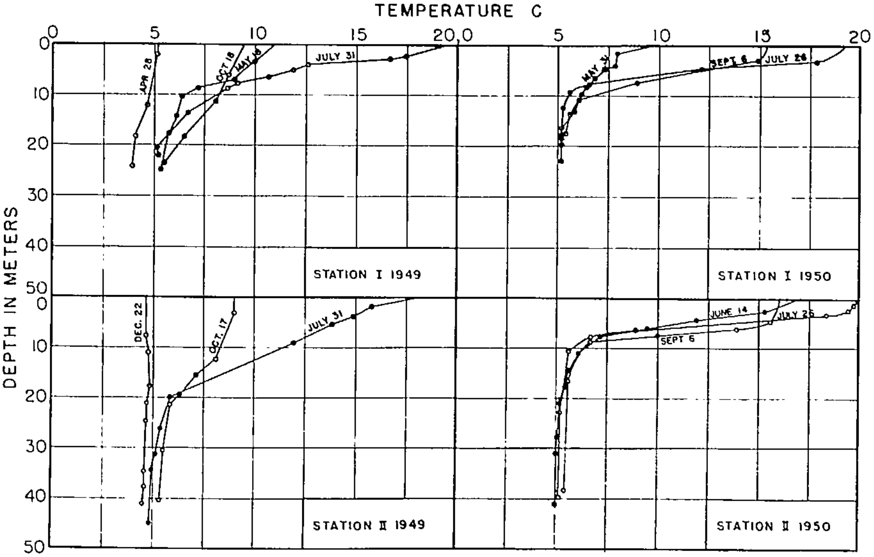

FIG. 40. Selected temperature curves for Port John Lake in 1949, 1950. (From Robertson, 1954, fig. 3.)

Temperature conditions are indicated in Fig. 40, as taken with a deep-sea reversing thermometer. While in some winters ice may cover the lake, as observed in 1949 and 1950 from January to mid-March, no marked inverse stratification was observed. Following the spring overturn in March–April, the surface waters quickly warm up and by May a thermocline appears. As Robertson (1954, p. 629) remarks "the proximity of the thermocline to the surface and a persistent stratification from May to October are characteristic of the vertical temperature distribution." Fluctuations in level and thickness of the thermocline occur but the typical midsummer thermal stratification is reported as:

Stratum	Temperature	Depth	Vol	Vol
	(*C*)	(*m*)	($m^3 \times 10^6$)	(%)
Epilimnion	19.7–18.2	0–3	2.43	10.6
Thermocline	18.2–6.5	3–8	4.04	17.8
Hypolimnion	6.5–5.1	8–49	16.33	71.6

OWIKENO LAKE

Owikeno Lake, situated at the head of Rivers Inlet in the central British Columbia coastal area (Fig. 2), is included in this review of sockeye lakes because it is characterized by high production of sockeye in spite of certain rather unusual

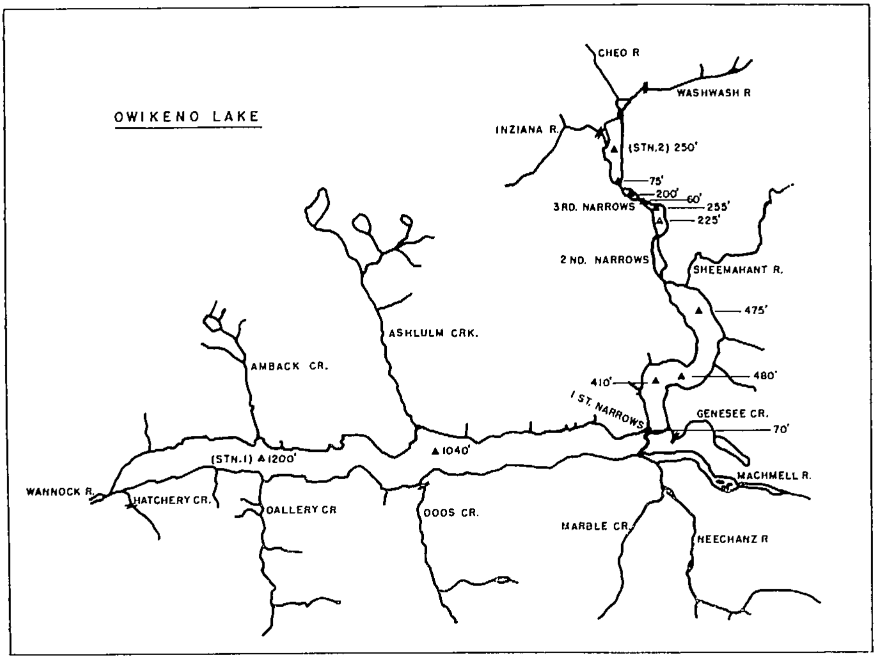

FIG. 41. Map of Owikeno Lake, British Columbia, at the head of Rivers Inlet. Area —8806 ha or 34 square miles; max depth at station 1—366 m. (From Foskett, 1958, fig. 1.)

limnological conditions. The lake consists (Foskett, 1958) of a chain of four basins (Fig. 41), separated by relatively shallow "narrows." Its area is recorded as 34 square miles (8806 ha), the depth as: basin 1—366 m (1200 ft), basin 2—146 m (480 ft), basin 3—78 m (255 ft) and basin 4—76 m (250 ft). The water of the two lower basins is heavily silted while in the upper two the water is relatively clear. The lake above First Narrows is reported to freeze over every winter but the main basin is thought to remain open, probably because of high prevailing winds.

No comprehensive limnological study has been made of the lake but a number of scattered temperature observations are available (Foskett, 1958). These indicate that (1) in basin 1, on May 27, 1956, the lake was still practically homothermal, with temperatures varying from 3.0 C (37.3 F) at a depth of 49 m (150 ft) to 3.3 C (38.0 F) at 6.5 m (20 ft) and 4.7 C (40.5 F) at the surface; (2) in September and October, 1952, well-developed thermoclines occurred at around 33 m (100 ft) in the upper basins, while in basin 1 a thicker thermocline, though with not so sharp a gradient, was centred at about 56 m (170 ft).

In Fig. 42, temperature profiles, as reported by Foskett (1958, p. 871), are shown to reveal the deep hypolimnion, the relative position of the relatively flat and narrow thermocline, except in basin 1 where wind action may have had a marked effect, and the varying depth of the epilimnion. As remarked earlier, the surface

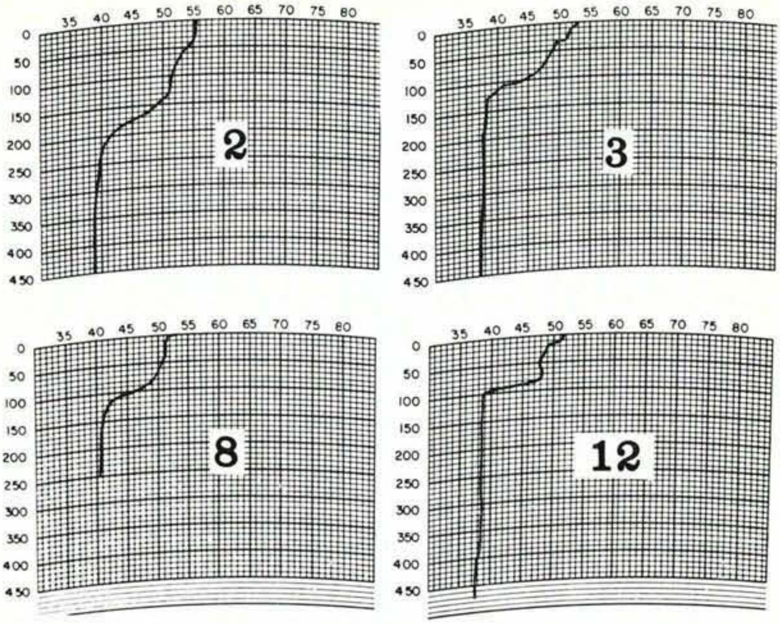

FIG. 42. Bathythermograph tracings taken from Owikeno Lake. Depth scale in feet; temperatures in degrees Fahrenheit. Tracing No. 2, Sept. 2, 1952, Basin 1 at Station 1: between Ambach and Dallery creeks. Bottom at 1200 ft. Tracing No. 3, Sept. 11, 1952, Basin 2 in the bend north of Genesee Creek. Bottom at 480 ft. Tracing No. 8, Sept. 19, 1952, Basin 4 at Station 2. Bottom at 250 ft. Tracing No. 12, Sept. 20, 1952, Basin 2 in northern part. Bottom at 475 ft. (From Foskett, 1958, fig. 2.)

temperatures of Owikeno Lake, ranging in summer and early autumn from 11 to 14 C (52–57 F), are very low and, in combination with the glacial silt-laden water, seem not to be good plankton-producing waters, and hence would not be expected to be exceptionally good for producing sockeye. Yet, as Fockett (1958, p. 867) notes, "Rivers Inlet sockeye production is almost the best in British Columbia, in relation to the size of the watershed which maintains it." It is true, however, that the smolts produced from Owikeno Lake are of unusually small size.

KARLUK LAKE

By way of comparison, the conditions existing in Karluk Lake, Alaska, another excellent sockeye-producing area, may be outlined. Situated on Kodiak Island, on the western margins of the Gulf of Alaska, Karluk Lake (Juday et al., 1932) is long (19.6 km or 12.2 miles), narrow (3.1 km or 2 miles at greatest width) and straight-sided (Fig. 43). Its area is 39.5 km^2 (15.2 square miles, 9728 acres or 3937 ha) and its maximum depth 126 m (413 ft). The volume of the lake is 1920×10^6 m^3,

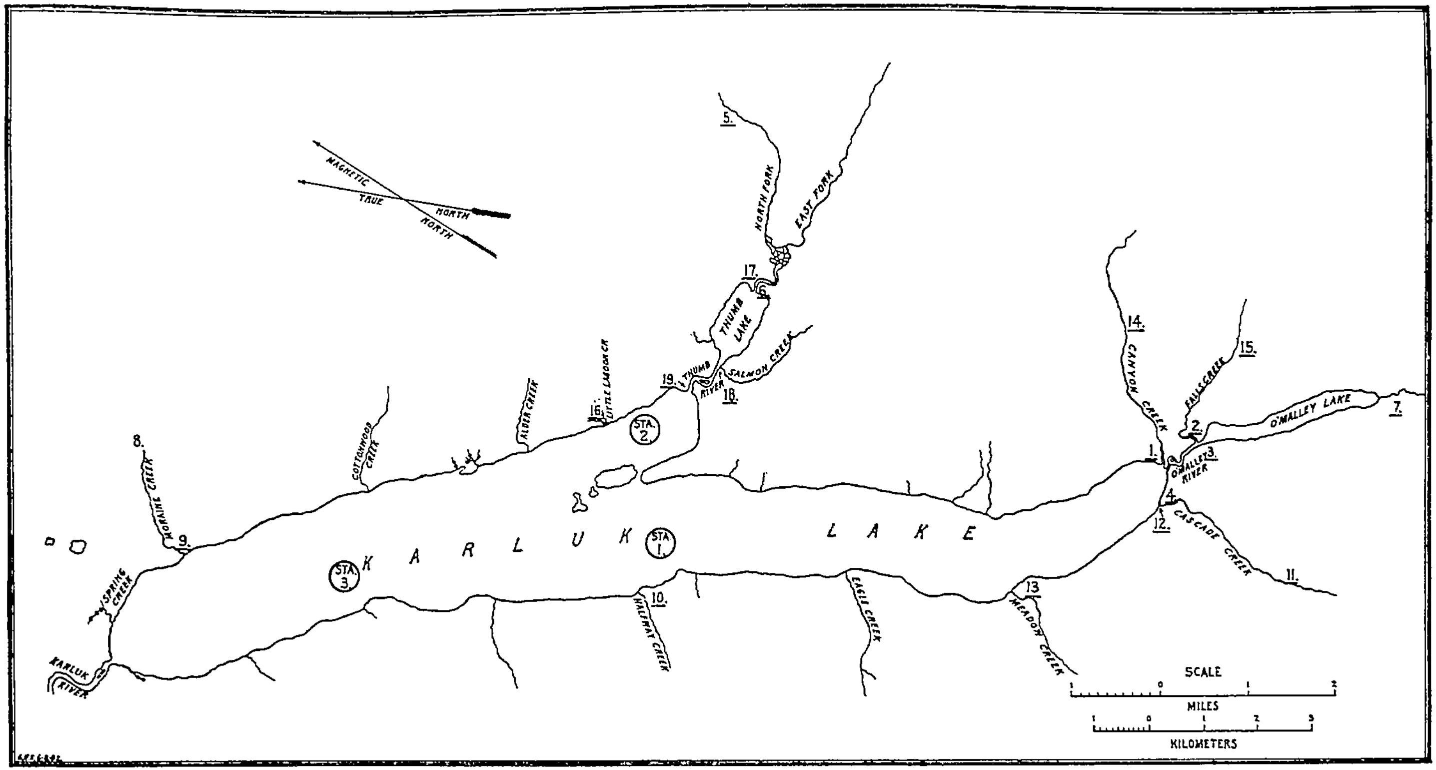

FIG. 43. Map of Karluk Lake, Kodiak Island, Alaska (from Juday et al., 1932, p. 409). Area—3937 ha or 9728 acres, 15.2 square miles. Vol—1920 × 10^6 m^3. Max depth—128 m; mean depth—48.6 m.

with 52% contained in the 0–20 m stratum. The lake freezes over in the winter (mid-December to April).

As revealed by the temperature conditions in the upper 30 m during the summer months (Fig. 44), a thermocline may occur in some years, e.g., 1926 and 1929, while in others, such as 1928, 1930, only a gradual rise in temperature with decreasing depth is indicated. In 1926, the three thermal strata (epilimnion, 0–8 m; thermocline, 8–15 m; hypolimnion, 15 m-bottom) were well marked. Since it is noted that during the winter of 1925–26 the lake did not freeze over, one wonders if the degree of

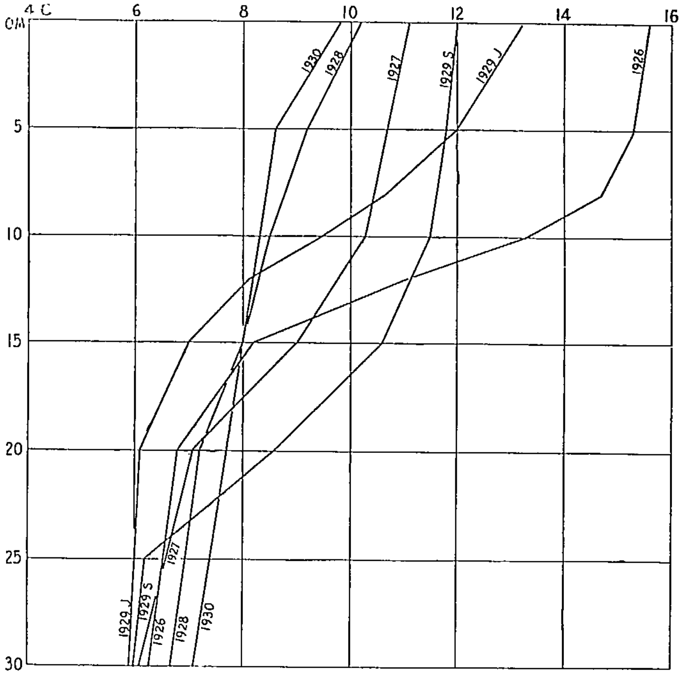

FIG. 44. Summer temperatures (in degrees Centigrade) of the upper 30 m of Karluk Lake, 1926–30 inclusive. (From Juday et al., 1932, p. 412.)

summer stratification may not be related to the mildness of the winter period. Appearance of a distinct epilimnion and a real thermocline may depend largely upon a rapid and appreciable warming up of the lake's surface waters, since the surface temperature in August, 1926, was the highest recorded, namely 15.6 C (60.1 F). It is of interest to note that, in early July, the temperatures at 20 m are around 6 C (43 F) or higher. It may well be that in general the young feeding sockeye are to be found principally in this upper 20 or 25 m, together with the bulk of the crustacean plankters.

EFFECT OF TEMPERATURE ON YOUNG SOCKEYE

It has been intimated earlier (p. 161), in discussing the vertical distribution of young sockeye in a lake, that they are usually found in the epilimnial zone, or, for Cultus Lake, in the thermocline and adjacent strips of the epilimnion or hypolimnion. Tests conducted to ascertain the effect of temperature on young sockeye, by retaining them in tanks at different temperature levels (Donaldson and Foster, 1941) and by field observations elsewhere, revealed that "young sockeye salmon are very selective in their choice of water of uniform temperature, choosing that water near the thermocline in preference to warmer surface water or colder water in the depths of the lakes." Specimens held at temperatures near 78 F (25.6 C) refused to eat and the respiration rate became excessive. When the temperature was reduced to 70 F (21.1 C) they were able to make a very slight increase in weight. At temperatures between 70 F and 60 F (15.6 C) growth rate increased and mortality dropped; at temperatures between 63 F and 53 F (17.2–11.7 C) the rate of growth was greatly accelerated and there was much less mortality. In one tank temperatures fell to as low as 38 F (3.3 C) toward the end of the experimental period. At those low temperatures food consumption was much reduced and, consequently, the rate of growth. The mortality rate increased.

In a tank in which the water temperature was kept at that prevailing just below the thermocline of Skaha Lake, a natural sockeye-producing area in the south Okanagan "dry-belt," not only was the growth rate better than in all other tanks but the utilization of the food and its conversion into fish flesh was highest. Not one fish died. In a survey of three lakes in the same hot, dry climatic zone as Skaha Lake, Chapman is reported (Donaldson and Foster, 1941, p. 345) to have found the young sockeye salmon in the zone of cool water near the thermocline during August and September. The warm surface layers of the lakes were devoid of sockeye, as were the depths of the lakes examined.

It seems likely, however, that different races of sockeye, native to geographic areas with more or less specific climatic conditions, whereby the ranges of water temperature may differ quite markedly, may be racially acclimated to different water temperature conditions. Thus, the sockeye of the Columbia River, which are produced in the lakes of the hot, dry Okanagan region, may thrive effectively in waters much warmer than those, for example, to which the sockeye of Bristol Bay, Alaska, or of Kamchatka are accustomed and which they would prefer. The probability of this is confirmed by experiments on temperature tolerances of Pacific salmon (Brett, 1952b) which revealed, for sockeye, an upper lethal temperature of 24.4 C (75.7 F), a lower lethal temperature for the highest acclimation, 23 C, of 6.7 C (44 F), and a region of greatest preference between 12 and 14 C (53.6 and 57.2 F). Young sockeye were very sensitive to low temperatures, unable to tolerate long exposure (4 days) to 0 C, even when taken from holding temperatures as low as 5 C (41 F).

RELATION OF LAKE SURFACE TEMPERATURES TO GROWTH OF YOUNG SOCKEYE

By utilizing data on the effect of water temperature on growth of young sockeye of the Baker Lake stock (Skagit River, Washington), as reported by Donaldson and Foster (1941), Rounsefell (1958a, p. 117) has plotted a curve to show the efficiency of growth (i.e., the increase or decrease in the weight of a fish, divided by the weight of the food fed to the fish) as related to or influenced by the water temperatures in which the fish are held. This curve is reproduced in Fig. 45. Concerning it, Rounsefell reports that:

> "as expected, growth is very slow below 40°F, increasing rapidly with increase in temperature until a plateau of favourable growth conditions is reached extending from about 45° to 68°F. The optimum range of temperature is about 48° to 56°, after which growth declines gradually

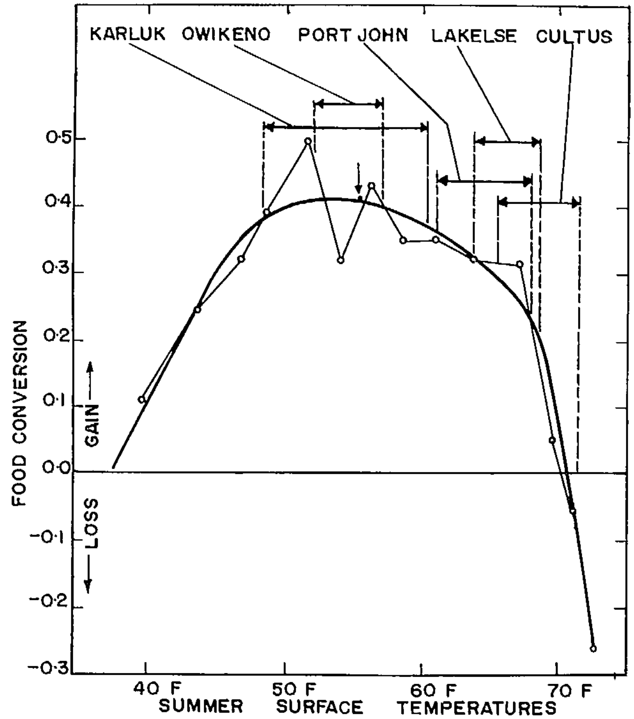

FIG. 45. Growth of young sockeye in 2-week periods, as shown by food conversion, at different water temperatures, according to data from Donaldson and Foster, 1941. Original curve prepared by Rounsefell (1958a, fig. 30) showing general position of Karluk Lake and Cultus Lake summer surface temperatures. The positions for Owikeno, Port John, and Lakelse lakes have been added, as well as the mean position for Babine Lake (arrow).

> with increasing temperature to about 67.5°F. At this point the growth curve falls steeply, and above 70°F the sockeye lose weight."

This curve was prepared originally to demonstrate that the difference in production of young sockeye salmon between Karluk Lake and Cultus Lake could not be due solely to the greater abundance of plankton at Karluk. It was felt that the related factor of temperature should be considered. In so doing it was revealed, according to Rounsefell, that in Cultus Lake the surface waters during summer became too warm for the sockeye, forcing them to seek deeper water where feeding conditions were presumably less suitable. Cultus Lake was taken to represent, therefore, a "marginal" sockeye-producing area.

On Rounsefell's curve we have indicated also (see Fig. 45) the relative positions of the summer surface temperatures of the several lakes which have been considered above, and, in addition, Babine Lake. The physicochemical conditions prevailing in this highly productive sockeye area of the Skeena River system (see Fig. 7) have not been dealt with in detail because of the multibasin character of the lake (see p. 220). However, mean summer (mid-June to mid-October) temperature data for the surface stratum (0–5 m) are available (Johnson, 1958, table I) for 3 years, showing a range of from 11.9 C (53.4 F) to 14.9 C (58.8 F) and an overall mean of 13.1 C (55.6 F). The position of this point on the curve (Fig. 45) is shown by the arrow and may be taken to indicate, relatively, that conditions for sockeye development in Babine Lake are very good, perhaps similar to those for Karluk.

As far as temperature conditions in the epilimnial zone of the lakes are concerned, then, Babine and Owikeno lakes, like Karluk, occupy the peak of the curve. The other three British Columbia lakes have higher surface temperatures, in the ascending order of Port John, Lakelse, and Cultus, though there is overlap among them all. They fall on the descending arc of the growth curve, suggesting that, so far as temperature conditions are concerned, each of the three lakes is progressively less suitable for sockeye production. Other factors have to be considered, however, as will be shown below. Nevertheless, this temperature:growth relationship of the various lakes is an important feature to keep in mind.

In this regard, an observation concerning conditions in Kamchatka sockeye-producing lakes is pertinent. Krogius (1953, p. 221) records that:

> "at the end of July and the beginning of August there were observed, in the epilimnion, maximum temperatures which reached, in certain lakes, 20°C. Because of such high temperatures and a drop in the abundance of *Cyclops* [presumably due to the heavy consumption by the feeding young fish] a change took place between the intensity of the metabolic processes at these temperatures and the availability of the food. In some lakes this resulted in a slowing-down in the growth rate, which was reflected in the scale structure of the young sockeye. In these instances, the retardation in the growth rate had no effect on survival."

Krogius' opinion, as we interpret it, is that the scarcity of food, brought on by the heavy cropping of the plankton supply by the masses of feeding young sockeye, led to a slowing-up of the growth rate and that, had adequate food been available, the more rapid metabolism, resulting from the high temperature of the epilimnion, would have continued the growth of the young fish without any retardation. According to the findings of Donaldson and Foster (1941) and the opinion of Rounsefell (1958a) the high temperatures themselves would tend to slow down growth, quite irrespective of availability of food, though, of course, an insufficiency of the latter would aggravate the situation.

For those sockeye which are produced in the Karymai Springs of the Bolshaya River system, where August-September surface temperatures of from 6.5 to 7.4 C (43.7 and 45.3 F) are reported (Semko, 1954a, table 37, p. 60), growth conditions would be the reverse. This low temperature range falls along the ascending left-hand side of the curve, and so would tend to provide a reduced food conversion and slow growth. Any rise in temperature would be advantageous, assuming that with the higher metabolism and presumed greater activity of the fish, a requisite proportion of the food consumed would go to growth and not all of it be expended on increased activity.

HEAT BUDGETS AND SUMMER HEAT INCOMES

It is recognized that, within tolerable limits, the higher the temperature of a lake, the greater the production of plant and animal life within it. Therefore, for sockeye-producing lakes, the overall temperatures must be of appreciable significance and the extent to which the amount of solar energy falling on a lake is converted into heat units, to be measured on the basis of temperatures attained by the lake water, may prove a useful gauge of productivity within a lake, other factors being equal or their effect calculable. The *annual heat budget* of a lake is considered to be (Welch, 1935, p. 59) the amount of heat required to raise its water from the minimum temperature of winter to the maximum summer temperature, while the *summer heat income* is the amount of heat required to raise the water of a lake from 4 C to the maximum summer temperature. The latter unit may be used, consequently, for comparison of lakes when the minimum winter temperatures of all are not available.

Whatever the significance of heat budgets or summer heat incomes may really be, with respect to a lake's production of plankton or fish, it is of interest to make a comparison of the conditions prevailing in the several lakes for which pertinent data are available (Table 40).

TABLE 40. Heat budgets and summer heat incomes of certain sockeye-producing lakes.

Lake	Area (*ha*)	Mean depth (*m*)	Heat budget (*kcal:cm²*)	Summer heat income (*kcal:cm²*)	Authority
Karluk	3937	48.6	33.50	18.90	Juday et al., 1932
Cultus	626	32.1	24.35	23.89	Ricker, 1937a
Lakelse	1347	7.9	13.11	11.19	Brett, 1950
Port John	91	25.1	–	10.72	Robertson, 1954

It has been suggested (Rawson, 1939, p. 14) that heat budgets and summer heat incomes "may be more readily compared and interpreted in lakes of more than 30 metres depth." Thus, perhaps, only Karluk and Cultus lakes should be compared. The former has a higher heat budget than the latter but, on the other hand, Cultus Lake has a higher summer heat income, the difference being due to the fact that the winters at Cultus Lake are milder and minimum lake temperatures higher. This higher summer income would imply a greater plankton production—at least to the extent that water temperature is a controlling factor—in Cultus Lake, which, as discussed below (p. 218) does occur.

On the other hand, as pointed out by Rawson (1939), "in the basic question of productivity we are less concerned with the total heat acquired than with the temperature of the trophogenic region (chiefly the epilimnion) and the length of the growing season." If this be the case—and it seems to be applicable to sockeye in lakes—then the summer heat incomes, and particularly the heat budgets of sockeye lakes, are of less consequence for sockeye production than the temperature conditions in the upper strata of sockeye-producing lakes. The relationships shown in Fig. 45 are, then, pertinent.

TRANSPARENCY OF LAKE WATER

Another physical factor of significance in plankton production and young sockeye production is the degree of transparency of the water. This is usually measured by lowering into the water a Secchi disk, a white crockery, metal, or weighted wooden plate, 20 cm (8 inches) in diam, and observing the depth at which it disappears, as well as the depth at which it reappears when lifted again. Some transparencies measured in midsummer are as shown in Table 41.

Upon the degree of transparency of the water of a lake depends the amount and extent of light penetration. Upon the latter depends, in turn, the amount of photosynthesis and the depth of the stratum of water where phytoplankton will flourish and where plankters which feed on the phytoplankton will be concentrated. Here also will be found the young sockeye which utilize plankton for food. At the same time, however, the clearer the water the greater the amount of radiant energy and thus the greater the warming effect.

Assuming that young sockeye actively seek out the plankters on which they feed, the greater the water transparency the better the feeding conditions. On the other hand, however, the clearer the water the more available will the young sockeye be to their enemies.

In general, then, the transparency of the water of a lake will have both a direct and an indirect influence on where young sockeye are to be found during the active feeding period and also on the growth rate. In cold, heavily silted lakes, such as Kitsumgallum Lake (0.5 m transparency) and Owikeno Lake (for which no transparency measurements are available) plankton production will presumable be confined to the near-surface stratum and the young sockeye will, in all probability,

TABLE 41. Secchi disk transparencies of 12 sockeye nursery lakes.

Region	Lake	Transparency	Authority
		(*m*)	
Kodiak I.	Karluk, July, 1928	8.6	Juday et al., 1932
	Karluk, July, 1929	5.5	Juday et al., 1932
	Karluk, July, 1930	7.5	Juday et al., 1932
Fraser R.	Shuswap, Aug., 1943	10.0	Ward, 1957
	Cultus, Sept., 1936	17.0	Ricker, 1937a
Central B.C.	Port John, summer, 1950	3.8–5.0	Robertson, 1954
Skeena R.	Lakelse, 1945–48	3.0	Brett, 1950
	Lakelse, Aug. 30, 1947	5.3	Brett, 1950
	Kitwanga, summer, 1945	7.8	McConnell and Brett, 1946
	Kitsumgallum, summer, 1945	0.5 (approx)	Brett, 1946
	Bear, summer, 1945	5.0 (approx)	Foskett, 1947a
	Sustut, summer, 1945	9.0	Foskett, 1947b
	Asitka, summer, 1945	5.5	Foskett, 1947b
	Johanson, summer, 1945	9.0	Foskett, 1947b
Kamchatka	Kurile, 1932	8–11	Krokhin and Krogius, 1937b

be concentrated there too. In more transparent waters the plankton production zone will be appreciably deeper and the distribution of sockeye likewise. In extremely clear water, such as Cultus Lake, however, due to the high temperatures in the surface strata (and perhaps the actual high light intensity) the main plankton crop is located at greater depths, with the young sockeye concentrations at a deeper level too. To what extent the high transparency of the water and the high temperatures of the surface strata limit growth and production of young sockeye, as Rounsefell suggests for Cultus, requires further study.

In some cases, e.g., Lakelse Lake (Brett, 1946), obstruction to light penetration may be partly due to the abundance of zooplankton or to the periodic "blooming" of certain phytoplankters. It may be caused by an unusual accumulation of organic detritus, as at Port John Lake (Robertson, 1954). In such instances, the situation may be of short duration. Where glacial silt is the responsible agent, e.g., Owikeno and Kitsumgallum lakes, the turbid condition may be prolonged and prove more detrimental to plankton production.

Reference might be made to the fact that, in considering the productivity of a lake, the surface area is of much greater significance than total volume or depth. Since photosynthesis, insofar as it depends upon solar radiation, is a function of surface *area*, rather than volume or depth, lakes of moderate depth will, other things being equal, be more productive for plankton and for plankton-consuming fish than deep lakes. For young sockeye, then, assuming that high temperature conditions do not become a limiting factor to their distribution in epilimnial areas, lakes of shallow or moderate depth should prove most effective for production. In a later section, the production of sockeye, based on lake area, will be discussed (see p. 271).

CHEMICAL CONDITIONS IN LAKES

Limnological surveys of sockeye lakes have usually included, as routine procedures, the determination of dissolved oxygen content, free carbon dioxide content and hydrogen ion concentration, and the quantities of the four inorganic salts, nitrates, nitrites, phosphates, and silicates, the first three primarily with respect to the extent that they may limit the within-the-lake distribution of the young sockeye, the last four, the inorganic salts, in regard to the production of plankton.

Dissolved Oxygen

So far as dissolved oxygen content is concerned, no instance can be found where, in any natural sockeye-rearing areas, it has been a limiting factor. Made available not only directly from the atmosphere by absorption from the air (largely as the result of wind and wave action), but also by the photosynthesis of plant life, there appears to be a high saturation in the epilimnion and thermocline at all times and a quite adequate supply in the hypolimnion, even in the deepest lakes.

At Cultus Lake (Ricker, 1937a) there is supersaturation in the early months of the season—up to 108% at 5 m—which declines gradually throughout the summer and is followed from mid-September to late October, by a period when the oxygen content remains close to saturation. At 10 m a slight supersaturation exists in the thermocline up to late October. Even in the hypolimnion a high saturation prevails, no doubt partly maintained by photosynthesis. At Karluk Lake (Juday et al., 1932) the deep water was well supplied with oxygen, 85–92% of saturation. In Kurile Lake (Krokhin and Krogius, 1937b) an oxygen saturation, in spring, of 91–92%, at depths of 10–20 m, was found. For Lakelse Lake (Brett, 1950) "dissolved oxygen remains high all year round and is only reduced in a very restricted hypolimnial zone. The minimum on record was 45% (5.2 ppm, 9.7° C)."

Brett (1950) points out that "unless oxygen concentrations of 30% (i.e., about 3.5 ppm or 2.5 cc per litre at 10°C) or less, are discovered in some regions of the water body of a lake, then it is most likely that oxygen is not a limiting factor to either the distribution or existence of any species of fish within the water system." Experiments (Chapman, 1938) indicated that sockeye fry (yolk sac absorbed but not yet feeding) weighing approximately 0.192–0.20 g consumed from 0.099 cc of 0_2 per gram of fish per hour at 7.8 C to 0.116 cc of 0_2 per gram of fish per hour at 8.5 C, while fingerlings of around 10 g consumed 0.232 cc of 0_2 per gram of fish per hour at 9.5 C. These values may be compared with averaged values of "routine" or ordinary metabolism for fish of different sizes (Winberg, 1956, equations 6.1.2 and 7.3.3), after adjustment to a standard temperature (20 C, using Winberg's table 1) and conversion to terms of milligrams per gram per hour:

Avg wt	Temp	Observed oxygen consumption	Winberg's averages for: Salmonid fishes	All fishes
(g)	*(C)*	*(mg/g/hr at 20 C)*		
0.196	7.8	0.505	0.735	0.416
0.196	8.5	0.541	0.735	0.416
10.	9.5	0.946	0.286	0.189

The rate of metabolism of the fry lies within the range of expected values for fish that are resting but not necessarily completely motionless, while that for fingerlings is several times the expected figure. Chapman suggested that this rate of oxygen consumption, which was obtained in experimental jars (5-gal or 20-litre glass demijohns), may have been due to the fact that the sockeye were nervous and sensitive to external stimuli when under confinement. Some of them were always swimming around and around, up and down, and at no time were they all quiet on the bottom.

CARBON DIOXIDE

Carbon dioxide is made available to the water of lakes either by (1) direct absorption from the air, (2) respiration of animals and plants, (3) decomposition of organic matter, or (4) from carbonate and bicarbonate salts. It is essential for the photosynthesis of phytoplankton and aquatic plants. As Coker (1954, p. 20) remarks, "Carbon dioxide is, then, the crux of the synthetic problem in respect to the storage of energy and is of equal importance with oxygen."

It is generally believed that fish can tolerate relatively wide ranges in carbon dioxide content and, in most cases, can make appropriate physiological adjustments to ordinary fluctuations. In experiments on the respiration of chinook salmon (*O. tshawytscha*) fry and fingerlings (Chapman, 1940, p. 203) "a gradual increase of the carbon dioxide content of the water to as much as 14.5 ppm caused no visible deleterious effects on the young salmon within forty-eight hours so long as the oxygen content of the water was maintained above 4.0 ppm." For trout, Gutsell (1929) reported that a carbon dioxide content as high as 28 ppm did not appear "markedly harmful."

Determinations of the carbon dioxide content of sockeye lakes revealed that it is present in relatively small amounts only, even in deep water. The available data are

Free carbon dioxide content *(mg/litre)*

Lake	At surface	At bottom	Authority
Cultus	up to 5	up to 5 (40 m)	Ricker, 1937a
Karluk	1.0	3.5–4.0 (125 m)	Juday et al., 1932
Kurile	1.0–2.0	4.3 (270 m)	Krokhin and Krogius, 1937b

HYDROGEN ION CONCENTRATION (*p*H)

In general, the *p*H of sockeye lakes, i.e., the measure of its acidity (*p*H below 7.0), its alkalinity (*p*H above 7.0) or its so-called neutrality (*p*H 7.0), is fairly uniform, especially in the upper strata and seldom departs too appreciably from a neutral to slightly alkaline state. Seasonal variations are relatively minor. For Cultus Lake (Ricker, 1937a) the range of variation is not great, being from neutral to moderately alkaline (*p*H 6.9–7.8). Lowest values occur in the hypolimnion in autumn, highest in the epilimnion in summer. Winter values are intermediate—7.3–7.6. For those lakes for which data are available, the *p*H determinations are presented in Table 42.

TABLE 42. Hydrogen ion concentration (*p*H) of seven sockeye nursery lakes.

Lake	Surface	Bottom	Authority
Cultus	7.3–7.8	6.9–7.6 (40 *m*)	Ricker, 1937a
Lakelse	7.1	6.6 (32 *m*)	Brett, 1950
Owikeno	7.0	7.0 (305 *m*)	Foskett, 1958
Karluk	8.6	7.0 (120 *m*)	Juday et al., 1932
Thumb	8.2	6.8 (10 *m*)	Juday et al., 1932
O'Malley	8.0	6.6 (12 *m*)	Juday et al., 1932
Kurile			
(southern part	7.6	7.45 (270 *m*)	Krokhin and Krogius, 1937b
northern part)	7.6	7.6 (190 *m*)	Krokhin and Krogius, 1937b

DISSOLVED MATERIALS

In a study of the productivity of 100 lakes in different regions of British Columbia (Northcote and Larkin, 1956) which considered the relative effects of climate, lake morphology, readily measurable physical and chemical characteristics, and estimates of plankton, bottom fauna, and fish abundance, one conclusion reached was that "dissolved nutrients must rank as a primary factor in determining levels of productivity." It was also indicated that in areas where annual precipitation is high and evaporation rate low, the rapid flushing out of lakes and a heavy demand on soil nutrients by a lush ground cover may contribute as much to a low dissolved nutrient content as does relative insolubility of the surrounding rocks. Conversely, however, the low annual precipitation and the hot, dry summers of the Interior Plateau area may cause concentration of dissolved nutrients in the inland lakes.

Four of the limnological regions of British Columbia, as defined by Northcote and Larkin, contain sockeye-producing lakes, and the lakes they studied in these regions were characterized by different average contents of total dissolved solids (TDS), which they determined by electrical conductivity. In the Coast and Insular Mountains Region, 17 lakes had an average TDS of 46 ppm; 33 lakes of the Southern Interior Plateau averaged 229 ppm; 10 lakes in the Columbia Mountains Region averaged 135 ppm; and 8 lakes of the Northern Interior Plateau averaged 104 ppm.

Most of the lakes studied by Northcote and Larkin are rather small, and only two contain sockeye populations. Information on the mineral content of these two and of other sockeye producers is shown in Table 43.

TABLE 43. Total dissolved solids of 16 sockeye nursery lakes of British Columbia, classified by physiographic regions.

Region	Lake	TDS (*ppm*)	Source
Coast and Insular	Alastair	12	Johnson, unpublished
	Lakelse	29	Johnson, unpublished
	Kitsumgallum	20	Johnson, unpublished
	Morice	34	Johnson, unpublished
	Port John	39	Robertson, 1954
	Owikeno	26 (19–35)	Foskett, 1958
	Cultus	104	Northcote and Larkin, 1956
	Sproat	32	Northcote and Larkin, 1956
South Interior Plateau	Kamloops	78	Original
Columbia Mountains	Quesnel (river)	127	Original
	Shuswap	81 (61–112)	Ward, 1957
North Interior Plateau	Bear	40	Johnson, unpublished
	Babine	47 (40–51)	Johnson, 1964
	Morrison	72	Johnson, unpublished
	Fraser	100	Original
	Nechako (river)	122	Original

A majority of the big sockeye-producing lakes of British Columbia are in the Northern Interior Plateau or the Columbia Mountains Region, and those for which data are available are intermediate in respect to mineral content (75–125 ppm). This includes Shuswap, Quesnel, Fraser, and the Nechako system. Babine Lake, in the Skeena drainage, has a considerably lower mineral content, though its tributary, Morrison Lake, is close to the intermediate range. Kamloops Lake, though situated in the Southern Interior Plateau, gets nearly all its water from the Columbia Mountains Region and has a similar TDS. No sockeye-producing lake is known to have the high mineral content typical of most lakes of the Southern Interior Plateau.

Ward (1957, p. 42), showed that TDS varied between different basins of Shuswap Lake, and he found a significant and rather high correlation between the volume of zooplankton and the TDS at five stations, whereas the correlation with temperature was smaller and non-significant.

In the Coast and Insular Region nearly all the lakes listed have the low TDS characteristic of the region. Owikeno Lake (Fig. 41) is extremely turbid in the summer months, due to glacial silt, and harbours a very large sockeye stock in spite of its low content of dissolved substances. Cultus Lake has a mineral content much larger than average for the Coastal Region, due to the presence of considerable sedimentary rocks in its drainage basin.

Nutrient Chemicals

Chemical analyses to determine the quantities of some of the individual substances used in plankton metabolism in the waters of sockeye-producing lakes have been made in only a few cases. These are gathered together in Table 44. For ready comparison, all values are expressed in milligram-atoms, a unit which permits ready comparison of the quantities of the various elements, being proportional to the number of units of each present (Ricker, 1937a, p. 396).

Table 44. Results of the chemical analyses of the waters of certain sockeye-producing lakes to determine amounts of various dissolved solids.

		Nitrogen		Silicon	Phosphorus		
Lake	Date	Nitrite (*mg:m*^{3})	Nitrate (*mg:m*^{3})	(*mg:m*^{3})	Total (*mg:m*^{3})	Phosphate (*mg:m*^{3})	Authority
Cultus	1932	0.02	4.2	100 (S) 150 (40 *m*)	–	0.1	Ricker, 1937a
Karluk	July, 1927	Trace	0.3 (S) 0.84 (125 *m*)	0–20	0.2	–	Juday et al., 1932
Kurile	Apr. 1933	–	–	77.3 (1.5 *m*) 83.9 (270 *m*)	–	0.6 (S)[a] 0.3 (150 *m*)	Krokhin and Krogius, 1937
Dalnee	–	–	–	–	–	0.9[b]	Krokhin, 1959
Owikeno	Oct. 1953	–	–	93 (S) 33 (305 *m*)	–	–	Foskett, 1958

[a] Sample taken in the bay at the outlet to the Ozernaya River, October 12.

[b] "The average of many years," according to Krokhin.

Critical comparison of the tabulated results of the analyses seems to be of dubious value unless the circumstances prevailing at the time of the water sample collection are taken into account. For example, the relatively low value for silica in Karluk Lake in July, 1927, may have been due to a preceding diatom "bloom," for it is reported for Karluk (Juday et al., 1932, p. 417) that "a large crop of diatoms may completely exhaust the supply of available silica," though at Cultus Lake (Ricker, 1937a, p. 397) observations indicated that "the spring pulse of diatoms appears in no way to diminish the silicate content of the water."

Furthermore, the greater quantity of phosphate in Kurile Lake may well have been due to the addition of this salt to the lake water from the decomposing carcasses of spawning salmon. This likelihood is discussed below (p. 201). Further study of the relation of the amount of nutrient salts to actual plankton production is desired. Theoretically, these salts are supposed to accumulate in the deep, hypolimnial stratum and be released to the upper waters at the time of spring and autumn overturn. The year-round studies at Cultus (Ricker, 1937a) do not show this too clearly, except for silicates, and here the indicated early autumn increase in the bottom waters is at variance with the situation found in Owikeno Lake (Table 44).

While, therefore, a definite positive relationship between the amounts of inorganic nutrients in a lake and the production of phytoplankton and, subsequently, of zooplankton is to be expected, other factors intervene to complicate and confuse the picture. For example, it has been pointed out (Hutchinson, 1944) that no clear-cut relationship between the chemical conditions in a lake and the qualitative composition of the phytoplankton can be expected, because of the physiological condition of the phytoplankton population and its relationship to populations of other species. It has also been found (Tucker, 1957) that the variations in phytoplankton periodicity (i.e., the occurrences of phytoplankton pulses), may be due to factors other than the nutrients present, when these nutrients are present in adequate supply in a lake throughout the year.

TABLE 45. Phosphorus, nitrogen, and silica contents (in mg:m^3) of the upper parts (above spawning areas) and lower parts (near mouth) of streams flowing into Karluk Lake in 1927. The numbers of sockeye reported to have spawned in these streams in 1927 are indicated. (Juday et al., 1932, p. 419, table X.)

	Moraine Creek		Cascade Creek		Upper Thumb	
	Upper	Lower	Upper	Lower	Upper	Lower
Date (August)	25	25	27	27	21	21
Temperature (*C*)	–	7.5	8.3	8.3	8.9	–
Phosphorus						
Soluble	4	60	Trace	16	4	25
Organic	18	130	3	–	6	15
Total:	22	190	3	–	10	40
Nitrogen						
Ammonia	0	400	Trace	80	Trace	328
Nitrite	0	9	–	4	0	18
Nitrate	40	85	40	30	5	60
Silica	2,000	2,000	3,000	2,000	2,200	2,000
No. of sockeye	10,000	10,000	?	?	50,000–	60,000

CONTRIBUTION TO NUTRIENT SALT SUPPLY BY SALMON CARCASSES

KARLUK LAKE

During a study of the chemistry of the streams flowing into Karluk Lake in 1927 (Juday et al., 1932) it was observed that there was marked difference in the quantities of soluble and organic phosphorus and of ammonia, nitrites, and nitrate nitrogen in samples of water from the upper parts and from the lower reaches, as indicated in Table 45. Since the presence of many thousands of decomposing carcasses of spawned-out sockeye between the upriver and downriver sampling sites seemed to be the essential difference between them, it was assumed that in large part these decomposing carcasses had contributed the additional nutritive salts. The differences are indeed quite appreciable and significant.

They are confirmed by a later 4-year study (Nelson and Edmondson, 1955, p. 415) which showed almost a fourfold increase (from 8–29 mg/m^3) in the phosphate content between upper and lower sections of streams in which sockeye were spawning or had spawned.

For the whole lake's nutrient phosphorus and nitrogen supply, however, contributions would be made not only by the fish spawning and decomposing in the tributaries, as indicated in Table 45, but also by (1) the fish which spawn in the streams but drift down into the lake and (2) those fish which spawn along the lake beaches. The latter are estimated at 25% of the total spawning escapement. Assuming, then, a spawning escapement of a million sockeye annually, at an approximate average weight of 4 lb (1.8 kg), and a wet weight content of 0.3364% for phosphorus and 3.5% for nitrogen, there would be released into Karluk Lake a total of approximately 7.6 tons (6100 kg)* of phosphorus and 70 tons (63,500 kg) of nitrogen (Nelson and Edmondson, 1955, p. 416).

This matter of the phosphorus content of Karluk Lake and of the contribution made to the phosphorus supply by the spawning salmon has received considerable attention. The sockeye runs there, originally about the largest anywhere per unit of lake area, have declined since about 1920. There has been a tendency for the average age at maturity to increase (Barnaby, 1944), as indicated by a greater representation of the older and larger 4th-year seaward migrants than of the 3rd-year migrants. This has been interpreted by some authorities as a tendency for the Karluk sockeye to remain *now* a year longer in the lake than formerly. Assuming the time (age) of seaward migration to be related to size, hence to rate of growth and to abundance of food in the lake, the inference is (Barnaby, 1944; Nelson and Edmondson, 1955) that the appreciably smaller spawning runs have led to a diminution in the amount of phosphorus in the lakes which is basic to plankton production. The plankton crops have thus been lower, and the rate of growth of young sockeye accordingly reduced.

Rounsefell (1958a, p. 144) is of the opinion that, for Karluk, "the importance of the salmon carcasses as the source of nutrient materials may have been overemphasized in the past." Pointing out that, according to his calculations, the amount of phosphorus added to the lake each year is considerably in excess of that brought in by the salmon carcasses, he suggests that if more adequate data confirm that the phosphorous contribution from normal runoff water proves to be around twice that from the spawning salmon carcasses, "then the reduction in the total phosphorous content of the lake caused by reduced escapements will be in the order of 10 to 15 per cent over a period of about 75 years."

It is estimated (Rounsefell, 1958a, p. 167) that the phosphorus content of Karluk Lake water is 31,680 kg, that from the annual inflow of tributary streams is 8785 kg,** and the annual contribution from 1 million salmon carcasses is 6100 kg, giving a total phosphorus content of 46,565 kg.

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* This phosphorus content is higher than the estimate of Juday et al. (1932) because of more precise data on average weights of spawning sockeye and on the phosphorus content of the flesh.

** Rounsefell gives 11,450 kg here but it appears to be an error, through using the wrong figure for total yearly inflow.

It becomes a question, therefore, as to whether the contribution to the lake phosphorus supply provided by the salmon carcasses should be considered in relation (1) to the total lake phosphorus content or (2) to the annual replenishment of phosphorus. The latter would seem to be of greater significance since obviously the phosphorus supply or reserve in the lake, upon which the developing supplies of plankton may draw, must be intimately related to the sources by which the supply or reserve is maintained and replenished. At Karluk Lake the annual contribution of 1 million salmon carcasses would provide roughly 40% of the annual supply of phosphorus to the lake, whereas a small spawning run (500 thousand individuals) would add but 25%, approximately, and a heavy run (2 million individuals) would contribute roughly 60%.

LAKE DALNEE

Considered from this viewpoint, the significance of the size of a spawning run in adding nutrients to the lake is quite appreciable. It is admirably demonstrated by results obtained at Lake Dalnee, Kamchatka, (Krokhin, 1954, 1957a, 1959), shown in Table 46. The conclusion reached (Krokhin, 1957a, p. 30) is that "the addition of phosphorus brought in by the dead carcasses amounted, on the average, to more than 20% of the total quantity introduced annually into the lake and around 5% of the total supply in the Lake Dalnee water mass." Also, "under certain conditions the contribution of phosphorus brought in by dead carcasses can be much greater (up to 600 kg a year) and can drop almost to zero (8 kg a year)."

TABLE 46. The estimated intake and outgo of phosphorus in Lake Dalnee (Krokhin, 1957a, p. 30).

	P_2O_5 (*kg*)	Amount of phosphorus: of total income or discharge (%)	Amount of phosphorus: of total quantity in lakes (%)
Income:			
1) from runoff discharge	800	70	14.4
2) from rainfall over the lake surface	75	7	1.3
3) from sockeye carcasses	260	23	4.7
Total:	1135	100	20.4
Withdrawals:			
1) by outflow into Dalnee River	890	98	16.0
2) in seaward-migrating sockeye	20	2	0.3
Total:	910	100	16.3
Total quantity of P_2O_5 in Lake Dalnee water	5560	–	100

In two quite different ways the importance of the contributions made to a lake by spawning salmon carcasses was corroborated. In one, by means of the Frantsev "biological productivity" method,* samples of water from a number of lakes were tested to determine where any difference could be found between lakes in which sockeye naturally spawn and lakes where no sockeye occur (Krokhin, 1957a).

Two sockeye lakes and four non-sockeye lakes were included in the study. It was found, firstly, that in the control samples, to which no nutrients were added, the increase in numbers of *Scenedesmus* cells was much greater in those from the sockeye lakes than from the non-sockeye areas; secondly, that when similar amounts of the biogenic elements, nitrogen, phosphorus, and iron, were added to all samples, alga growth in the waters from non-sockeye lakes increased markedly whereas in the water samples from the two sockeye lakes there was little or no increase over that occurring in the controls. Thus, the supply of the nutrient element, phosphorus, in the waters of lakes in which sockeye spawn (fluctuating within limits of 46–129 mg/m^3) was appreciably greater than in the non-sockeye waters (13–26 mg/m^3) and it is concluded that the difference was due to the fertilizing effect of the decomposing sockeye carcasses.

The second confirmation of the role of the sockeye carcasses in contributing to a lake's nutrient elements came from a comparison of the phosphorus (in the form of P_2O_5) in Lake Dalnee, at the time of autumn overturn each year, for a period (1937–47) when the escapements were good and when they were poor (1948–58) (Krokhin, 1959). The results are summarized in Table 47. They indicate that during the second period, with relatively low spawning escapements, the phosphate level of Lake Dalnee was much lower. Furthermore, the reduction in phosphate was apparent

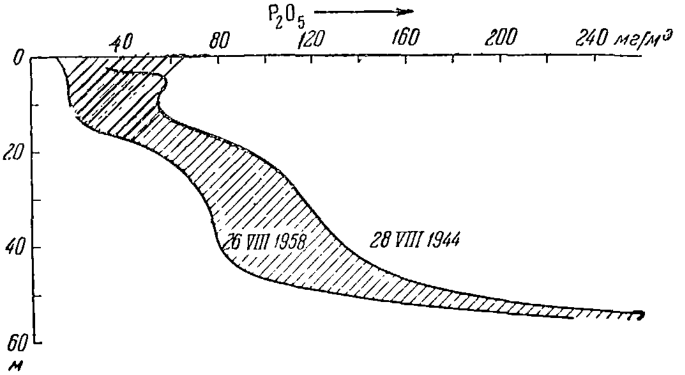

FIG. 46. Vertical distribution of phosphates in Lake Dalnee. Shaded area represents the difference between phosphate content in 1944 and 1958. (From Krokhin, 1959, fig. 2.)

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* The Frantsev (1932) "biological productivity" test, as described by Krokhin (1957a, p. 31): "To a filtered sample of the water from a body of water being investigated is added a known quantity of an element, the abundance of which, in that water basin, it is desired to determine; one sample of the water is kept, without addition of anything, as a qualitative control. To all the samples are added known quantities of a culture of *Scenedesmus quadricauda*. On certain days a calculation is made on the number of cells of this alga in the samples; from the increase in number of cells it is possible to determine the scarcity or abundance of any of the food elements in the body of water under investigation."

at all depths (Fig. 46). The double-acting adverse effect of a serious decline in a sockeye run is emphasized: "all indications point to the fact that the escapement of an insufficient number of sockeye to a spawning basin has not only a direct negative influence on the resulting population, but also at the same time results in profound changes in the quantities of nutrients in the lake which, indirectly affecting the food supply, appreciably reduce the effectiveness, success of propagation" (Krokhin, 1959, p. 627).

TABLE 47. Lake Dalnee sockeye spawning escapements and the phosphorus (P_2O_5) content at end of autumn circulation period (Krokhin, 1959, p. 626).

	Spawning escapement (thousands of fish)		Phosphorus (P_2O_5) (in $mg{:}m^3$)	
Period	Range	Avg	Range	Avg
1937–47	20–100	55.2	130–150	138
1948–58	1–20	9.2	83–112	98

One wonders whether sufficient significance has been given to this feature of the phosphate balance. With sockeye populations in all areas showing such evident declines, despite legislation on regulation and limitation of fishing, it might well be that some basic factor such as this may be having a much more limiting effect on productivity than seems apparent. In addition to the smaller amounts of phosphorus introduced into a lake in the carcasses of fewer sockeye spawners, there may also be occurring a steady decline in the phosphate content of the runoff waters as the phosphates of the soil and rock become leached out over the years. Future studies of the phosphate balance of sockeye-producing waters and the direction of its trend may prove most enlightening. Addition of suitable fertilizers may be found advantageous.

THE PLANKTON IN LAKES

Since sockeye salmon spend a portion of their early life cycle in lakes and, while resident there, frequent primarily the open waters (i.e., the pelagic areas) of the lake, they are dependent, for growth and development, on the quantities of food available to them there. They feed chiefly on small, microscopic Crustacea—the Cladocera and Copepoda—as discussed in a subsequent section below. Since, however, the Crustacea, in turn, are dependent on the phytoplankton for their food, the abundance of phytoplankton—the algae and diatoms—of the lake is of prime, though indirect, significance to sockeye production.

PHYTOPLANKTON

Despite its importance, however, in the consideration and evaluation of a lake as a food-producing unit for young sockeye and its intimate role in the food-chain,

PLATE IX. Clarke-Bumpus plankton sampler in operation.

Top left: preparing to lower sampler to desired depth for towing. *Bottom right:* after towing for a required period the net is raised and the lower end released from the supporting frame for washing off the plankton into terminal plankton bucket. *Top right:* removing plankton bucket from end of net. *Bottom left:* pouring contents of plankton bucket into glass jar.

phytoplankton production has been, thus far, but cursorily studied in sockeye lakes. Extremely little information is available concerning even the "standing crop," i.e., the amount of phytoplankton present at the time of lake sampling. This has resulted, of course, largely from the fact that any real study of phytoplankton abundance and distribution, the factors responsible for its production, and its relation to zooplankton, is an extremely complex problem and requires much time, extensive field work, and special equipment. As Ricker has remarked, in explaining why his plankton studies at Cultus Lake (Ricker, 1938b) were restricted to the larger or "net" organisms (i.e., those that could be captured, to some extent at least, by plankton nets with mesh no finer than No. 20 bolting silk), "such eclecticism can be justified only because of the press of other work and because of unfamiliarity with the easiest method of enumerating the smaller plankters."

The outstanding and most striking feature of phytoplankton populations is the occurrence of cyclic or seasonal pulses or "blooms" of different species throughout the year. During these pulses the abundance of the species "blooming" increases tremendously and often can be noted by the increase in turbidity of the lake water and its colour. In Fig. 47 (two bottom graphs) are depicted the fluctuations in abundance of two species of diatoms in Cultus Lake (Ricker, 1938b, p. 41) over a period of years.

These pulses are due largely to (1) changes in water temperature resulting from seasonal changes in solar radiation and local weather condition and also to (2) changes in nutrient conditions (McCombie, 1953, p. 279). McCombie suggests that weather conditions affect both the degree and time of development of the alga pulse, whereas changes in nutrient conditions influence primarily the degree of development. In other words, very warm weather may bring on an earlier spring diatom pulse than would otherwise normally occur; an increase in the quantity of nutrients in the water, however, would not cause the pulse to occur before the proper water temperature was reached.

Hutchinson (1944, p. 3), in considering the influences of the chemical changes in lake water on the fluctuations in abundance of phytoplankton, refers to the findings of Pearsall (1932), summarizing them as follows:

1. Diatom populations increase when the water is richest in phosphate, nitrate, and silicate, i.e., in the winter and spring.
2. The diatom, *Asterionella*, develops at a higher nutrient level than does *Tabellaria*.
3. Green algae and desmids occur primarily during summer depletion of nutrients, the latter group being formed by a low calcium content and low nitrogen: phosphorus ratio.
4. Blue-green algae are abundant when the dissolved organic content of the water is high and can increase at very low concentrations of dissolved inorganic nutrients. Lakes which support large populations of blue-green algae in summer generally contain the diatom *Melosira* at other seasons.

From his own studies, Hutchinson (p. 25) suggests "that in general, clear-cut correlations between chemical conditions and the qualitative composition of the

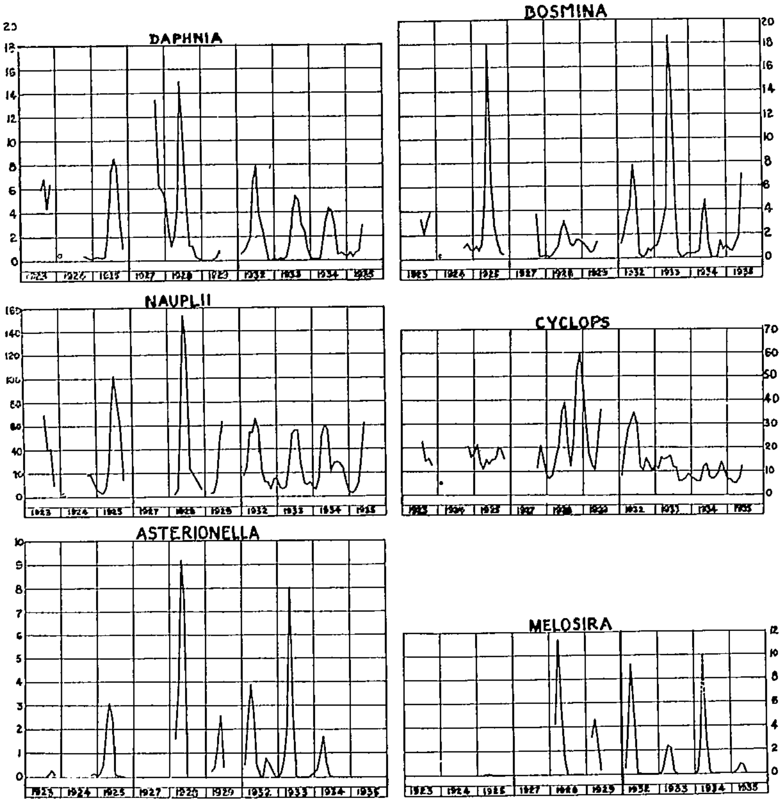

FIG. 47. Fluctuations in abundance of plankters in Cultus Lake, British Columbia, over a 10-year period. Scale in metres of filaments per litre for *Melosira,* thousands of colonies per litre for *Asterionella,* and individuals per litre for *Daphnia, Bosmina, Cyclops* and the nauplii. (From Ricker, 1938b, fig. 2.)

phytoplankton are not to be expected, and that the physiological condition of a population and its relation to populations of the species are likely to explain many of the apparent inconsistencies observed when different seasons and different lakes are compared."

In view of (1) the wide fluctuations in phytoplankton abundance due to the seasonal diatom and algae pulses and the variations from year to year, as well as (2) the fact that the abundance of the nannoplankton—minute plankton forms not collected by a No. 20 silk bolting cloth net (mesh, 0.03–0.04 mm)—has not been included in plankton studies of sockeye-producing waters, though these organisms are considered to greatly exceed in quantity those of the net plankton, there seems to be little value in discussing in detail the production of phytoplankton and its relation to the production of crustacean plankters which are the principal food of young sockeye. Suffice it to say that in any serious study of the productivity of a sockeye lake and the relation of the production of sockeye to the food supply, either under natural conditions or when increased by addition of appropriate fertilizers, attention will have to be given to all phases of or links in the food chain from the basic physicochemical conditions, through production of bacteria, nannoplankton and net phytoplankton to the zooplankton which are dependent upon the former for food. As stated by Welch (1935, p. 237):

> "While the plankton is an organic community in which exist many interdependencies, it must be remembered that each component of this heterogeneous assemblage has its own form of life cycle, its own problems of maintenance, and its own characteristic reactions to stimuli; also, that these features may differ even among those species which are most closely related taxonomically. The plankton community is, in this respect, no different from some terrestrial community in which each of the various species, while influencing associated organisms in many ways, has its own individual sequence of life-history stages, generations and reactions."

One very interesting and illuminating experiment in fertilizing a lake to increase its plankton supply and thus increase the production of young sockeye has been undertaken (Nelson and Edmundson, 1955). It was conducted on a small lake primarily to determine whether, if the serious decline in the sockeye runs to the adjacent highly important sockeye-producing Karluk Lake was due to the reduced quantities of nutrient inorganic substances, the addition of commercial fertilizers would correct the situation, to what extent and at what cost.

Addition of calculated amounts of fertilizer (19% superphosphate and sodium nitrate) was followed by a large and prolonged increase in photosynthesis and a rapid increase in phytoplankton, as shown in Fig. 48. However, as pointed out by the authors (Nelson and Edmundson, 1955, p. 433), interpretation of population trends depends on specific knowledge of alga physiology, much of which is as yet non-existent. Furthermore, the physiological condition of a population, as quoted above from Hutchinson, is very important in determining its productivity under a given set of conditions. More information is needed before proper assessment can be made of productivity and of the effect of fertilization. One factor that must always be borne in mind is the fact that where the measure of a fertilization test or of any change in conditions is the increase in the standing crop, the extent and significance of the increase *may not be fully apparent* because of the active grazing by other plankters, thus absorbing, in whole or in part, the increased production.

PRIMARY PRODUCTION

Reference may be made here to the renewed interest shown in the practical significance of studying and evaluating the primary production of lakes, as a measure of their potential in producing crops of fish of either commercial or sport-fishing value. Primary production pertains, essentially, to the building up, through the photosynthesis by plant-life in lakes, of crops of aquatic plants—phytoplankton, in particular—from the stores of inorganic substances present in the lake or brought into it by inflowing streams, etc.

Thus, all of the factors pertaining to lakes, which have just been discussed come into play in the manufacture, by the phytoplankton, of plant life, the first link in the

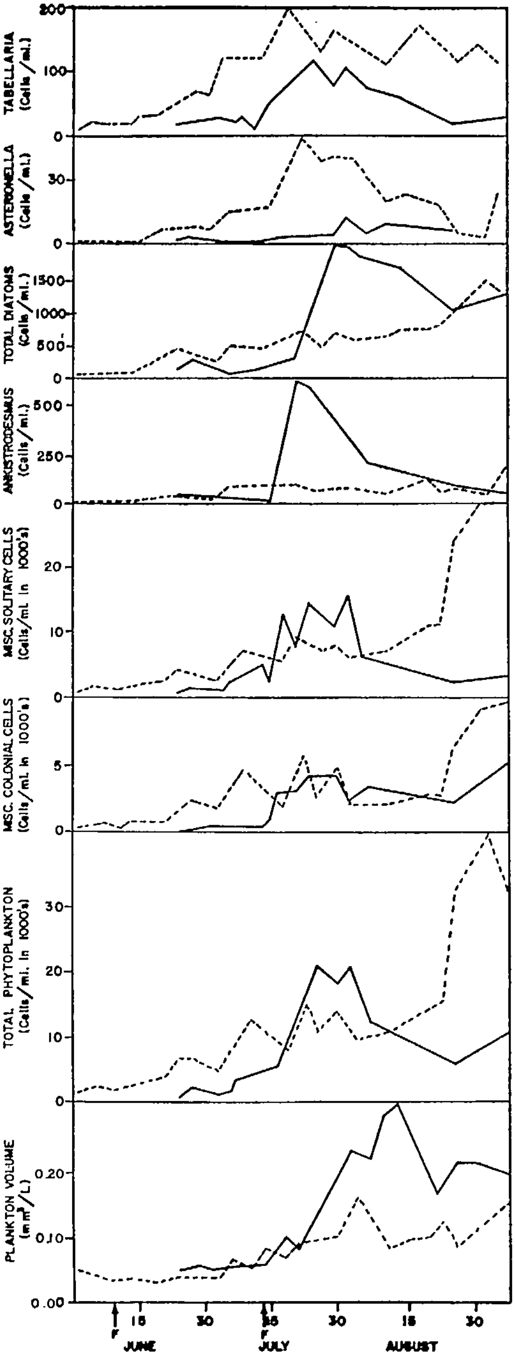

FIG. 48. Seasonal abundance of phytoplankton in Bare Lake, Kodiak Island, Alaska, during 1951 (solid line) and 1952 (broken line). Arrows denote fertilization dates—July 12, 1951, June 11, and July 16, 1952. (From Nelson and Edmondson, 1955, fig. 5.)

food chain of fishes. The inorganic salts present in the water are transformed by the plants, through photosynthesis, into organic substances necessary in the metabolism and development of zooplankton, the next link in the food chain. Temperature regulates the rate of photosynthesis while the transparency of the water determines the degree of photosynthesis and the depths, within the lake, to which photosynthetic activity may operate.

For sockeye salmon, where the production of the young fish depends so directly on the amount of zooplankton food in the nursery lakes, the importance of zooplankton production cannot be too greatly stressed. Since the production of zooplankton depends on the abundance of phytoplankton and this, in turn, on the quantities of the essential inorganic substances and on favourable conditions for rapid and extensive photosynthesis, a thorough study of primary production* in sockeye-producing lakes is of paramount importance.

Evidence has been presented of the significance of phosphates in the development of zooplankton crops in sockeye lakes. Other essential inorganic salts may be likewise of great significance. While at the present time our sockeye lakes may be considered sufficiently rich in the necessary inorganic salts, sufficiently productive with respect to phytoplankton or zooplankton crops to provide maximum production of sockeye, if optimal spawning escapements to them can be maintained, it is conceivable that, by providing greater stores of the basic inorganic salts, production of greater plankton crops and sockeye populations may result. In any case a thorough understanding of primary production will reveal, when sockeye production declines, what the limiting factor or factors may be and whether they can be rectified.

As one notable authority in this field, Winberg (1960, p. 288), has remarked,

> "There is a definite interrelationship between the extent of primary production and the production of fish in bodies of water. This is clearly shown, in particular, in the fertilization of fish ponds. Therefore, there can be no doubt but that the quantitative study of primary production is of paramount importance in the understanding of the fundamentals of the biological and commercial productivity of bodies of water."

The matter is especially stressed at this time, because of its great potentialities in sockeye production. The matter may not be of critical importance at the present time, but if the facts are obtained and the inherent relationships clearly understood, there need be no delay in applying appropriate measures to correct any adverse development when, in the future, it may occur.

ZOOPLANKTON

PROTOZOA AND ROTATORIA

The next links in the food chain for young sockeye in a lake are represented by the protozoan plankters and the rotifers. They are consumers of phytoplankton and, in turn, are consumed by larger zooplankters, particularly the crustaceans, represented by the Cladocera and Copepoda. Many of the rotifers no doubt feed on

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* An excellent and thorough review of techniques involved in the study of primary production in fresh water is given by Lund and Talling (1957).

Protozoa and also on smaller rotifers; some Protozoa are known, also, to be carnivorous.

Coker (1954, p. 212) has stated, concerning Protozoa, that probably the most numerous animals, and the greatest number of animal species in a pond, are these generally invisible but active agents in the "conversion" of bacteria, algae, and dissolved nutrients into forms of "meat" available to small carnivorous animals. This probably applies also to lakes, but information is decidedly limited concerning the Protozoa of the limnetic areas of such bodies of water. Plankton samples have generally been collected by means of nets of No. 20 or the coarser No. 10 silk bolting cloth, through which the smaller protozoan species would escape. In any event, the only protozoans taken from Karluk Lake (Juday et al., 1932, p. 426) were the ciliates *Epistylus* and *Vorticella*, attached to copepods, and a flagellate form, *Peridinium*, the largest number being taken on July 31, 1927, at Station 1 (see Fig. 43) i.e., 1279/litre in a bottom to surface haul. On the other hand, for Cultus Lake (Ricker, 1938b, p. 38–39), the flagellates *Ceratium* and *Dinobryon* were reported as having peak abundance in summer and early autumn, the former having a maximum usually in September of 200 individuals per litre, the latter, up to several hundred colonies per litre in late August and early September. Both species were quite erratic in abundance from year to year, as indicated, for *Ceratium* in Fig. 49.

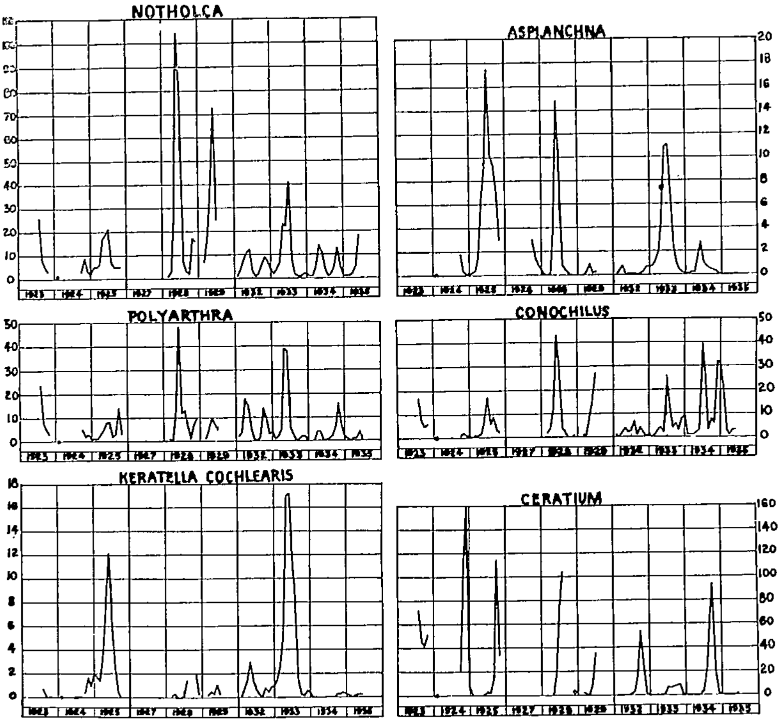

FIG. 49. Fluctuations in abundance of 5 species of rotifers and one protozoan, *Ceratium*, in Cultus Lake over a 10-year period. Scale in numbers of individuals per litre. (From Ricker, 1938b, fig. 1.)

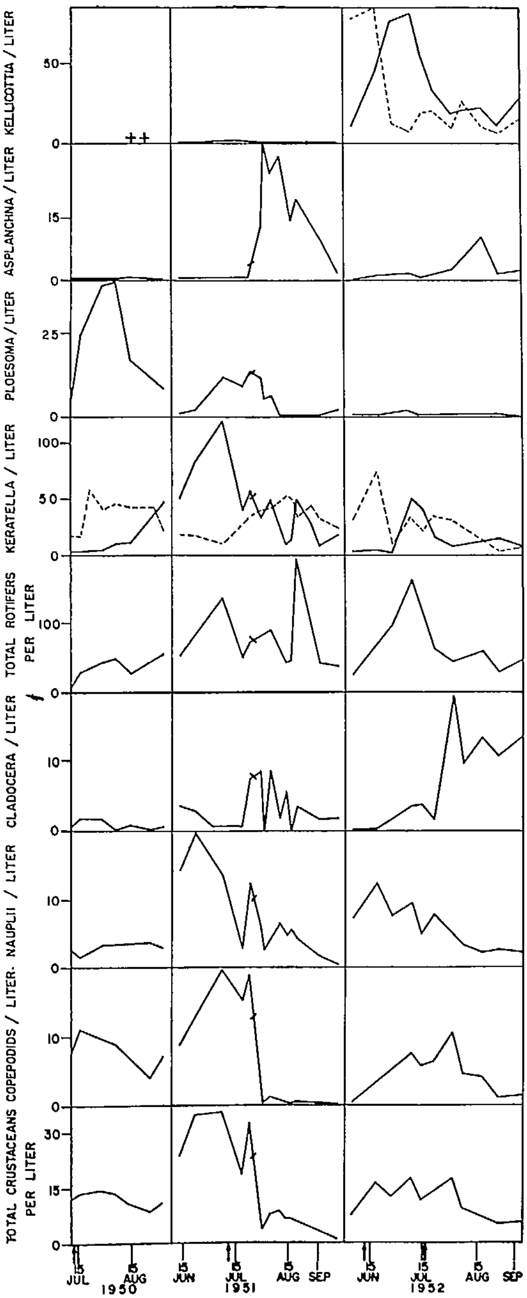

FIG. 50. Seasonal abundance of rotifers during 1950, 1951, and 1952 at Bare Lake, Alaska. Arrows denote lake fertilization dates. Broken lines indicate the number of eggs per female. (From Nelson and Edmondson, 1955, fig. 6.)

In an earlier study at Cultus Lake (Foerster, 1925) occasional specimens (0.3–0.4/litre) of the amoeboid protozoan (*Difflugia*) had been taken in the limnetic area in autumn. Oddly enough, in the fertilization tests at Bare Lake, Alaska (Nelson and Edmondson, 1955) Protozoa are not mentioned, though one would have expected them to flourish as and when the nutritive substances were added and the abundance of phytoplankton increased.

Among the rotifers appreciable fluctuations in abundance occur from year to year (Fig. 49). Within the year, also, some species may show one or more peaks or pulses, the spring pulse being generally the most prominent one. In Fig. 50 is shown the effect of fertilization on rotifer abundance, as observed in the Bare Lake, Alaska, experiment.

CRUSTACEA

The crustacean plankters, the *Cladocera* and *Copepoda*, are, as already intimated in a previous section, p. 166, the principal food of young sockeye during lake residence. Hence, their distribution, abundance, and production are of prime concern in any plankton study.

YEAR-TO-YEAR VARIATIONS

As has been demonstrated for phytoplankton, (Fig. 47), Protozoa (Fig. 49) and rotifers (Fig. 49), marked fluctuations occur also from year to year in the crustacean plankton populations, as revealed by the plankton studies at Cultus Lake (Fig. 47). While at Cultus Lake "little success has been achieved in attempting to assess their causes" (Ricker, 1938b, p. 43), an interesting correlation has been suggested for the crustacean plankton variations in Lake Dalnee, Kamchatka (Krogius and Krokhin, 1948). In Table 48 are listed the average crustacean plankton measurements for 7 years and the phytoplankton and physical conditions which, in the opinion of Krogius and Krokhin, were associated with and contributed to the crustacean plankton variations.

In 1937, 1938, 1940, and 1941, the plankton was relatively abundant (Table 48, item 1), though varying appreciably from year to year. It was least abundant in 1939, 1942, and 1943. The same relationship prevailed, in general, in the case of the phytoplankton, item 2. Reference to the conditions in the lake, item 4, reveals that in 1937, 1938, and 1941 a complete spring overturn of lake water occurred after the ice cover had disappeared. As a result, a complete circulation of the lake waters occurred and the nutritive substances in the lake became uniformly distributed. When there is only a partial or incomplete overturn, the nutritive substances required for phytoplankton development remain in the deeper strata of the lake and are inaccessible to the plankton above the thermocline. Within the thermocline there is a rapid drop in temperature with depth, which acts as an effective boundary to the vertical movement of plankton and some fish. Following the complete overturn in 1937, 1938, and 1941 the upper waters of the lake warmed up considerably, item 3c, thus aiding the more extensive production of phytoplankton.

TABLE 48. Conditions in Lake Dalnee relating to the production of plankton, as reported by Krogius and Krokhin, 1948, p. 12–13.

Item	1937	1938	1939	1940	1941	1942	1943
1. Avg wet wt of plankton during the June to Nov. growing period (cm^3m^3)	5.95	3.52	2.62	4.01	3.63	3.22	2.46
2. Approximate growth of the phytoplankton biomass (*mg:l dry wt of diatoms*)							
Si	17.1	14.5	–	8.2	6.7	4.4	6.6
P	17.3	14.7	–	13.4	10.7	8.8	10.0
3. Thermal conditions in the lake during the spring circulation period, (*C*)							
a) Initial temp	3.2	2.9	3.8	3.7	3.0	3.7	3.6
b) Final temp	4.0	3.8	3.9	3.8	4.0	3.7	4.0
c) Heat uptake	0.8	0.9	0.1	0.1	1.0	0.0	0.4
4. Extent of spring overturn (C = complete; P = partial)	C	C	P	P	C	P	C
5. Avg air temp (*C*)	13.05	14.37	11.70	12.59	12.21	14.11	10.15
6. Avg wind velocity (*m:sec*)	1.09	2.0	2.3	2.0	1.5	1.5	1.1
7. Thickness of epilimnion (*m*)	7.5	5.0	10.0	7.5	4.0	4.0	7.5
8. Lake temp at time of autumn homothermy	3.1	3.8	3.8	3.0	3.7	3.6	3.9
9. Avg air temp in Nov. (*C*)	–4.59	–5.26	–3.96	–4.18	–4.20	0.46	–8.14
10. Avg wind velocity in Nov. (*m:sec*)	1.8	1.1	1.2	1.8	1.1	2.0	1.0

As indicated in Table 48, item 4, a complete spring overturn occurred in years when the lake water temperature, prior to the spring circulation period, was low. This temperature, item 3a, appeared to be influenced by the final temperature at the time of autumn cooling of the upper waters in the preceding year when the lake temperatures were the same (homothermal) throughout, item 8. These temperatures, in turn, depended on the autumn air temperatures prior to ice cover, item 9, and on the extent of wind action at that time, item 10.

Thus, heavy winds in November, particularly in the latter part of the month, when air temperatures are normally quite low, led to a cooling of the lake. This resulted in a complete overturn of the lake water the following spring which, in turn, caused a general distribution of nutritive substances from the lower strata to the upper and made possible a greater growth of plankton in the epilimnion during the spring and early summer growing period. The data for 1942 are of interest in showing that, although wind action on the lake was severe, the unusually high air temperatures in November (0.4 instead of −4 or −5 C) led to but a slight cooling of the lake prior to freeze-up.

In 1938 and 1941 the plankton supply in Lake Dalnee, though relatively high, was much less than in 1937. This is attributed to the fact that, in 1938 and 1941, the epilimnial layer, item 7, was much thinner (5 m and 4 m, respectively) than in 1937 (7.5 m). Since, after stratification of the lake waters in early summer, the production of plankton depends on the amount of nutritive substances in the epilimnion, then the thinner it is the less the potential supply. In 1939 the epilimnion was thickest (10 m), item 7. It is suggested, however, that the absence of a complete spring overturn, item 4, and quite low spring air temperatures, item 5, provided poor conditions for plankton growth; air temperatures were also quite low in 1943, item 5, although a complete spring overturn did occur, item 4.

The depth of the epilimnion depends on the meteorological conditions prevailing in the spring, after the ice-cover has left the lake. Hot and calm weather at this time, item 5, results in the quick formation of a narrow band of warm water above the thermocline, as in 1938 and 1942, item 7; conversely, cold and windy weather leads to a deeper well-mixed epilimnion, as in 1939.

The above description of the general relationship of the meteorological and limnological factors of Lake Dalnee to plankton production is, of course, merely indicative of the complex nature of the mechanics, as it were, involved in production of plankton. Other factors pertaining to a lake, such as its size, its shape, the climatic condition of the area in which it is situated, are important. Each lake will have its

TABLE 49. Monthly average abundance of the four principal crustacean plankters in Cultus Lake, expressed as (a) the number of individuals per litre, the mean of 3 years' observations (Ricker, 1937b, p. 462) and (b) as a percentage of the total plankton, as represented by the four species.

	No. of individuals/litre					Percentage of total plankton			
Month	*Epischura*	*Cyclops*	*Daphnia*	*Bosmina*	Total	*Epischura*	*Cyclops*	*Daphnia*	*Bosmina*
May	0.26	31.5	3.7	10.4	45.86	0.5	68.7	8.1	22.7
June	0.25	16.3	5.4	6.7	28.65	0.9	56.9	18.8	23.4
July	0.43	10.2	4.4	1.7	16.73	2.6	60.9	26.3	10.2
Aug.	0.46	8.0	3.6	0.2	12.26	3.8	65.3	29.3	1.6
Sept.	0.35	10.7	1.6	0.1	12.75	2.7	83.9	12.6	0.8
Oct.	0.22	11.3	1.1	0.8	13.42	1.6	84.2	8.2	6.0
Nov.	0.10	9.7	0.5	0.6	10.90	0.9	89.0	4.6	5.5
Dec.	0.09	9.0	0.2	0.8	10.09	0.9	89.2	2.0	7.9
Jan.	0.04	8.0	0.3	0.7	9.04	0.5	88.5	3.3	7.7
Feb.	0.03	8.9	0.2	0.9	10.03	0.3	88.7	2.0	9.0
Mar.	0.01	8.6	0.3	1.1	10.01	0.1	85.9	3.0	11.0
Apr.	0.11	11.3	0.9	3.1	15.41	0.7	73.4	5.8	20.1
Yearly avg:	0.20	12.0	1.9	2.3	16.26	1.2	73.2	11.6	14.0

own peculiarities which will tend to influence or affect its sockeye-rearing potentialities. Only through a study of different sockeye-producing lakes can some understanding of the relationships of the locally prevailing limnological, climatic, and other conditions to production of young sockeye be realized. It is important to know how the many interrelated factors influence the productive capacity of the lake, with respect, firstly, to the plankton and, secondly, to the sockeye in order (1) that the fluctuations which occur from year to year may be understood and their effect perhaps predicted, (2) that the overall productive capacity may be calculated and (3) that, if remedial or improvement measures may be introduced, such as the addition of fertilizers to increase the amount of nutritive elements, their practicability may be assessed.

WITHIN-YEAR VARIATIONS

In Table 49 are shown the average monthly abundance records for the four principal zooplankters in Cultus Lake, each month's average being the mean of 3 years' observations, 1932–34, (see Ricker, 1937b, p. 462). *Cyclops*, by far the most abundant of the crustacean plankters, exhibits a major peak of abundance in the spring and a minor one in autumn. The cladoceran *Daphnia*, on the other hand while not nearly as abundant, has but one peak of abundance, in midsummer, when it con-

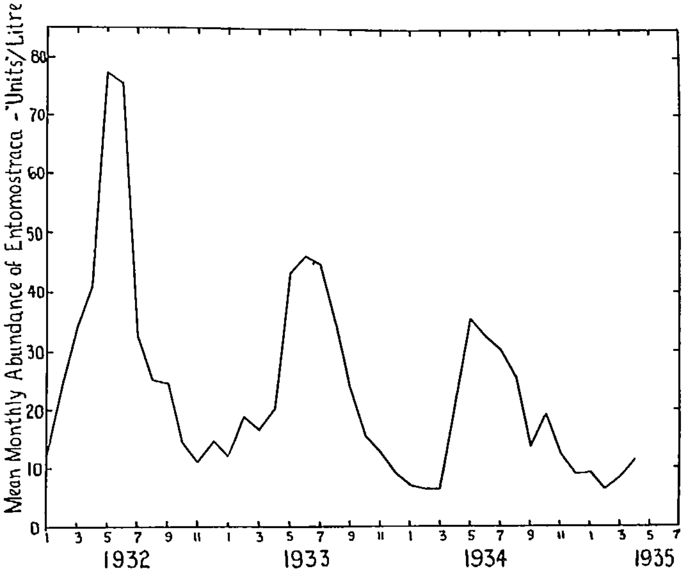

FIG. 51. Mean monthly abundance of adult Entomostraca in Cultus Lake in "units" per litre. Each species is weighted approximately according to its bulk: *Epischura*—5 units; *Cyclops*—1; *Bosmina*—1; *Daphnia*—5 (May–Sept.) or 3 (Oct.–April). One unit is equivalent to about 0.005 mg wet wt. (From Ricker, 1937b, fig. 4.)

tributed approximately one-quarter of the crustacean plankton. It is quite apparent that the zooplankters are most abundant in early summer, May and June, at Cultus Lake.

This is again brought out when considering the crustacean plankton biomass, i.e., the plankton supply in bulk, rather than in numbers of individuals. To a feeding fish the size of meal, i.e., its mass or bulk, would seem of greater significance than the numbers of organisms consumed. From Fig. 51 it is quite apparent that the zooplankton food is most plentiful in the later spring and early summer months, May–July, under Cultus Lake conditions.

At Lakelse Lake, lower Skeena River area, a somewhat different situation prevails. Here three of the important crustacean plankters show an increase in abundance in August and September, with a marked drop occurring toward the end of Septem-

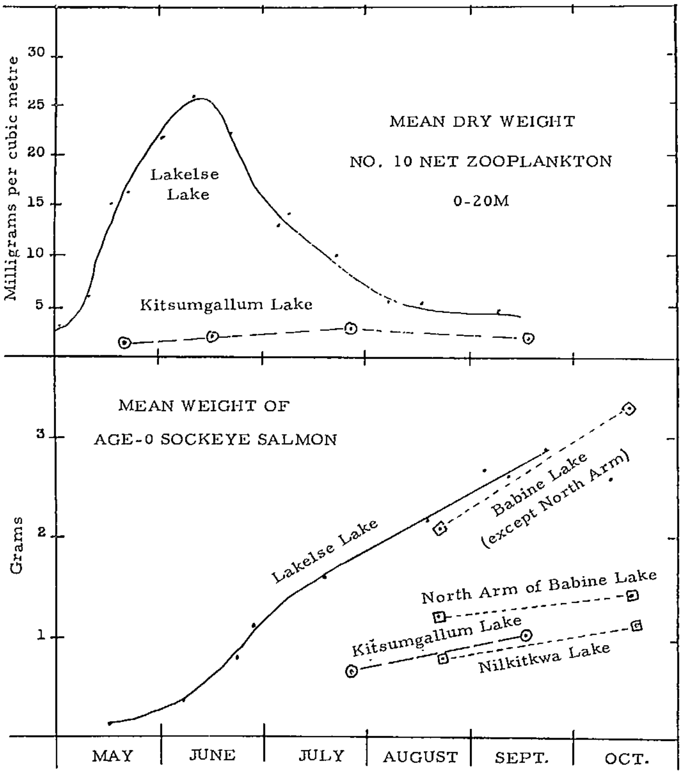

FIG. 52. Mean dry weight of standing crop of zooplankton in the 0–20 m stratum of Lakelse Lake during the summer of 1955 (solid line of upper graph) as determined from catches with Clarke-Bumpus plankton sampler equipped with No. 10 standard net, and mean weight (solid line of lower graph) of Age 0 (fingerling) sockeye taken from the lake by tow net in 1955. Curves for other lakes are included, purely for comparison with the Lakelse data.

ber (McMahon, 1954, p. 493). One cladoceran, *Holopedium*, appeared only in May to July samples, reaching a peak of abundance in June. This cladoceran, though never very plentiful in the lake, may have, however, because of its bulk, constituted an important item in the diet of young sockeye. This may be one reason why, in a special test with a Clarke-Bumpus plankton net in 1955 (W. E. Johnson, unpublished data) the mean dry weight of zooplankton in the 0–20 m regions of Lakelse Lake (Fig. 52) was greatest in the mid-May to mid-July period. In vertical distribution, the five plankters were found, with the exception of the copepod *Cyclops*, to be predominantly in the upper 15 m (McMahon, 1954, p. 484).

PRACTICAL ASSESSMENT OF PLANKTON ABUNDANCE

The available evidence indicates that (1) the most active period of growth and, hence, of feeding, is during the summer season, (2) the crustacean plankters upon which young sockeye feed are most abundant at that time, and (3) both plankters and young sockeye are present in the upper strata of the lake. Therefore, in relating the food supply to the young sockeye population, for whatever purpose desired, it

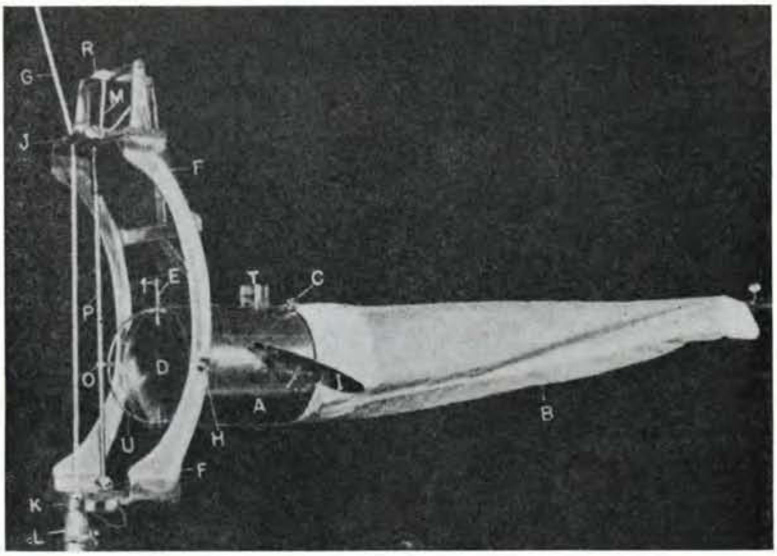

FIG. 53. Side view of Clarke-Bumpus plankton sampler with shutter in initial closed position. The plankton cup at the free end of the net and the rod which holds the net in a straight position are not shown. (A) Tube, (B) Net, (C) Bayonet lock, (D) Shutter, (E) Pivot for shutter, (F) Frame, (G) Cable, (H) Pivot for tube, (I) Plane, (J) Spring pin, (K) Gate lock, (L) Supporting clamp, (M) Rod fixed to trigger, (O) Long finger lug, (P) Rod, (R) Trigger, (T) Counter, (U) Semicircular bar, (1) Spring. (From Welch, 1948, p. 250.)

would seem sufficient to concentrate attention upon the upper 0–10 m or 0–20 m of a lake, during the summer months, in order to obtain the pertinent data.

This has been nicely shown for Babine Lake by Johnson (1956, 1958, 1961). With a minimum of effort, excellent data on the relation of plankton crops to size of feeding sockeye populations have been obtained. At the same time, however, information on the plankton present in the lower strata of the lake has been collected and is available for consideration of their relation to the upper-strata plankton crops.

It may be of interest to note that, throughout his plankton work, Johnson has used a Clarke-Bumpus plankton sampler, Fig. 53, rather than the standard Wisconsin net (Fig. 54). The Clarke-Bumpus sampler measures the volume of water strained during each haul or tow and thus gives a reasonably accurate record of the plankton strained from a measured volume of water. Horizontal tows are made at various levels within the stratum being studied (e.g., 0–5 m, 0–10 m, 10–15 m, 15–20 m, 20–30 m, and 30–100 m), for definite periods of time, thus minimizing the error due to unequal horizontal distribution of plankton which must be inherent in the direct vertical plankton haul through a known stratum of water. (See Plate IX.)

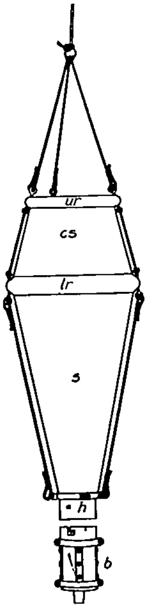

FIG. 54. Wisconsin plankton net. (b) detachable bucket, shown detached from headpiece, (cs) canvas sleeve between upper and lower rings, (lr) lower ring, (h) headpiece, (s) sleeve of silk bolting cloth between lower ring (lr) and headpiece (h), (ur) upper ring. The third supporting cord, extending from lower ring to headpiece, and the third supporting wire connecting upper and lower rings, are not shown in the figure. (From Welch, 1948, p. 240.)

Having obtained the plankton samples by Clarke-Bumpus sampler, analysis was made (Johnson, 1958) for *quality* by examining and counting sub-samples and for *quantity* by taking the dry and ash weights. On the basis of ash content, correction was made for diatoms, the only phytoplankton taken in abundance.

MULTIBASIN LAKES

Studies in British Columbia have indicated that the large, irregularly shaped lakes present special problems because of their multibasin character. This might

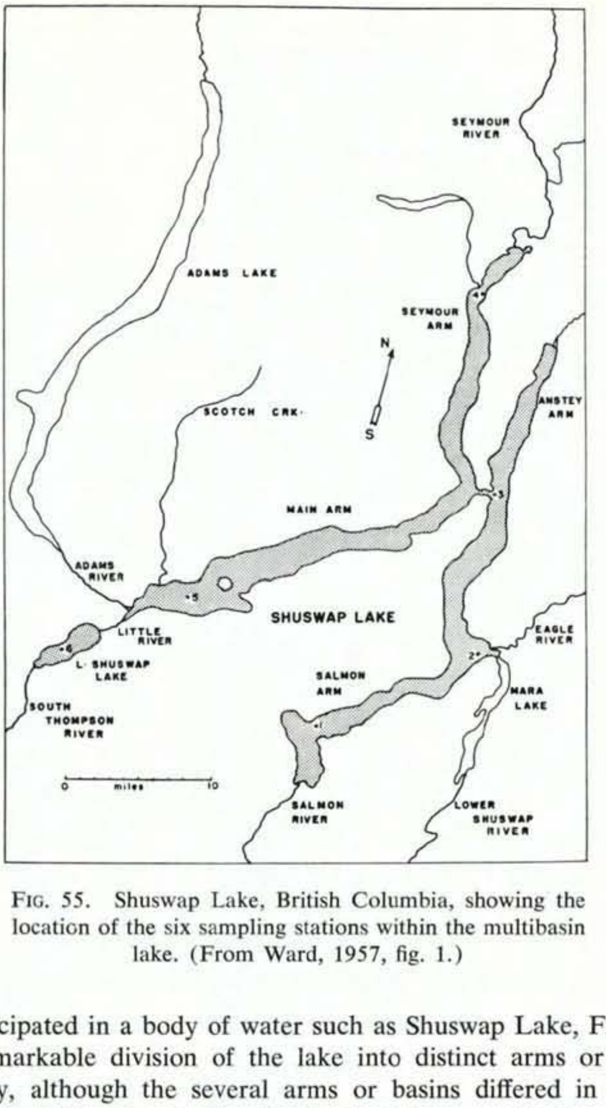

FIG. 55. Shuswap Lake, British Columbia, showing the location of the six sampling stations within the multibasin lake. (From Ward, 1957, fig. 1.)

perhaps be anticipated in a body of water such as Shuswap Lake, Fig. 55, because of the very remarkable division of the lake into distinct arms or fairly discrete basins. Actually, although the several arms or basins differed in many respects (Ward, 1957) the differences in the dissolved solids seemed to be most significant and to have had greatest effect in producing the marked differences found to occur in the plankton abundance. It seems then (Ward, 1957, p. 40) that the differences in plankton productivity between the major sections of the lake were real. Such plankton productivity differences will cause differences in the capacity of the various parts of a multibasin lake of this kind to produce sockeye. Each basin or division will require separate investigation.

Babine Lake, the major sockeye producing area of the Skeena River, a long, extremely narrow lake (see Plate X), is also of a multibasin type (Johnson, 1956). Seven distinct divisions, Fig. 56, have been recognized, based largely on morphometric characteristics, but other differences no doubt occur. Not only do substantially

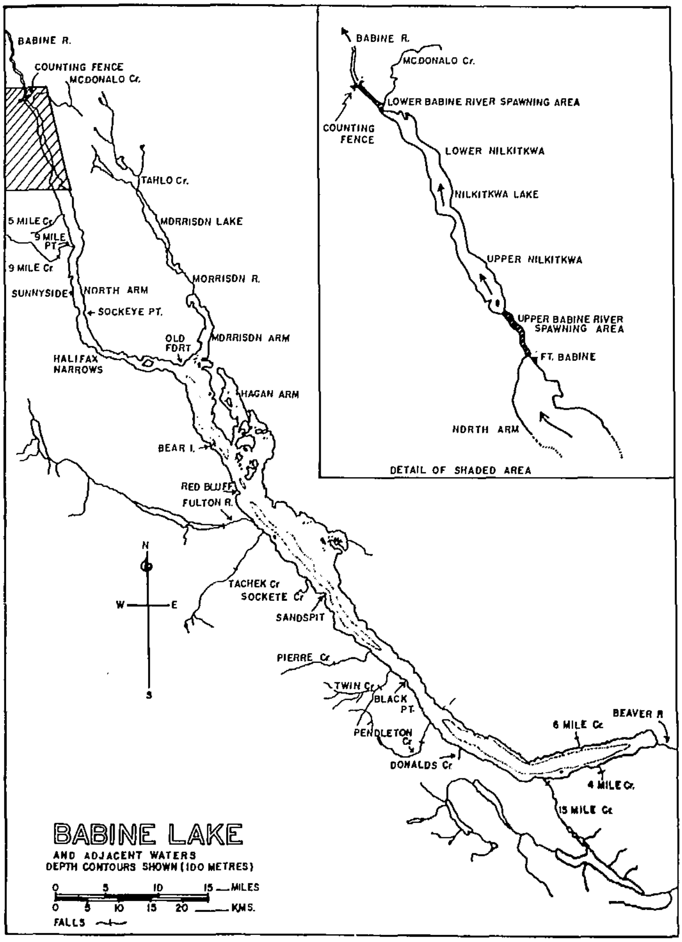

FIG. 56. Outline map of Babine Lake and adjacent waters. The seven basin areas into which the lake has been divided, as noted in the text, are shown.

varying levels of abundance occur in the young sockeye populations (Johnson, 1958) but there are differences also in the plankton biomass (Johnson, 1961). The latter involve not only quantitative, but also qualitative differences. Thus, as sockeye-producing areas, whose capacity is closely related to food conditions, each sub-basin must be dealt with separately.

Much the same situation prevails in Owikeno Lake, tributary to Rivers Inlet, Fig. 41. Although only preliminary studies have been made (W. E. Johnson, unpublished), plankton collections revealed that "zooplankton was considerably more abundant in the large main basin than in the others, but the quantity was generally low throughout (roughly in the range 2 to 15 mg/m^3 dry weight for the surface 20 meters)."

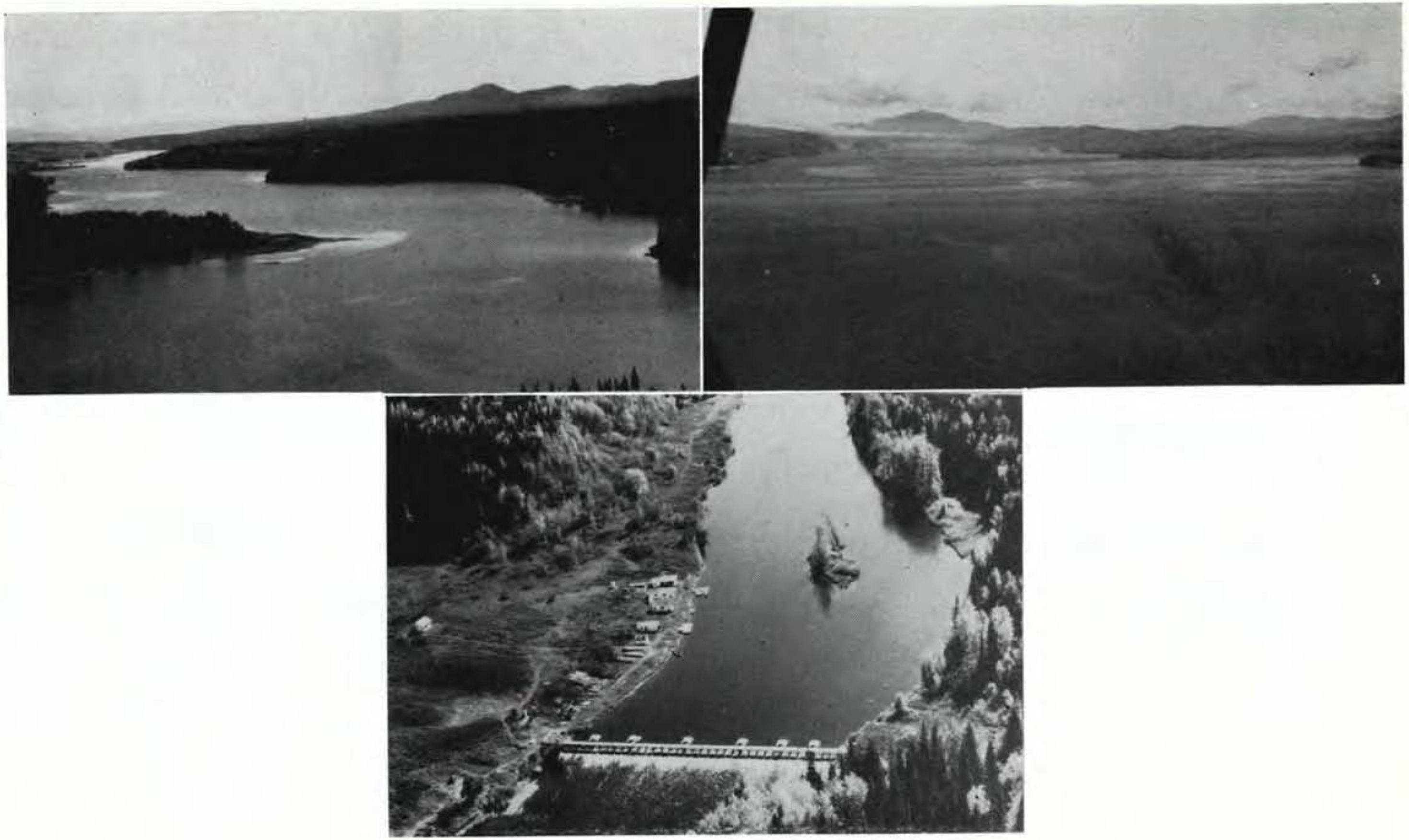

PLATE X. Babine Lake and Babine River.

Left: looking northward up Babine Lake from Halifax Narrows area, see Fig. 56.
Right: looking northward up Babine Lake from the Fulton River, (Fig. 56). The solitary high hill behind Old Fort can be seen in the distance.
Bottom: adult counting weir across the lower Babine River. The weir is provided with six traps into which the adult fish proceed for counting, examination, etc., see Plate II. The Babine River field station buildings are located on the left river bank.

STANDING CROP OF PLANKTON

RELATION OF STANDING CROP TO PLANKTON PRODUCTION

It is necessary, of course, to keep in mind, in any plankton study of a lake, that the plankton collections when they are made represent only the plankters present in the lake at that specific time. They represent what has been termed "the standing crop." During the year several generations of Cladocera and Copepoda may appear and disappear. In endeavouring to assess what the sockeye-producing capacity of a lake would be it thus seems necessary to multiply the amount of the standing crop of plankton by the number of generations occurring, or by the extent of "overturn," as it is called.

Accurate data on the number of generations of a plankter per year, i.e., of the "overturn," are lacking for sockeye lakes. Some estimates have been attempted, however, on the basis of available information.

For Cultus Lake, Ricker and Foerster (1948, p. 200) calculated the yearly consumption of plankton by the young sockeye to be 154 tons as compared with a standing plankton crop in the lake of 23.6 tons; this indicates a minimum turnover of crustacean plankters of 6.5 times a year. On the other hand, at Lake Dalnee, Kamchatka, it was found (Krogius and Krokhin, 1956a, p. 12) that the production of the copepod *Cyclops* was from 2 to 2.5 times greater than its biomass.

Both of these production estimates must be considered preliminary. Further research is required. It is to be expected that each genus, if not species, will differ in the number of generations per year; undoubtedly the conditions prevailing in a lake each season will have a bearing also. All factors must be made known if an estimate of the total plankton production of a lake, rather than merely its "standing crop," is to be obtained. An understanding of the plankton production during the active growing period in summer is of particular interest.

SUMMER STANDING CROP OF CERTAIN LAKES

The availability of comparable plankton data for a number of sockeye-producing lakes (Table 50) makes possible a consideration of their *relative* productiveness with respect to the crustacean plankters. When ranked according to *number* of plankters per litre the relative order—Cultus, Karluk, Dalnee, Lakelse, Blizhnee, Port John—is quite different from that when wet *weight* is considered—Dalnee, Karluk, Lakelse, Cultus, Port John, Blizhnee—which again emphasizes the value of considering the plankton on a weight or volume basis, rather than according to number. Too great reliance cannot be put on the comparative wet weight data in some instances, for in some cases weights have been computed from numbers, using average individual weights obtained in other areas. However, the data are quite sufficient to indicate how lakes can differ in plankton abundance and to stress that each sockeye lake must be studied individually to reveal its capabilities and potentialities.

For instance, the differences in plankton crops recorded for Cultus Lake and Lake Dalnee may be cited. According to Table 50 the differences in biomass or wet

TABLE 50. Average monthly abundance of crustacean plankters, during the summer season, July to Sept. in six lakes. All quantities are per litre of water (average, top to bottom).

	Cultus[a] B.C.	Lakelse[b] B.C.	Port John[c] B.C.	Karluk[d] Alaska	Dalnee[e] Kamchatka	Blizhnee[e] Kamchatka
Area						
(*Acres*)	1550	3520	224	9720	336	–
(*Hectares*)	627	1425	91	3934	136	–
Volume ($m^3 \times 10^6$)	201	22.4	22.8	1920	42.8	–
Depth, maximum (*m*)	42	25	49	126	60.0	–
Depth, mean (*m*)	30	6	25	4.8	31.5	–
Copepoda	12.2	5.0	7.1	12.6	11.3	5.1
Epischura	0.2	2.0	7	–	–	–
Diaptomus	–	–	0.07	–	1.1	–
Cyclops	12.0	3.0	0.03	–	10.2	5.1
Cladocera	4.2	0.66	0.57	2.4	2.1	0.4+
Daphnia	1.9	–	–	–	2.1	0.4
Bosmina	2.3	0.5	0.03	–	–	+
Holopedium	–	0.06	0.04	–	–	–
Polyphemus	–	–	0.07	–	–	–
Pseudosida	–	–	0.43	–	–	–
Diaphanosoma	–	0.1	–	–	–	–
Total no:	16.4	5.66	0.67	15.0	13.4	5.5
Wet wt (*mg*)	0.124[f]	0.246[g]	0.095[h]	0.597[i]	0.982[j]	0.36[j]

[a] Ricker, 1937b, p. 462. Average for three seasons, see Table 49.

[b] McMahon, 1954, p. 495. For one season only, 1949.

[c] Robertson, 1954, p. 645. Average of two seasons, 1949 and 1950.

[d] Juday et al., 1932. Average of four summers, 1927–1930.

[e] Krogius and Krokhin, 1948, p. 11. Average yearly quantity, 1937–38.

[f] *Epischura*—0.025 mg; *Cyclops*—0.005 mg; *Daphnia*—0.025; *Bosmina*—0.005 (Ricker, 1937b).

[g] *Epischura*—0.1 mg; *Cyclops*—0.01 mg; *Bosmina*—0.01 mg; *Holopedium*—0.1 mg; *Diaphanosoma*—0.5 mg (McMahon, 1948b).

[h] The weight units for Lakelse[g] have been used, with *Diaptomus*—0.1 mg.

[i] Weights, as established for Morrison Lake, Babine System (McMahon, 1948b): *Diaptomus*—0.09 mg; *Cyclops*—0.01 mg; *Daphnia*—0.05 mg; *Bosmina*—0.01 mg. Assumed that representation of Copepoda is 40% *Diaptomus* and 60% *Cyclops* and of Cladocera: *Daphnia*—50%, *Bosmina*—50%.

[j] *Diaptomus*—0.108 mg; *Cyclops*—0.062 mg; *Daphnia*—0.11 mg (Krogius and Krokhin, 1948, p. 11).

weight per litre are: Cultus Lake—0.124 mg; Lake Dalnee—0.982 mg. Cultus Lake is thus approximately one-eighth as rich in crustacean plankton as Lake Dalnee. It is clear, then, according to Krogius and Krokhin (1948, p. 12) that, in order to obtain adequate food, the young in Cultus Lake are forced to expend much more energy in searching for food than at Lake Dalnee. Hence, one can understand why the young sockeye at Cultus Lake are much smaller than in Dalnee. It also suggests that the abundance of food in a lake may be one of the factors which de-

TABLE 51. Species of crustacean plankters occurring in 10 lakes of the Skeena River system and in certain other sockeye-producing lakes. A—abundant; N—numerous; C—common; O—occasional; R—rare. Relative abundance of plankters in lakes 11–19 are the author's approximations.

Name of lake	Area (mi^2)	Area (ha) (1×10^3)	Volume (m^3) (1×10^6)	Depth (ft)	Depth (m)	Copepoda: Heterocope	Copepoda: Diaptomus	Copepoda: Epischura	Copepoda: Cyclops	Cladocera: Daphnia	Cladocera: Bosmina	Cladocera: Diaphanosoma	Authority
Skeena River system:													
1. Morice	40	10.36	10,326	775	236	–	–	N	A	–	N	–	McMahon (1949)
2. Kitsumgallum	6.8	1.76	1,248	400+	122+	–	N	–	N	–	–	–	McMahon (1949)
3. Babine	171.8	44.50	26,549	680	207	N	A	R	A	O	O	–	McMahon (1949)
4. Swan	10.8	2.80	636	210	64	N	N	–	A	N	N	–	McMahon (1949)
5. Alastair	2.3	0.60	137	236	71.9	–	–	–	A	N	A	–	McMahon (1949)
6. Morrison	5.6	1.45	297	200	61	N	A	–	A	N	N	–	McMahon (1949)
7. Bear	7.3	1.89	240	240	73.1	N	A	–	A	O	N	–	McMahon (1949)
8. Lakelse	5.5	1.42	108	98	32.2	–	–	A	A	–	N	N	Brett (1950)
9. Stephens	3.1	0.80	85.6	85	25.9	N	A	–	A	–	N	–	McMahon (1949)
10. Kitwanga	3.0	0.73	5.2	44	13.4	–	A	–	A	A	O	–	McMahon (1949)
Fraser River system:													
11. Harrison	–	–	–	–	–	–	N	–	N	O	A	–	Foerster (1925)
12. Cultus	2.4	0.63	201	137	42	–	–	O	A	C	C	–	Ricker (1938)
13. Shuswap	119.5	31.0	19,128	530	161.5	–	A	O	C	C	C	–	Ward (1957)
14. Anderson	10.9	2.8	3,701	705	215	–	C	O	A	A	C	–	Geen and Andrew (1961)
15. Seton	9.4	2.4	2,110	494	157	–	C	O	A	A	C	–	Geen and Andrew (1961)
Central British Columbia coast:													
16. Port John	0.35	0.09	23	160	48.8	–	N	–	C	–	A	–	Robertson (1954)
Alaska:													
17. Karluk	15.2	3.9	1,919	413	126	–	N	–	A	C	C	–	Juday et al. (1932)
Kamchatka:													
18. Dalnee	0.5	0.136	42.8	197	60	–	C	–	A	C	–	–	Krogius and Krokhin (1948)
19. Kurile	29.0	7.52	13,200	1,004	306	–	–	–	A	A	–	–	Egorova et al. (1961)
Wet wt in mg/100 individuals—													
(McMahon, 1948)						25	9	10	1	5	1	5	
(Ricker)								5	1	5	1		
(Krogius and Krokhin)							10.8		6.2	11			

termines the length of residence of the young sockeye in fresh water (migration of 1- and 2-year-old smolts from Lake Dalnee, mostly yearlings from Cultus Lake, and chiefly fingerlings from the streams and springs of Kamchatka). This matter is discussed below, p. 269.

VARIATION IN COMPOSITION OF PLANKTON AMONG LAKES

It is to be expected that, among lakes, there will be quite a variation in the species and genera of crustacean plankters found in them. Though studies of the food of young sockeye in lakes (see p. 166–170) have indicated that certain crustaceans seem to be preferred, probably related to the size of the young fish and the time of year and the availability of the plankton in adequate numbers, the actual food constituent must obviously depend on what crustacean plankters occur in a lake and are available as fodder.

In Table 51 are shown the distribution and relative abundance of the more common crustacean plankters in a variety of sockeye-producing lakes, as revealed by plankton samplings during the summer months. Although the species may be different in the various lakes, the genera occur quite widely. The nonrecording of a genus in any area does not necessarily mean that it is altogether absent for in many of the Skeena lakes, the samplings were largely exploratory and preliminary. An

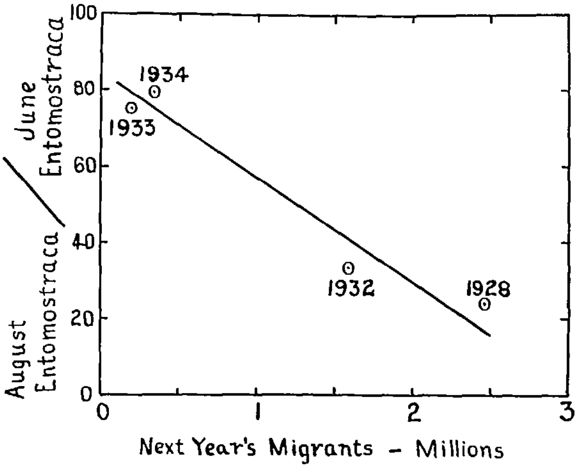

FIG. 57. Relationship between abundance of planktonic crustaceans in Cultus Lake in the summer and the number of young sockeye feeding in the lake. The ordinate scale represents the mean abundance of plankton in August, as a percentage of the mean abundance in June for each year. The abscissal scale relates to the number of sockeye migrants counted leaving the lake the following spring, here regarded as roughly proportional to their abundance the previous summer. (From Ricker, 1937b, fig. 5.)

indication of the relative importance of the genera from a biomass or weight point of view is given by noting, last item of Table 51, the approximate weight which is indicative, more or less, of size or bulk. One point worthy of notice and further investigation is the wide disparity in size of the *Cyclops* and *Daphnia* at Cultus Lake and Lakelse Lake and those in Kamchatka (Lake Dalnee). When queried on this point, Dr Krokhin (personal communication) intimated that this difference had amazed him also, and, since the weights of Lake Dalnee crustaceans agree with other weight records known to him, he marvels at the low Cultus Lake weights rather than the high ones in Kamchatka lakes.

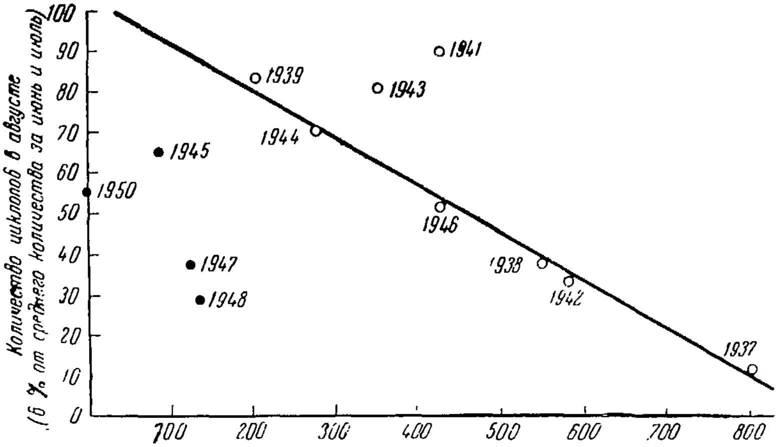

FIG. 58. Relationship between the consumption of *Cyclops* in Lake Dalnee (abundance in August as a percentage of the abundance in June and July) and the numbers of seaward-migrating young sockeye in the following year. Since the ration of yearling sockeye is four times greater than that of fingerlings, the number of young is expressed as the sum of the number of migrating yearlings and four times the number of 2-year-old migrants. (Taken from Krogius, 1953, fig. 2.)

REDUCTION OF PLANKTON CROP BY FEEDING OF YOUNG SOCKEYE

The fact that the quantity of plankton food in a nursery lake may be of real significance is suggested by evidence obtained at Cultus Lake (Ricker, 1937b, p. 465) and at Lake Dalnee (Krogius, 1953, p. 219), which showed the decrease in plankters during the summer as a result of the "cropping" by the young sockeye. In Fig. 57 and 58, the August plankton standing crops, computed as a percentage of the numbers of plankters present in June, i.e., before active feeding has commenced, are shown in relation to the presumed population of young sockeye in the lake.*

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* In a recent paper (Egorova et al., 1961, p. 445) reference is made to the use, by Krohkin (1958), of copepod nauplii, a juvenile stage of copepods and which are rarely eaten by sockeye, as a measure of plankton abundance rather than the adult stages, as here discussed.

For 4 years at Cultus and 12 years at Dalnee an inverse relationship occurred between the size of the sockeye population feeding in the lake and the abundance of crustacean plankters in August, thus indicating a keen competition for food. This competition became most severe in years of large populations of young feeding sockeye in a lake, bringing about a slower growth-rate, a smaller size at migration time and an increase in the carryover of the smaller nonmigrants for a 2nd year. In addition to the competition among the sockeye, there is present also the demand for food by other fish in the lake. In Lake Dalnee the consumption of plankton by large populations of the three-spined stickleback is an important factor. This will be further discussed below (p. 236).

Reference may be made again to the quite interesting situation at Lakelse Lake in 1955 (W. E. Johnson, unpublished data). Here, where the young sockeye population in 1955 was known to be of relatively low density, the greatest growth occurred during June (Fig. 52) when zooplankters were most abundant. Water temperatures throughout the summer period varied little and thus the decline in growth rate of the sockeye from July on was felt to be due to the declining availability of the zooplankton food. Extremely low phosphate levels in August and September and the paucity of phytoplankton suggest low nutrient levels as the basic cause of the decline in zooplankton abundance.

OTHER PERIODS OF PLANKTON SCARCITY

There may well be other periods during the lake residence of sockeye when a scarcity of plankton occurs. This may cause not only a retardation in the growth-rates, but even an increase in mortality. Adequate supporting evidence is lacking, but we may hypothesize.

A comparison of the qualitative composition of the food in the stomachs of young sockeye from Cultus Lake with the crustacean plankters in the lake (see Fig. 30) revealed that the young sockeye ate relatively few *Cyclops* that were abundant in the lake in May and June, but fed more heavily on the much scarcer *Bosmina* and *Daphnia*. Thus, in the early part of the season there may be a period of severe scarcity of the types of plankton food suitable for the very young fish.

Actually, one very critical period in the life of young sockeye may indeed be that when the young newly hatched fry first take up lake residence. Very little study has been given to the nutritional needs of the fry at this time when a natural transfer is being made from yolk feeding to ingestion of plankton food substances. There would seem to be good chance, here, for heavy mortality to occur, if, at the time the young fry appear in the lake, the appropriate small plankters are not readily available to them.

How close and precise a synchronization of the proper food at the moment of entry into the lake Nature normally provides is not known. It is a period when mass mortality could occur and contribute to the lack of correlation between (1) the eggs deposited or fry hatched and (2) the numbers of seaward migrants produced or adults returning to spawn.

This may indeed be a very critical situation in the case of hatchery-produced fry released into a lake. Large-scale liberation at an inopportune time, so far as available food of the proper size is concerned, may be utterly ruinous and lead to heavy mortality of the released fry. Normally Nature may arrange the proper timing of availability of the right plankton food to the newly arrived fry so that there be but little loss. There may, however, be years when the timing is not right, and heavy losses in fry occur. In artificial propagation and release of fry, is any consideration given to such timing? Little pertinent data are available. They should be obtained and fully utilized, if success in artificial propagation is to be effectively undertaken.

Chapter 9. Young sockeye in the lake's community of fishes

FISH ASSOCIATES OF THE SOCKEYE IN FRESH WATER

In considering the development and survival of young sockeye during their period of lake residence, it must be recognized that they constitute but one segment of a very active and dynamic community within the lake. Many other species of fish are also present whose relationships with the young sockeye may be either quite close or quite remote. In some cases the interrelationships may be relatively intimate throughout the period of the sockeye's residence; in others, they may be temporary, either in time (i.e., season), in stage of development (i.e., as young fish or as adults), or in location (i.e., when their areas of distribution overlap).

In Table 52 are listed the various species of fish which have been encountered in those sockeye-producing lakes of British Columbia which have thus far been examined. The species have been arranged according to general location within a lake, but the divisions are by no means hard and fast. There are many species which change their habitat as they grow and develop, or according to the season of the year, even as do the young sockeye. In one lake, the habitat and habits may be quite different from those in another. Nevertheless, so far as is known, those species which frequent the open-water or limnetic regions of a lake are of greatest interest to us and of greatest concern to the young sockeye.

Early in the investigation of sockeye production in the Skeena River system, northern British Columbia (Fig. 7), a study of the various lakes in the Skeena Basin was initiated in order to get some understanding of their fish fauna, i.e., of those species of fish with which the sockeye would be associating during their period of lake residence. Gill nets were used and a standard form of fishing was set up in order that the fishing effort from lake to lake might be more or less comparable. A standard "gang" of nets consisted, then, of a series of five nets, each 50 yards (46 m) long, including one each of meshes 1, 2, 3, 4, and 5 inches stretched (between every second knot). A series of nets was either completely of linen or of cotton thread, but not mixed. If sets were made at right angles to the shore and thus from shallow water out into deeper areas, the sequence of the graded meshes was changed from time to time so that, for instance, each small-mesh net was in shallow water as often as in deep. No set was allowed to remain out for more than 24 hr. The catches in each lake could then be expressed as the catch per net night.

The data obtained for the Skeena River lakes are given in Table 53 and may serve as a guide to the relative abundance of the various species of fish, other than the anadromous salmon. Since catches were made by gill net, only those fish which

Table 52. List of fishes, other that young sockeye salmon, found in sockeye-producing lakes of British Columbia. X indicates presence of a species. Sources as follows: Cultus (Ricker, 1933); Port John (Robertson, 1954); Lakelse (Brett and Pritchard, 1946a); Morice (Brett and Pritchard, 1946b); Kitwanga (McConnell and Brett, 1946); Kitsumgallum (Brett, 1946); Bear (Foskett, 1947a); Upper Sustut (Foskett, 1947b); Morrison (McMahon, 1948a); Lac-de-dah (Withler, MS, 1948); Babine (Withler, McConnell, and McMahon, 1949); Shuswap (Clemens et al., 1938).

		Cultus	Port John	Lakelse	Morice	Kitwanga	Kitsumgallum	Bear	Upper Sustut	Morrison	Lac-de-dah	Babine	Shuswap
Open lake areas:													
Cutthroat trout	*Salmo clarki*	x	x	x	–	x	x	–	–	x	–	–	–
Rainbow trout	*S. gairdneri*	–	x	x	x	–	–	x	x	x	x	x	x
Dolly Varden (char)	*Salvelinus malma*	x	x	x	x	x	x	–	x	–	x	–	x
Coho salmon	*Oncorhynchus kisutch*	x	–	–	–	–	–	x	x	x	–	–	x
Kokanee salmon	*O. nerka kennerlyi*	–	–	–	–	–	–	x	–	x	–	x	x
Squawfish	*Ptychocheilus oregonense*	x	–	x	–	x	–	–	–	x	–	x	x
Deep water:													
Lake trout	*Cristivomer namaycush*	–	–	–	x	–	–	x	–	x	–	x	–
Burbot	*Lota maculosa*	–	–	–	–	–	–	x	x	x	–	x	x
Lake whitefish	*Coregonus clupeaformis*	–	–	–	–	–	–	x	–	x	x	x	x
Rocky Mountain whitefish	*Prosopium williamsoni*	–	–	x[a]	x	x	–	x	x	x	x	x	x
Largescale sucker	*Catostomus macrocheilus*	x	–	x	–	–	–	–	–	–	–	–	x
Longnose sucker	*C. catostomus*	–	–	–	x	x	–	x	–	–	x	x	x
White sucker	*C. commersoni*	–	–	–	–	x	–	x	–	–	–	x	–
Shallow water:													
Peamouth	*Mylocheilus caurinum*	–	–	x	–	x	–	–	–	x	–	x	x
Redside shiner	*Richardsonius balteatus*	x	–	x[a]	–	x	–	x	x	–	–	x	x
Lake chub	*Hybopsis plumbea*	–	–	–	–	–	–	–	x	–	–	x	–
Longnose dace	*Rhinichthys cataractae*	–	–	–	–	–	–	–	–	–	–	x	–
Leopard dace	*R. falcata*	–	–	–	–	–	–	–	–	–	–	–	x
Carp	*Cyprinus carpio*	–	–	–	–	–	–	–	–	–	–	–	x
Threespine stickleback	*Gasterosteus aculeatus*	x	x	x[b]	–	x	–	–	–	–	–	–	–
Prickly sculpin	*Cottus asper*	x	x	x[a]	x	–	–	x	–	–	–	x	x
Coast-range sculpin	*C. aleuticus*	x	–	–	–	–	–	–	–	–	–	–	–

[a] Taken in fyke nets.

TABLE 53. The relative abundance of various species of fish in the lakes of the Skeena River drainage basin, as indicated by the catch per net night of a standard series of gill nets 1- to 5-inch mesh (+ = present).

Lake	No. of years of netting	Total no. of sets involved	Kokanee	Pea-mouth	Squaw-fish	Dolly Varden char	Cut-throat trout	Rain-bow	Lake trout	Burbot	Lake white-fish	Rocky Mountain whitefish	White sucker	Large-scale sucker	Long-nose sucker
Lakelse	6	1083	–	5.16	1.56	0.04	0.88	+	–	–	–	0.31	–	0.30	–
Babine	4	2152	1.60	0.82	0.44	–	–	0.16	0.17	0.04	0.17	0.84	0.09	–	0.25
Kitsumgallum	2	60	–	23.14	–	1.39	2.61	–	–	–	–	1.22	–	–	–
Kitwanga	3	75	0.15	3.29	2.16	0.08	0.99	–	–	–	–	0.71	–	–	0.31
Stephens	2	40	–	–	–	0.60	–	0.15	–	–	–	2.30	–	–	2.30
Morice	1	50	–	–	–	0.18	–	0.16	–	–	0.72	1.02	0.02	–	3.12
Alastair	1	15	–	1.10	–	0.30	1.20	–	–	–	–	0.60	–	–	0.90
Morrison	3	140	0.42	0.33	0.52	0.00	0.03	0.10	0.34	0.05	1.65	0.11	0.02	–	0.11
Bear	3	150	0.30	–	–	0.65	–	–	–	–	1.27	2.58	0.08	–	–
Sustut	1	6	–	–	–	1.67	–	0.33	–	–	–	11.50	–	–	–
Johanson	1	3	–	–	–	0.89	–	–	–	–	–	3.00	–	–	–
Motase	1	3	–	–	–	0.33	–	–	–	–	–	0.33	–	–	0.33
Kluayaz	1	3	–	–	–	–	–	–	–	–	–	2.33	–	–	3.25
Damshilgwit	1	3	2.33	–	–	1.83	–	0.17	–	–	–	3.83	–	–	–
Slamgeesh	1	6	0.02	–	–	2.67	–	0.33	–	–	–	4.33	–	–	0.50

could be caught by a 1-inch or larger mesh net are included. Many species of small size may be present in the lake, but not indicated in the list. Then, too, since in many lakes only limited time could be given to the netting, a full coverage of the lake area was impossible. Therefore, there may have been other species of fish in the lake which frequented areas not netted. In other words, Table 53 is not to be taken as a complete record of the fish in any lake. It represents merely a carefully conducted survey.

Two types of fishes are of greatest significance to the well-being of young sockeye—those which compete with them for plankton food and those which prey on them. We shall discuss these in turn below.

COMPETITORS FOR FOOD

For Cultus Lake it is reported (Ricker, 1937b, p. 464) that, though a number of fish which eat plankton are present,

> "during the summer season of rapid growth none of these appear to be serious competitors of the sockeye. The Aleutian sculpins may intrude on the sockeyes' feeding grounds from below, and the minnows and sticklebacks impinge on its lateral borders. But throughout the whole pelagic region, comprising four-fifths of the lake's area, the sockeye appear to be without serious rivals."

This suggested lack of competition for plankton food during the summer months would seem to prevail in most of the British Columbia lakes which have been examined. During the summer most of the likely competitors—peamouth and redside shiners—are restricted largely to inshore areas, as are also the young of the squawfish. The situation during winter months may be quite different and many of the species may, at that time, be present in the deeper waters of the lake and in competition there for the available food. At that season, of course, there is little growth and presumably a decreased amount of feeding.

LAKE WHITEFISH *(Coregonus clupeaformis)*

This species, locally known as "eastern" whitefish, is in most places mainly a bottom feeder. At Morrison Lake, tributary to Babine Lake, they had adopted an unusual feeding habit and ate the same plankters as young sockeye, their diet being made up almost entirely of copepods (McMahon, 1948a, p. 8). Since eastern whitefish are rather abundant in Morrison Lake, they "thus become a serious food competitor." To what extent this same situation may apply in other lakes frequented by eastern whitefish is not known. The feeding of this species and of the Rocky Mountain whitefish on plankton in Babine Lake has been recorded (Withler et al., 1949, p. 9), but the overall significance of the competition with young sockeye needs further study.

THREESPINE STICKLEBACK *(Gasterosteus aculeatus)*

This species, though present in several British Columbia sockeye-producing lakes, has not been observed to be a serious food competitor. It has been recorded as present in Owikeno Lake, tributary to Rivers Inlet, in very large numbers (FRBC, 1958, p. 99). At Cultus Lake, there seemed to be an increase in the abundance of sticklebacks, after an intensive predator fish reduction campaign had been waged for 2–3 years, thus suggesting that a decline in predators might produce an increase in competitors. No actual data to substantiate these observations are available.

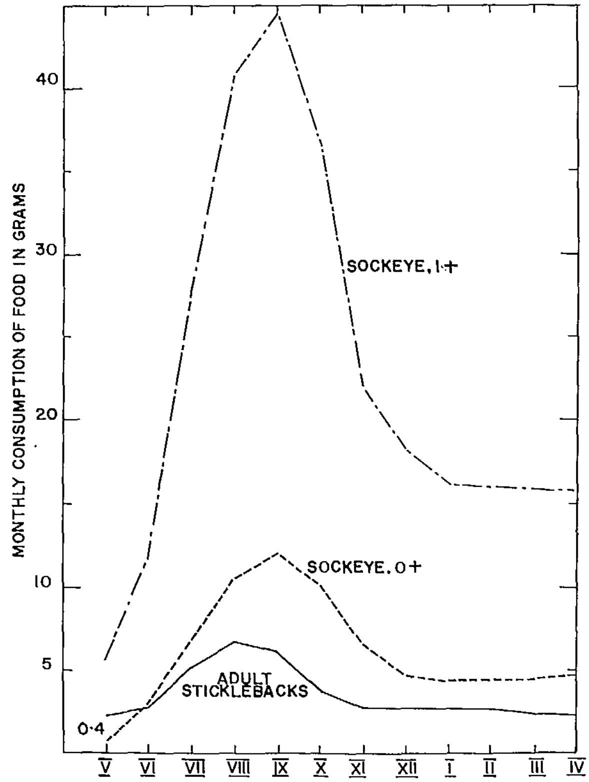

FIG. 59. Monthly consumption of food (copepods), in grams of wet weight, of adult sticklebacks, sockeye fry, and fingerlings (O+ age-group) during their 1st year in the lake and yearling sockeye (1+ age-group) during their 2nd year in the lake. (Data from Krokhin, 1957b.)

In Alaska (e.g., the Wood River Lakes, Karluk Lake) and Kamchatka (e.g., Lake Dalnee), however, the threespine stickleback* has been recognized as the most serious food competitor of young sockeye. It subsists on the same planktonic Crust-

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* For a description of the life history, habits, growth, etc. of the species, see Greenbank and Nelson (1959).

acea; it frequents the same lake areas—inshore waters during early fry stage, and the pelagic region in fingerling and yearling stages. It can be very abundant. In Lake Dalnee, unusual numbers were reported for 1945, 1947, 1948 (Krogius and Krokhin, 1956b, p. 147) when "500–1000 specimens were taken at a time in a fine-meshed net when this net usually caught 20–30 specimens;" in Lake Nerka (Burgner, 1960) much larger catches of sticklebacks than of sockeye fry were made in both inshore and pelagic regions.

Because of its importance as the principal competitor of the young sockeye for food, a very careful study was made at Lake Dalnee, Kamchatka, of the food ration of sticklebacks, for comparison with that of the young sockeye (Krokhin, 1957b). Only adult sticklebacks, having an assumed weight of 4.5 g, were considered, since only the older fish are present in the open waters of the lake and compete with the young sockeye there, probably for at least 2 years. The life span of *Gasterosteus aculeatus* has been given as 2¼ years for Alaskan waters (Greenbank and Nelson, 1959) while elsewhere it is stated (Jones and Hynes, 1950, p. 60)that "the most widely accepted opinion is that they live for 3 or 4 years."

The monthly consumption of food by an adult stickleback, expressed as grams wet weight of the copepod, *Cyclops*, during the year, is indicated in Fig. 59. A marked increase occurred from June to October. Also shown are similar curves for young sockeye during their 1st year in the lake (0+) and during their 2nd (1+). In these cases, however, the actual weights, in grams, attained by the fish (an average of 2 years' data) are used.

For the year the total food consumption for stickleback amounts to 42.49 g, while that for the 0+ sockeye is 72.7 g. In other words, each adult stickleback consumes, during the active summer growing season and also over the whole year, over one-half as much food as a young fingerling sockeye. It can readily be appreciated, therefore, how serious a heavy crop of actively feeding sticklebacks can be in affecting the growth and well-being of young sockeye in the same waters.

KOKANEE *(Oncorhynchus nerka kennerlyi)*

This fish, a nonmigratory form of the sockeye salmon, eats plankton almost entirely and so constitutes the anadromous sockeye's greatest competitor for food (Withler et al., 1949, p. 9). Present in varying abundance in many of the larger sockeye-producing lakes, kokanees present a serious problem, for in some areas they are quite abundant and thus must cause a heavy drain on limited plankton resources.

Unfortunately, very little information is available, primarily because there has been, as yet, no way of distinguishing young kokanee from young sockeye in a lake. Therefore, it has been impossible to determine, from catches of the young in a lake, the relative abundance of the two forms. No data are available, either, on the relative densities of spawning within a lake on which one might attempt to compute the relative fry hatch and abundance of feeding young.

At the present time the problem is being attacked at Babine Lake where competition among the young of the two forms may be a very important factor in sockeye production. Populations of both forms are present at varying levels of abundance.

Reference may here be made to observations carried out at Cultus Lake (Ricker, 1938c) on kokanee present in the lake and apparently resulting (Ricker, 1959b, p. 900) from the accidental and undetected escape of individuals being reared in ponds for transplantation purposes (Foerster, 1947). In size the 26 specimens netted in the lake were appreciably heavier (mean weight of 8 specimens—500 g or 1.1 lb) than found in a variety of British Columbia lakes where the average weight was "considerably less" than 1 lb (Dymond, 1936); they were longer (range in fork length of 20 specimens captured in 1935—30.0–40.3 cm) than those found in Kootenay Lake where the variation in mean fork length during 1951–54 was 15.62–24.66 cm (Vernon, 1957, p. 587); and they were fully mature when caught (last week of August and first of September). Both sexes were equally represented. At the present time, the kokanee are not known to have persisted in Cultus Lake; at any rate they are too scarce to be competitive with young sockeye for food.

YOUNG SOCKEYE OVER ONE YEAR OLD

In Fig. 59 there is also given the curve of food consumption for those young sockeye that remain in the lake for a second season. The heavy drain on the food resources of a lake during the summer months is readily apparent. There is also distinct competition for food, even though it be intraspecific. Each yearling or older sockeye (1+) consumes 271.5 g of *Cyclops* during the year or as much as 3.7 fingerling (0+) sockeyes would.

Since in Kamchatka there appears to be no greater percentage return from the ocean of young sockeye which have gone to sea as 2-year-olds than as yearlings (Krogius and Krokhin, 1948, p. 17),

> "it follows that two years' residence of young sockeye in a lake, from the fish management point of view, is irrational since, on the basis of the food eaten by the 2-year-old young, 4 times as many yearlings could be fed and be available for seaward migration. This, in turn, would give a much greater absolute return from the sea. It is desirable, therefore, to investigate thoroughly the causes of the different periods of lake residence of young sockeye and find some means of controlling it" (Krokhin, 1957b, p. 108).

DWARF OR RESIDUAL SOCKEYE

In some Kamchatka lakes, e.g., Lake Dalnee (Krogius and Krokhin, 1954), dwarf male sockeye are found which, like the kokanee referred to above, mature in fresh water without going to sea. They are present, also, in some British Columbia lakes and have been designated as "residual" sockeye (Ricker, 1938c). A more comprehensive discussion of them is given below, p. 285.

From studies at Cultus Lake (Ricker, 1938c) it is suggested that in the spring of each year at the time of seaward migrations, three overlapping length groups occur among the young sockeye. One group of large average size does not migrate but remains in the lake to mature mainly that same autumn, rarely in 1 of the following 2 years. The second group of intermediate size migrates seaward as yearlings. The third group of small average size remains in the lake. Of these, when next year's migration time approaches, the larger continue to reside in the lake and mature as 3rd-year residuals; the smaller mostly take part in migration, but a few remain in the lake and mature in their 4th year.

Residuals in Cultus Lake were predominantly of male sex, maturing usually in the autumn of their 2nd or 3rd year but to some extent in the 4th. The less common females matured in the autumn of their 3rd and 4th year. In size the residuals were, like the kokanee, relatively small—16–38 cm in fork length. At spawning time they did not exhibit, in Cultus Lake, the brilliant scarlet-red colouration of normal sockeye and most kokanee, tending rather to be of a dull olive-gray hue; but this is not true in all lakes (Ricker, 1938c, p. 209).

Subsisting, like the kokanee, on identically the same plankton crustaceans as young sockeye, but on obviously a much greater quantity per fish, the residuals are also a distinct competitor for food. Although, according to Krogius and Krokhin (1954), dwarf sockeye males occur in Lake Dalnee every year they may, in some years, be unusually abundant. The year-classes of 1946 and 1949 were phenomenally numerous. Populations of dwarf males were found in Lake Blizhnee in 1952 for the first time. It is thought they probably exist also in Kurile Lake, one of the best sockeye-producing areas of Kamchatka.

OTHER FOOD COMPETITORS

In addition to the threespine stickleback, other food competitors of lake-dwelling young sockeye, recorded as occurring in Kamchatka waters, are the pond smelt (*Hypomesus olidus*) and the ninespine stickleback (*Pungitius pungitius*) (Krogius and Krokhin, 1956a). The former, found principally in one of the few important lakes of the Kamchatka River basin, Azabach Lake, is quite abundant, apparently, and bears the same interspecific relationship to the young sockeye as the threespine stickleback in other areas. Azabach Lake lies at quite a low elevation, is within tidal influence and is brackish in part; the smelt is a migratory form.

For those sockeye found in the Kamchatka River and in springs elsewhere (e.g., Karymai Spring on the Bolshaya River; see p. 138) the competition for food involves all of the spring-resident young fish, the fry and fingerling sockeye, the young coho and char which feed principally on the tiny bottom organisms (larval insects, Crustacea) and on the adult insects that fall onto the surface of the water (Semko, 1954a, p. 74). Synkova (1951) reports that the fry of almost all species of salmon were feeding primarily on larval chironomids, adult insects, harpacticids (small copepods), ostracods, and the cladoceran *Chydorus*.

CONSIDERATION OF THE FOOD-COMPETITION FACTOR IN ENDEAVOURING TO INCREASE PRODUCTION OF YOUNG SOCKEYE SALMON

The evidence is clear that there is definite competition for food in lakes between young sockeyes and young sticklebacks, and that where and when the latter are abundant they may seriously reduce the quantity of plankton food for the sockeye.

In order, then, to improve conditions for production of young sockeye, one obvious approach would be to cut down the populations of sticklebacks.

Solution of the problem is not quite so simple, however. Further investigation must be made of the full role of the stickleback in the lake community. It has been found, as referred to in the next section, that the sticklebacks are the food of the char, *S. malma*, which also preys heavily on young sockeye. The sticklebacks, therefore, may be an important buffer for young sockeye in the predation by char. Before reducing their numbers it is desirable to ascertain whether the sticklebacks are more beneficial as a buffer food for char than more harmful as a food competitor. Complete satisfaction might be provided by the large-scale removal of *both* sticklebacks, a food competitor, and char, a predator. The feasibility of such action deserves careful attention.

The same situation undoubtedly applies to the kokanee and residual sockeye populations in a lake. These wholly lake-resident forms of sockeye are most intimate and serious food competitors wherever they are present in abundance but to what extent they act as a valuable alternative food for sockeye predators has yet to be determined. Here again, in any management scheme which attempts to increase sockeye production, the reduction of both competitors and predators may be quite effective. Reduction of kokanee and residual sockeye populations may be readily accomplished by netting or by trapping in the spawning streams.

PREDATION

That type of community association of fishes which is commonly known as the predator-prey relationship represents one link in the normal food chain of the fishes involved. It is a natural development within a lake or stream community, but under certain circumstances it may be a quite serious one in limiting the survival of species which it may be desired to increase.

The feeding of predator fish on young sockeye fry between the time of their emergence and their entrance into the lake has already been discussed (p. 154–159). During the young sockeye's residence in a lake it is of equally great significance, if not greater. Its extent depends largely on the distribution and activities of both the predator and the prey (i.e., where they are in the lake at the different seasons of the year or how closely they may be associated), and on the particular behaviour of the predator and prey species. Some predators are most active at certain times or on particular size ranges of the prey; others at other times and on different size groups.

Since there is a close, direct relationship between the number of seaward-migrating young (generally called "smolts") and the return from the sea of adults, the most important predators are those which prey on the young sockeye just prior to or during seaward migration. In any attempt to increase sockeye production, these predators should have first attention leading to reduction in numbers. All predators, however, are of significance and their depredations should be limited as much as possible.

PREDATION STUDIES AT CULTUS LAKE

An investigation of the propagation of sockeye salmon at Cultus Lake (Foerster, 1929b) revealed that the losses of young sockeye during their year's residence in the lake were very heavy. They amounted to approximately 96% of the eggs contained in all the females going to the spawning grounds. The activities of predator fish were considered as perhaps responsible in greater or lesser degree. A study was, therefore, initiated to ascertain what predators were present in the lake, to what extent and at what times of year they preyed on the young sockeyes, and just how much destruction they caused.

TABLE 54. Total number of net-nights of gillnet fishing, arranged according to size of mesh used, Cultus Lake, 1932–38 (Foerster and Ricker, 1941, p. 317).

Mesh size (*inches*)	5	4.5	4	3.5	3	2.75	2.5	2.25	2	1.75	1.5	
(*mm*)	127	114	102	89	76	70	64	57	51	44	38	
Year						Net-nights						Total
1932[a]	8	22	22	22	22	22	21	21	21	21	21	223
1933[a]	7	15	15	9	15	15	15	15	15	15	15	151
1934[a]	17	17	21	17	17	21	17	17	21	10	21	196
1935[b]	71	371	419	440	423	341	318	241	250	–	–	2854
1936[b]	–	414	332	624	768	1390	1917	548	688	66	66	6813
1937[c]	–	52	36	63	431	1508	1844	610	934	–	–	5551
1938[c]	–	10	19	105	330	759	1004	761	461	–	–	3458

[a] Exploratory gillnetting, with a very limited amount of gear and at a few selected setting locations.

[b] In May, 1935, the netting programme was expanded. From then until October the number of nets was increased and the settings were made fairly continuously. In 1936, a further increase in netting occurred, especially among the medium-sized meshes, i.e., from 2 to 3 inches (51 to 76 mm).

[c] In 1937, the larger meshes, catching but few fish, were used less often, and similarly in 1938, but in this year the data cover only netting operations from January to June.

In 1932–34 exploratory gillnetting was carried out in the lake (Ricker, 1933, 1941) with a graded series of meshes (see Table 54), the gang of nets being set from shore outward and left in the water for periods of around 24 hr (overnight), rarely for 2 nights.

The fish caught by the gill nets in the early years are included in the tabulated data of Table 55. It was found (Ricker, 1933, p. 3) that the lake contained two very consistent salmon eaters; the squawfish and the Dolly Varden char, as well as several others of lesser importance. These latter were cutthroat trout, coho salmon, and prickly sculpins. One Rocky Mountain Whitefish was found to contain 12 small sockeye fingerlings, though this species was primarily a bottom feeder.

A preliminary study of the stomach contents of the fish caught by gill net was made during 1932–33 (Ricker, 1933), and gave the following picture.

TABLE 55. Catch of gill nets in Cultus Lake, 1932–38, arranged by species (Foerster and Ricker, 1941, p. 317).

Date	Squawfish	Trout	Char	Coho	Residual sockeye	Whitefish	Peamouth	Large scale sucker	Prickly sculpin	Kokanee	Total
1932	317	1	87	2	71	3	4	47	8	–	540
1933	109	4	22	0	6	1	1	7	1	–	151
1934	48	9	68	10	67	1	0	38	6	–	247
1935	2,046	225	232	44	72	17	8	853	42	13	3,552
1936	4,513	720	258	239	954	11	13	1,098	14	2	7,882
1937	1,783	764	177	268	21	4	1	900	227	–	4,145
1938	1,726	587	91	167	7	16	0	807	129	–	3,530
Total:	10,602	2,310	935	730	1,198	53	27	3,750	427	15	20,047

1. *Dolly Varden char* were individually the most destructive species to sockeye. Netted specimens ranged in length from 11 to 27 inches (28 to 68.5 cm) and all fed principally on young salmon. Heaviest predation occurred in May and in mid-July when an average of 17 sockeye per stomach was found. As many as 90 sockeye were found in individual stomachs. At two seasons the Dolly Varden utilized alternative foods, in June feeding heavily on the small, coast-range sculpins and in January gorging on the decaying carcasses of adult spawned-out salmon. Small Dolly Varden char, 5–6 inches (12–15 cm) long, were captured in the spring. Even these small char were able to feed on seaward-migrating sockeye, as well as on small coho fingerlings.

2. *Squawfish* were caught more frequently than all other species combined and on the basis of winter net catches they appeared to be five times as abundant as the char. Sockeye predominated in their stomachs, with sticklebacks and sculpins as alternative food items. Sockeye were found in stomachs of squawfish of all sizes from 5 inches (12 cm) upward, but consumption per squawfish seemed to be much less than for the char, most of the squawfish examined containing only one fingerling or the remains of one. At sockeye seaward-migration time, April–June, capture is easier and at this time, in 1932, the average number per squawfish stomach was two.

3. Only a few *cutthroat trout* were available for examination, but young sockeye appear to be an important food, possibly the main food item of the larger individuals.

4. The *coho salmon* which remained in the lake for a year or more before seaward migration, as well as those which did not migrate, fed extensively on sockeye. Specimens taken in the outlet stream, at the time of seaward migration of the sockeye, contained only insects, however.

5. *Prickly sculpins* consumed sockeye fry at the time they emerged from the gravel of the redds, which, at Cultus Lake, are located along the shore of the south end of the lake. Sculpins taken in the outlet stream at migration time almost in-

variably contained small coho fingerlings. Hence, since the sculpins are relatively abundant in the lake, they may prove very destructive at fry-emergence time.

The 1932–34 study of the food of predator fish in Cultus Lake provided clear evidence that predation may be an important cause of the high mortality of young sockeye in the lake. It was decided, therefore, to ascertain just how much the mortality could be reduced by cutting down the populations of these various species in the lake, if such action be feasible. As shown in Table 54, the netting program was greatly expanded in 1935 and, as noted in Table 55, the catches of fish were much greater.

This provided much more material for a study of the food of the predator fishes of the lake, particularly of the consumption of young sockeye (Ricker, 1941), to confirm previous findings, as already reported above, and to supplement them. Drawing heavily on Dr Ricker's observations the revised status for each of the predator species may be summarized as follows:

SQUAWFISH *(Ptychocheilus oregonense)*

Except during the summer period, May–September, young sockeye up to 1 year of age are the most important food of all squawfish over 100 mm (4 inches) in fork length. The number of sockeye found per stomach seldom exceeded three and the average for any large series was never more than one, more commonly only 0.2–0.5 per stomach.

TABLE 56. Number of sockeye salmon found in stomachs of Cultus Lake squawfish of fork length 200–299 mm (7.5–12 inches) in early spring (from Ricker, 1941, p. 308).

Date		Stomachs examined	No. with sockeye	Avg no. per stomach	Avg no. per stomach containing sockeye
Jan. and Feb.	1932	50	15	0.30	1.00
	1933	21	12	0.95	1.70
	1937	19	8	0.47	1.10
	1938	416	135	0.41	1.30
Mar. and Apr.	1932	30	7	0.23	1.00
	1933	53	23	0.53	1.20
	1936	184	12	0.08	1.10
	1937	60	22	0.48	1.30
	1938	614	139	0.28	1.20

During the summer season very few squawfish were caught in the pelagic region of the lake, presumably not being common there. In inshore areas the food was made up in coarse fish (chiefly shiners and sticklebacks), terrestrial insects, and some plankton.

Over the several years of investigation the variation in early spring sockeye consumption by the larger squawfish was as shown in Table 56.

CHAR *(Salvelinus malma)*

Individuals less than 300 mm (12 inches) long have quite a uniform diet of fingerling sockeye and other fish, particularly the coast-range sculpin. Larger char, while using young sockeye and coast-range sculpins as staple items of the diet, add variety by consuming also shiners, sticklebacks, squawfish, and prickly sculpins. In May and June the consumption of small sockeye averaged 10–12 per stomach, the highest number in any one stomach being 93. From July to the following April, the char appear to eat fewer sockeye, on the average, than do the trout.

In various years of investigations, the variations in fingerling sockeye found in the stomachs of char up to 499 mm (19.5 inches) were as in Table 57.

TABLE 57. Number of sockeye salmon found in stomachs of Cultus Lake Dolly Varden char up to 499 mm (19.5 inches) in fork length (from Ricker 1941).

Date		Stomachs examined	No. with sockeye	Avg no. per stomach	Avg no. per stomach containing sockeye
July and Aug.	1932	21	17	6.40	11.00
	1933	3	1	2.70	8.00
	1934	32	6	0.50	2.50
	1935	82	2	0.50	19.00
	1936	19	10	2.10	4.00
	1937	30	9	3.00	10.00
Jan. to Apr.	1932	11	7	1.60	2.60
	1933	6	5	5.30	6.40
	1936	25	1	0.04	1.00
	1937	18	5	0.70	2.40
	1938	64	22	0.90	2.60

In 1936, a considerable number of small char, less than 12 inches (299 mm) long were examined. They had confined themselves even more strictly than middle-sized individuals to a small-fish diet, principally to sockeye in their 1st year of life As these small char contained a greater volume of fingerling sockeye per stomach and fewer empty stomachs were found, it seems clear that, at that size and age, they are more destructive to potential sockeye migrants than when larger and older.

TROUT *(Salmo clarki)*

Trout do not appear to be fish eaters so exclusively as the char, since stomachs examined sometimes contained large quantities of insects or sticklebacks as well. In general, the smaller trout seem to eat more insects, the larger individuals more fish, yet when midge pupae or ants are very abundant almost all sizes of trout gorge on them. Among fish eaten by trout, the smaller individuals feed principally on the very young larvae of the prickly sculpin, while for large trout, the stickleback is perhaps the important food item. Sockeye salmon seem most commonly eaten by trout of the intermediate 300–399 mm range (12–16 inches), slightly more frequently than in the 200–299 mm (7.5–12 inch) group.

Trout, unlike the squawfish, take young sockeye at all times of year. In May and early June they feed heavily on sockeye fry, as high as 60 per stomach in 1937. The number eaten tends to drop during the summer, after which it remains fairly steady at 2 or 3 per stomach. An increase in the number eaten may occur in April when the young sockeye move into shallower water preparatory to migrating seaward.

The variations per year of examination in fingerling sockeye consumed by the trout of the 300–399 mm (12–16 inch) size group were as in Table 58.

TABLE 58. Number of sockeye salmon found in stomachs of Cultus Lake cutthroat trout of fork lengths 300–399 mm (12–16 inches), arranged to show the numbers taken from four different sockeye year-classes, spawned in 1934 (A), 1935 (B), 1936 (C), and 1937 (D). Data from Ricker (1941).

	Year-class	Year	Stomachs examined	No. with sockeye	Avg no. per stomach	Avg no. per stomach containing sockeye
May–June	A	1935	32	0	0	0
	B	1936	72	12	2.2	13.2
	C	1937	48	3	3.8	60.7
	D	1938	26	0	0	0
Sept.	A	1935	47	7	0.55	3.30
	B	1936	27	17	1.78	2.80
	C	1937	8	2	0.38	1.50
Oct.	A	1935	20	2	0.10	1.00
	B	1936	41	26	2.12	3.30
	C	1937	9	2	1.33	6.00
Dec.	B	1936	38	20	1.42	2.70
	C	1937	89	22	0.51	1.90
Jan.	B	1937	12	6	1.10	2.20
	C	1938	35	16	0.77	1.80
Feb.	B	1937	7	7	3.00	3.00
	C	1938	65	21	0.88	2.70
Mar.	A	1936	36	2	0.08	1.50
	B	1937	36	27	1.80	2.40
	C	1938	52	17	0.86	2.60
Apr.	A	1936	65	5	0.14	1.80
	B	1937	41	20	1.46	3.00
	C	1938	47	29	1.81	2.90

COHO SALMON *(Oncorhynchus kisutch)*

Individuals ranging from 200 to 399 mm (7.5 to 16 inches) were captured by the gill nets in 1936–38 in almost the same abundance as char. Young sockeye were found in their stomachs in every month of the year. In their consumption of sockeye they seemed to be more consistent predators than even the trout. The fact that sticklebacks were seldom found in the stomachs, and sculpins never, indicates that the coho of this size-range confine themselves to the pelagic region of the lakes which the young sockeye also frequent.

A tabulation of the variation in numbers of sockeye found per stomach for coho of the 200–299 mm (7.5–12 inches) size range caught in April shows the following:

Date	Stomachs examined	No. with sockeye	No. of sockeye per stomach
1935–36	24	9	0.5
1936–37	3	2	2.3
1937–38	45	24	1.6

PRICKLY SCULPIN *(Cottus asper)*

Being bottom-dwelling fish of relatively shallow inshore waters these fish would appear to be sockeye predators at only two seasons of the year, namely when the newly hatched sockeye fry are emerging from the gravel and are present for a time in shallow water and again when the lake-resident fingerling sockeye move into the shallow regions of the lake preparatory to leaving the lake on seaward migration. Sculpins present in the outlet stream from the lakes may also, at this time, feed abundantly on the young sockeye. In many lakes the sockeye spawn in the tributary streams, from which the newly emerged fry in due course move down into the lake. These young fry, scouting around in the shallow water adjacent to the streams preparatory to moving into deeper water, are easy prey for the hungry, lurking sculpins and undoubtedly suffer serious loss. Evidence of such loss was not available at Cultus Lake but in May, 1937, sculpins were taken which had been feeding (111 fry in one stomach) on sockeye fry recently liberated from the hatchery.

RELATIVE EFFECTIVENESS OF PREDATOR FISH AT CULTUS LAKE

By way of summarizing the findings obtained at Cultus Lake with respect to the consumption of young sockeye, it has been computed, from the stomach content analysis data, that over the whole 12-month period a trout may be considered as the equivalent of 5 squawfish, a coho of 4 squawfish, and a char of 3 squawfish. Although seemingly much less numerous in the lake (see Table 55) than the squawfish, the salmonid population (trout, char, coho) exceeds it in total effectiveness as predators. Since the trout population seems to be reasonably large and quite stable, it may be looked upon as being the basic predator in the lake to which must be added the depredations of the squawfish, char, and coho, as they fluctuate in abundance and seasonal predaceousness from year to year.

Consumption of sockeye by the predators appears (Ricker, 1941, p. 313) to be, in general, proportional to young sockeye abundance. This seems to apply particularly when the young sockeye populations are large. When they are small, the predation may be less than in proportion to abundance. Conversely, there is no indication, according to Ricker (1941, p. 312), that predation in Cultus Lake upon young sockeye has ever been limited by the appetites of the predators. Even when the young sockeye were quite numerous in the lake the number of empty predator stomachs was quite considerable.

THE LAKELSE LAKE FISH COMMUNITY

Observation on the fish present in Lakelse Lake formed an important part of the investigations there during the period 1944–55. Early studies (Brett and McConnell, 1950) revealed that the squawfish represented an important predator of young sockeyes there, constituting an average of 31% of the stomach contents of 623 squawfish examined during the 1944–47 period. At the same time, however, the remainder of the squawfish stomach contents was made up of 27.7% sticklebacks, 19.2% peamouth, and 21.8% prickly sculpins, thus indicating that though the squawfish preyed on young sockeye to a quite appreciable degree it also consumed a known food competitor of the sockeye, the stickleback, and a predator of the fry and quite young fingerlings in streams and shallow lake margins, the sculpin. A more intensive study of the fishes in Lakelse Lake seemed warranted.

Ten species were found to be present (Table 52). Of six of these (those amenable to sampling by gill nets), the distribution within the lake during three seasons of the year was determined as shown in Table 59.

A tendency for certain species to concentrate in certain areas at different times of the year was noted and has been attributed either to spawning or to better feeding facilities. In general, the spring appears to be a time of movement shoreward and

TABLE 59. Distribution of fish in Lakelse Lake during different seasons of the year, as revealed by gillnetting in 1951–53 (Shepard and Bilton, 1953, p. 25).

	Vertical offshore distribution			Horizontal distribution		
Fish	Spring	Autumn	Winter	Spring	Autumn	Winter
Peamouth	Deep	Deep	Few present	Inshore	Dispersed	Inshore
Squawfish	Deep	Deep	Few present	Inshore	Offshore	Inshore
Cutthroat	Shallow	Shallow	Shallow	Inshore	Inshore	Dispersed
Whitefish	Few present	Few present	Few present	Inshore	Inshore	Inshore?
Sucker	Few present	Few present	Absent	Inshore	Inshore	?
Dolly Varden	Few present[a]	Dispersed	Deep	Inshore	Inshore	Dispersed

[a] A comparison of angler's catches in Lakelse Lake and in the upper part of the Lakelse River suggests that, during spring and summer months, char are to be found mainly in the river.

downriver from the lake while the autumn and winter period is one of upstream movement into the lake and a tendency for fish to disperse throughout the lake.

Regarding the abundance of the various species in the lake, only very tentative and approximate data are available. They indicate that during the autumn and winter the adult fish population in Lakelse Lake, in 1953, was

Peamouth – 40,000
Squawfish – 50,000
Cutthroat trout – 20,000[a]
Dolly Varden char – 8,000
Rocky Mountain whitefish – 9,000
Largescale suckers – 10,000[b]

[a] Includes 5000 fish resident in the upper Lakelse River.

[b] Represents only the population contributing to the spawning in the upper Lakelse River and therefore is a minimal estimate.

Stomach content analyses were made of all the fish netted in Lakelse Lake. Three species were found to be piscivorous, and, therefore, potential predators on young sockeye salmon. These were cutthroat trout, Dolly Varden char, and squawfish. It was of interest also to ascertain what the alternative foods of these potential predators might be and how the diet might vary according to (1) the place of residence of the predator when caught, i.e., whether in shallow, inshore waters or well out in the lake, and (2) the season of the year.

SUMMER DIET OF LAKE-RESIDENT PREDATORS

Most of the fish whose stomachs were examined had been caught during the late spring or summer—May–September. The diets for cutthroat and squawfish during this period for the years 1945–51 were as shown in Table 60.

TABLE 60. Stomach contents of cutthroat trout and squawfish caught in Lakelse Lake May to Sept. for 1945–51 (Shepard and Bilton, 1953).

		Captured inshore				Captured offshore			
Species of fish	Organisms in stomach	Stomachs examined	Total no.	Avg no. per stomach	Per cent of total contents	Stomachs examined	Total no.	Avg no. per stomach	Per cent of total contents
Cutthroat trout	Insects	598	9025	15.09	82	146	1162	7.27	71
	Sockeye		127	0.21	1		101	0.69	7
	Stickleback		838	1.40	8		110	0.75	7
	Unidentified fish remains		1057	1.77	9		211	1.45	15
Squawfish	Insects	610	164	0.27	30	210	6	0.03	3
	Sockeye		57	0.09	10		15	0.07	8
	Stickleback		90	0.15	17		54	0.26	29
	Unidentified fish remains		231	0.38	43		111	0.53	60

For the trout, insects made up a very substantial portion of the diet of fish caught in the inshore area, due, no doubt, to the large hatches of insects along the shallow, reedy shores of the lake. Squawfish which were caught inshore had also subsisted heavily (30%) on insects. It is surprising that trout caught in offshore, deeper waters had apparently fed so heavily on insects (71%). Squawfish caught in similar regions had not done so.

Trout captured inshore had consumed few young sockeye (1% of stomach contents or 0.21 fry per stomach) but those caught in deeper waters had preyed more heavily on them (7% of stomach contents or 0.7 fry per stomach). Squawfish had been slightly more predaceous, particularly in inshore areas, and if a fair portion of the unidentified fish remains be considered as representing young sockeye, the predation would be even more serious, perhaps amounting to 1 fry per stomach.

Sticklebacks appeared to be an important alternative fish food in both inshore and offshore areas during the summer period. Inshore-captured trout had consumed seven times as many sticklebacks as young sockeye, no doubt due to the much greater availability of the former. This was not so apparent among the squawfish.

Further studies during the summers of 1952 and 1953 served to fully confirm the earlier data just summarized. One important observation was the increase in consumption of fish by trout and squawfish as the season advanced. Between May and November the incidence of sticklebacks and unidentified fish remains doubled while the occurrence of young sockeye was almost fivefold.

It should be explained that Dolly Varden char do not appear in the summer lake fish studies at Lakelse Lake because at this time of year they are chiefly downriver. They apparently tend to leave the lake and move into the outlet river during the spring, returning again to the lake in the autumn. Evidence of these seasonal movements was presented by creel census data taken at Lakelse Lake, 1950–52. These gave the relative catches by a representative sample of anglers during the May–September period in the lake and in the upper section of the outlet stream, the Lakelse River.

WINTER DIET OF LAKE-RESIDENT PREDATORS

It is quite to be expected that there will be an appreciable difference between the summer and winter foods of fish. Due to the different hydrological conditions in the lake in these seasons, the normal habitats of the fish will be different, hence the associations between the fish and their foods, particularly between predators and their prey.

During the winter of 1951–52, an attempt was made to conduct gillnet operations in Lakelse Lake under the ice. Weather conditions limited the operations to a 6-week period—mid-February to end of March. A total of 23 sets was made with a single 46-m length of 2.5-inch (6.35-cm) mesh, 12 sets being made at the lake surface just beneath the ice and 11 at the bottom (approximately 20 ft or 6 m deep) of that part of the lake selected, namely near the centre of the lake (Fig. 37).

The results of the netting operations may be recorded as follows:

No. set at:	Surface		Bottom	
No. of net-days:	22		25	
Species of fish caught:	Cutthroat	Dolly Varden	Cutthroat	Dolly Varden
No. of specimens caught:	19	2	1	9
No. of stomachs containing:				
Sockeye	3	2	–	7
Stickleback	11	–	1	–
Fish remains	1	–	–	1
No. of stomachs empty:	5	–	–	1
No. of fish in all stomachs:				
Sockeye	3	16	–	31
Stickleback	132	–	10	–
No. of sockeye per stomach:	0.16	8.0	–	3.4
No. of sticklebacks per stomach:	6.95	–	10	–

Too great reliance cannot be placed on these limited data, but they do suggest that:

1. The Dolly Varden char are, during the winter months, an important predator on young sockeye in the lake.
2. Cutthroat trout are less predaceous on sockeye; they appear to feed much more heavily on stickleback.
3. Dolly Varden char seem to be more abundant in the deeper strata of the lake, the cutthroat trout more common near the surface.

RELATIONSHIP OF SIZE OF PREDATOR TO EXTENT OF PREDATION

Is it correct to assume that the larger the size of the predator fish, the more young sockeye it is likely to consume? Data available from the Lakelse Lake studies were examined in this regard, using all the records, irrespective of place or season of capture of the fish (Table 61).

Larger cutthroat trout and probably also Dolly Varden (although the numbers of the latter were much smaller) feed more heavily on young sockeye than smaller individuals. The stomachs of the larger fish—up to 41 cm long—contain more young sockeye than the smaller ones for both species, and, in the case of the cutthroat, the frequency of occurrence varied directly with size.

For squawfish, however, there was an apparent inverse relationship between size and the extent of sockeye consumption. There was evidence that the largest squawfish were relatively more abundant in shallower inshore areas where young sockeye would be less common, but, nevertheless, when offshore and inshore samples were examined separately, the inverse trend seemed to persist.

Summarizing the predation-on-sockeye situation as it seems to occur in Lakelse Lake, it may be said that:

1. During the spring season both cutthroat trout and squawfish tend to move inshore where the abundant emergence of insects provides a ready source of alternate

TABLE 61. The relation of size of predator to number of sockeye consumed, Lakelse Lake, 1945–51. (No. = number of stomachs examined; F(%) = per cent of stomachs containing sockeye; Avg no. = average number of sockeye per predator stomach.)

Species	Size class (*cm*)					
	11–20	21–25	26–30	31–35	36–40[a]	Over 41
Cutthroat						
No.	218	529	758	565	174	–
F(%)	2.3	3.0	6.6	11.5	16.7	–
Avg no. sockeye	0.07	0.16	0.29	0.33	0.56	–
Squawfish						
No.	485	489	434	122	33	–
F(%)	4.5	3.7	2.5	0.9	0	–
Avg no. sockeye	0.07	0.08	0.04	0.01	0	–
Dolly Varden						
No.	13	132	98	73	29	36
F(%)	0	0	6.12	9.6	6.9	0
Avg no. sockeye	0	0	0.24	0.35	0.52	0

[a] All cutthroat trout and squawfish over 36 cm long are included in this category.

food. At the same time the Dolly Varden char leave the lake and move downriver shortly after ice breakup.

2. During the summer a gradual return of trout and squawfish to offshore, cooler water occurs. This movement is likely due also to the cessation of insect emergence and to the greater availability of fish food in the pelagic areas of the lake.

3. In autumn a dispersion of fish to offshore waters is apparent; the incidence of sockeye feeding increases. Dolly Varden char return again to the lake from downriver areas.

4. During winter the trout and char are widely dispersed, with the char seemingly more common at deeper depths than the trout. Squawfish were rarely taken in nets set under the ice in winter. Young sockeye were actively consumed, particularly by the char, the trout containing a much greater percentage of sticklebacks.

A preliminary and very rough estimate of the removal of young sockeye by predators in Lakelse Lake was made by combining the available data on consumption of sockeye by predators, abundance of predators and rate of digestion in predator stomachs. Cutthroat trout, most active in the autumn, could remove some 800,000 young sockeye annually. Squawfish, approximately three times as numerous in the lake, probably are most predaceous in summer and autumn, removing some 900,000 young sockeye. The predation by Dolly Varden char, concentrated largely in autumn and winter, may account for the consumption of 400,000 young sockeye. Total removal of young sockeye in Lakelse Lake by these three predators could, then, according to these estimates, amount to roughly 2 million fry and fingerlings.

It was at one time anticipated that a predator control plan might be instituted at Lakelse Lake, replacing that which had to be abandoned at Cultus Lake. A selective removal of the squawfish only was considered desirable since it was felt that an energetic sport fishery for cutthroat trout and Dolly Varden char might well keep the numbers of these two species in check. However, no further action was taken.

PREDATION ON YOUNG SOCKEYE IN ALASKAN LAKES

Evidence bearing upon the mortality among young sockeye during their years of lake residence in Alaskan lakes, as a result of consumption by predator fishes, is not too clear. Certainly the situation appears to be quite different to that just revealed for lakes in British Columbia.

In the first place, the predator fishes seem to consist primarily of two species of char, the Dolly Varden (*S. malma*) and the alpine or Red Lake char (*S. alpinus*), the freshwater sculpin (*Cottus aleuticus*), and young coho salmon (*O. kisutch*). No doubt further studies in other lakes will extend this list of sockeye predators, but thus far our information has been confined to Karluk Lake (Barnaby, 1938; DeLacy and Morton, 1943; Rounsefell, 1958a), Chignik Lake (Roos, 1959, 1960) and certain lakes of the Kitoi Bay area of Afognak Island, Alaska (Parker and Vincent, 1956, p. 40; Parker, 1957).

Secondly, the predatory activities of the very abundant chars are decidedly limited. According to Barnaby (1938, p. 33):

> "At Karluk Lake it was noted that chars take a very heavy toll of red salmon fry in the spring at the time the young fish are entering the lake from the spawning streams. However, during the summer and fall relatively little damage is done to the salmon populations by these chars. . . . An analysis of stomach contents of chars in Karluk River showed that the chars in the river were not feeding on seaward migrants."

These observations are confirmed by DeLacy and Morton (1943) who found that the Dolly Varden char were, in the spring, feeding "mainly on larval and adult insects, snails and leeches" and that, during both downstream migration in the spring and upstream ascent in the autumn, "fewer than 20 per cent of the fish had been recently feeding." Of the lake resident chars, *S. alpinus*, insects were the most common food eaten in the spring prior to late June and again in September. It is remarked that char caught in shallow portions of the lake were feeding quite heavily on sticklebacks during certain seasons and that "cottids, salmon fingerlings and young chars are found occasionally in their stomachs."

At Chignik (Roos, 1959) insects were the most common food item of Dolly Varden during the entire summer in all areas examined. Predation on young sockeye occurred principally in the fast water below the lake outlet where they were attacking not only seaward migrating smolts, but also young fry ascending to the lake. Here 31.1% of the fish examined had consumed young salmon. None of the Dolly Varden captured in the lake itself had been feeding on salmon, and only a small percentage (5.3%) in the river.

These Chignik observations indicate, therefore, that the char were most destructive to young sockeye in the fast water below the lake outlet where sculpins, which are abundant, had been noticed with sockeye fry in their mouths. Since the

Dolly Varden prey upon sculpins also, they have some beneficial effect in this regard, added to which they feed actively also on sticklebacks, thus mitigating to some degree the damage they do through consuming young sockeye.

Young coho salmon in the two lakes of the Chignik system were found to be consuming young sockeye, though the principal food again was insects, primarily Diptera larvae. Of all the cohos examined (182) during May, June, and July of 1956, 1957, and 1959, 30% had fed on sockeye salmon fry, with an average of 2.3 fry per stomach. This is seven times greater, according to Roos (1960), than the number of young sockeye found in Dolly Varden stomachs. It is of interest to note that, although sticklebacks were more abundant in seine hauls than young sockeye, none was found in coho stomachs. It is inferred, therefore, that at Chignik the young coho "prefer young sockeye over sticklebacks as a source of food" and that "coho salmon are more detrimental than beneficial to sockeye salmon."

PREDATION ON YOUNG SOCKEYE IN KAMCHATKA LAKES

While quite definite evidence is available (see text, p. 159) of the serious predation of 1- and 2-year-old coho salmon, 1-year-old sockeye and 1-, 2-, 3-year-old (and older) *S. malma* on young sockeye fry which have been hatched in spring-fed areas, such as the Karymai Springs on the Bolshaya River system (Semko, 1954b), the activities of predators on the young sockeye during their year or years of lake residence are not as damaging.

Char appear to be the main predator in lakes (Krogius and Krokhin, 1948, 1956a). However, their detrimental influence is largely mitigated by the fact that they also prey heavily on sticklebacks, which, quite abundant in many Kamchatka sockeye-producing lakes, are a serious food competitor of the young sockeye. The char, therefore, in Kamchatka present a somewhat different picture to that found at Cultus Lake, British Columbia, and the adverse effects of their predation on young sockeye must be balanced against the beneficial effect of their consumption of an important food competitor of the young sockeye.

That Dolly Varden char are, in Kamchatka as in Alaska (DeLacy and Morton, 1943), being unjustly maligned in respect to their fish predation propensities, is em-

TABLE 62. The food of lake-resident char in Lake Dalnee (Savvaitova, 1960).

Food Component	Individual index of stomach fullness June	July
Sticklebacks	94.10	120.00
Gammarids	5.35	1.68
Molluscs	1.40	0.98
Insects	2.64	0.18
Vegetation	1.60	0.14
Miscellaneous	0.53	0.41
Total index of stomach fullness	105.62	123.39

phasized by interesting researches recently conducted in Kamchatka (Savvaitova, 1960; Savvaitova and Reshetnikov, 1961). It has been found that *S. malma* exists in three quite distinct forms. One is anadromous, spawning in fresh water but feeding in the sea; the second is a lake and stream inhabitant which never enters salt water; the third is exclusively a lake-dwelling form.

Extensive analysis of stomach contents has revealed that the anadromous type of *S. malma* is essentially insectivorous, feeding primarily on aquatic insect larvae and on terrestrial insects, with molluscs playing a minor role. The lake-stream variety, on the contrary, subsists chiefly on molluscs, with aquatic insect larvae being of secondary importance. Only the lake resident *S. malma* presented evidence of a predaceous propensity, the main food item being sticklebacks, while amphipods, molluscs, and insect larvae were present in small quantities only (Table 62). Char larger than 300 mm in length were reported to feed almost exclusively on fish. It is most surprising that young sockeye are not recorded as found in the Lake Dalnee char stomachs, since they are actively consumed by char (Krogius and Krokhin, 1948, 1956a). It is possible, perhaps, that the collections of June and July are not too typical of the situation in Lake Dalnee.

Chapter 10. The production of young sockeye in lakes

It seems appropriate, now, that consideration be given to the growth and survival, i.e. to the production, of young sockeye in the lake. During this period which extends from the time of entrance into the lake as newly emerged and free-feeding fry in the spring of the year, April–June, to the time when the young fish (now called "smolts") leave the lake on seaward migration—again in the spring—the young fish are growing actively.* Successful production is directly associated with and influenced by those conditions prevailing within the lake which promote and assure good growth and survival.

Since, as will be discussed later (p. 399), the larger (within limits) the seaward migrants the higher the percentage return from the sea, growth during lake residence is an important feature. Furthermore, if, as some evidence indicates (see p. 359), the age at maturity also is related to the size of the seaward migrants, growth in the lake is a quite significant factor. Thirdly, since seaward migration of young sockeye at the end of their 1st year is much more efficient than a more extended period of lake residence and seaward migration as 2- or 3-year-olds (Krogius and Krokhin, 1948, p. 18; Krogius, MS, 1949, p. 11), it may have added significance here, too.

While each of the many factors within the lake has an intimate relationship to and effect upon the young sockeye's growth rate, some of them, particularly those related to the climate—temperature, precipitation, hours of sunshine, etc.—are largely beyond man's control. Others, however, may be altered in an attempt to achieve the objective of maximum sockeye production. These would include: (1) the nutritive substances in the water which limit the production of plankton, (2) the presence of species of fish which are food competitors, also older age-classes of young sockeye in the lake which are also active and serious food competitors, and (3) predator fishes. Just how and to what extent these adverse factors in the lake community may be controlled or eliminated is not clear, but the possibilities are deserving of investigation. Therefore, any facts that can be brought to light have great value.

THE ADEQUACY OF PLANKTON FOOD SUPPLIES

Having available, from plankton studies in three sockeye-producing lakes, a measure of the abundance of the food available to the young sockeye resident in

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* Those young sockeye which are hatched and reared in spring areas, principally in Kamchatka, e.g., the Bolshaya (Semko, 1954b) and Kamchatka rivers, are produced under quite different conditions. These will be discussed in a later section, p. 323.

them, it is of interest to determine how adequate the food supply is for the feeding fish. Calculations cannot be too precise since the data on quantity of plankton and of young sockeye are largely approximations. Nevertheless, they may serve to indicate the general relationship.

CULTUS LAKE

From the monthly plankton abundance data (Ricker, 1937b, table IV), converted to gram wet weight per cubic metre, the average quantity for the main growing period, June–August, for the years 1928, 1932, 1933, and 1934 has been considered in relation to the estimated population of young sockeye feeding in the lake during these months. This latter estimate was obtained by considering, in years of natural propagation (1927 and 1931*) that 60% of the eggs presumed to have been deposited produced virile fry and that, at the end of June, 50% of the original fry hatch survived (Foerster, 1938b). In 1931 (see footnote on p. 265) and 1933, liberations of fry were made from the Cultus Lake hatchery and a mortality of 50% among the fry, to the end of June, was again assumed. In 1934 a planting of "eyed" eggs was made in the streams flowing into the lake, and a total mortality of 60%, to the end of June, was assumed.

TABLE 63. The calculated relationship of the plankton food supply in Cultus Lake to the population of young feeding sockeye.

Year of lake residence	Calculated no. of feeding sockeye $(\times 10^6)$	Estimated avg abundance of Crustacea in June and July (*g wet wt* $\times 10^6$)	Amount of food per sockeye (*g*)	Avg wt of seaward migrants in following spring (*g*)
1928	75.00	43.3[a]	0.6	3.06
1932	20.20	31.0	1.5	3.67
1933	2.40	25.8	10.8	6.53
1934	1.75	17.8	10.2	7.55

[a] The volume of the pelagic feeding grounds of the young sockeye in Cultus Lake is considered (Ricker, 1937b, p. 464) as 57×10^6 m^3.

The pertinent data are shown in Table 63 along with the average weight of the seaward migrating sockeye in the following spring. Despite the broad assumptions made it is apparent that in the first 2 years, when the populations of feeding sockeye were vastly greater than in the last 2 years, there was much less plankton food available for each young sockeye fingerling, around one-tenth as much. As a con-

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* In 1931 part of the spawning run to Cultus Lake was trapped and artificially spawned (10,685 females stripped, egg content of 51,660,000) and most of the resulting fry transferred to other areas. Only 6,031,000 fry were released into Cultus Lake. The remainder of the spawning run (6861 males and 12,869 females, egg content—54,000,000) was allowed to ascend to the lake and spawn naturally.

sequence the seaward migrants of the following spring were much smaller in size. A better survival in the years with relatively abundant food per fingerling in the lake might be anticipated also, but unfortunately comparative data are not available to substantiate or negate it.

TABLE 64. The relationship of the number of young sockeye in Lake Dalnee[a] to the quantity of plankton food available. (Data taken from Krogius and Krokhin, 1948.)

Year of growth in lake	Initial no. of young in the lake ($\times 10^6$)	Avg quantity of food in lake June–July (unit $\times 10^6$)	Amount of food per fry (*g*)	Size of yearly seaward migrants in following year (*g*)	Survival of fingerlings to following year (per cent of initial no.)
1937	3.1	372.0	120.0	12.8	12.8
1938	1.8	195.7	108.7	23.0	7.0
1939	0.7	143.1	204.5	17.4	24.6
1940	22.4	156.0	8.3	14.1	0.9
1941	15.4	140.1	9.2	12.5	2.2
1942	35.6	202.0	5.7	18.8	0.4

[a] The volume of Lake Dalnee is reported as 42.8×10^6 m^3 (Krokhin, 1957a, p. 30).

LAKE DALNEE

Similar data on the quantities of plankton in relation to the estimated abundance of young feeding sockeye in Lake Dalnee are available (Krogius and Krokhin, 1948, p. 16–17) and are shown in Table 64, together with the average weights of the yearling migrants in the following spring. It is explained that "the most favourable food relationship prevailed in 1939, in spite of the scarcity of plankton. Very good conditions also existed in 1937 and 1938. In 1940 and 1941 the prevailing situation was much worse; the amount of food available per fingerling was from 10 to 20 times less than in the preceding years. In these years the survival of the fingerlings dropped greatly."

In comparing the data for Lake Dalnee (Table 64) with those for Cultus Lake (Table 63) the vastly greater quantity of plankton in the former is readily apparent. When the sockeye populations are small the plankton available for each fish is around 10 times as great as at Cultus (1938 at Lake Dalnee compared to 1934 at Cultus Lake). When the fish are numerous (1940 at Lake Dalnee) the food available per fish is five times that at Cultus (1932). It is of particular interest to note, however, that the difference in quantity of food available per sockeye in Lake Dalnee is not reflected in the size of the migrants in the following year as it is for Cultus Lake. Krogius and Krokhin (1948, p. 20) state that "in different years the different conditions of life for the young in the lake are reflected not only in survival but also in growth and, consequently, in the size which the migrants attain at time of migration." It is further intimated (Krogius and Krokhin, 1948, p. 17) that "in evaluating the quantity of food available to each fingerling the fact must not be overlooked that the young can never exterminate the food completely. There is a certain limit, however, to the dispersion of the food forms beyond which their capture requires a greater consumption of energy than they provide in nutriment. To determine this limiting concentration of food is very important in the evaluation of the food resources of a lake."

From the data just reviewed, Lake Dalnee presents no problem in this regard. It is not typical, apparently, of other sockeye-rearing lakes in Kamchatka for, in Lake Kurile, the principal sockeye-producing area at the present time, the young sockeye are much smaller, more comparable with those in Cultus Lake, Table 65. In lakes of this kind the abundance of plankton food forms for the young sockeye in them, particularly in years when the sockeye populations are large, may become an important limiting factor, as far as growth is concerned.

TABLE 65. Average lengths (L) and weights (W) of 1-, 2-, and 3-year seaward-migrating sockeye from different lakes.

		1-year			2-year			3-year		
Lake	Year	No.	L (*cm*)	W (*g*)	No.	L (*cm*)	W (*g*)	No.	L (*cm*)	W (*g*)
Cultus	1929	4,761	6.84	3.06	30	11.76	12.64	–	–	–
Cultus	1930	376	8.76	6.55	778	11.83	16.44	–	–	–
Cultus	1931	719	9.08	7.10	50	13.13	22.60	–	–	–
Cultus	1934	609	8.65	6.53	499	10.60	12.07	–	–	–
Cultus	1935	1,503	9.07	7.55	76	12.73	20.33	–	–	–
Dalnee[a]	1939	–	13.30	23.00	–	15.50	36.50	–	–	–
Dalnee[a]	1941	100	11.10	14.10	100	16.10	43.70	14	20.3	79.6
Dalnee[a]	1942	–	11.20	12.50	–	16.10	37.90	–	–	–
Blizhnee[a]	1941	21	9.40	9.20	251	10.80	13.40	13	11.2	13.0
Kurile[a]	1943	10	5.60	–	680	9.70	9.40	402	11.4	14.3
Karymai Spring[b]	1948	–	8.33	–	–	–	–	–	–	–
Bolshaya River[b]	1949	–	6.81	–	–	–	–	–	–	–

[a] Krogius and Krokhin, 1948, tables 14 and 16.

[b] Semko, 1954a, p. 90.

Due consideration must be given also to the abundance of those species of fish which compete with the young sockeye for plankton organisms. In areas where sticklebacks, for example, are very abundant, such as at Lake Dalnee and in the Wood River lakes (Burgner, 1960) the interspecific competition for plankton food "can reach such proportions that, in addition to a general decrease in the rate of growth and retardation in development of the young fish to the migratory stage, there occur specimens which show extremely poor growth and poor condition" (Krogius, 1951, p. 12).

Furthermore, the small and poorly developed fingerlings become easy prey for predators and mortality becomes more severe. This is clearly indicated in Fig. 58 when, for the years 1945, 1947, and 1948 (Krogius, 1953, p. 220) in Lake Dalnee, exceptionally large populations of threespine stickleback occurred and for 1950 when many of the older age-groups of sockeye (2+, 3+, and 4+) were found in the lake. In 1947 and 1948, particularly, the relationship of abundance of food to numbers of seaward-migrant sockeye in the following spring was far below normal, thus suggesting that the lack of food due to food competition had dire consequences.

It is of particular interest to note that in considering the significance of amount of plankton food available to the young sockeye in Lake Dalnee during the main growing season, as shown in Table 64, a high correlation (regression coefficient, 0.95) is found for the effect of amount of food on survival of smolts the following spring. But between the amount of food and the size (average weight) of yearling smolts a very low regression prevailed, 0.26.

BABINE LAKE

In this lake much more precise data are available with regard to numbers of feeding sockeye and the available plankton food. Babine Lake (Fig. 56) is multibasin in character and observations have indicated (Johnson, 1958) that each basin must be considered a separate production unit, as far as density and distribution of young feeding sockeye are concerned. Therefore, in studying the production of sockeye it becomes necessary to devise and utilize methods whereby the conditions within the various basins, particularly the density of the young sockeye and the abundance of plankton food per unit area or volume, could be ascertained.

For plankton collection, a Clarke-Bumpus recording collector was used, as outlined earlier (p. 220). For capturing young sockeye, a relatively recent development, made possible by the availability of high-speed and high-powered outboard motors,* the cone-shaped tow net, (Fig. 28) already described (p. 164) was used, as shown in Plate VIII.

The plankton collections and young sockeye catches at Babine Lake thus give directly the numbers of plankters per unit volume (milligram dry weight per cubic metre) and the numbers of sockeye per unit area (per hectare, i.e., per 2.47 acres) (Johnson, 1961, table I). For convenience the population density of the young sockeye, originally expressed in fish per hectare, has been considered as fish per hectare × 1 m, in order to convert it into volume measure, since the tows for young sockeye are considered to fish the surface 3 ft.

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* During the studies at Cultus Lake, 1925–38, many varied attempts were made to capture young sockeye in the lake. Stationary traps were tried. Large wire cages were suspended at different depths in which lights (flashlights) with coloured lenses were placed, in order to attract the plankton and the young sockeye or both. Small-mesh gill nets [¼-inch (approximately 0.635 cm), ½-inch (approximately 1.27 cm) and ¾-inch (approximately 1.90 cm)], all handmade, were also used. None was successful. At Lake Dalnee, however, special small mesh gill nets were used successfully (Krogius and Krokhin, 1948, p. 8).

In Table 66 are given the pertinent data for each of the seven basin areas of Babine Lake. As pointed out and illustrated by Johnson (1961), three important relationships are indicated. These are:

1. A general direct relationship between the mean abundance of zooplankters (within the range of 0.067–1.000 g/m^3 wet wt) and the June–October growth of the young sockeye. Naturally, the more food available per fish, the greater the amount of growth attained by the fish.
2. A definite inverse relationship between population density and growth, particularly when the population density is relatively high, i.e., above 0.5/m^3 in the upper 1 m sampled by the tow net. In other words, the more young sockeye in the area the less food per fish and, hence, the less growth attained.
3. A similar inverse relationship between quantity of plankton during the mid-June to mid-October period and the numbers of young fingerling sockeyes in the lake, especially when the populations in the lake are appreciable, i.e., 0.5/m^3 and greater.

These records of plankton abundance in Babine Lake embrace the whole of the summer and early autumn period, mid-June to mid-October. They include, therefore, not only the main growing period, June and July, as do the data for Cultus and Dalnee lakes, Tables 63 and 64, but also the late summer and early autumn period,

TABLE 66. The relationship of young sockeye population density in each basin area of Babine Lake to the quantity of plankton food available during the summer feeding periods of 1957 and 1958. (Data from Johnson, 1961.)

Year of lake residence	Lake basin[a]	Population density[b] (*fish/m^3*)	Quantity of food in lake[c] (*g/m^3, wet wt*)	Amount of food per fry (*g wet wt*)	Size of sockeye mid-October (*g*)
1957	1	1.230	0.100	0.081	2.20
	2	1.460	0.092	0.063	1.70
	3	0.665	0.300	0.451	3.60
	4	0.500	0.575	1.150	3.80
	5	0.063	0.667	10.600	5.70
	6	0.170	0.792	4.660	5.00[d]
	7	0.220	1.000	4.540	5.00[d]
1958	1	0.990	0.067	0.070	2.00
	2	1.690	0.067	0.040	1.20
	3	0.930	0.175	0.190	2.20
	4	0.905	0.283	0.310	2.50
	5	0.755	0.350	0.460	3.10
	6	0.170	0.850	5.000	4.20
	7	0.225	0.983	4.370	4.20

[a] Locations of lake basins are shown in Fig. 56.

[b] As computed by Johnson for late August.

[c] As determined for the mid-June to mid-October period in the 0–5 m stratum of each basin and converted to wet wt.

[d] These average weights are only approximate (Johnson, 1958, p. 974).

August to mid-October, when it has already been shown (Fig. 57 and 58) that plankton abundance is substantially decreased through the heavy summer consumption by the young sockeye during the active growing period. They will represent, consequently, a lower unit plankton abundance and a correspondingly lower amount of food per sockeye fry in the lake than do the records for Cultus and Dalnee lakes.

SOCKEYE FEEDING CAPACITIES OF THE THREE LAKES

For a very rough and approximate comparison of the sockeye feeding capacities of the three lakes in question, the calculated plankton food rations for young sockeye salmon at Lake Dalnee (see Table 38) may be used. These (the average for June and July over 2 years) amounted to 21.25 mg dry wt or 0.18 g wet wt of plankton crustacea per day.

At Cultus Lake (Table 63, column 4) there would seem to be ample food, i.e., 3–8 times the amount of the daily ration, in the years of large populations. However, it may be quite scattered and require an undue amount of energy to capture—hence using up the energy in motion rather than in adding to the size or weight. In years of low populations, viz. 1933 and 1934, with around 60 times the daily ration available per fingerling, much more food is available, hence more can be devoted to growth.

In considering the situation at Lake Dalnee itself, Table 64, it is apparent that there is a great deal more plankton food available to each sockeye fingerling than at Cultus Lake. Comparing the situation in the two lakes in years when lake populations were closely similar it is found that, with the much greater (5×) quantity of plankton available per fingerling, growth was much greater (4×):

Year	Lake	No. of sockeye	Amount of food per fingerling	Size of yearling seaward migrant in following year
1940	Dalnee	22.4×10^6	8.3 g	14.10 g
1932	Cultus	20.2×10^6	1.5 g	3.67 g

For Babine Lake, Table 66, the calculated amounts of plankton food available per fingerling are much less than calculated for Cultus Lake or Lake Dalnee, particularly in the heavily populated basins 1 and 2. Actually in these areas there is present only from roughly one-third to one-half as much plankton food as required by each young sockeye, if the Lake Dalnee standard of 0.18 g/fish applies. The relatively small size of the fingerlings in these areas can be readily understood. The sizes noted in Table 66 for fingerlings in October are hardly comparable with the sizes set down for Cultus Lake and Lake Dalnee since the latter refer to the seaward-migrating smolts. It is known, however, that the seaward-migrating yearling sockeye from Babine are characteristically small, e.g., 4.9±1.5 g in 1952, 5.5±1.3 g in 1950, 5.6±1.5 g in 1951, and 6.2±1.5 g in 1953 (Dombroski, 1954, p. 32).

YEARLINGS

While the amount of plankton food available to each young sockeye in a lake is of prime importance and, in some respects, is the most important factor, there are other features that have a significant bearing upon production, particularly the number of feeding sockeye in the lake throughout the period of lake residence. In this section the word "production," by itself, is used in the sense defined by Ivlev—the total amount of live substance elaborated in a stated period of time, regardless of whether or not it survives to the end of the period. "Net production," however, refers to the biomass (weight) of stock present at the end of a period of time less the biomass present at its beginning.

In Fig. 60 there is presented diagrammatically the situation which prevailed in Cultus Lake for one 1-year-class of young sockeye (1933) for which the pertinent data are available (see Ricker and Foerster, 1948). The sockeye populations resident in the lake, showing a decline in numbers during the year* but at the same time an increase in total weight as well as individual weight** are represented as the biomass of young sockeye or "standing crop." This suffered a sharp decrease early in the year, late May and early June, reaching a low point about mid-June but increased rapidly and greatly during the summer and early autumn, amounting in mid-September to roughly 1.8 times the subsequent migration size. During late autumn

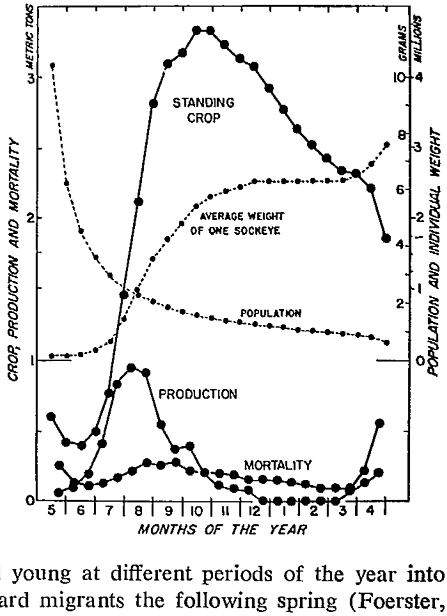

FIG. 60. Diagram illustrating the interrelationships of abundance, individual weight, standing crop, production and mortality for fingerling sockeye of the 1933 year-class in Cultus Lake. (From Ricker and Foerster, 1948, fig. 3.)

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* As determined from the release of marked young at different periods of the year into Cultus Lake and the subsequent recovery of seaward migrants the following spring (Foerster, 1938b) and revised to include nonmigrating individuals (reproduced in Fig. 61).

** Individual weights were determined by Ricker from young sockeye taken in stomachs of predator fishes (Ricker, 1937b, 1938d), since other means were, in those early days, not available to capture young sockeye in the lake.

and winter growth fell off and finally ceased. Mortality, however, remained fairly high so that the stock continued to decline. During April both growth and mortality increased but the losses were sufficiently great to reduce the biomass or standing crop to its final level. This, being three times the original weight of fry, means that, during their year in the lake, the young sockeye of this 1933 year-class increased to three times their initial bulk.

Production is, as intimated above, the gross increase in growth (i.e., weight) of the young fish, not adjusted for losses due to mortality. Fig. 60 indicates that the absolute production fluctuated widely during the year, with a peak in late summer and an extended low during the winter, while the mortality maintained a much more uniform trend.

TABLE 67. Production (sense of Ivlev) and mortality of fingerling and yearling sockeye during their year of residence in Cultus Lake (kg) (Ricker and Foerster, 1948, p. 189, 196).

Year-class	Initial wt of fry	Wt of yearling stock	Mortality	Production	Ratio of production to yearling stock	Ratio of production to mortality
Fingerlings						
1925	500	1,600	3,750	4,850	3.03	1.29
1926	1,030	1,980	5,280	6,230	3.15	1.18
1927	7,500	8,540	26,500	27,500	3.22	1.04
1928	220	420	1,130	1,320	3.15	1.17
1929	870	2,500	5,990[a]	7,620[a]	3.05	1.27
1930	1,900	5,770	13,700	17,600	3.06	1.29
1931	5,300	6,690	20,200	21,500	3.22	1.06
1932	650	1,360	3,520	4,270	3.14	1.21
1933	610	1,860	4,390	5,700	3.05	1.30
1934	590	5,030	6,140	10,700	2.13	1.74
1935	3,300	18,840	25,100	40,700	2.16	1.62
1936	1,700	11,790	15,100	25,200	2.14	1.67
Yearlings						
1926	290	105	540	350	3.36	27,800(1928–29)
1927	1,120	1,095	4,150	4,130	3.77	5,450(1929–30)
1928	160	118	470	430	3.64	8,050(1930–31)[b]
1931	920	763	3,030	2,860	3.75	7,130(1933–34)
1932	570	288	1,320	1,040	3.61	6,740(1934–35)

[a] In the original table these figures were incorrect.

[b] Corrected from the 6350 kg of the original table.

In Table 67 are given the calculated mortality and production data for Cultus Lake during the 12 years of investigation. Vast differences in production occurred. These were, in large part, brought about by widely varying original fry populations in the lake, which, in turn, resulted from the differences in (1) the numbers of spawning fish returning to the lake and (2) the different methods of propagation

TABLE 68. The three methods of propagation tested at Cultus Lake in the years indicated, showing: (1) the extent of the seeding, either of (a) eggs contained in females proceeding to the lake spawn naturally, (b) of eggs planted at "eyed" stage or, (c) free-swimming fry liberated; (2) the calculated fry or known fry release; (3) yearling stock in lake; and (4) the percentage survival at end of first year in lake (Ricker and Foerster, 1948, p. 184, but column 3, calculated fry release, has been added).

Brood year	Seeding (1×10^3)	Calculated fry release (1×10^3)	Yearlings in lake (1×10^3)	Survival (%)
A. Natural spawning				
1925	17,470	3,300	200	1.14
1927	250,000	51,500	3,092	1.24
1930	24,900	13,100	788	3.17
1935[a]	40,000	–	3,161[b]	7.90
B. Eyed egg planting				
1928	2,650	2,332	91	3.44
1933	4,371	3,846	246	5.63
1934[a]	5,590	–	571	10.22
C. Fry liberation				
1926	5,916	5,916	419	7.07
1929	9,093	9,093	352	3.87
1932	4,825	4,825	263	5.45
1936[a]	12,468	12,468	1,637	13.13

[a] During these years predator control was being practised.

[b] In the original table, the figure of 2204 was in error.

being tested (see Foerster, 1938a). These latter, three in number, were carried out as shown in Table 68, where the pertinent data are also shown.

With reference to Table 68, it should be pointed out that:

1. The fry releases in column 3 have been computed as follows: for natural propagation, as 100/6 × numbers of yearlings, since, from the marked sockeye releases into the lake (see Fig. 61) around 6% of the fry survived to yearling migrant stage; for "eyed" egg planting, as 88% of the eggs planted, since from special experiments (Foerster, 1935a) this survival of healthy fry resulted.

2. The number of yearlings in the lake, column 4, relates to the numbers of yearlings surviving, whether they migrate seaward at the end of the first year or remain in the lake. In general, the nonmigrants have been found to be of minor significance except for the year-classes (1928 and 1932) which follow immediately *after* the extremely large spawnings. For these 2 year-classes the nonmigrants were more numerous than the migrants: 1928—52,000:39,000; 1932—142,000:121,000 (Ricker and Foerster, 1948, table I, p. 178).

As far, then, as consideration of production of young sockeye in Cultus Lake is concerned, it is apparent that, as might be expected, absolute productions and net productions of sockeye varied greatly from year to year, but one general feature remained about the same: the ratio of production to size of yearling stock varied only from 3.03 to 3.22. This ratio indicates, generally, that, of the total amount of

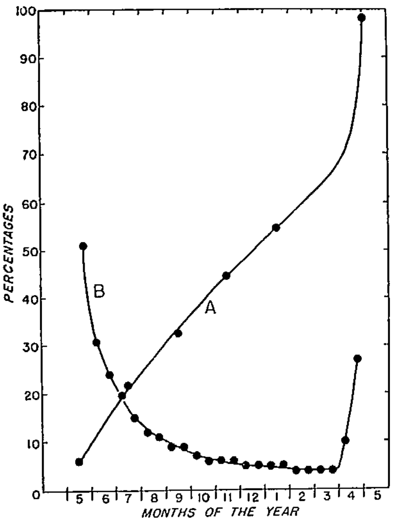

FIG. 61. A. Number of yearling sockeye migrants of the 1933 year class in Cultus Lake surviving from fingerlings released during the months indicated, as a percentage of the number released. B. Instantaneous mortality rates, in terms of percentage, computed from curve "A" for successive half-months. (From Ricker and Foerster, 1948, fig. 2.)

fish produced per year, only three-tenths was represented in the fish that survived to become yearlings. The other seven-tenths was represented by fish which died during the year.

Of course, a large additional quantity of energy in the food of the young fish was expended in swimming, seeking food, and in maintenance of metabolism, while another portion was not assimilated into the fish's body. For the year 1931, for example, for which (Ricker and Foerster, 1948, p. 201) there are data on the amount of plankton food consumed (103 metric tons) by the young sockeye in the lake, it was found that but 21.5 tons or 20% went actually into production of sockeye flesh. Of the 21.5 tons of sockeye produced during the year, only 6.69 tons or 31% was in the live yearling sockeye at the end of the year, which represents but 6.5% of the total biomass of food consumed.

In Fig. 62 are plotted curves of biomass (i.e., young sockeye) production throughout the year's residence in the lake, from fry to yearling stages for 1931 and 1935, and from yearling (I) to 2-year-old (II) stages for 1927. The methods used in calculating growth, mortality and resulting biomass production, in half-monthly intervals, are outlined elsewhere (Ricker and Foerster, 1948) and while, as intimated therein (p. 209), "the picture of production and food relationships obtained is incomplete from the standpoint of the lake's economy as a whole" and "even the information on the sockeye is quite imperfect in places," the findings serve to suggest the general trends in production of sockeye in a nursery lake and for that reason are exceedingly valuable. Future studies elsewhere, with more efficient techniques, will no doubt clarify the picture.*

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* As Ricker and Foerster remark (1948, p. 209) "in our work it was always tantalizing to realize that while millions of young salmon were present in the lake, it was necessary to depend on partly digested stomach samples for information on growth and feeding. . . ." Using methods developed by Johnson (1956) at Babine Lake and by other investigators elsewhere in recent years, samples of young sockeye resident in the lake can now be collected for study.

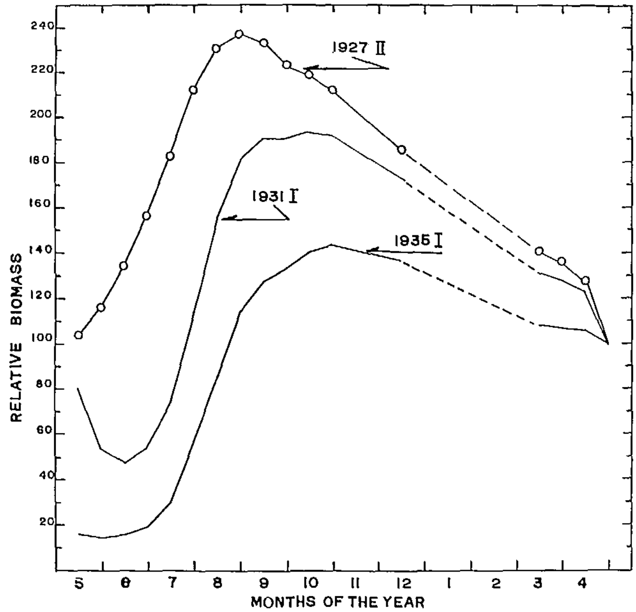

FIG. 62. Comparison of curves of relative biomass of young sockeye in Cultus Lake, expressed in terms of 100 wt units of yearlings (1931 and 1935) and 2-year-olds (1927). (From Ricker and Foerster, 1948.)

In comparing the seasonal course of change in biomass for the 1931 year-class in Fig. 62, with that for the 1933 year-class in Fig. 60 (there referred to as "standing crop") it will be noted that the initial decrease in biomass in 1931 was relatively greater, so that the stock decreased rapidly to almost one-half its weight at time of entrance into the lake. The summer growth did not reach as high a level as in 1933. Mortality was relatively higher in 1931. As a result, as shown in Table 67, the final stock at migration time in 1931 weighed only about one-quarter more than it did at the fry stage while, in 1933, the yearling stock was triple the weight of the initial fry escapement.

The 1931 year-class was a large one (1,571,000 yearling migrants and 633,000 nonmigrants) with a total weight of 6690 kg.* On the other hand, the 1933 year-class was relatively small—242,000 yearling migrants and 4,000 nonmigrants, having

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* This 1931 brood-year is not shown in Table 68 because, of the total spawning run of 32,438 fish (7,269 males, 25,169 females), roughly one-half (12,869) of the females were allowed to proceed to the lake to spawn naturally giving a possible deposition of 54 million eggs. The remainder (12,300) of the females (egg content—51,660,000) were stripped and the eggs placed in the hatchery. In the spring of 1932, 6 million of the resulting fry were liberated in the lake while the remainder were transferred to other areas. Due to the confusion in assigning the yearlings in the spring of 1933 to either of the two methods of propagation, the year's results were not included in this propagation test.

a total biomass of 1860 kg. Thus, the two series of data may be looked upon as close to the upper and lower limits of the lake's production and net production under natural conditions.

In Fig. 62, the seasonal biomass curve for the 1935 year-class yearlings is of interest, because it represents the situation prevailing when control of predators was undertaken. As shown in Table 67, (fingerlings), the last 3 years tabulated, 1934, 1935, 1936, have an appreciably lower ratio of production to yearling stock (2.14) than in earlier years (average of 3.13); they also have a higher ratio of production to mortality (1.68 as compared with 1.20). These were years in which a vigorous campaign to remove predators from Cultus Lake was conducted (see p. 240 and 396). As a result of the decrease in predation, it was found that while in the years prior to predator control, 1925–33, an average of only 12.6% (1349 kg) of the total average yearling production (10,732 kg) went into the development of the final yearling stock (weight of yearling stock, 3413 kg, less the initial weight of the fry, 2064 kg), in the years of predator control, 1934–36, 40% (10,024 kg) of the total average yearly production (25,533 kg) was converted into net yield of yearling sockeye (11,887–1,863 kg).

It will be observed from Fig. 62 that, in comparison with the curve for 1931, that for 1935 shows important differences. In the first place, the early drop in production in spring is very much less pronounced and, secondly, the increase from lowest to highest production is greater, namely from 14 to 144 wt units or 10-fold, as compared to from 48 to 193 or 4-fold. It will be recalled that the year 1931 was considered to represent the lower limit of net production of biomass (relative to the initial fry biomass) because it was a "big" year, i.e., a large population of sockeye was resident in the lake. However, comparison of the 1935 curve, Fig. 62, with that for 1933, Fig. 60, considered as representing the upper limit of (relative) net production of biomass, shows that 1935 maintains its advantages, though less pro-

TABLE 69. Comparison of young sockeye biomass production of the 1927 and 1936 year-classes in Cultus Lake, when total production was similar.

Sockeye	Year-class 1927	Year-class 1936
Initial wt of fry (*kg*)	7,500	1,700
No. of yearling migrants ($\times 10^3$)	2,426	1,627
Avg wt of one migrant (*g*)	3.06	7.2
Total wt of migrants (*kg*)	7,420	11,720
No. of yearling non-migrants ($\times 10^3$)	666	10
Avg wt of one non-migrant (*g*)	1.68	7.0
Total wt of non-migrants (*kg*)	1,120	70
Total wt of yearling stock (*kg*)	8,540	11,790
Calculated biomass mortality (*kg*)	26,500	15,100
Total calculated biomass production (*kg*)	27,500	25,200
Net production of biomass of young sockeye (*kg*) (yearling stock less wt of fry)	1,040	10,090

nounced. The early spring drop in 1935 is less than in 1933; the summer peak in biomass is also less. For the 1933 year-class the initial fry biomass (see Table 67) was tripled during the year, whereas for the 1935 group there was an increase of 5.7×.

The fact of particular significance here is not the beneficial effect of predator control, which is discussed later, p. 396, but the capacity of the lake to get more sockeye biomass into the form of yearlings. Table 69 compares 2 year-classes, 1927 (prior to predator control) and 1936 (during predator control) when the Ivlev production of young sockeye was of the same order. In 1936, with roughly one-quarter as many fry released into the lake, the growth per fingerling during the year in the lake was much greater (7.2 g as compared with 3.06 g) and the total biomass of the yearling stock (11,790 kg) was 6.9 times that of the initial fry release; while, in 1927, the yearling stock was only 1.14 times the initial calculated weight of the fry. In 1936, the net production of young sockeye biomass was practically 10 times that of 1927; not only was there better growth per fish, but many more carried through the year due to decreased mortality (which was 15,100 kg in 1936 and 26,500 kg in 1927).

It is clear, then, that while the biomass production data for early years, 1927–33, may have accurately revealed the productive capacity for young sockeye development *under the conditions prevailing* in the lake during those years, they by no means represent the maximum net production potential had the lake been "managed" to achieve greatest sockeye production. This will be further discussed later (see p. 387).

Refer briefly to Rounsefell's treatment of the Cultus Lake data (Rounsefell, 1946) (see Fig. 36). He suggests that at low levels of abundance (under 1 million) the young fish were not competing with one another for food. The actual size attained depended, therefore, on factors other than competition. Since there is a natural limit to the growth potential of the individual fish, the maximum productivity of the lake was not achieved when the populations were small (Area A of Fig. 63). As the population increased the total weight of sockeye resident in the lake increased. At high levels of population, however, e.g., in 1929 and 1933, growth rate of the individual sockeye dropped and competition for food appeared to be the principal factor. From Fig. 63, according to Rounsefell, it would seem that "at Cultus Lake the maximum yield is in the neighbourhood of 9000 kg (about 20,000 lb) with a population of about 1¾ million sockeye." When the population is greater than this, the decline in growth rate brings about a smaller total weight.

TWO-YEAR-OLDS

At Cultus Lake the number of young sockeye which did not migrate to sea as yearlings but which remained in the lake a second season was never great. They occurred in largest numbers (Foerster, 1929b, 1944) as a carry over of an abundant year-class (Table 67, year-classes of 1927 and 1931) constituting, roughly, 3–4% of the total number of smolts produced by the year-class. They occurred in

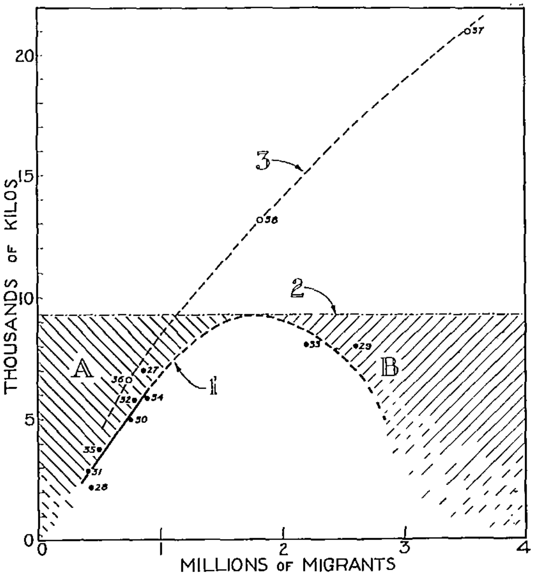

FIG. 63. Production of seaward-migrating young sockeye, Cultus Lake from 1927 to 1938. Curve 1 shows the probable production in kilograms under natural conditions, the broken line portion being empirically determined. Curve 2 shows the line of approximate maximum production under natural conditions. Curve 3 shows the indicated production for the 3 years in which the predator and competitor species of fish in the lake were suppressed. Area A—weight lost from the maximum natural production caused chiefly by a population insufficient to utilize the total food supply. Area B—weight lost from maximum natural production when too large a population is present, probably due to (1) the large amount of food used to sustain life without growth and (2) the actual impairment of the food supply owing to the large number of fish per unit area. (From Rounsefell, 1946, fig. 3.)

largest proportions in the years following the "big" year (i.e., 1928 and 1932 year-classes, Table 67 yearlings), when they represented 12–13% of the year-class. In these latter year-classes, while the sockeye not migrating as yearlings were estimated to be greater in actual numbers than the yearling migrants (38,000 migrants and 52,000 nonmigrants of the 1928 brood; 122,000 and 140,000 for 1932), they were notably smaller and represented less biomass, as shown in Table 67.

In the case of the 1927 and 1931 year-classes, however, the 2-year-old migrants (Table 67 yearlings) appreciably exceeded in weight the yearling migrants which were resident in the lake with them, i.e., those of the 1928 and 1932 year-classes (Table 67 fingerlings), and the 2-year-olds of the 1927 brood even exceeded the

1928 brood yearlings in numbers. In these years, therefore, the production of 2-year sockeye is of significance, particularly in relation to that of the yearlings.

In Fig. 62 is shown a curve of biomass production for the 2-year sockeye of the 1927 year-class in Cultus Lake. Though the data with respect to production, mortality, etc. of the 2-year fish are sketchy, because of the limited information (Ricker and Foerster, MS, 1948, p. 193–196), they are at least suggestive of the general trend and, when compared with similar data for yearlings, they serve to bring out certain important facts to substantiate certain opinions voiced by other investigators concerning the production of 2-year fish (see p. 270).

During their 2nd year in the lake, the 1927 year-class 2-year-old fish, based on the limited data available (Ricker and Foerster, MS, 1948, p. 195), though appreciably larger in size at the start of the year than the 1-year fish (at that stage only fry), merely doubled their mean individual weight and actually decreased slightly in total biomass. Throughout the year, as indicated in Table 67, mortality was high, practically as great, in biomass weight, as the production. In other words, in general the 2-year-old fish made no gain whatever, during their 2nd year in the lake, when considered in terms of weight. They, at best, were able merely to hold their own. When considered from the point of view of their weight at the beginning of the year and that at the end, i.e., migration time (Table 67, columns 2 and 3), the 2-year-olds decreased substantially in bulk in all years except 1927—in two instances, 1926 and 1932, by 50% or more.

OCCURRENCE OF TWO-YEAR-OLD MIGRANTS

Sockeye which remain in lakes for more than 1 year prior to seaward migration are not numerous in most of the prominent sockeye rivers of British Columbia, except for the Nass River, the most northerly, where they represented over the years 1912–55, an average of 62% of the run each year (Foskett, 1956). In the other rivers examined, they, recorded as 5_3 fish, occur as follows:

Skeena —1916 to 1955—8.7% (Foskett, 1956, p. 37)
Rivers Inlet —1922 to 1955—1.5% (Foskett, 1956, p. 41)
Fraser River—1952 to 1959—2.0% (Henry, 1961, p. 19)

In the Fraser River system, the 2-year-in-lake sockeye are found principally (Henry, 1961, p. 18) in three spawning stocks, Taseko, Chilko, and Birkenhead, but they may occur in small numbers in any race, as they do at Cultus Lake.

In Alaskan and Kamchatkan waters these 2-year-in-lake sockeye are much more common and in some areas there are large numbers of individuals that migrate seaward only after 3 years' residence in a lake or more (Barnaby, 1944; Rounsefell, 1958a; Krogius, 1961a; Krogius and Krokhin, 1948). From studies at Lake Dalnee, Kamchatka, Krogius and Krokhin (1948, p. 17) have concluded that:

> "if a large population of yearlings is present in the lake and the amount of food is limited, the unfavourable conditions will result in weaker fingerlings which will bring about a greater

> loss. . . . Since the return of adults with one- and two-year-lake residence is almost equal, from an economic point of view a two-year sojourn of the young in the lake is disadvantageous. Two-year-olds consume considerably more food than yearlings; in their place, four times as many yearlings could be produced which would give a correspondingly greater return of adults (in absolute numbers of fish). Therefore, an understanding of the reasons for the different lengths of lake residence of the young becomes a very important problem."

Recently Krogius (1961a, p. 139) has presented some most interesting data, pertaining to Lake Dalnee, on *why* some young sockeye remain in a lake for a second season. She points out that while, in some instances, the prolonged lake residence may be caused by a retarded rate of growth of some of the young sockeye, due to insufficient food in years when the lake populations are usually great (as at Cultus Lake and Kurile Lake in some years), there are occasions when, because of a severe decline in the populations of young sockeye feeding in the lake, the food resources of the lake are not fully utilized. In such cases either (1) the fish which compete with the young sockeye for food increase in numbers, such as the three-spine stickleback in Lake Dalnee and in Karluk Lake or the smelt in Lake Azabach, or (2) the young sockeye themselves strive to make use of the extra food resources by remaining in the lake an additional year. Some of these, therefore, continue to stay in the lake as "dwarf" sockeye or "residuals" (Ricker, 1938c).

Fig. 64 is a reproduction of Krogius' diagram of the relation of numbers of young sockeye migrating from Lake Dalnee (1- and 2-year-old migrants) to their biomass or weight, to which have been added comparative data for Cultus Lake. According to Krogius, the central curve of the three serves to divide the 1-year from

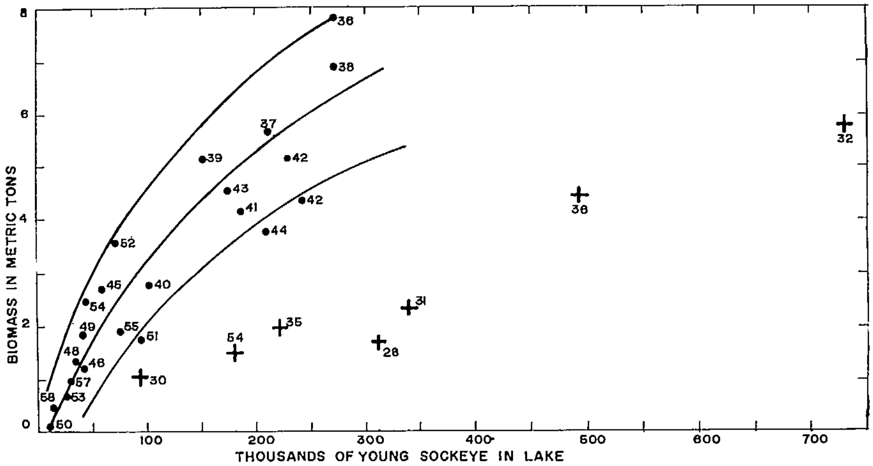

FIG. 64. The numbers of young sockeye (in thousands) in relation to their biomass (in metric tons) for Lake Dalnee (solid circles) and for Cultus Lake (crosses). The numerals indicate the year of migration. Each year's population includes both 1- and 2-year migrants (see Krogius and Krokhin, 1948, p. 19, for the 1936–43 Lake Dalnee data and, Ricker and Foerster, 1948, p. 178, for the Cultus Lake data.) The graph is taken from Krogius (1961a, fig. 4), to which the Cultus Lake data have been added.

the 2-year fish. All the points lying above and to the left of this central curve represent years in which the lake's food resources are not fully utilized, in which the fish are of very large size, migrate predominantly as 2-year-olds or become dwarf "residuals." Conversely, those points lying below and to the right of the central curve represent years in which the food resources are fully utilized. Frequently there is a shortage of food. In these years the sockeye migrate as yearlings; they are of relatively small size and no dwarf residuals occur.

Because of this apparent superfluity of food in some lakes, according to Krogius' hypothesis, and the resulting tendency for young sockeye to remain in the lake for one or more additional years, if not permanently—a situation which is of no particular benefit to sockeye production and may be even detrimental (see discussion, p. 237 and p. 269)—it is suggested (Krogius, 1961a) that the remedy for the situation lies in restoring, in those lakes, the much greater populations of young sockeye to the levels that the plankton food resources would seem to warrant.

This is actually quite the reverse of any situation which has been found to occur in British Columbia sockeye lakes. Here there has not been found any great number of 2-year-old seaward migrants except in a few lakes, e.g., Morice Lake on the Skeena and lakes in the Nass River system. In these cases the evidence available suggests that the rate of growth is so slow—due to very low temperatures and to the presence of glacial water with low transparency and hence poor food conditions —that the young sockeye are not sufficiently developed at the end of the 1st year to be stimulated to migrate seaward. It must be noted, in passing, that in Owikeno Lake (p. 185) these same environmental conditions occur, yet the seaward migrants there are principally yearlings. Where 2-year-old seaward migrants have been found to occur in company with yearlings these have always been found to be of smaller average size at the migration season than the yearlings which did migrate. This was found to occur also at Karluk Lake (Barnaby, MS, 1932) in the case of 3-year-olds which did not go seaward when the normal 2-year-old seaward migration occurred. It even occurs at Lake Dalnee. Here (Krogius, 1961a, p. 138), "yearling sockeye, captured in Lake Dalnee after the seaward migration had occurred, were always smaller in length and weight than the sockeye of the same year-class which had just gone to sea."

GROWTH OF YOUNG SOCKEYE DURING LAKE RESIDENCE

On the basis of data available for certain sockeye areas around the Pacific, as shown in Table 70 and reported by various investigators, it is of interest to relate the growth of young sockeye in four lakes, expressed as biomass in kilograms per hectare of lake area, to the population density of the sockeye in the lake. It is at once evident, from Table 70, that there are two quite different types of lakes, one in which the growth or production of sockeye is quite low, relatively speaking, i.e., Cultus and Chilko lakes, and one in which it is much greater, i.e., lakes Dalnee and Karluk.

A comparison of the relation of population density to the total biomass of young sockeye migrating from four different lakes has been made by Krogius (1961a,

p. 140), to which have been added the comparable data for Chilko Lake, as taken from Table 70:

Lake	Area	Vol	Avg no. of seaward migrants		No. of seaward migrants per ha	
	(ha)	*($m^3 \times 10^6$)*	*(millions)*	*(tons)*	*(no.)*	*(kg)*
Kurile	7,490	13,160	60.000	416.0	8,000	56.0
Karluk	3,950	1,920	8.500	193.7	2,000	49.0
Cultus	626	201	1.300	6.8	1,900	11.0
Dalnee	136	43	.115	3.1	850	23.0
Chilko	19,426	–	10.000	42.0	513	2.1

TABLE 70. Comparison of numbers of seaward migrating sockeye per year and their biomass (in kg) calculated on a "per hectare of lake surface" basis, for four lakes.

Cultus Lake[a]		Chilko Lake[b]		Karluk Lake[c]		Lake Dalnee[d]	
No.	Biomass	No.	Biomass	No.	Biomass	No.	Biomass
168	1.7	67	0.38	1100	24	750	19
300	2.3	165	0.63	1400	32	1100	39
410	3.2	435[e]	1.48	1500	25	1250	35
540	2.7	607	2.68	1500	31	1370	28
567	4.0	1293[f]	5.64	1800	37	1600	41
803	7.1			1800	38	1840	32
1260	9.2			1800	40	2100	50
2510	9.2			1900	45	2100	54
2600	19.0			2000	46		
3900	12.0			2100	41		
5000	30.0			2700	64		
				2800	63		
				2900	67		
				3300	72		
				3300	85		
				3400	89		

[a] Area of lake—626 ha. Sockeye data from Foerster (1944).

[b] Area of lake—19,426 ha. (IPSFC, 1949). Sockeye data from Clutter and Whitesel (1956, p. 24), and Henry (1961, p. 79).

[c] Area of lake—3,950 ha. Sockeye data from Rounsefell (1958a, table A-10).

[d] Area of lake—136 ha. Sockeye data from Krogius and Krokhin (1948, table 14).

[e] For 1953 no weight was recorded for the yearlings, but since the fork length of the migrants was the same as in the preceding year, the weight was considered to be approximately the same.

[f] In 1 year (1951 brood year) no weight was given for the 2nd-year migrants. A weight of 10 g has been taken as approximate. The number of 2nd-year fish was small.

Here again the two types of lakes show up. Karluk and Dalnee lakes produce, per hectare of lake surface, a small number of quite large smolts. Their period of lake residence is, in general, more than 1 year (Lake Dalnee— 50%; Karluk Lake —90%). Cultus, Chilko, and Kurile lakes, however, produce a much larger number of small seaward migrants. At Cultus and Chilko lakes most of these migrants are yearlings, but at Kurile Lake they are mostly of the 2- and 3-year lake residence type. The Kurile Lake sockeye production or growth picture represents, consequently, a compromise between the two lake types. It does not correspond to Krogius' hypothesis concerning food utilization and growth of large 2-year-in-lake sockeye, as discussed above.

In the Bristol Bay area of Alaska, an extremely productive sockeye area, there is also a similar variation in length of lake residence of the young. In most areas, e.g., Kvichak, Naknek, etc., 2 years in the lake is general; in the Wood River system, with five individual lakes involved, 1-year-in-lake migrants predominate (FRI, 1959, p. 6). In another Alaskan area, Chignik, an unusually high proportion of yearling sockeye in the 1959 seaward migration, 34.3% (FRI, 1961, p. 7), has aroused interest. In the 1920s when the Chignik sockeye runs were large the majority of the adults were of the 1-year-in-lake type. The implication that the dominance of 2-year seaward migrants from Chignik is associated with smaller runs and hence of reduced sockeye production is in line with Krogius' hypothesis.

In British Columbia, as has already been intimated (p. 269), the occurrence of 2-year-in-lake sockeye in the sockeye-producing areas of British Columbia is confined to a few localities only. Yet were the Krogius hypothesis to apply in the lakes of the upper Fraser River system and at Babine Lake on the Skeena River there should have been ample opportunity for 2-year-in-lake smolts to occur in those many years on the Fraser, 1915–47, when the annual sockeye runs were strikingly reduced by the Hell's Gate slide and the continued heavy fishing in subsequent years, and, on the Skeena, 1951–53 (Godfrey et al., 1954), when a serious rock slide also severely reduced the extent of spawning.

In the years following these disastrous slides the populations of young sockeye in the nursery lakes were very light, relatively speaking, and the available plankton food must have been only partially utilized. There are no records of the development of unusual populations of 2-year-in-lake sockeye nor of greater crops of "residuals." Neither is there any evidence of unusual increase in competitor fishes though the data in this respect are perhaps inadequate. This phase of the problem requires further careful study.

All available evidence for British Columbia sockeye production suggests, therefore, that the young sockeye, in general, proceed seaward after 1-year residence in a lake. In years when the population density of the feeding fish in a lake is unusually high the smaller fish may not migrate but remain a second season in the lake.

RELATIVE INCREASES IN GROWTH INCREMENT PER YEAR

In order to give some idea of the relative growth of young sockeye in a lake, Table 71 has been prepared from available published data to show the average lengths and weights of seaward migrating yearlings, 2-, and 3-year-olds in various lakes of Washington, British Columbia, Alaska, and Kamchatka. A wide range of variation is to be expected, having regard to the productive capacities of the lakes,

TABLE 71. Average lengths and weights of seaward-migrating sockeye of ages from I (yearlings) to IV (4-year-olds).

	Avg length (*cm*)				Avg wt (*g*)			No. of years'	
Region and lake	I	II	III	IV	I	II	III	data	References
Fraser system									
Cultus	8.5	12.0	–	–	6.3	16.8	–	11	Foerster, 1944, p. 272
Harrison	9.5	–	–	–	9.2	–	–	2	Clutter & Whitesel, 1956, p. 24
Lillooet	7.7	–	–	–	4.5	–	–	1	"
Shuswap	6.3	–	–	–	2.3	–	–	2	"
Chilko	7.6	10.7	–	–	4.3	10.9	–	5	"
François	10.5	–	–	–	12.0	–	–	1	"
Stuart	9.5	–	–	–	8.4	–	–	1	"
Skeena system									
Lakelse	8.2	11.3	–	–	5.5	13.6	–	1	Foerster, 1952, p. 30
Babine	8.3	10.8	–	–	5.7	11.6	–	4	Dombroski, 1954, p. 32
Central B.C. coast									
Owikeno	6.1	–	–	–	2.0	–	–	–	Foskett, 1958, p. 873
Port John	8.4	10.4	12.6	–	6.2	11.2	21.7	5	FRBC data
Alaska									
Karluk	–	13.2	14.2	–	–	21.0	26.5	16	Rounsefell, 1958a, p. 161
	11.1	13.3	14.2	15.0	–	–	–	6	Barnaby, 1944, p. 274
Chignik	–	7.6–8.4	–	–	–	–	–	–	FRI, 1959, p. 11
Little Kitoi	6.2	7.9	–	–	2.0	4.1	–	1	ADF, 1959, p. 32
Ruth[a]	11.2	14.2	–	–	13.6	27.9	–	1	"
Midarm	7.2	8.7	–	–	2.7	5.9	–	1	"
Kamchatka									
Dalnee	11.5	15.6	19.1	–	15.5	39.1	69.2	?	Krogius, 1961a, p. 133
Achchei	–	15.7	17.2	–	–	34.3	41.5	?	"
Azabach	10.0	–	–	–	9.3	–	–	?	"
Kurile	–	9.0	10.9	–	–	18.0	21.0	?	"
Columbia system									
Wenatchee and Osoyoos	8.9–12.7	–	–	–	–	–	–	1	Fish and Hanavan, 1948, p. 25
Same[b]	10.8	22.2	–	–	–	–	–	5	Anas and Gauley, 1956, p. 42–46

[a] Ruth Lake had been poisoned and the scrap fish eliminated prior to planting of sockeye fry.

[b] These sockeye were trapped at Bonneville Dam during the year, most of them in April and May, as they migrated down the Columbia River.

as influenced by climatic conditions, food resources, density of population, presence of competitor, and predator fishes, etc.

One-year-old migrants (i.e., yearlings, age I) vary from a low of around 6 cm in length and 2 g in weight to a high of 11.5 cm and 15.5 g in very richly productive Lake Dalnee or 11.2 cm and 13.6 g in Ruth Lake where competition from other competitor and predator fishes had been eliminated. Two-year-old migrants (age II) vary from 7.6 cm in length at Chignik, and 9.0 cm and 18 g at Kurile, to 15.6 cm and 39.1 g at Lake Dalnee. Three-year-olds, in areas where they occur in abundance, vary from 10.0 cm and 21 g at Kurile to 14.2 cm and 26.5 g at Karluk.

For the British Columbia area, the vast majority of the sockeye migrate as yearlings with an average size of around 8.0 cm in length and 5 g in weight.

VARIATIONS IN SIZE FROM YEAR TO YEAR

In each lake the sizes of the young sockeye would be expected to fluctuate about the averages given in Table 71. The extent of these variations may be indicated by a study of Table 72 where records for several areas are given. In general, the fluctuations in size are not too extreme, except when there are very great differences in population density of young sockeye in the lake, as at Cultus in 1929 and 1933. This feature is not apparent in 1937 because of predator control which substantially raised the productive capacity of the lake. For Shuswap Lake the 1948 and 1952 data represent years when the very abundant quadrennial-cycle migrations occurred. In 1953, a relatively "low" year, the migrants were much larger and the differences in weight would most likely have been more remarkable.

TABLE 72. Examples of size differences (length and weight) from year to year of seaward-migrating 1-, 2-, and 3-year-old sockeye from various North American lakes and, in some of the areas, the numbers of migrants counted or estimated.

		1-year-olds			2-year-olds			3-year-olds		
Lake	Year	No. ($\times 10^3$)	Length (*cm*)	Wt (*g*)	No. ($\times 10^3$)	Length (*cm*)	Wt (*g*)	No. ($\times 10^3$)	Length (*cm*)	Wt (*g*)
Cultus[a]	1927	183.4	9.22	8.10	–	–	–	–	–	–
	1928	336.2	8.06	5.04	–	–	–	–	–	–
	1929	2,426.2	6.84	3.06	8.3	11.76	12.64	–	–	–
	1930	38.6	8.76	6.55	66.6	11.83	16.44	–	–	–
	1931	349.9	9.08	7.10	5.2	13.13	22.60	–	–	–
	1932	788.4	9.02	7.32	–	–	–	–	–	–
	1933	1,571.0	7.22	3.67	–	–	–	–	–	–
	1934	121.2	8.65	6.53	63.3	10.60	12.07	–	–	–
	1935	242.5	9.07	7.55	14.2	12.73	20.33	–	–	–
	1936	102.6	9.49	8.83	–	–	–	–	–	–
	1937	3,101.0	8.38	5.96	–	–	–	–	–	–
Babine[b]	1950	–	8.30	5.50	–	11.04	11.90	–	–	–
	1951	–	8.24	5.60	–	10.07	9.40	–	–	–
	1952	–	8.04	4.90	–	10.44	10.10	–	–	–
	1953	–	8.60	6.20	–	11.47	14.80	–	–	–
Chilko[c]	1951	3,146.8	7.20	3.72	–	–	–	–	–	–
	1952	1,170.5	8.24	5.08	–	11.33	12.41	–	–	–
	1953	11,581.9	7.71	4.29	–	10.79	10.70	–	–	–
	1954	24,688.4	7.71	–	–	10.75	11.52	–	–	–
	1955	8,316.1	6.99	3.30	–	10.11	9.08	–	–	–

(Continued.)

TABLE 72. (Concluded.)

Lake	Year	1-year-olds			2-year-olds			3-year-olds		
		No. (× 10^3)	Length (*cm*)	Wt (*g*)	No. (× 10^3)	Length (*cm*)	Wt (*g*)	No. (× 10^3)	Length (*cm*)	Wt (*g*)
Shuswap[c]	1948	–	6.30	2.58	–	–	–	–	–	–
	1952	–	6.39	2.02	–	–	–	–	–	–
	1953	–	8.48	–	–	–	–	–	–	–
Karluk[d]	1925	–	11.20	–	10,023	13.53	–	–	14.56	–
	1926	–	10.00	–	9,120	13.55	–	1,237	15.07	–
	1927	–	11.12	–	3,345	13.40	–	1,498	14.60	–
	1928	–	11.05	–	4,477	12.76	–	817	14.23	–
	1929	–	–	–	5,195	12.82	–	3,132	14.26	–
	1930	–	11.04	–	6,011	12.64	–	2,101	13.94	–
	1931	–	11.08	–	10,212	12.97	–	2,058	14.07	–
	1932	–	10.69	–	5,850	13.20	–	3,100	14.29	–
	1933	–	11.38	–	4,052	13.55	–	1,957	14.62	–
	1934	–	12.15	–	11,172	14.03	–	1,319	15.29	–
	1935	–	11.61	–	11,448	14.14	–	1,778	15.19	–
	1936	–	11.07	–	11,092	13.30	–	1,922	14.63	–
Port John[e]	1950	0.1	8.60	4.9	–	10.00	8.5	–	–	–
	1951	1.6	9.44	–	13.0	9.78	–	–	–	–
	1952	2.1	7.67	4.4	8.3	10.81	13.0	0.6	12.03	17.9
	1953	4.3	8.30	5.9	9.6	10.90	12.6	0.2	–	–
	1954	6.0	8.70	6.8	13.5	10.74	11.7	–	–	–
	1958	–	8.80	–	5.2	10.66	–	0.6	12.66	–
Owikeno[f]	1914	–	5.95	–	–	–	–	–	–	–
	1915	–	5.86	–	–	–	–	–	–	–
	1916	–	6.02	–	–	–	–	–	–	–

[a] Data from Foerster, 1944.

[b] From Dombroski, 1952.

[c] Size data from Clutter and Whitesel, 1956; numbers of migrants from Henry, 1961.

[d] Size data from Barnaby, 1944, p. 274; numbers of migrants from Rounsefell, 1958a, p. 161.

[e] From unpublished data of Fisheries Research Board of Canada.

[f] From Gilbert, 1915, 1916, 1918.

VARIATIONS IN SIZE DURING THE PERIOD OF MIGRATION

Whenever two or more age-classes of young sockeye participate in migrating seaward, the individuals of the older age-class appear to migrate earlier, i.e., they occur early in the migration period. This has been found to occur with respect to yearlings and 2-year-olds at Cultus Lake (Foerster, 1929b, p. 11), at Kitoi Lake (ADF, 1955, p. 51) and Lake Dalnee (Krogius and Krokhin, 1948, p. 19), and for 2-year-olds and 3-year-olds at Karluk (Barnaby, 1944, p. 273). In the case of each individual age-class, however, early data collected at Cultus Lake tended to suggest that the population density of young sockeye in a lake may have an important bearing on the time of migration. For example, as shown in Table 73, at Cultus Lake in 1927 and 1928 when 183,400 and 336,200 yearlings, respectively, occurred there

TABLE 73. Average fork lengths and weights of yearling sockeye migrants at different periods of the annual seaward migration from Cultus Lake in 1927, 1928, and 1929.

Date	No. in sample	Length (*mm*)	Weight (*g*)
1927[a]			
Mar. 28	15	87	6.5
Apr. 18	18	91	7.8
Apr. 22	17	93	7.4
Apr. 28	5	92	7.2
Apr. 30	9	92	7.2
May 2	10	94	10.2
1928[b]			
Apr. 2–3	53	80.5	5.67
Apr. 4–11	141	79.5	4.80
Apr. 12–13	187	79.3	4.97
Apr. 14–16	155	81.5	5.42
Apr. 17–19	126	80.3	5.13
Apr. 20–22	189	78.6	4.89
Apr. 23–24	179	81.2	5.55
Apr. 25–26	158	81.6	5.02
Apr. 27–28	150	82.0	5.12
Apr. 29	191	79.1	4.85
Apr. 30–May 1	180	82.2	4.96
May 2–3	154	82.1	5.00
May 4–6	172	79.3	4.89
May 7–28	137	81.2	5.00
1929[c]			
Apr. 3–19	158	78.0	4.38
Apr. 20	161	76.8	4.02
Apr. 21–23	129	78.7	4.52
Apr. 24	220	76.3	4.02
Apr. 25–26	246	74.0	3.71
Apr. 27–28	558	70.9	3.23
Apr. 29–30	869	68.9	3.05
May 1–3	670	66.4	2.89
May 4–5	645	64.4	2.70
May 6–10	738	63.6	2.48
May 11–24	311	62.7	2.39
May 25–June 5	56	66.0	2.76

[a] From Foerster, 1929b, p. 19.
[b] From Foerster, 1936b, p. 316–317.
[c] Unpublished data.

seemed to be no pronounced changes in size during the period of migration. In 1929, however, when a large migration of 2,426,000 yearlings left the lake, a very marked decrease was observed as the migration proceeded. The varying trends are clearly shown in Fig. 65.

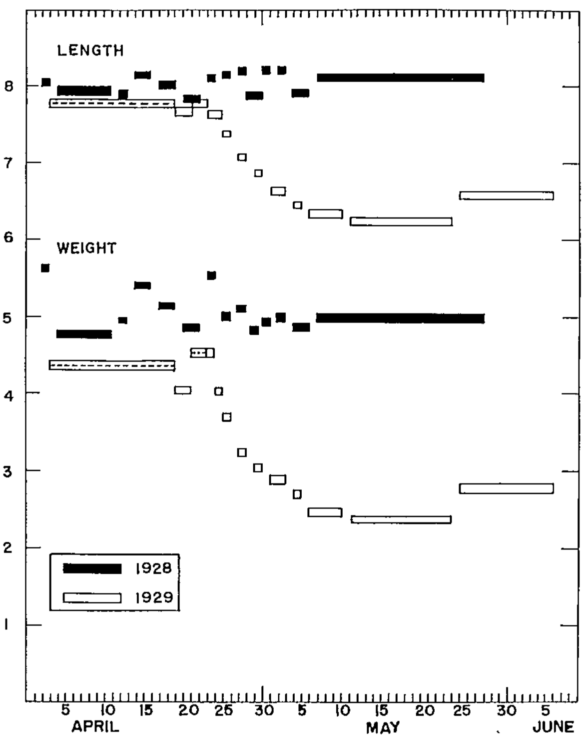

FIG. 65. Variations in average length (in centimetres) and weight (in grams) of seaward-migrating yearling sockeye from Cultus Lake at different periods during the migrations of 1928 (336,200 yearlings migrating) and 1929 (2,426,000 yearlings migrating). For the data in question, see Table 60: 1928—solid blocks; 1928—open blocks.

This evidence of the progressively declining size of migrants leaving a lake in years when population density is high and feeding conditions are limited, fits in well with the general picture of the largest, most virile and fastest-growing fish going to sea first, to be followed by smaller and yet smaller fish as the season advances with the very smallest unable to escape the lake but remaining over for a 2nd year. This was sugested as early as 1914 by Gilbert (1915, p. 74) when he remarked that:

> "both in the Fraser and in the Skeena there seemed grounds for the belief that the question of size at the close of the first year played an important role in determining the matter, for it appeared that the delayed migrants consisted in the main of that portion of the brood which had made the least growth up to the time when yearlings undertake their downward movement."

A comparison was made of the numbers of 1st-year nuclear rings on the scales of 5-year-old Nass River sockeyes, one group of which had migrated seaward as yearlings, the other as 2-year-olds. In a sample of 172 of the former and 233 of the latter, the 1-year-olds averaged 10.4 nuclear rings and only 11% had less than 9 rings, whereas the 2-year-olds averaged only 7 rings and 80% had less than 9. Thus,

> "this furnishes abundant confirmation of the theory that smaller yearlings with fewer nuclear rings are more likely to remain an additional year in the lake than are the larger yearlings. The smaller individuals may be drawn from those latest spawned, or they may be those of less vigorous growth. We have as yet no means of determining this point, but the probabilities are in favour of the theory of slow growth."

Examination of data from a quite larger collection of seaward migrants in the spring of 1916 (Gilbert, 1918, p. 62–66) quite clearly verified this hypothesis. It is remarked that:

> "the tendency to reduction in size is well marked throughout in each sex, and becomes strongly pronounced near the close of the season. The smaller sizes remaining in the lake then push forward, and in Owikeno Lake pretty thoroughly exhaust the yearling supply by the time the migrating season closes. Only a few remain over in this lake until their third spring, and these, as we can determine by the rings on their scales, were on the average the smallest of the yearlings at the time they failed to accompany their fellows of the preceding year."

However, reverting to the Cultus Lake data, cognizance must be taken of evidence presented by Clutter and Whitesel (1956, p. 59) showing a variety of size changes as the migrations of 1941, 1942, 1943, and 1944 proceeded (Fig. 66). The average weights obtained during each season were calculated "from the daily average counted number of smolts per six-pound weighing" (Clutter and Whitesel,

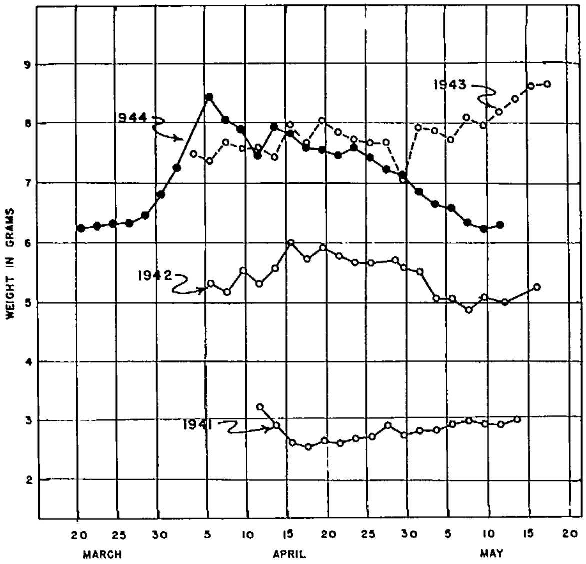

FIG. 66. Comparison of average weight of Cultus Lake seaward-migrating yearling sockeye at different periods of migration in 1941, 1942, 1943, 1944. Calculated from a total of 2087 counted 6-lb weighings (Clutter and Whitesel, 1956, p. 59).

1956, p. 58) and therefore represent "live" weights. Even though the earlier curves for Cultus Lake (for 1928 and 1929, Fig. 65) were based on formalin-preserved material, which introduces a certain error (Parker, 1963), the error would scarcely affect the comparisons made for 1928 and 1929, nor would they be such as to produce a progressive change as revealed for 1929. In 1941, 1942, and 1944 the migrations from Cultus were all relatively large—3,958,000, 1,752,500, and 2,012,500, respectively—hence, comparable with 1929; in 1943, however, 691,000 yearlings were recorded, thus perhaps falling into the category of a medium density lake-population and within the range depicted by the 1927 and 1928 migrations.

No explanation can, at the moment, be offered for the lack of the clearcut decrease in size in these 3 years, 1941, 1942, and 1944 (Fig. 66) at Cultus Lake, as so well shown for 1929, unless there was a marked increase in the productivity in the lake. That this situation may have developed is perhaps borne out by the fact that the average weights for 1942 and 1944, both well above 5 g, are appreciably

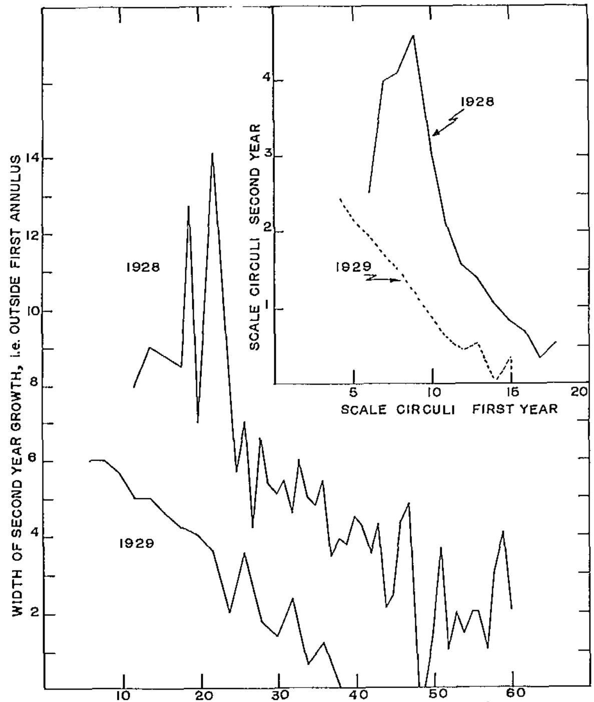

FIG. 67. The relationship (inverse) of width of that portion of 2nd year scale growth up to time of seaward migration of yearling sockeye, to width of 1st year growth band (in millimetres magnified 100 ×) for sample of 543 migrants in 1928 and 895 in 1929 from Cultus Lake. In the inset is shown the relationship of numbers of circuli laid down in the 1st year to the number laid down in the early portion of 2nd year in fresh water.

higher than the average for 1929, 3.06 g, for a closely similar (2,426,500) migration. The 1941 migration was greatly in excess of 1929, yet showed no appreciable change in migrant size.

One feature to be considered in connection with change in size of migrants during the migration period is the extent to which later-migrating individuals put on new growth prior to leaving the lake. As noted by Gilbert (1916, p. 48) for Owikeno Lake (Rivers Inlet) sockeye migrants "in general, the smaller the individual at the close of its first season's growth, the earlier it begins the growth of the next year, and the greater the amount of this growth will have been made by the time it leaves the lake." This phenomenon was also observed in studying the rate of growth of seaward migrants from Cultus Lake (Foerster, 1929b, 1936a, and unpublished data for the migration of 1929) and the 1929 findings confirmed conclusions reached for the 1928 migrants, namely, of a tendency for scales showing a relatively small amount of growth in the 1st year (i.e., a quite narrow 1st-year annulus) to have a greater amount of growth during that part of the 2nd year prior to migration, the so-called "accessory" freshwater growth. This is shown in Fig. 67 for the 1928 and 1929 migrant samples from Cultus Lake. The numbers of scale circuli or sclerites laid down, respectively, during the 1st year and that portion of the 2nd year prior to seaward migration, inset in Fig. 67, show the same pattern.

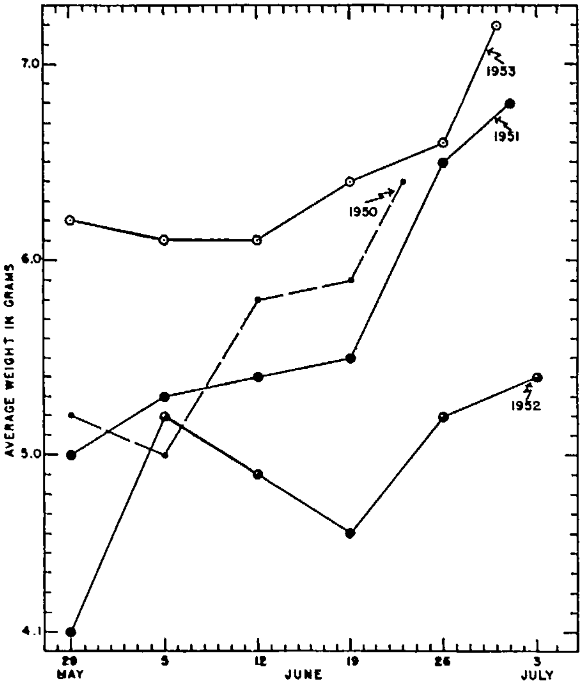

FIG. 68. Weekly average weight of yearling sockeye migrants from Babine Lake. (From Dombroski, 1954, fig. 5.)

While at Cultus Lake the amount of 2nd-year accessory freshwater growth of the young sockeye does not appear to be to any extent sufficient to mask the differences in growth for the 1st-year's lake residence nor any appreciable gradual decrease in size between early and late migrants, at least for 1929, the second season's growth prior to migration was found, at Babine Lake in 1951, to have been quite appreciable. Here (Dombroski, 1954, p. 32) while there was a quite obvious variability in size of migrants as the migration progressed, there was no evident decrease in weight (see Fig. 68) but, in all years examined, an increase in the latter part of the season (Dombroski, 1952, p. 25), especially after June 19th, Fig. 69. "Examination of stomachs showed that the migrants are feeding throughout their migration period (May to July). However, the new season's growth does not seem to be generally evident on their scales until the week ending June 19."

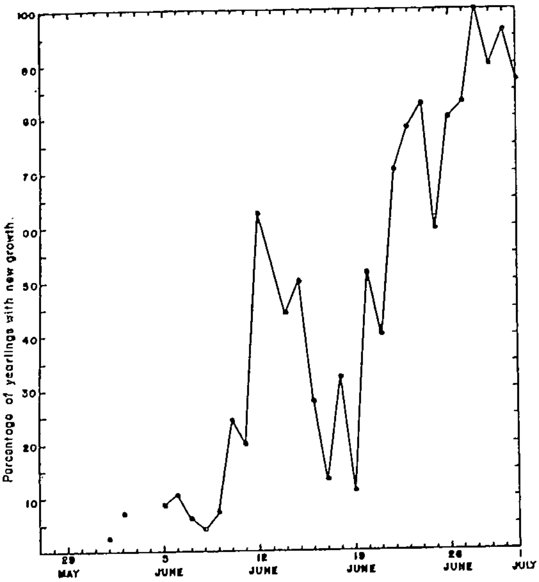

FIG. 69. The percentage of yearling sockeye with new 2nd-year growth, in daily samples taken at Babine River weir, 1951. (From Dombroski, 1952, fig. 10.)

The laying down of new 2nd-year growth on the scales of seaward migrants prior to migration has also been observed at Wood River, Alaska, (Burgner, MS, 1958). This new growth appeared on the scales of migrants collected after June 12th and increased in amounts as the season advanced, representing 30% of the total scale growth, hence of the fish's growth at the end of the migration period, mid-July. Thus, in such situations, the acquisition of new growth would tend to mask any indication of a general decrease in size as seaward migration proceeds.

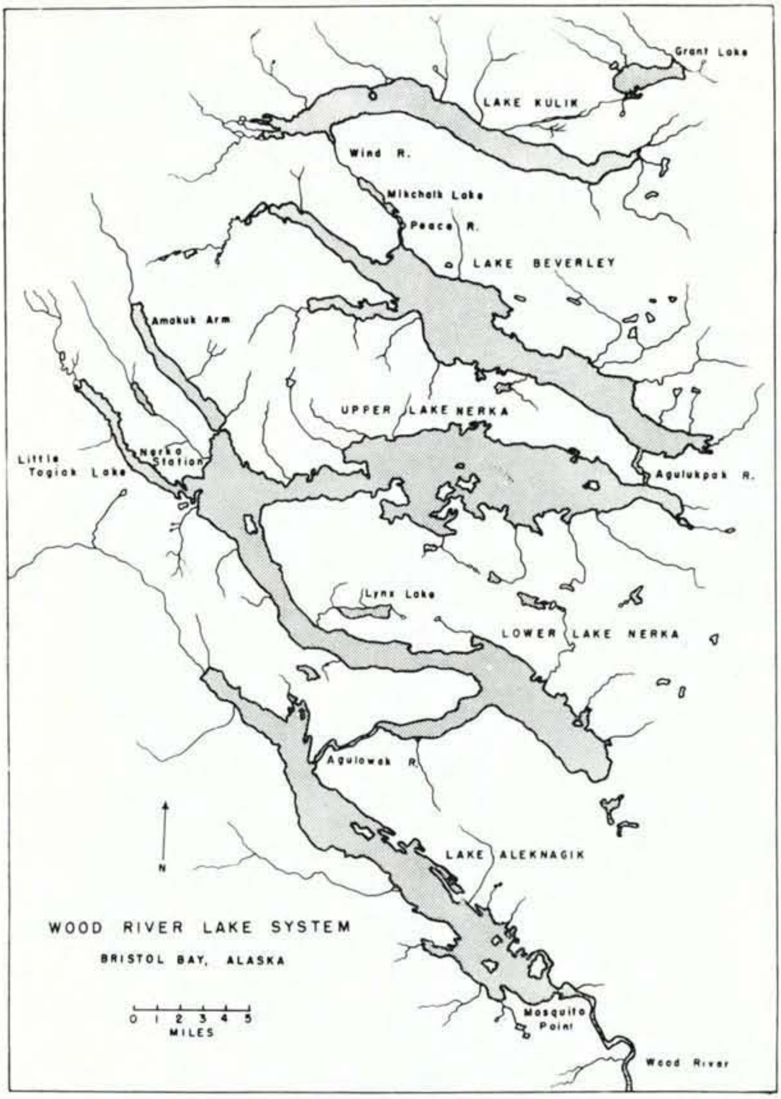

FIG. 70. The Wood River Lakes system, Bristol Bay, Alaska. (From Burgner, 1958, fig. 1.)

The situation in a multiple-lake river system such as the Wood River (see Fig. 70) or in a multibasin lake, such as Babine (see Fig. 56), may well be such that the succession or intermingling of runs of young seaward migrating sockeye from the different lakes or rearing basins may mask any evidence of a general decrease in size of migrants as the migration proceeds. For the Wood River system it is intimated (FRI, 1961, p. 5) that the "lack in progression in sizes of the smolts as the season advanced merely indicates that later smolts had come from other populations than the earlier ones." Whether the otherwise anticipated progression in size is thought to be due to the increased accessory 2nd-year growth is not clear. The graph presented, reproduced as Fig. 71, clearly shows a somewhat decreasing size trend during the season, but a marked increase at the end. The several peaks in migration during the season may well mark the arrival of new populations from upper lake nursery areas which would naturally change the size trend picture.

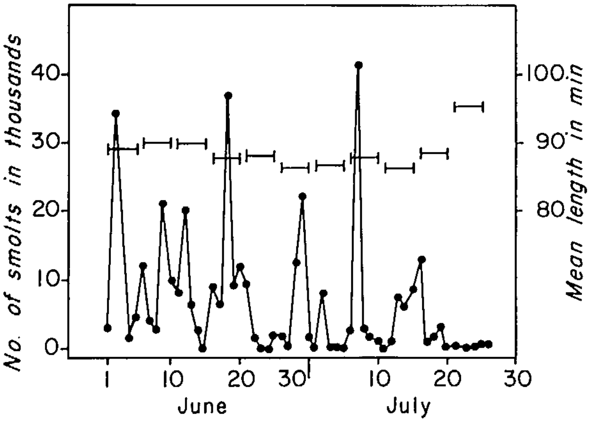

FIG. 71. The 1960 sockeye smolt migration from Wood River. Horizontal bars indicate the average lengths of samples in 5-day periods. (From FRI, 1961, fig. 2.)

All these data have been included in the discussion, merely to show the complicated nature of the study of size trends among migrants. Size of migrants is of particular significance in view of its relation to ocean survival. The larger the migrants as a result of good growth in the lake, the greater the ocean survival (p. 399) and consequently the more adults returning, but a too-rapid growth, leading to an extra year's stay in the lake, as discussed above, p. 237, is undesirable.

SEX RATIOS OF SEAWARD-MIGRATING SOCKEYE

Samples of yearling and 2-year-old migrants from Cultus Lake were examined to determine the male:female ratio (Foerster, 1954b). No significant departure from a 50:50 sex distribution was found among yearlings for the 7 years for which the sex determinations were made. Among the much smaller samples of 2-year-olds, an excess of females was found only in one season, 1939, out of three in which samples were available.

In order to ascertain whether a seasonal change in sex ratio may take place within an age-group, samples (1541 individuals in all) of the 1937 seaward migration of 3,102,000 sockeye were analyzed. From the sex distributions obtained:

Period	Total sample	Males	Females	Chi-square	Probability
April 1–24	734	339	395	3.830	0.05
April 25–June 15	807	447	360	9.210	>0.01
Total:	1541	786	755	0.584	0.3–0.5

it is apparent that while the females were more numerous in the first part of the run, the males predominated in the latter. For the total migration there was no significant difference in sex representation.

Observations made in other areas confirm the findings of a 50:50 sex ratio among sockeye migrants at Cultus Lake. At Babine (Dombroski, 1954, p. 31) examination of samples from four migrations (1950–53) revealed an equal representation of the sexes, and at Karluk Lake (Barnaby, 1944, p. 275) for 2-year and 3-year migrants in 10 migrations the sexes were, in general, equally represented. While slight variations occurred from year to year, none was statistically significant. For a number of Fraser River areas (Clutter and Whitesel, 1956, p. 53) examination of relatively small samples indicated, in general, an equal sex ratio. In some cases statistically-significant differences did occur but, since no one sex consistently predominated in these cases, they may have been due to inadequate or incomplete sampling.

For Owikeno Lake, Rivers Inlet area, however, the quite comprehensive sample of seaward migrants collectd in 1916 (Gilbert, 1918, p. 63–66) provides evidence of a predominance of males. Of the 2460 migrants examined, the sex ratios were:

Period (1916)	No. of Males	No. of Females	Chi-square	Probability
May 18–31	440	369	6.05	0.01
June 1–17	859	792	2.64	0.10

To what extent this unequal sex representation may be characteristic of the Owikeno Lake area in other years remains to be determined by further sampling. It does indicate that, for 1916, the sex ratios in the first part of the season were quite the reverse of those established for Cultus Lake in 1937. For the latter part of the migration, however, it agrees with Cultus Lake in having a preponderance of males.

OCCURRENCE OF "RESIDUAL" SOCKEYE IN A LAKE

Having discussed the characteristics of seaward-migrating sockeye from a lake with respect to age, size, sex ratios, it may be appropriate now to deal with those members of the lake population which do not migrate and to review the information which has thus far become available concerning them.

In the course of certain gillnetting operations carried out at Cultus Lake, originally (1932–34) of an experimental nature, but later (1935–37) to reduce the populations of predator fishes (squawfish, char, trout) in the lake, it was found (see Ricker, 1938c) that young sockeye of a greater-than-seaward-migrant size were present in the lake. The great majority of these, when captured in autumn, were in mature condition. Because these fish differed markedly from the normal nonmigratory kokanee or landlocked sockeye in breeding colour, time of spawning and certain other characters, Ricker proposed the name "residual" since it was apparent that they were "at least in large part, the progeny of anadromous parents" (Ricker, 1938c, p. 192).

In view of the fact that (1) gill nets are highly selective in the sizes of fish they catch, (2) the numbers of mesh sizes of nets varied from month to month and from year to year, (3) the fish resident in the lake undoubtedly varied greatly from year to year in size attained, the catches each year cannot pretend to be other than gross indices of the numbers of "residuals" in the lake each season. The particulars of the catches in 1932 to 1937 may be set down as follows:

Year caught	No. of fish caught	Sex		Age-groups present
		Male	Female	
1932	48	48	0	46 II, 1 IV
1933	1	1	0	1 III
1934	59	59	0	41 III, 2 IV
1935	72	70	2	4 III, 31 IV
1936	952	889	63	25 II, 60 III, 22 IV
1937	20	19	1	3 II, 4 III, 9 IV

From a consideration of the sizes and comparative annual growth increments each year Ricker suggests that, in the spring of the year and within a certain size range which may vary from year to year, certain forces come into play which bring about migration from the lake. Those young sockeye which have enjoyed exceedingly good growth and are of relatively large size are not affected by the migratory stimuli, perhaps because of factors associated with approaching maturity, and remain in the lake. These fish are chiefly males; they mature principally that same autumn at age II, but a few continue on in the lake and mature as large as III's or IV's. Among the spring yearlings there is another and larger group of small average size, for which the migratory stimulus fails to operate and these also remain in the lake for a 2nd year. As the next vernal migratory season approaches, again some of the larger individuals have developed beyond the stage at which the migratory stimulus is operative; these fish continue their lake residence and mature that autumn as III's, or carry on to mature the next year as IV's. These III's and IV's are much smaller and much more numerous than those of the fast-growing group described above. The smaller of the 2-year-old sockeye leave the lake.

In this way, on the basis of size, growth rates, and sex, it seems possible "to arrange in some kind of order an otherwise chaotic mass of data" (Ricker, 1938c, p. 208). The food of the residuals consists chiefly of the large plankton Crustacea, the main food constituent of the young sockeye in Cultus Lake, but some chironomids and terrestrial insects, in addition. Residuals in their fourth year have been found to consume very small fish, including newly emerged sockeye fry. They are, therefore, both competitors of and predators on the young sockeye in the lake.

More recently Ricker reports (1959b) on the occurrence of residuals in Crawford Lake (in the Stuart Lake area of the upper Fraser River system), a barren lake teeming with natural food (Crawford, 1933), which had been adopted as an excellent nursery area for sockeye fry from the Stuart Lake hatchery. Subsequently it was found that part of the young sockeye being reared in the lake were not migrating, but were becoming permanent residents or "residuals." Many were recaptured in mature condition, females greatly outnumbering the males. Of 307 fish caught up to September 4, 1929, only 36 were males. As Ricker remarks (Ricker, 1959b, p. 899) "it is impossible to know whether the Crawford Lake mature fish taken in 1928–1930 were the direct survivors of the fry planted (true residuals) or were the progeny of such survivors, or were a mixture of both. The excess of females taken is the reverse of what was found among Cultus Lake residuals, where there was a very heavy excess of males."

At Lake Dalnee, Kamchatka, it would appear (Krogius and Krokhin, 1956a, p. 13; Krogius, 1961a, p. 138) that both types of residuals occur, those that do not migrate because they develop too rapidly in 1st year and those that develop too slowly the 1st year and then put on greatly increased growth. Such residuals are chiefly males maturing in 3rd or 4th year of life; females are much scarcer, spawning principally in 4th year but sometimes in 5th.

Needless to say, the development of populations of residual sockeye in any sockeye-rearing lake is much to be discouraged. The residuals constitute competitors for food of young anadromous sockeye and to some extent may be predators as well. If, as Krogius and Krokhin (1948, p. 16) have pointed out, young sockeye remaining in a lake for a 2nd year consume four times as much food as fingerlings during 1st year, older residuals would take even more, hence seriously cutting into the capacity of a lake to produce anadromous young sockeye. On the one hand it would appear desirable to radically increase the population density of young feeding sockeye, thus decreasing the overall growth rate; on the other, the productive capacity should be built up by increasing the food supply, removing food competitors, etc.

FACTORS INFLUENCING SEAWARD MIGRATION

During the many years of study at Cultus Lake an effort was made to find out the trend of environmental conditions prior to and during the period when the young sockeye left the lake on their seaward migration. It was hoped that a study of these might provide some insight into the factors bringing about the phenomenon of migration from the lake each spring.

It had already been determined that the Cultus Lake sockeye normally spend 1 year in the lake before migrating seaward and that during this time they appeared to inhabit chiefly strata of the lake below the surface region, subsisting on the crustacean plankton (Foerster, 1925; Ricker, 1934). With the arrival of spring, there was gradual increase in amount of daylight each day and a gradual increase in temperature of the surface water of the lake took place which led, greatly assisted by wind action, to a change in the lake conditions from winter stratification to a spring overturn (see p. 178). At about the same time, young sockeye were observed in the surface waters of the lake and in the lake outlet stream.

WATER TEMPERATURES

Consideration of the water temperatures prevailing in the surface strata of Cultus Lake during (1) the year of residence and (2) during only the spring months, as read from a thermograph installed in the outlet stream, Sweltzer Creek, provided the following relationships between mean lake temperature conditions and the date when 20% of the migration had taken place in a series of 8 years, 1929–36 (Foerster, 1937):

No. of days from Jan. 1 to date when 20% of migration occurred	Correlation coefficient	Probability
Mean yearly water temperature	—0.12	0.8 to 0.7
January–March water temperature	—0.77	0.05 to 0.02
February and March water temperature	—0.85	less than 0.01

There was, therefore, a highly significant correlation between the temperature conditions occurring in the lake during February and March just preceding the seaward migration from the lake. This has been interpreted as indicating that the activity of the young sockeye in the lake, which culminates in their migration from it, is definitely influenced by pre-migratory lake temperatures. While movement out of the lake usually occurs toward the end of April its relative occurrence is advanced or delayed by the mildness or severity, respectively, of the lake's climate in January to March. If February and March mean water temperature be represented by x, and the number of days between January 1 and the time of 20% of the migration by y, a relationship was calculated of the form:

$$x = 15.85 - 0.11y$$

$$y = 144.1 - 9.1\ x$$

Thus, if the February–March water temperature in the lake is 2 C, 20% of the migrants will have left the lake 126 days after January 1st or by May 6th, and with each 1 C degree increase in temperature the date is advanced by 9.1 days.

In Fig. 72 the progress of each year's seaward migration from 1929 to 1936 is shown, with the period during which from 20% to 80% of the run occurred blocked in. It was thought that while the earliest migrants each year might very likely be individuals which had, by reason of their particular location in the lake in early spring, been more readily stimulated to migrate and appeared at the counting weir more quickly than the general body of sockeye in the lake, that portion of the migration making up from 20% to 80% of the migrants would much more realistically represent the migration as a whole.

Considerable variability from year to year occurs in regard to the time (1)

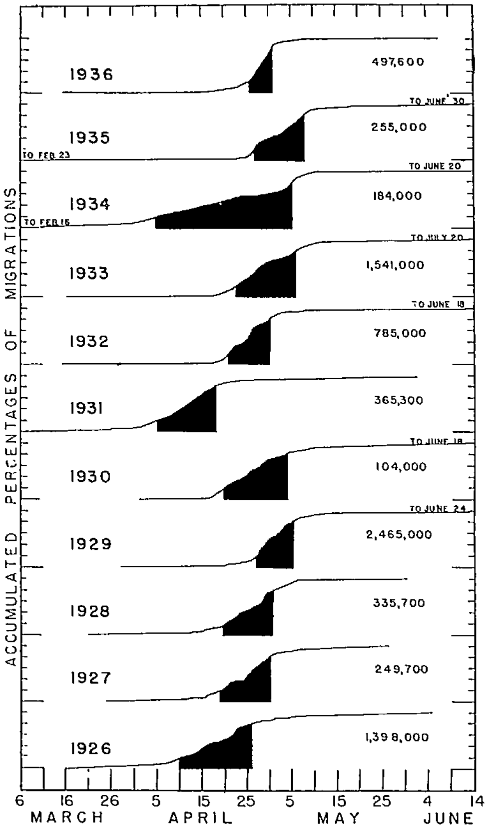

FIG. 72. The seaward migration of young sockeye from Cultus Lake each year from 1929 to 1936, plotted as accumulated percentage curves. The dates of commencement and termination of each season's run are given. The period during which from 20 to 80% of the run left the lake is shown as a solid block. The total number of migrants counted each year is given at the right of each year's curve. (From Foerster, 1937, fig. 2.)

when the migrations begin, (2) when the majority of the migrants (20–80%) leave the lake and (3) when the runs terminate. The start of migration, as indicated by the date when 0.05% of the run occurs, Table 74, follows a definite increase in lake temperatures. In 6 of the 8 years for which temperatures of Sweltzer Creek water—assumed to represent the conditions prevailing in the upper strata of the lake—are available, an average increase of 2.8±0.22 C in temperature was noted above the winter minimum. In the other 2 years, 1931 and 1934, when increases of only 0.6 and 0.1 C, respectively, had occurred, the minimum winter temperatures were usually high. There appears to be no relation between the time of migration

TABLE 74. Temperature readings (*C*) of Sweltzer Creek and dates when stated percentages of the seaward migration of young sockeye from Cultus Lake had taken place, 1929–36. Data on minimum water temperature and on the total number and average length and weight of migrants each year are also given.

	Year							
	1929	1930	1931	1932	1933	1934	1935	1936
No. of migrants: (× 10^3)	2,465	104	365	785	1,541	184	255	497
Avg length (*cm*)	6.84	8.76	9.08	9.02	7.22	8.65	9.07	9.49
Avg wt (*g*)	3.06	6.55	7.10	7.32	3.67	6.53	7.55	8.83
Minimum winter temp (*C*)	2.0	1.1	4.8	2.5	2.2	4.5	2.8	1.7
Date:	Feb. 9	Feb. 2	Feb. 26	Feb. 2	Feb. 17	Feb. 4	Feb. 12	Feb. 24
Temp (*C*) and dates when following percentages of migration occurred:								
0.05%	5.3	4.6	5.4	5.1	5.5	4.6	4.6	3.8
Date:	Apr. 10	Apr. 2	Mar. 10	Mar. 29	Apr. 10	Feb. 10	Apr. 3	Apr. 8
0.10%	5.2	4.4	5.4	5.4	6.1	5.1	4.8	4.0
Date:	Apr. 15	Apr. 3	Mar. 12	Apr. 1	Apr. 12	Feb. 15	Apr. 6	Apr. 10
0.5%	5.5	5.2	5.8	5.1	6.5	4.8	6.0	4.9
Date:	Apr. 18	Apr. 8	Mar. 17	Apr. 6	Apr. 14	Feb. 24	Apr. 10	Apr. 14
1.0%	6.6	4.6	6.2	5.2	6.0	5.4	8.1	4.3
Date:	Apr. 19	Apr. 11	Mar. 20	Apr. 9	Apr. 15	Mar. 4	Apr. 12	Apr. 15
5.0%	8.8	6.2	5.9	6.8	6.9	6.5	8.8	6.3
Date:	Apr. 22	Apr. 18	Mar. 26	Apr. 18	Apr. 20	Mar. 23	Apr. 24	Apr. 18
10%	9.3	6.2	6.4	6.9	8.4	7.7	8.0	8.1
Date:	Apr. 25	Apr. 18	Apr. 3	Apr. 20	Apr. 21	Mar. 31	Apr. 26	Apr. 23
20%	8.4	6.6	7.0	7.9	8.9	10.1	6.7	9.9
Date:	Apr. 28	Apr. 20	Apr. 5	Apr. 21	Apr. 23	Apr. 5	Apr. 27	Apr. 26

and the numbers of young sockeye in the lake just prior to migration—no population pressure, as it were—and no relation between the start of migration and size of migrants, i.e., within the size limits observed.

When migration definitely gets under way, the temperatures of the upper strata of the lake, as judged by the Sweltzer Creek readings, are in the neighbourhood of 4.9 C (41 F). From this it was suggested (Foerster, 1937, p. 431) that

> "there would appear to be a definite threshold temperature range at which migration commences, for an inverse relationship is shown between the extent of increase required to stimulate migration and the minimum winter temperature. In those years when the minimum lake temperatures were high (4.5° to 4.8°C) a much smaller increase was related to a definite percentage of migration than in years when the winter minima were low. Thus, threshold temperature would appear to be in the neighbourhood of 4.4° to 5.0°C (40–41°F)."

Prevailing weather conditions over the lake while the migration is in progress play a large part on the daily variations in numbers of migrants. Bright, calm days invariably resulted in a rush of fish, provided such conditions were not too prolonged whereas dull weather, with or without rain, caused a slackening, of the run. Winds blowing up-lake, i.e., toward the outlet, retarded migration presumably because of wave action and turbulence set up at the lake outlet. Figure 72 shows the speed with which the major portion of the migration took place (the blocked-in area). In 1929, for example, the bulk of the 2,465,000 migrants left the lake in slightly over 10 days whereas in 1930 the bulk of the 104,000 sockeye appeared over a period of 15 days. In 1936, two-thirds of the migration occurred in a 5–6 day period, April 26 to May 1.

Cessation of migration seemed to be associated with a high temperature regime in the upper waters of the lake. When the Sweltzer Creek water temperatures reached 13.0 C, the daily migrations decreased greatly. Thereafter only stragglers appeared, the last migrants appearing at temperatures ranging from 14.4 C in 1930 to 20.1 C in 1933—the average for 8 years being 17.5±0.78 C. It was suggested that migration from the lake ceased with the creation in the epilimnial waters of the lake of a warm water temperature blanket through which the yearling sockeye, presumably late in responding to the migration stimulus, are unable to pass. Such a "temperature barrier or blanket" was first proposed by Ward (1932) to explain the origin of "land-locked" salmon (actually "residual" salmon) in Baker Lake. It would seem equally applicable in explaining the nonmigration of small sockeye at the end of their first year and their occurrence the following season as 2-year-olds, though there must be a differential response of fish of different sizes.

While carrying through this comprehensive study of the seaward migration of young sockeye from Cultus Lake and the environmental factors seemingly related thereto, it was recognized that Cultus Lake presented an unusual situation in that it seldom froze over and, even when it did, the ice-cover was quite light and very temporary. Nevertheless, observations in other more northern areas tend to confirm the Cultus Lake findings.

For example, in the Wood River system of Alaska Burgner (MS, 1958) found that seaward migration of young sockeye occurred consistently only when the Lake Aleknagik outlet temperatures approached 38–39 F (close to 4 C), after the breakup of the ice in late May or early June. As shown in Table 75 there was often a considerable delay in appearance of the migrants at the observation point after the ice breakup had occurred, due to the slower warming up of the lake's surface waters, presumably. Although the prevailing climatic conditions tended to alter the sequence of time intervals, the relationships were apparent even up to the time when the migration was well underway (when 20% of the migration had passed). It was also noted that the end of the migration coincided closely with an epilimnial temperature of 50 F (10 C). At Lake Nerka, 90% of the smolt run had left the lake within a very few days of the lake surface water reaching 10 C.

TABLE 75. Relationship between date of ice breakup in Lake Aleknagik and early migration of young sockeye at Wood River observation site. The years are arranged in order of ice breakup date (from Burgner, 1958, table 55).

Year	Date of ice breakup	Dates when indicated percentages of migration had occurred		
		5%	10%	20%
1954	May 26	June 1	June 2	June 2
1953	May 27	May 31	June 3	June 11
1957	May 28	June 2	June 7	June 12
1951	May 30	June 4	June 7	June 9
1956	June 1–3	June 10	June 12	June 15
1952	May 7	June 11	June 12	June 14
1955	May 10	June 23	June 26	June 29

Whether this cessation of migration as the lake epilimnial waters rose above 10 C suggests the setting up of a temperature barrier to further migration is not clear. It is reported that the greatest concentrations of young fingerlings in the Wood River lakes occurred inshore and near the surface during the week or 10 days after the surface temperatures had exceeded 50 F and that a record catch of sockeye fingerlings was made in the lake traps at Lake Nerka on a day when the surface temperatures at the trap site were 61 F (16.1 C). This was taken to indicate that young sockeye may inhabit relatively warm water but it is not clear whether these were lake-resident, nonmigrating young sockeye or yearlings on their seaward migration.

At Lake Dalnee, Kamchatka (Krogius, MS, 1949, p. 9; Krogius and Krokhin, 1948, p. 19), the seaward migration of young sockeye commences shortly after the ice-cover has disappeared. "With the setting up of the spring circulation the young fish ascend into the upper strata and then migrate from the lake" (Krogius, MS, 1949, p. 9). As shown already in Fig. 25, the young sockeye in Lake Dalnee tend to concentrate in the epilimnial stratum in June and early July. The seaward migration usually terminates around July 20.

Observations at Lakelse Lake, lower Skeena River system, in 1952 and 1953 (Table 76), revealed that there also the young sockeye did not seek to leave the lake and proceed seaward until the ice had left the lake and an appreciable warming of the upper waters had taken place over a period of from 9 to 10 days.

TABLE 76. Spring temperature conditions at Lakelse Lake, B.C., and sockeye migrations.

	1952	1953
Date of ice breakup in lake	May 1	Apr. 10
Date of appearance of first migrant at counting weir below the lake	May 11	Apr. 19
Daily avg water temp on above date	8.4 C	–
Date of peak daily run	May 21	May 8
Daily avg water temp at peak	8.5 C	–
Date when last migrant counted	Aug. 1	July 11
Total number of smolts in migration	600,000	398,000

The latest available evidence from Babine Lake serves to confirm an earlier observation of 1951 that the sockeye seaward migration from Babine Lake followed closely the disappearance of the ice-cover. Since 1960 a trap for the collection of downstream migrants has been operated at the foot of Nilkitkwa Lake, a 2.75 mile enlargement of the Babine River, roughly 1.5 miles below Babine Lake (see Fig. 56). Early season operation of this trap has made it possible to ascertain when the sockeye start to migrate and the relationship of migration to time of ice breakup and to water temperatures taken at the Babine River counting weir a mile downriver from the smolt trap. The data are as follows:

Year	1960	1961
Date of ice breakup, Nilkitkwa Lake	April 26	April 26
Water temperature, Babine River (min–max)	33–38 F	32–40 F
Date of appearance of migrants	May 3	May 2
Water temperature, Babine River (min–max)	37–41 F	38–41 F

The relation of the seaward migration from the Babine Lake system to the breakup of the ice-cover, the prevailing water temperatures, and the conditions in the epilimnial layer of the lake, is somewhat complicated by the multibasin nature of the lake system, the separate sockeye populations in each area, and the conditions within each basin. The information given above refers specifically to the Nilkitkwa Lake area immediately below Babine Lake proper (see Fig. 56) where the ice-cover disappears first. The first migrants observed are believed to migrate from this nursery area.

It is now apparent, from observations in 1960 and 1961, that in the earlier years, 1951–59, the information provided by the catches at the trap at the outlet of Babine Lake had reference only to the population of young sockeye from Babine Lake proper. Within this multibasin lake a number of separate populations occurred, the activities of which, insofar as onset of seaward migration was concerned, differed and, in all likelihood, depended largely on the time of disappearance of ice-cover and warming up of the epilimnial waters, etc. Records of the ice-cover breakup in the northern half of the lake and of the first appearance of migrants in the Babine Lake outlet trap are recorded in the field reports as:

Year	Date of ice breakup	First smolts appear	Peak daily catch
1951	May 10	May 23	June 3
1952	May 17	May 29	June 2
1953	May 15	May 28	June 12
1954	May 27	June 5	June 10
1955	May 15	May 30	June 3
1956	May 13	May 24	May 26
1957	May 14	May 30	June 4
1958	May 6	May 16	
1959	May 15	May 24	May 28

Having regard to the limitations of the data, it seems apparent that from Babine Lake the seaward migrations commenced, as indicated for Nilkitkwa Lake, some days after ice breakup brought about by the same conditions that prevailed in Lakelse and Cultus Lake and elsewhere, namely, a warming up of the upper waters of the lake in early spring.

PHYSIOLOGICAL CONDITIONS WITHIN THE FISH

A most illuminating review of the physiological changes which take place within the young sockeye prior to migration and which may stimulate them to migrate is given by Baggerman (1960). Many carefully planned experiments by many investigators show that a definite change takes place in the physiology of salmon, as well as in many other animals, which, under appropriate environmental conditions, induces and initiates migration.

The first step in the chain of circumstances to migration, according to Baggerman (1960), is the response of the organism, i.e., its internal mechanism, to the increasing length of day, termed the "length of the daily photo period." The regular increasing amount of daylight in spring each year is thought to activate the pituitary-thyroid system, one of the endocrine gland mechanisms of the young fish, which, in turn, causes a change in the freshwater–saltwater preference of the fish which leads to "the induction of a migratory-disposition" (Baggerman, 1960, p. 320).

Young coho salmon yearlings were confined in an apparatus where they were exposed to (1) naturally increasing day lengths or to controlled photo periods of (2) 8 and (3) 16 hr of light per day. In this apparatus they could make a choice between fresh and salt water (salinity of 18–24‰). It was found that in the first test made in March–June, 1957, the fish exposed to 8-hr day length still preferred fresh water at the end of March whereas those subjected to naturally increasing day lengths and to 16-hr day length showed a preference for the salt water. At the end of May the 8-hr group still remained in fresh water while the 16-hr group still preferred salt water. Those fish under natural day length showed, at that time, no preference. In a second test in 1958, starting in mid-January the 8-hr fish maintained their freshwater preference until June when the experiment ended whereas those exposed to natural day length changed to a saltwater preference in April, i.e., at the normal time of year. The reactions of the 16-hr fish were somewhat erratic and confusing and require further study.

That these reactions of young coho to the changing length of day would apply also to sockeye is suggested but was not tested. Reference to Fig. 72, where the periods of sockeye migration from Cultus Lake are shown, indicates that there was considerable variation from year to year in the date when the first migrants or the first 20% left the lake. Moreover, when, over a period of 11 years, the number of hours of sunshine, as measured at Agassiz, British Columbia, occurring from January 1 each year to the time when 0.05% of the sockeye migrated from Cultus Lake was considered, they varied from 145 hr in 1931 to 275 in 1930 (Foerster, 1937, p. 432). It was concluded that "the seaward migration of young sockeye, therefore, is not directly influenced by the amount of sunshine in the months prior to migration." However, many external factors may intervene and affect migration in the period between initiation of the "migration disposition" and actual departure from the lake. Therefore, the Cultus Lake data merely emphasize the need for further clarification of the intervening reactions or behaviour of the young sockeye.

Baggerman (1960) has clearly demonstrated that at the time of seaward migration of young sockeye there is also increased activity of the thyroid which, in turn, is accompanied by a salinity preference. It not only increases appreciably prior to onset of migration, but remains high throughout the migration period (mid-April to June) and then declines. In fact, thyroid activity was found to decrease even before the preference from salt to fresh water had changed, thus before the actual termination of the migration period. This suggests, then, that "it is very likely that increased thyroid activity may be one of the factors inducing migration-disposition, whereas decreased thyroid activity may be a factor involved in terminating the migration season" (Baggerman, 1960, p. 310).

Thus, the increased activity of the thyroid, causing a rise in the thyroid hormone level in the blood of the young sockeye, changes the salinity tolerance or preference and develops within the fish a "migratory-disposition." In this condition the young fish become readily susceptible to those external environmental stimuli which bring the fish—may we say without too much confirmatory evidence—into the upper strata of the lake and eventually to the lake outlet.

THE SPEED OF SEAWARD MIGRATION

As indicated in Fig. 72, once seaward migration began at Cultus Lake there was a rather long period during which the daily migrations were relatively small. Then within 5–15 days the bulk (20–80%) of the run occurred. Prevailing weather conditions played a large part in the daily variations in numbers of migrants leaving the lake. On calm evenings following bright, warm days the surface of the outlet end of the lake would be literally alive with young sockeye jumping from or finning the surface, and the migrations after dark would be heavy. On dull days, with or without rain, no sockeye would be seen at the surface and the night migration would drop off appreciably.

At Lakelse Lake and at Babine Lake the migrations, once begun, also quickly rise to a peak (Brett and McConnell, 1950; Foerster, 1952; Johnson and Groot, 1963). Here, too, the prevailing weather conditions no doubt have considerable influence on the progress of the migration and the speed with which the seaward migrants reach the outlet.

MOVEMENT WITHIN A LAKE

At Babine Lake tests were made in 1960 and 1961 (Johnson and Groot, 1963) to ascertain the rate of travel of seaward-migrating sockeye from certain release sites in Babine Lake to the lake outlet, as indicated in Fig. 73. In 1960 only one release was made, at Halifax Narrows, and the mean rate of travel for the 27 miles to the recovery trap was 3.5 miles/day (5.6 km/day). In 1961 a release at the same site showed a mean travel rate of 4.9 miles/day (7.9 km/day). Two other release points were used in 1961—Morrison River and Sandspit, 46 and 63 miles from the outlet recovery site. The mean rates of travel from these points were 4.2 and 4.4 miles/day, respectively, not significantly different from the 4.9 miles/day from Halifax Narrows, nor from the average for all three release sites—4.6 miles/day. The increase in rate

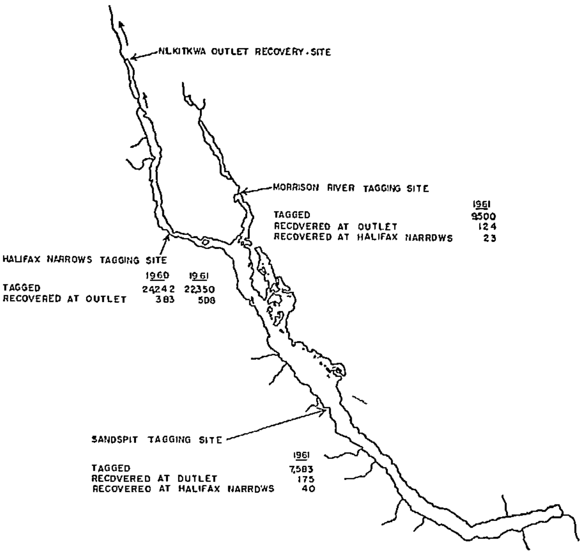

FIG. 73. Tagging and recovery sites, Babine Lake, for seaward-migrating young sockeye, 1960 and 1961, showing the numbers of smolts tagged and released at each of the three tagging sites and the number recovered at the lake outlet. (From Johnson and Groot, 1963, fig. 3.)

from 1960 to 1961 from 3.5 to 4.9 miles/day was accompanied by increased sunshine: 296 hr between May 1 and June 20 in 1960, and 376 in 1961. A positive relationship was also found between mean hours of sunshine for the days immediately following release and the rate of travel to the outlet. Johnson and Groot (1963, p. 935) suggest "that in 1961, with the sunshine record indicative of more clear skies, the sockeye smolts were able to orient better to keep on a more direct course to the outlet, thus showing a higher rate of travel." However, this does not imply a continuous directed migration, for they state that "most near-surface schools observed during the day are either stationary or moving slowly and randomly and are obviously feeding." Directed migration must commence toward dusk, for they note that in calm weather the direction, speed, and horizontal distribution of actively migrating schools could be determined from boats and from high observation points along the lake using field glasses and a surveyor's transit.

Cruising speeds of sockeye salmon smolts had been found experimentally (Brett, Hollands, and Alderdice, 1958) to vary from 0.8 to 1.1 ft/sec (24 to 34 cm/sec) for the temperature range and smolt sizes applying at Babine. These compared well with direct measurements of near-surface swimming schools of smolts at Babine: 0.65–1.0 ft/sec, mean 0.8 ft/sec (20–30 cm/sec, mean 24). Johnson and Groot (1963, p. 926) inferred, therefore, that the Babine smolts "would have to swim on direct course at this speed (0.8 ft/sec) for a total of 6.5 (1960) to 8.5 (1961) hours each day" to accomplish the rate of travel indicated by the tagged fish. Observations suggest that about this length of time each day, i.e., principally from dusk to midnight but also again in early morning, is spent in active migration (Johnson and Groot, 1963, fig. 5C).

For migrating sockeye smolts of the Wood River chain of lakes (Fig. 70) rate of travel tests were made on migrants which had been tattooed for recognition at the Wood River trap (Burgner, MS, 1958). Smolts released in Little Togiak Lake were recovered again, 13 in all, within 11 days, after traversing a distance of 40 miles (64 km), whereas smolts released in Lake Nerka were recaptured 34 miles (55 km) away within 8 days.

MOVEMENT DOWNRIVER

Once in the outlet stream of a lake and bound for the sea, rate of travel will depend largely on the speed of the current and the character of the flow, i.e., the extent of rough, turbulent water and the amount of smooth, quiet flow. It is common knowledge that in migrating downstream the young sockeye, in schools of varying size and seemingly led by one larger individual or "leader," swim rapidly with the current where the flow is uniform and quiet but when a stretch of broken, turbulent water is approached the school swings about, tends to tarry a bit, and gradually passes downstream tail first. Where weirs obstruct their downriver progress the schools are seen to turn upstream, move back and forth across the channel until they find an opening and then proceed tail first through it. How much manoeuvring of this kind occurs must depend on the character of the river, the number and length of such turbulent fast and broken water passages, each of which will retard the seaward movement.

Experiments in the Babine River with marked smolts (Withler, 1952b, p. 19) in traversing an 8-mile stretch of stream gave the following results:

Year	No. of smolts recovered	Range of time out days	Mean time out days
1951	11	2–6	3.4
1952	100	1–11	3.4
1953	62	1–8	2.9
1954	179	1–9	2.4

or an average of roughly 2.5 miles/day (4 km/day).

For the Columbia River (Anas and Gauley, 1956) releases of marked sockeye from hatcheries above Bonneville Dam and their recapture at Bonneville indicated that the rate of travel of smolts released in the spring at distances of 350 and 400 miles above Bonneville averaged from 12 to 25 miles/day (19 to 40 km/day). A spring release at a distance of approximately 20 miles above Bonneville, however, averaged less than 2 miles/day (3 km/day).

FACTORS GUIDING SMOLTS TO A LAKE OUTLET

Just how young sockeye resident in a lake and stimulated by internally developing physiological changes which induce a migration disposition, as outlined above, p. 288, find their way to the lake outlet and commence their seaward migration has long puzzled investigators. While experimentally it was found (Hoar, 1954; Hoar, Keenleyside, and Goodall, 1957) that young sockeye in the smolt stage exhibited an increased sensitivity to light and retreated to darker and deeper areas, numerous observations in many lakes attest that in the spring of the year and prior to and during the period of migration many sockeye lose this light sensitivity and appear in the bright surface waters of a lake. Most of them may remain below the surface and rise only as daylight wanes but it would seem that they, too, are in epilimnial waters where they carry on extremely active feeding.

Opinions as to how the smolts find the lake outlet and descend to the sea have varied appreciably, from those which admit no specific directional influences to those which involve orientation to certain celestial phenomena. To the former the situation is merely that of the young moving into relatively shallow waters and following along the shoreline, though some distance offshore, until they detect the current of the outflowing stream or river to which they respond like plankton and drift downstream. It is assumed that the smolts might swim either clockwise or counterclockwise, in which case some schools would have to more or less circle the lake while others might have only a short distance to go. All of these shore-paralleling peregrinations would have to be accomplished, of course, within a matter of 4–6 weeks in order to conform to the well-documented pattern of a specific spring seaward migration. Those smolts not finding the outlet within the time period would have to remain in the lake a 2nd year.

Others there are who envisage a reaction, on the part of the fish, to a current-flow influence within the lake, a current-pull attraction as it were, which guides them, not as passively drifting organisms, but as actively moving schools responding to some sensory-recognizable stimuli, toward the lake outlet. As yet no proof of such a reaction has been obtained, in fact all the evidence collected regarding wind currents and surface water movements suggests a heterogeneous and confusing current pattern of surface water displacement, but some observers of the migration-from-the-lake phenomenon, including this writer, are not convinced that all the salient facts have been revealed. They prefer to withhold judgment until more convincing evidence is presented. Attempts were made at Cultus Lake over a number of years to solve the problem but without success. It was recognized that the movements of the schools of yearling sockeye, no matter where seen, were primarily in the direction of the lake outlet. The occasional countermoving school was observed but these may have subsequently swung back again into the normal pattern. Most of the fish were, without question, on a directed course toward the lake outlet.

Johnson and Groot (1963, p. 929) report that "Groot (MS) has demonstrated that sockeye salmon smolts are able to use celestial phenomena to orient themselves in a certain preferred compass direction during a number of hours of the day; hence, a time-compensated celestial orientation mechanism is apparent." Field tests carried out at Babine Lake in the spring of 1960 at three different locations around the lake (see Fig. 74) revealed that under conditions of relatively clear skies (0–60% cloudcover) the smolts taken at the three test sites showed directional preferences that correlated remarkedly well with the direct route of migration to the sea. The overall picture for the Halifax Narrows tests (comprising observations at 3- to 5-hr intervals between noon and midnight) does not conform to this interpretation but, if those observations made during the dusk period, at which times the smolts are migrating most actively, are selected, they show a northwest directional preference, i.e., down the lake toward the outlet. In other words, at the appropriate time of day, these Morrison River smolts also do conform. On the other hand, when the skies were overcast (70–100% cloudcover) the orientation was found to be in the opposite direction at all three test points.

Throughout the whole of the migration period the smolts at the Nilkitkwa and Halifax Narrows sites exhibited the same constant one-direction preference, that toward the northwest. This is toward the lake outlet and toward the sea. For the Morrison River smolts, a one-direction preference is not sufficient. They must subsequently make an almost 180° shift in direction, from southeast to northwest, to get out of the lake. Tests made with Morrison River smolts periodically throughout the migration period in 1961 revealed that, if migrants from the early part of the run were retained in tanks and then tested at a later date with the then-migrating normal

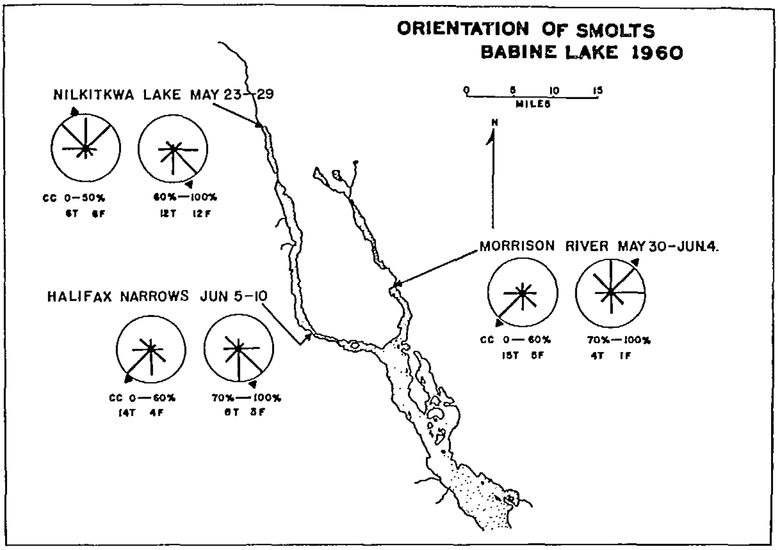

FIG. 74. Direction preferences of smolts with view of the sky only, captured and tested at three different locations in Babine Lake in 1960. The results are separated as to those obtained with relatively clear skies and those with relatively overcast skies (CC). Under each diagram the number of tests (T) and the number of smolts used (F) are indicated, also the mean choice of direction (Δ). (From Johnson and Groot, 1963, fig. 8.)

smolts, a shift in direction preference occurred with time. The normally running fish changed from a southeast to a west preference, the retained, early migrating individuals from a southeast to a west-northwest. Such shifts, it is noted (Johnson and Groot, 1963, p. 933), "swimming first in a southeast direction would lead the fish out of Morrison Lake and down Morrison Arm, then a shift over south to southwest, west, and northwest would bring them into Halifax Narrows and through the North Arm to the outlet."

Confirmatory evidence of a shift in direction-preference was provided by testing again tagged smolts from Morrison River which were recaptured at Halifax Narrows and Nilkitkwa Lake. Whereas, when tested originally at Morrison River, the smolts had shown a direction-preference toward the southeast, the subsequent tests showed preference for southwest to west.

The idea that young salmon possess a built-in compass and chronometer whereby, through some form of celestial navigation varying according to time of migration, they may respond to an inherited direction-preference orientation and make their way through and out of a lake to the sea is a novel and challenging one worthy of close attention and further investigation both experimentally in appropriate apparatus and in the field under natural conditions. It is a further extension of the suggestion that in their return from the ocean feeding areas to natal spawning rivers the adult salmon respond to some form of celestial navigation (see p. 30).

THE SITUATION WHEN TRANSPLANTATION OF STOCKS IS UNDERTAKEN

The significance of a well-oriented, non-random movement of sockeye smolts toward a lake outlet, if factually established, should present a distinct problem in the case of transplantation of sockeye, either as eggs or fry, from one area to another. The results of some earlier transplantations and their success or failure may be briefly reviewed:

1. Transfer of "eyed" eggs from Cultus Lake to Eagle River, Shuswap Lake system (Fig. 6). Here no success was achieved (Foerster, 1946). It was surmised that either the young sockeye succumbed during their year in Shuswap Lake or remained in the lake. These fish, if migrating from Cultus Lake, would have proceeded in a northerly direction (see Fig. 35) to leave the lake. When released at Eagle River the fingerlings, upon reaching Shuswap Lake, and taking up residence in that section of the lake off Eagle River outflow, would have to move (see Fig. 55) first northward, then westward through the Narrows, then south-southwest to the lake outlet; in other words, quite the reverse of their inherited or inbred direction, if there be such.

2. Transfer of "eyed" eggs from Seymour River, Shuswap Lake system to the upper Adams River in 1951 (see Fig. 55). A shipment of 667,000 "eyed" eggs from the 1950 spawning run to Seymour River was made to the upper Adams River in the spring of 1951 and the eggs planted in prepared redds. In 1954 a return of 205 adults was reported (IPSFC, 1955). These sockeye, in migrating to sea as smolts from their natal Seymour River area, would have had to travel south, then west to the Shuswap Lake outlet. In their new environment, upper Adams Lake, however, they would have to move south-southwest, then southeast, then down the lower Adams River, in a southeasterly direction to Shuswap Lake, and then make a sharp shift to the southwest in order to find the south Thompson River. The recovery of returning adults in 1954 indicated that, for some of the transplanted fish at least, their "built-in" or inherited direction-guiding orientation mechanism was so altered in their new environment that they were successful in getting to sea and returning 2½ years later. In the next 4th year, 1958, a spawning escapement "greater than in the brood year" returned to the upper Adams but (IPSFC, 1959, p. 17) "it cannot be stated that the second return in 1958 is the entire result of natural spawning in 1954 since eyed eggs were again transferred in the latter year from the Seymour River." In 1960, however, (IPSFC, 1961, p. 15) "only a very few individuals returned to upper Adams River from a planting of 253,000 eggs originating from the Seymour population."

3. Transfer of "eyed" eggs from the lower Adams River, Shuswap Lake sytem, to Portage Creek, Anderson-Seton Lakes system (see Fig. 6). From a planting of 300,000 eyed eggs in 1951 a return of 3505 adults occurred in 1954. In their natal area, Shuswap Lake, the smolts take a westerly direction in leaving the lake. In their new environment they would have to proceed east through Seton Lake to reach the lake outlet, a 180° change in their inherited mechanism of orientation to any celes-

tial phenomenon. This they apparently accomplished successfully. In the following cycle year, 1958, there was a spawning escapement of 4803 sockeye to Portage Creek area. "The 1954 natural spawning in Portage Creek not only returned a run of sockeye to that area but provided for an increased run sufficient to allow an escapement through the fishery of 4803 adults" (IPSFC, 1961, p. 17).

4. Transfer of "eyed" eggs from Forfar Creek, Stuart Lake system to the Nadina River, Fraser-François system. A total of 318,000 eggs was involved in this transfer in 1956. No adults returned in 1960 (IPSFC, 1961, p. 15). In this case the shift in orientation would have been simply from a southeasterly through Stuart Lake to the outlet stream, to an easterly through François and Fraser lakes.

The above transplantation experiments are cited primarily to present evidence which would seem to controvert the theory of an inherent direction orientation response to a celestial stimulus. For those tests in which no adults returned the lack of success could be due to any one or more of a number of factors other than failure to find the nursery lake's outlet, for there is no proof that the young fish reached the seaward migrant stage. For those tests which did produce returning adults, and in which a marked change in direction orientation occurred, explanation is required from the proponents of the celestial orientation hypothesis. It need only be pointed out again that a delicate, active rheotactic response to a current movement within the lake, which accompanies the migratory-disposition condition of the young sockeye that brings them into the epilimnial waters of the lake, could well explain all the migration-from-the-lake situations. These must be still further investigated.

Suffice it to say that added interest will attach to transplantation experiments already in progress. Up to the present, according to the International Pacific Salmon Fisheries Commission (1961, p. 25) "only eyed-egg transplants from donor streams having the same environmental cycle and located the same distance from the sea have proven to be of value." These two criteria have been the significant ones in proposing transplantations from areas which have abundant sockeye populations to others in which the sockeye are scarce or nonexistent (see also IPSFC, 1957, p. 23). Transplants undertaken with eggs of the 1958 (IPSFC, 1959, p. 18) and 1959 (IPSFC, 1960, p. 19) brood years are shown in Table 77 (see Fig. 6 for lake locations).

In the autumn of 1961 a shipment of over 5 million sockeye eggs, collected in Pinkut Creek on Babine Lake (see Fig. 7) was made to Nanika River, tributary to Morice Lake on the Bulkley River branch of the Skeena River system (Anon., 1962, p. 18–19). Normally these sockeye hatched in Pinkut Creek and reared, presumably in the southern end of Babine Lake would traverse the length of Babine Lake in a westerly, then northwesterly direction—to reach the lake outlet. The smolts, resulting from the hatch of fry transplanted to Nanika River and a year's residence (or more) in Morice Lake, would have to orient in a northeasterly direction to locate the lake outlet. The results of these transplantations will be awaited with keen interest. If unsuccessful in producing returning adult runs, they may indicate that a third factor, in addition to distance from the sea and suitable environmental conditions, has to be taken into account in transplantation endeavours. If successful, on the other hand, they may suggest a rejection of or a drastic modifi-

TABLE 77. Transplantation of eyed sockeye eggs in 1958 and 1959 by the International Pacific Salmon Fisheries Commission.

No. of eggs transplanted	Donor area	Main direction of migration to reach lake outlet	Area where transplanted	Main direction of migration to reach lake outlet
		1958		
850,000	Taseko L.	N	Upper Adams	S, SE
483,000	Seymour R.	S, SW	Upper Adams	S, SE
582,000	Raft R. (N. Thompson R.)	[a]	Barrière R. (N. Thompson R.)	[a]
273,000	Seymour R.	S, SW[b]	Eagle R.	N, W, SW[b]
3,429,000[c]	Stellako R. (Fraser-François system)	E	Horsefly	W on Horsefly L., then W and NW in Quesnel L.
		1959		
490,000	Raft R.	[a]	Fennell Cr. (N. Barrière L.)	SW
900,000	Seymour R.	S, SW	Upper Adams	S, SE
600,000	Taseko L.	N	Upper Adams R.	S, SE

[a] There is no lake on the Raft River system to which the sockeye fry might go for their year in fresh water except Kamloops Lake, an enlargement of the main Thompson River, below the junction of the North and South branches. No indication is given as to where the Barrière River plantings were made, whether below the two lakes in the system or above.

[b] It is assumed that the young sockeye hatching out in these two tributaries of the multibasin Shuswap Lake would tend to remain for feeding in the lake basin which they first entered.

[c] Total. A release of 3,003,000 fry made from the hatchery and artificial spawning area in the spring of 1959.

cation of the direction orientation of seaward migrating sockeye smolts to some celestial phenomenon or guiding influence.

CESSATION OF MIGRATION

As indicated in Fig. 72 for Cultus Lake migrations and as observed also at Lakelse Lake (Foerster, 1952) and at Babine Lake, there is a long period during which the last of the migrants leave the lake. This would seem only natural. All of the migrants cannot escape from a lake at one and the same time. Stragglers always occur. However, in many years there are considerable numbers of young sockeye remaining in the lake for a second season, which are appreciably smaller in size than those that migrate. Whether these are merely inherently slow-growing individuals, or fish which hatched out considerably later than those that migrated, is not known. At Cultus Lake such 2-year-in-lake individuals were much more abundant in 3 years following a heavy migration whose fish were small in size (Foerster, 1937, p. 435). This suggested that the high population density had limited the amount of food per fish and had resulted in the slower-growing or weaker ones putting on insufficient growth to respond soon enough to the migratory impulse, however caused. Meanwhile rapidly rising temperatures of early summer had so warmed up the epilimnial waters of the lake that a temperature barrier, as suggested by Ward (1932) to explain the origin of landlocked salmon in a lake, had been created, through which the young sockeye could not pass to reach the lake outlet.

The coincidence of the slowing down and eventual termination of seaward migration with rising epilimnial water temperature of the nursery lake has been remarked upon by many investigators. As early as 1904 Chamberlain (1907, p. 37) had observed in the Naha River, Alaska, that seaward migration began to drop off "when the water had reached a surface temperature of over 50°" (10 C). At Cultus Lake (Foerster, 1937, p. 436) 80% of the migration had occurred—average for 8 years—by the time the mean outlet stream temperature had reached 10.6±0.44 C and as these temperatures approached 13 C "the daily migrations decreased greatly." In the Wood River system (Burgner, MS, 1958) 90% of the migrants had passed the checking point "within a very few days of the date the surface temperatures had reached 50° [10°C] at Lake Nerka." It is further remarked that sockeye fingerlings during their period of lake residence do not appear to have their movements in epilimnial waters curtailed by any "temperature blanket" barrier since greatest concentrations are observed at or near the surface of the lakes *after* surface temperatures have risen above 10 C. A record catch was made in the lake traps at Lake Nerka on a day when the surface temperature at the trap read 61 F (16.1 C). For Bare Lake (Nelson, 1959) the sockeye smolt run begins in late May, reaches a maximum in June and is practically over by the end of July. Usually the older (2+ years in the lake) and larger smolts move out in early June, with the 1+ year-in-lake individuals migrating in the latter part of June. For the 4 years in which temperature records are available (Nelson and Edmondson, 1955, p. 423) the percentages of the seaward migration and the surface lake temperatures to June 28 were as follows: 1950—96%, 12 C; 1951—90%, 11 C; 1952—86%, 13 C; 1953—97%, 14.5 C. In 1954, however, only 26% of the migration had passed out by June 28 and around 60% of the smolts appeared in the subsequent 2 weeks. In 1955 a similar but much less pronounced July migration occurred (38% of the total run) for reasons that are not clear. Temperature records for these two seasons are not reported.

The discovery by Hoar, Baggerman, and others of the development of a physiological state, within the migrants, whereby, as a result of increased pituitary-thyroid activity induced by the vernal increasing hours of daylight (photoperiodism), they develop an acute migratory disposition, has already been discussed (p. 294). Reacting, then, to environmental factors the migrants leave the lake. A close correlation also was observed (Baggerman, 1960, p. 310, 318) between a *decrease* in thyroid activity in sockeye yearlings and the termination of migration, which suggests (to Baggerman) a "causal role of this gland in the termination of migration."

Can this finding be interpreted as extending further Hoar's conclusion (Hoar, 1953, p. 444) that "environmentally regulated endocrine changes give the downstream migration of species, which reside for a prolonged period in fresh water, its precisely timed and controlled characteristic" in order to embrace also the cessation of migration as the season advances and lake conditions change? Such a hypothesis would conveniently fit the situation, such as prevails at Cultus Lake, Babine Lake, the Wood River lakes, Kurile Lake, etc., where only two age-groups of migrants occur (1+ and 2+), the older one appearing to be a carryover of the smaller non-migrating fish until the next year.

Where, however, the young sockeye remain in the lake for 3 years (3+), as at Karluk Lake, Lake Dalnee, etc., and even for 4 (4+), the above hypothesis cannot apply as simply. Other factors must come into play to render inoperative the factors stimulating a migration-disposition in the third spring season but yet cause them to be operative in the succeeding year. By the third spring season the size of the fish, then in their 4th year of age, should not, of itself, be the limiting factor.

On the basis of data for Karluk Lake sockeye (Barnaby, 1944, table 27) and Lake Dalnee (Krogius, 1961a, table I) the average lengths at the time of seaward migration were:

	Karluk Lake	Lake Dalnee
	(cm)	*(cm)*
1 year in lake	11.06	11.5
2 year in lake	13.29	15.6
3 year in lake	14.24	19.1
4 year in lake	15.00	

For each year, in all sockeye areas examined, it has been found that those young sockeye that do not migrate in any one year but remain in the lake for a further season's residence are on the average always smaller, as calculated from scale growth pattern, than those smolts that do migrate. For example, Barnaby (MS, 1932) provides data on the average computed fork lengths (cm) of Karluk sockeye, at the time various freshwater annuli were formed on the scale as follows:

		Age-group (adults)		
Freshwater annulus	4_3	5_4	5_3	6_4
1	6.9	5.7	6.7	6.8
2	12.7	10.4	12.6	10.6
3	–	14.2	–	15.1

Similarly, Krogius (1960, table VII) reports for Lake Dalnee the following computed average fork lengths (cm) at the end of each year in fresh water:

		Age-group (adults)		
Freshwater annulus	4_2	5_3	5_2	6_3
1	12.8	10.3	12.9	10.4
2	–	17.6	–	17.1

But although the average rates of growth of sockeye that remain in the lake for later migrations are becoming progressively slower, there is much overlap in size among the individual fish of the two migrating and nonmigrating groups, so that size alone is not the factor determining migration. Indeed size as such is not likely to be involved at all, but rather some physiological condition positively, but far from perfectly, correlated with size.

The reason why such consideration has been given to this matter of period of lake residence is that, as intimated elsewhere above, any time spent in a lake over and above 1 year—or in cold, northern lakes, more than 2 years—is to some extent a waste of time and an unnecessary drain on a lake's sockeye-producing potentialities. Although older migrants are larger and thus have a somewhat greater ocean survival, it is questionable whether this increase in ocean survival counterbalances the extra freshwater mortality during the extra year or years' residence in the lake. In addition, 2-year-old sockeye in the lake consume four times as much food as yearlings, hence reduce by one-quarter (more for still older individuals) the lake's sockeye-rearing potentialities.

The objective then should be to produce only yearling or, in certain lakes, only 2-year-old migrants. A knowledge of what factors bring about migration or, conversely, what causes extended lake residence, is extremely important. To know whether or not they can be controlled or manipulated is equally important. As above intimated, seaward migration is not perfectly correlated with size. Any size threshold must, according to Rounsefell (1958a, p. 123) vary from year to year, dependent, to some extent, on population density within a lake. Otherwise in years of great abundance and small size there would be no seaward migration while in years of low abundance all migrants would go out as yearlings. According to Krogius (1961a,

TABLE 78. Number and weight of yearling migrants from Cultus Lake and those non-migrants which remained in the lake for a second season, for the brood years 1926–33. Yearling migrants went out early in second year, e.g., those of 1926 brood year in the spring of 1928.

Brood year	No. of migrants ($\times 10^3$)	Avg wt (*g*)	No. of non-migrants[a] ($\times 10^3$)	Avg wt (*g*)
1926	336	3.04	83	3.5
1927	2426	3.06	666	1.68
1928	39	6.55	52	3.0
1929	350	7.10	2	7.0
1930	788	7.32	0	–
1931	1571	3.67	633	1.46
1932	121	6.53	142	4.0
1933	242	7.55	4	7.5

[a] Non-migrants were computed as 10 times the actual number of 2-year-old smolts in the seaward migrations of 1929–36, respectively (Ricker and Foerster, 1948, table I and p. 199).

p. 140) the data obtained at lakes Dalnee and Kurile are in agreement, as were the Cultus Lake observations up to a point (Table 78). However, the Cultus data include two very anomalous year-classes, 1928 and 1932, for which the carryover of nonmigrants was much greater than the actual yearling migrations, although the number of migrants was less than average.

IS THE LENGTH OF LAKE RESIDENCE PARTLY A GENETIC CHARACTER?

There remains for consideration, as a possible factor influencing the age of a migrant, the matter of heredity as determined by genetic selection. In other words, do 4_2 adults tend to produce offspring that migrate seaward after 1 year in a lake, 5_3 parents give rise to 2-year-old migrants, etc.? According to the literature examined, this matter has received little, if any, attention. It would seem to merit study, even if it were eventually to be eliminated as a significant influence.

At Cultus Lake separation of the returning adults into their appropriate age-classes is very difficult because of the breakdown of the outer portion of the scale as the fish mature. Only for the fresh-run, relatively immature individuals can the ages be satisfactorily determined. However, only the central area of the scale is required to indicate whether a sockeye has spent 1 or 2 years in fresh water prior to seaward migration and most of the scales, except for well-matured males, had scales sufficiently complete to provide this information. Table 79 indicates that, in 1925, 1926, and 1930, when the adults with a 2-year-in-lake history constituted 14, 13, and 11%, respectively, of the spawning escapement sampled, the offspring remaining in the lake (see Table 78) made up 8.5, 19.8, and 0.0% of the total crop of young sockeye in the lake (migrants and nonmigrants). For 1928, when the 2-year-in-lake adults made up less than 1% of the spawners sampled, over half of the offspring remained in the lake a second season. Yet for the brood year 1932 when 2-year-in-

TABLE 79. Numbers of adults returning to Cultus Lake, 1925–32, which had had (a) 2 years' or (b) 1 year's residence in the lake prior to seaward migration, as computed from examination of scales.

Brood year	Spawning escapement			2-year-in-lake			1-year-in-lake			References (R.E. Foerster)
	Male	Female	Total	Male	Female	Total	Male	Female	Total	
1925	1,543	3,883	5,426	421	361	782	1,122	3,522	4,644	1929a, p. 25
1926	3,122	1,949	5,071	293	359	652	2,829	1,590	4,419	1929b, p. 8
1927	26,049	56,376	82,425	0	373	373	26,049	56,003	82,052	MS
1928	3,878	11,461	15,339	51	71	122	3,827	11,390	15,217	MS
1929	1,645	3,437	5,082	46	255	301	1,599	3,182	4,781	1934, p. 7
1930	4,856	5,553	10,409	884	228	1,112	3,972	5,325	9,297	1934, p. 7
1931	10,368	27,105	37,473	0	0	0	10,368	27,105	37,473	1936, p. 327
1932	741	1,770	2,511	318	910	1,228	423	860	1,283	MS

lake spawners constituted close to ½ (48%) of the spawning run the nonmigrating yearlings made up 54% of the young sockeye.

This latter coincidence is most striking. It suggests that length of residence in fresh water might be in part a hereditary character, although the evidence presented by the other Cultus Lake data hardly supports such a hypothesis. Inadequate sampling in the early years to differentiate clearly the various age-classes in the spawning run may be a problem, and the 1928 spawners came in part from 2-year-old migrants of the big-year line spawned in 1923, so a large representation of 5_3 spawners in 1928 would have been expected on that ground. The problem deserves further close attention. Selective breeding may be required in order to provide a solution.

MORTALITY OF YOUNG SOCKEYE DURING LAKE RESIDENCE

CULTUS LAKE

Since almost all the spawning at Cultus Lake occurs along the lakeshore gravel areas in water from 0.5 to 20 ft (15 cm to 6 m) or more deep and the emerging fry move, in due course, into the deeper waters of the lake, there is no way of determining the numbers of fry entering the lake each year from natural spawning. Fry releases from the hatchery were made in 3 years, 1926, 1929, and 1932 (Foerster, 1938a, p. 156) and showed a survival to the seaward smolt stages of 5.83, 3.85, and 2.81%, respectively, or an average of 4.16%. When, however, consideration is given to those young sockeye which do not migrate at the end of their 1st year in the lake, the survival values (see Ricker and Foerster, MS, 1948, p. 178, table I and p. 184, table III) become 7.07, 3.87, and 5.45% of fry liberated, respectively, or an average of 5.5%. Whether these survival values would be typical for naturally hatched fry, however, is not known. It is quite probable that they may be appreciably lower, because of losses occurring during the release and distribution of the hatchery-reared fry around the lake in relatively shallow water from metal fry cans or from a specially built fry scow.

In order to get further information on the probable extent of the mortality in the lake during the year, groups of marked sockeye, which had been reared in retaining ponds at Cultus Lake, were released in each of three different years, each group in each year being distinctively marked by removal of certain fins in order to identify it at the time of arrival at the seaward-migrant counting weir (Foerster, 1938b). In the first two tests, 1930–31 and 1932–33, disease broke out in the rearing tanks and mortality was heavy. This not only reduced the numbers of young sockeye available for marking but very likely led also to abnormal loss of some of the marked fish after release into the lake. In both years only the final release in March gave what might be deemed a reasonable survival, probably because the fish that were then marked and released had recovered from the disease or had been immune. These liberations, included in Table 80, showed survivals of 63.1 and 66.3%, respectively.

TABLE 80. Survival rates for young sockeye according to length of residence in Cultus Lake as determined by the release of pond-reared fingerlings at various periods during the year (from Foerster, 1938b, p. 187).

Date of release	Period of pond retention (*months*)	Fins removed[a]	No. released	No. recovered	Period of lake residence (*months*)	Survival (%)
1934–35						
July 13–18	2.0	BV	25,000	5,480	9.5	21.9
Sept. 12–14	4.0	Ad	25,000	8,206	7.5	32.8
Nov. 14–21	6.0	LV	40,000	17,836	5.5	44.6
Jan. 14–17	8.0	RV	40,000	21,872	3.5	54.7
Mar. 11–18	10.0	AdBV	53,375	17,556	1.5	32.9
1930–31						
Mar. 16	9.5	BV	15,922	10,051	1.5	63.1
1932–33		AdBV	31,050	20,575	1.0	66.3
Mar. 29–31	11.0					

[a] BV = both pelvic fins; Ad = adipose fin only; LV = left pelvic fin; RV = right pelvic fin; AdBV = adipose fin plus both pelvic fins.

The third test, in 1934–35, was much more successful. It served to reveal (Table 80) a progressive decline in lake mortality as the period of lake residence was reduced and the fish were larger at time of liberation. The recoveries from the fifth and last release—10 months' pond retention and 1.5 months in the lake—do not conform to the general trend, possibly because the large size of the fish when released may have promoted nonmigration and adoption of the "residual" habit. The average lengths and weights of the test fish, at (1) time of release into the lake, and at (2) time of recovery when migrating from the lake, are given in Table 81. The

TABLE 81. Average lengths and weights of young sockeye at time of release from rearing ponds and at time of recovery as seaward migrants from Cultus Lake (other data in previous table).

	At time of release			At time of recovery		
Date of release	No. in sample	Length (*cm*)	Wt (*g*)	No. in sample	Length (*cm*)	Wt (*g*)
1934–35						
July	50	4.9	1.2	242	8.7	6.5
Sept.	50	7.8	5.3	296	9.4	7.9
Nov.	50	9.4	9.5	279	10.0	9.2
Jan.	50	9.7	10.1	138	10.6	10.6
Mar.	49	11.2	16.4	135	10.8	11.2
1930–31						
Mar.	–	–	–	20	9.5	–
1932–33						
Mar.	–	–	–	7	9.7	8.3

average size of the last group released in 1934–35, when recovered at the seaward migrant counting weir, was actually less than that at time of release into the lake. This would seem to be clear evidence that many of the March release did not migrate from the lake. (One of these marked fish was captured as a mature male residual sockeye in the fall of 1936.) In consequence, the 32.9% recovery does not indicate total survival. It is even possible that some of the preceding January, 1935, release also may not have migrated thus making the 54.7% recovery as seaward migrants a minimum figure of survival for the winter period. The recovery percentages obtained for the March releases in 1930–31 and 1932–33—63.1 and 66.3%, respectively—may be, then, a more accurate indication of the actual survival rates in early spring just prior to seaward migration.

On the basis of these data a curve of the probable trend in lake survival was constructed (Fig. 61A) and from it a curve of the instantaneous mortality rate (Fig. 61B), computed for fortnightly intervals during the year in the lake. The first (lowest) point in curve A has been arbitrarily set at 6.0%, as closely approximating a projection downward of the curve and the survival values found from the fry liberation tests, namely 5.5%.

OTHER LAKES

Just how typical of sockeye-rearing areas in general this 6.0% lake survival may be awaits further investigation in representative sockeye lakes. The following information is available, however, from a few specific and quite different localities where counts or estimates of the fry entering the lake have been made:

1. *Port John Lake* (Fig. 2 and 39; p. 135 and 184). Predator fish are thought to be quite limited in number (Robertson, 1954) which is said to account for a high survival of young sockeye from fry stage on. Survival values—fry to smolt stages (Table 83)—are recorded as: 19, 29, 54, 59, 25, 84, 13, 48+, with an average of 41% and range of 19–84%. Most of these smolts are age II, so these figures represent survival for 2 years of lake life.
2. *Lakelse Lake* (Fig. 7 and 37; p. 131 and 181). Predators here are relatively abundant, see p. 246, consisting of trout, char, and squaw fish. Two lake survival ratios are available, 21 and 11%, for 1-year-old fish.
3. *Chilko Lake* (Fig. 6). In this very important Fraser River sockeye-producing area (see p. 136) where the sockeye spawn in the outlet river and the fry migrate up into the lake, estimates have been made, for a number of years, of the numbers of fry ascending to the lake and of the surviving seaward migrants a year or 2 years later by the International Pacific Salmon Fisheries Commission (1959, p. 14). No description of the methods used is available as yet and it may be that these preliminary estimates are subject to revisions. As reported (see Table 86), the survival percentages for the fry-to-seaward-migrant period have varied from 45.4 to 56.65%, with an average, for the 7 years, of 52.6%. In comparison with most findings elsewhere this high level of lake survival seems fantastic, but the figures for

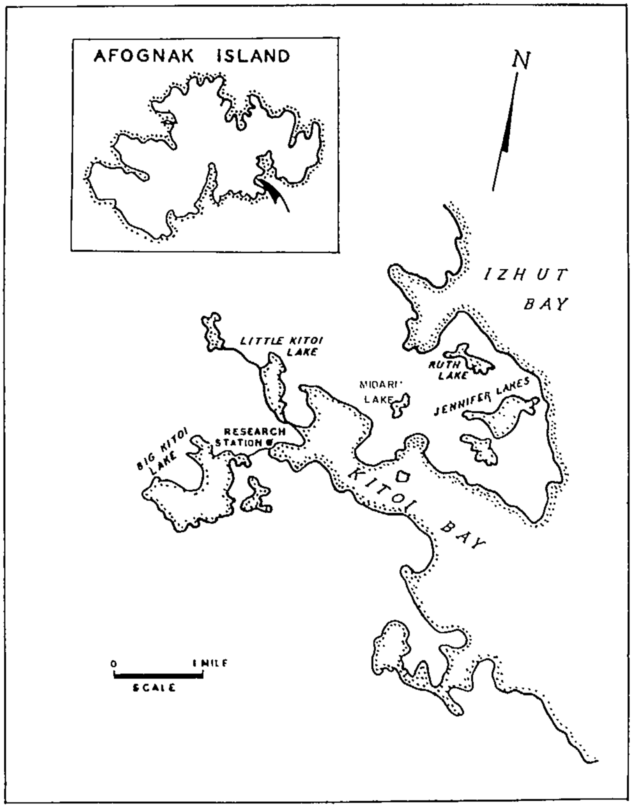

FIG. 75. Map of Kitoi Bay area of Afognak Island, Alaska. (From Meehan, MS, 1963, fig. 1.)

Port John Lake are of the same order if the 2-year lake life there is taken into account. No information is to hand regarding the prevalence of predator and competitor fishes in Chilko Lake.

4. *Midarm Lake, Kitoi Bay area of Afognak Island, Alaska* (Fig. 2 and 75). This is a small lake, 13 acres (5.3 ha) in area, inaccessible to migratory salmon because of a precipitous outlet stream (ADF, 1957, p. 35). To ascertain how sockeye would fare in such an area, a fry planting was made in 1956, 80,000 fry being transferred from the Kitoi Hatchery. In the spring of 1957, a total of 1142 yearling migrants resulted, in 1958, 1700 2-year-olds, and in 1959, 10 3-year-olds, or a total yield of 2852 smolts or 3.6% (ADFG, 1960, p. 30).

5. *Ruth Lake, Kitoi Bay area of Afognak Island, Alaska* (Fig. 2 and 75). From this somewhat larger lake of 48 acres (19 ha), also inaccessible to migrating salmon, all resident fish had been eliminated by rotenone poisoning (ADFG, 1960, p. 30). Sockeye fry were planted in 3 years, and smolts obtained have been as follows:

Year of planting	Fry planted	Smolts produced				
		Age 1	Age 2	Age 3	Total	To date
1956	90,000	31,400	8,600	1,000	41,000	46%
1957	66,000	9,300	5,000±	–	–	22%
1958	60,000	35,000±	–	–	–	58%

The survivals are in general, similar to Port John Lake, where predators are scarce, and much greater than in Midarm Lake, where the resident fish were not disturbed. This seems to indicate the significance of predaceous and competitor fish to sockeye well-being and survival.

6. *Karymai Spring*. In this most interesting Bolshaya area of the west coast of Kamchatka (Fig. 2) where the young sockeye have no recourse to lakes but live in the pools, lagoons, or the main river channel for a year, the calculated seaward migration of smolts from calculated natural fry hatches (Table 91), namely, 9.0, 1.0, 2.0, 1.6, 0.5, 1.7, 18.9, vary widely around an average of 5%. The varying quantities of 1- and 2-year-old coho salmon and 1-, 2-, and 3-year-old char in the streams contribute to the wide fluctuation, as indicated above (p. 159).

SUMMARY OF LAKE SURVIVAL

In view of the very wide fluctuations in survival from fry to smolt stages, depending so profoundly on the conditions under which the young fish are reared, it is extremely difficult to select what might be deemed a reasonably good survival value for the lake-residence period. In the hypothetical survival chart set up on page 67, the lake mortality of young sockeye was placed at 92%, thus providing a lake survival value of 8%. While perhaps not too far removed from the calculated survival value for Cultus Lake nor from the minimum values reported for Port John Lake and Lakelse Lake, this is far below the fry-to-migrant survivals estimated for Chilko Lake. Further comment is reserved for later discussion, page 371.

In a subsequent section, p. 396, the general effect of predation and competition is further discussed. Particular attention is given to the effect of removal, or, at least partial reduction, of the populations of predator and competitor species. The period in the lake is indeed a very crucial stage in the natural production of young sockeye, one in which the mortality is very heavy. By further study the responsible factors causing these extensive losses during lake residence may be made known for important sockeye-rearing areas and if it proves practicable to eliminate or control any or all of these factors the advantages may be exceedingly worthwhile.

Once the young sockeye have left their nursery lakes and have repaired to the sea for further development, they are beyond man's control. Since all evidence indicates, as discussed more fully later, that there is a close positive relationship between the numbers of smolts going to sea and the number of adults returning—the greater the smolt runs, the greater the adult returns—all significant increases in the numbers of smolts constitute greater returns of adult fish, which contribute to a higher catch and a greater economic return to the fishery, also to a greater spawning escapement which, in turn, means a higher productivity from the sockeye-producing areas.

THE NATURAL PRODUCTION OF SOCKEYE SALMON: FRESHWATER PERIOD

In order to assess the efficiency of natural propagation of sockeye salmon under the conditions which prevail in the various areas of the North Pacific region where they spawn and develop to the seaward-migrant stage, the data, thus far accumulated and reported, have been reviewed, where possible, stage by stage, from spawning to seaward migration. There are, however, certain areas where such stage-by-stage information has not been available and only the overall production

TABLE 82. Natural propagation of sockeye salmon to the seaward-migrant stage at Cultus Lake, British Columbia.

	Year of spawning									
	1925	1927	1930	1935[c]	1937[c]	1938	1939	1940[d]	1941[d]	1942[d]
No. of males	1,540	26,050	4,853	5,615	2,234	5,511	21,616	26,475	8,610	12,746
No. of females	3,883	56,376	5,542	10,174	827	7,831	51,565	47,646	9,554	24,559
Avg fecundity of females	4,500	4,500	4,500	4,067	3,764	4,237	4,273	4,300[d]	4,300[d]	4,300[d]
Presumed egg deposition (*millions*)	17.5	253.7	24.9	40.0	2.9	32.74	220.4	204.88	41.1	105.6
No. of 1-year smolts (*thousands*)	183.3	2,456	788.4	3,089	196.3	1,375	3,958	1,753	691.1	2,012
Per cent of egg deposition	1.05	0.97	3.16	7.72	6.77	4.20	1.80	0.86	1.68	1.91
Number of 2-year smolts (*thousands*)	1.7	67.0	15.9	22.9	0.1	1.0	20.7	12.0	2.6	unknown
Per cent of egg deposition	0.010	0.026	0.064	0.057	0.003	0.003	0.009	0.006	0.006	–
Total no. of smolts (*thousands*)	185.0[a]	2,523[b]	804.3	3,112	196.4	1,376	3,979	1,765	693.7	–
Per cent of egg deposition	1.06[a]	1.00[b]	3.23	7.78	6.77	4.2	1.8	0.86	1.69	–

[a] Not counting 12,500 fry migrants counted through the weir.

[b] Not counting 117,000 fry migrants counted through the weir.

[c] Predator control tested in 1936–38 when the young sockeye of these year-classes were resident in the lake. Lake survivals, consequently, much higher than normal.

[d] Spawning escapement counts taken from International Pacific Salmon Fisheries Commission Annual Reports. Sex ratios for 1940 only approximate. Fecundity per female also approximated for all 3 years.

of a known (estimated) number of seaward-migrating smolts from a calculated egg deposition can be determined. In order to present the most comprehensive picture of the natural production of sockeye up to the time of departure from their freshwater nursery areas to the ocean, all the available data will now be considered. As intimated in the Preface it was hoped, for British Columbia at least, that studies of sockeye propagation, in different areas and under differing prevailing local conditions, might bring to light the variations in the survival values at various stages of the life history and the causes thereof more quickly than a long-term study at one site only. It was expected that if the mortalities during the various freshwater life-cycle stages differed radically in different areas, these also would be revealed. A comparison of the findings in *all* areas where such studies have been conducted should, then, be even more illuminating and significant. For each locality, each year's data are given in order that the reader may appreciate the relative sizes of the runs and the ranges of variation from year to year and note in what way and to what extent the production of young is affected thereby.

Cultus Lake, British Columbia (Table 82) (Fig. 6, 35)

Counts of adult fish and of seaward migrants were made at appropriate weirs (see Foerster, 1936c). Most of the fish spawned along the lakeshore, down to a depth of 20 ft (6 m) or more. Most of the young fish migrate seaward at the end of their 1st year, i.e., as yearlings or age I. In 2 years, 1935 and 1937 year-classes, a relatively high production of smolts, 7.8 and 6.8%, respectively, was obtained due to predator control operations in the lake. Normally, production of smolts varied from 0.9 to 4.2% of eggs available for deposition, the average for 8 years being 2%.

Port John Lake, British Columbia (Table 83)

In this small sockeye spawning and rearing area, the adult sockeye enter and ascend Hooknose Creek for a distance of around 2 miles (3 km) to Port John Lake and spawn in the small streams tributary to the lake (Fig. 39). Most of the spawning was observed (Robertson, 1949) to take place in Tally Creek (No. 1 fence) not far from the lake outlet, and particular attention was given to the spawning, fry hatch, etc., in this stream in order to determine the efficiency of natural propagation up to the fry migration stage. As indicated in the footnotes to Table 83, some Tally Creek fry were taken, in some years, for experimental purposes, and thus subtracted from the fry release to the lake. The spawning in other creeks was inspected each year and in those years when the fry produced in them was considered to be of significance in computing the percentage of seaward migrating smolts resulting from the fry in the lake, the estimated fry release from these other creeks was taken into account. From 1957 to 1961, practically all the fry were collected at the Tally Creek weir and transferred directly to salt water to test the feasibility of releasing sockeye fry directly into the ocean and thus eliminating the hazards, etc., of a 1-

TABLE 83. Natural propagation of sockeye salmon to the seaward migrant stage at Port John Lake, British Columbia. A plus sign (+) in this and subsequent tables indicates the presence of unknown, but rather small, quantities, in addition to any indicated.

	Year of spawning								
	1948	1949	1950	1951	1952	1953	1954	1955	1956
No. of males	359	775	455	626	566	568	628	1,037	388
No. of females	149	821	197	122	156	274	244	370	500
Avg fecundity	1,830	2,425	2,157	2,632	2,436	2,809	2,809	2,577	2,627
Presumed egg deposition (*millions of eggs*)	0.273	1.991	8.425	0.321	0.380	0.770	0.662	0.954	1.314
No. of fry produced	74,900	35,400	21,600	30,100	19,100	103,000	64,300	81,700	75,200
Per cent of egg deposition	27.4	1.8	5.1	9.4	5.0	13.4	9.7	8.6	5.7
No. of fry released into lake	74,900	35,400	21,600	30,100[a]	14,000[b]	115,000[c]	154,000[d]	41,000[d]	17,100[d]
No. of 1-year smolts	142	1,587	2,090	4,270	6,000	6,764	452	0	47
Per cent of egg deposition	0.05	0.08	0.50	1.30	–	0.80	–	–	–
Per cent of fry release	0.20	4.50	9.70	14.20	–	6.00	–	–	–
No. of 2-year smolts	13,108	8,293	9,579	13,482	8,102	22,042	11,808	5,248	8,221
Per cent of egg deposition	4.8	0.41	2.2	4.2	–	2.9	–	–	–
Per cent of fry release	17.5	23.4	44.4	44.7	–	19.0	–	–	–
No. of 3-year smolts	675	196	0	56	57	0	641	105	+
Per cent of egg deposition	0.25	–	–	–	–	–	–	–	–
Per cent of fry release	0.90	0.60	–	0.20	–	–	–	–	–
Total smolts produced:	13,925	10,076	11,669	17,808	14,160	28,806	12,901	5,329	8,268+
Per cent of egg deposition	5.1	0.50	2.7	5.5	5.1[e]	3.7[e]	8.1[e]	1.1[e]	2.8+[e]
Per cent of fry release	18.6	28.5	54.3	59.1	?[f]	25.0	84.0	13.0	48+

[a] Fry (5075) marked by removal of fins and released again.

[b] Fry (5100) taken for experiments.

[c] A few sockeye spawned in other areas of the lake. The fry so produced, calculated on the same basis as established for Tally Creek, have been added, as an estimate of the total fry population in the lake.

[d] These are fry which hatched from spawnings elsewhere than in Tally Creek or escaped from Tally Creek. Most of the Tally Creek fry were taken to Port John for release directly into salt water.

[e] These percentages calculated on the egg deposition as computed back from the fry counted: fry in lake ratio as given in field reports.

[f] There is manifestly an error in the estimate of fry release to the lake, the nature and extent of which cannot be assessed from the data available.

or 2-years' residence in the lake. The results of these experiments are reported on p. 8.

Most of the young sockeye remain in Port John Lake for 2 years. Survival in the lake appears to be relatively high because of the apparent paucity of predators which results in a relatively high smolt production of, on the average, 3% of eggs available for deposition. The range of variation over the 10-year period is from 0.5 to 8%.

Lakelse Lake, British Columbia (Table 84) (Fig. 7, 37)

In this lower Skeena River sockeye spawning area, the studies embrace two periods: (1) 1944–46 when the spawning runs were relatively large, the numbers of adults were estimated and the seaward-migrating smolts were counted (Brett and McConnell, 1950), and (2) 1950–54 when the spawning escapements were much smaller and, while a new weir had been constructed, its operation for adult salmon enumeration was not too reliable and reliance had to be placed on small weirs installed in the main spawning streams, Williams and Scully creeks. The counting of seaward-migrating smolts at the weir in Lakelse River (Foerster, 1952) was carried out each season from 1952 to 1956. Practically all smolts migrated as yearlings.

Table 84. Natural propagation of sockeye salmon up to the seaward migrant stage at Lakelse Lake, lower Skeena River, British Columbia.

	Year of spawning								
	1944	1945	1946	1950	1951	1952	1953	1954	1955
No. of males	11,500	23,000	18,400	4,086	8,957	6,640	4,100	3,140[a]	1,837
No. of females	13,500	27,000	21,600	1,871	7,157	5,460	4,405	3,660[a]	1,881
Avg fecundity	3,890	3,890	3,890	3,800	3,800	4,050	4,050	4,010[a]	3,540
Presumed egg deposition (*millions of eggs*)	52.5	105.0	84.0	7.1	27.0	22.1	17.8	14.7+	6.6
No. of fry produced (*millions of fry*)	–	–	–	–	–	–	1.4	2.53	1.04
Per cent of egg deposition	–	–	–	–	–	–	7.8	17.2	15.8
No. of smolts (*thousands*)	557.0	373.0	1,500	594.3	393.6	379.5	311.5	300.7	–
Per cent of egg deposition	1.1	0.4	1.8	8.4	1.5	1.7	1.7	2.0+[b]	–
Per cent of fry liberation	–	–	–	–	–	–	22.0	11.9[b]	–

[a] Approximate only.

[b] The number of 2-year-olds in 1957 is not known.

In considering the significance of stream conditions, with particular reference to the quality of the stream bottom where the spawners deposit their eggs, McDonald and Shepard (1955, p. 37) point out that, although the egg deposition in 1953 was greater than in 1954, the number of fry produced from the 1953 spawning was only slightly less than one-half that of the fry resulting from the 1954 seeding. No great difference in climatic conditions was noted between the 2 years. Hence, it would seem that stream improvement, i.e., cleaner gravel, and more of it made available to the fish by enhanced and regulated flow of water, played a considerable part in bringing about an increased fry production in 1955.

In considering all the evidence available from the Lakelse area, it would appear that smolt production fluctuated around 1.5% of eggs deposited, if the unusual

8.4% for the 1950 year-class—smolts migrating seaward in 1952 (1-year-old) and 1953 (2-year-old)—be not included. There is some question as to the exact extent of the spawning escapement in 1950 but even when a quite high maximum is given the latter, a production of over 8% smolts results. The reason for this remarkably high value is not clear.

On the basis of the data for the 1953 and 1954 year-classes, approximately 92% mortality occurred in 1953–54 during egg deposition, fry emergence, and migration of the fry to the lake where subsequently around 80% mortality of the fry took place. For the 1954 year-class these mortalities were approximately 80 and 88%, respectively. The overall production of seaward migrating smolts was approximately the same for both year-classes.

BABINE LAKE, BRITISH COLUMBIA (TABLE 85) (FIG. 7, 56)

In this major sockeye-producing area of the Skeena River much effort has been devoted to obtaining reasonably accurate estimates of the numbers of seaward migrants produced each year. The size of the outflowing Babine River and volume and speed of the spring floods precluded the operation of a smolt weir. Therefore, a mark and recapture technique had to be adopted (Withler, 1952a, 1953) where-

TABLE 85. Natural propagation of sockeye salmon up to the seaward migrant stage at Babine Lake, upper Skeena River system, British Columbia.

	Year of spawning										
	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
No. of small males[a] (*thousands*)	48.0	179.3	11.0	27.9	28.0	9.7	30.6	18.2	50.2	30.8	31.9
No. of large males[a] (*thousands*)	179.0	159.4	73.4	205.6	303.1	196.1	33.7	172.8	212.2	319.8	309.7
No. of females (*thousands*)	282.1	205.0	68.0	143.4	383.5	297.6	37.7	182.6[d]	220.9[d]	492.3[d]	473.2[d]
Avg fecundity	–	–	–	3,206	3,498	3,555[c]	3,126[c]	3,071	3,063	3,261	3,343
Presumed egg deposition (*millions*)	853	591	194	409	1,241	1,020	105	523	653	1,543	1,554
No. of smolts (*millions*)	4.2	4.5	3.1	2.8	30.9	21.1	6.4	22	39	45	–
Per cent of egg deposition	0.5	0.8	1.6	0.7[b]	2.5	2.1	6.1	4.2	5.9	2.9	–

[a] At the weir small sockeye or Jacks, i.e., precociously-maturing (3_2) males, were enumerated separately from large sockeye which had to be sampled to determine the sex ratio.

[b] Only about one-third of the 1952 spawning escapement spawned successfully, due to the adverse effects (delay and injury) caused by the Babine River slide (see p. 89). The probable estimate of percentage smolt survival from eggs actually deposited would approximate 2%.

[c] Calculated on an egg-content-to-length-of-fish basis.

[d] In these years the numbers of female sockeye caught in the nets set by Indians in the Babine River between the weir and Babine Lake, amounting to 12,276; 8,102; 19,060; 8,259 respectively, were subtracted from the total females in computing the egg deposition. Such deductions were not made, presumably, prior to 1956, but it would seem that the percentage survival of smolts would not be changed appreciably.

by a sample of the migrant run from the lake was captured, the individuals distinctively marked and released. Lower down the Babine River samples of smolts were again caught. Assuming a normal mixing and distribution of marked and unmarked migrants, the ratio of marked to unmarked individuals caught should indicate the numbers of fish migrating.

More recent studies have indicated that in earlier years, i.e., prior to the 1958 smolt migration (brood year, 1956), the first part of the run may have been missed, due to inability to get the traps erected early enough in the season. According to observations in 1958, 1959, and 1960, from one-third to one-half of the migration may have been missed, depending on the degree of spawning at the outlet end of the lake. However, in the early years the spawning was believed to be fairly general throughout the Babine Lake area. Hence, probably not more than one-quarter to one-third, at most, could have escaped attention. To concede this would not greatly change the percentage smolt survival values recorded in Table 85, which show an average seaward migrant production of around 3% of total eggs.

Chilko Lake, British Columbia (Table 86) (Fig. 6)

For this important Fraser River sockeye-producing area where the International Pacific Salmon Fisheries Commission has been making a detailed study of

Table 86. Natural propagation of sockeye salmon up to the seaward migrant stage at Chilko Lake, upper Fraser River system, British Columbia (data taken from International Pacific Salmon Fisheries Commission reports as indicated).

	Year of spawning								
	1949	1950	1951	1952	1953	1954	1955	1956	1957
No. of small males[a]	59	8,700	18,000	2,500	500	1,800	10,300	800	2,300
No. of large males[a]	23,800	9,200	42,000	231,400	94,400	13,800	46,100	260,300	55,000
No. of females[a]	35,200	11,900	58,100	255,600	102,800	20,900	71,700	386,300	83,500
Estimated egg-to-fry survival[b]	6.71	6.49	11.90	6.04	4.97	9.50	9.86	–	–
Estimated no. of yearling seaward migrants[c] (*millions*)	3.147	1.170	11.582	24.688	8.316	2.997	9.410	28.512	–
Per cent of egg deposition	3.49	3.57	6.74	3.14	2.58	5.26	4.48	–	–
Per cent of fry release[b]	52.00	55.00	56.65	52.02	51.92	55.33	45.40	–	–
Migrant to returning adult survival[b]	11.85	11.50	5.49	7.08	5.36	20.00	13.77	–	–

[a] From IPSFC Annual Reports (1950–58).

[b] From IPSFC (1960, p. 14).

[c] From Henry (1961, p. 70).

natural propagation, the data thus far reported (IPSFC, 1960, p. 14; Henry, 1961, p. 70) are of interest.

As already intimated, p. 136, the indicated egg-to-fry survival seems unusually high, in comparison with data from other areas. However, the 4.2% smolt production from eggs deposited, although high in comparison with Cultus and Lakelse lakes, is of the same order as recorded for Babine Lake in recent years. Further data from Chilko and similar observations in other large lakes will be of great interest.

LITTLE KITOI LAKE, ALASKA (TABLE 87)

From this small sockeye area on Afognak Island, Alaska, (Fig. 2 and 75), data are available for six complete year-classes and partially for a seventh. The majority of the sockeye migrated seaward as yearlings (80%). Smolt survival for the 7 years averaged 4% of the presumed egg deposition, varying from 2 to 8.5%.

TABLE 87. Natural propagation of sockeye salmon up to the seaward-migrant stage at Little Kitoi Lake, Afognak Island, Alaska, for the brood years 1954–60 (from Meehan, 1963).

	Year of spawning						
	1954	1955	1956	1957	1958	1959	1960
No. of females	1,150	1,202	279	251	150	1,378	843
Potential egg deposition[a] (*thousands*)	2,300	2,000	515	442	251	2,226	1,466
No. of seaward migrants							
Yearling	50,000	34,200	17,476	25,091	7,240	33,840	49,862
Age 2	1,257	9,452	4,122	12,581	3,000	10,304	16,805
Age 3	153	3	54	2	0	0	?
Total smolts:	51,410	43,655	21,652	37,674	10,240	44,144	66,667
Per cent of egg deposition	2.24	2.18	4.20	8.52	4.10	1.98	4.55

[a] Based on the average number of eggs per female.

Consideration may be given also to two transplantation tests carried out in this area, one at Midarm Lake, the other at Ruth Lake (see Fig. 75). In the former, a small lake to which adult sockeye could not ascend because of impassible rapids, no change had been made in lake conditions. In Ruth Lake, however, also a "barren" lake, all resident fish had been killed by rotenone poisoning and allowed to decompose in the lake. The great differences noted (Table 88) in fry and smolt survival between the two lakes is attributed to the removal of predatory and competitor fishes. In Ruth Lake survival was remarkably high for the first 3 years and then dropped appreciably. No explanation is offered for this change in survival.

LAKE DALNEE, KAMCHATKA (TABLE 89) (FIG. 8)

From the long-term comprehensive study of sockeye salmon propagation at this small but important sockeye-producing lake on the east coast of Kamchatka,

TABLE 88. Survival of sockeye salmon fry liberated in Midarm and Ruth lakes, Afognak Island, Alaska (from the Alaska Department of Fisheries Annual Reports and from Meehan, 1963).

	Midarm Lake[a]	Ruth Lake[b]				
Year of spawning	1955	1955	1956	1957	1958	1959
No. of eggs planted	80,000	89,000	66,000	110,000	50,000	425,000
No. of seaward migrants						
Yearling	1,142	31,407	9,329	33,733	841	28,811
Age 2	1,700	8,641	5,761	705	2,607	6,506
Age 3	0	1,667	50	2,271	183	unknown
Total smolts:	2,842	41,715	15,140	36,710	3,661	35,317+
Per cent of eggs planted:	3.6	46.9	23.0	33.4	7.3	8.3+

[a] A "barren" lake, to which sockeye salmon could not ascend because of impassable rapids. Sockeye fry were introduced but the lake was not otherwise changed.

[b] Another "barren" lake. All resident fish were poisoned off before the planting of sockeye fry was undertaken.

exceedingly interesting data have been reported. An attempt has been made to bring together all the pertinent data from the several reports of Krogius and Krokhin.

The observations here draw attention to certain phases of natural propagation not clearly indicated in any of the other areas considered. One reason may be the fact that, at Lake Dalnee, lakeshore or "beach" spawning takes place, rather than spawning in tributary streams. Nevertheless, the hazards of low water and freezing during a severe winter should be equally as great, if not greater, in stream-located redds; freshet floods in streams should cause additional damage. In any event, the mortality in early developmental stages can be quite severe.

Thus, at Lake Dalnee in 1938 and 1947 the spawning areas were frozen over and mortality of eggs was very high. Digging up of already deposited eggs by later-arriving spawners can cause heavy loss, as, for example, in the 1936 and 1937 year-classes. On the other hand, mortality of young fish during lake residence may be of major significance, as in the year-classes of 1943 and 1944, and to a lesser degree in the 1946 year-class.

In general, the efficiency of natural propagation to the seaward migrant stage at Lake Dalnee was, in comparison with North American sockeye areas, exceedingly low—on average 0.3%—with a low of 0.006% and a high of 1.05%. But along with this low production of smolts there occurred, in Lake Dalnee, an exceptional growth of the young. Krogius (MS, 1949, p. 11) points out that while the percentage migration from Lake Dalnee, based on the number of eggs contained in all spawning females, averaged only one-tenth that at Cultus Lake, the biomass of the migrants was only a little less than one-half. Not only were the 1-year smolts at Lake Dalnee larger than those at Cultus Lake but there occurred also a goodly number of 2-year migrants. This larger size of smolts led, as will be noted below, to a higher survival in the ocean and a greater per cent return of adults from the sea.

TABLE 89. Natural propagation of sockeye salmon up to the seaward migrant stage at Lake Dalnee, Kamchatka. Data on the return of adult sockeye to the lake are also given.

	Year of spawning												
	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947
No. of males	?	68,800	47,200	37,650	22,850	36,450	14,000	11,000	13,600	76,000[b]	63,700[b]	55,000[b]	23,000[b]
No. of females	11,000	73,100	52,800	47,300	25,800	34,300	22,800	9,300	13,400				
Avg fecundity	?	2,300	2,600	2,660	2,500	3,080	2,370	2,440	–	–	–	–	–
Eggs available for deposition (*millions*)	28.2	166.9	138.0	125.8	67.7	86.0	70.4	22.0	32.7	111.0	93.4	57.7	35.9
No. of live eggs (*millions*)[a]	–	1.7	1.4	14.0	22.2	15.1	35.2	15.4	23.3	87.7	60.7	28.8	0.3
Per cent of eggs available	–	1.0	1.0	11.0	32.8	17.6	50.0	70.0	71.2	79.0	65.0	49.9	1.0
No. of yearling smolts (*thousands*)	12.8	113	23	68	145	200	70	–	–	–	–	–	–
No. of 2-year smolts (*thousands*)	169	131	34	40	50	100	–	–	–	–	–	–	–
Total smolts (*thousands*)	297	244	57	108	195	300	?	228	16	80	226	35	2
Per cent of eggs available	1.05	0.15	0.04	0.10	0.29	0.35	–	1.04	0.05	0.07	0.24	0.06	0.005
Per cent of live eggs	–	14.4	4.0	0.8	0.9	2.0	–	1.5	0.07	0.09	0.37	0.12	0.006
No. of returning adults (*thousands*)	72.7	72.7	88.2	19.0	49.2	–	–	85.0	2.0	7.4	25.0	–	–
Per cent from 1-year smolts	–	29.0	38.0	33.0	48.0	–	–	–	20.0	4.5	9.3	–	–
Per cent from 2-year smolts	21.1	33.5	38.0	–	–	–	–	37.0	10.0	11.7	20.0	–	–
Ratio of return per spawner	2.74:1	0.62:1	0.19:1	0.59:1	–	–	–	4.20:1	0.07:1	0.10:1	0.44:1	–	–

[a] From an examination of redds during the winter or early spring. The losses in eggs not properly buried at spawning time or dug up during subsequent spawning activities are not included.

[b] Total spawners, i.e., males plus females.

TABLE 90. Natural propagation of sockeye salmon at Kurile Lake, Kamchatka (from Egorova, Krogius, Kurenkov, and Semko, 1961, table 5).

	Year of spawning														
	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	Avg
No. of fish (*millions*)	0.50	0.50	3.20	0.85	4.19	1.70	3.20	0.75	4.20	0.96	2.40	2.35	1.20	0.32	1.98
Avg fecundity of females	3,160	3,600	3,370	3,420	3,500	3,810	3,300	3,700	3,530	3,590	3,590	3,480	3,400	3,320	3,483
No. of eggs (*billions*)	0.72	0.88	5.00	1.30	6.67	2.70	4.80	1.28	6.73	1.55	3.95	3.72	1.80	0.46	2.97
No. of eggs deposited (*billions*)	0.30	0.32	0.70	0.44	0.70	0.42	0.88	0.42	0.80	0.48	0.61	0.56	0.40	0.22	0.52
Per cent of eggs available	42	36	14	34	10	16	18	38	12	31	15	15	22	48	25
Per cent of egg loss in redds	9	18	26	22	65	20	36	29	36	30	36	30	22	10	28
No. of live eggs in redds (*billions*)	0.28	0.27	0.52	0.34	0.25	0.34	0.56	0.30	0.51	0.34	0.39	0.40	0.32	0.20	0.35
Per cent of eggs available	39	31	10	26	4	13	12	23	8	22	10	11	18	44	24
No. of adults (*millions*)	3.97	4.41	7.81	3.72	6.35	6.02	6.48	3.90	8.50	5.54	9.35	5.84	6.93	3.00	5.85
Per cent of eggs available	0.50	0.50	0.16	0.29	0.10	0.20	0.13	0.30	0.12	0.36	0.24	0.16	0.39	0.65	0.29
Per cent of live eggs	1.4	1.6	1.5	1.1	2.5	1.8	1.2	1.3	1.7	1.6	2.4	1.5	2.2	1.5	1.6
Ratio of adult return per spawner	7.9:1	8.8:1	2.4:1	4.4:1	1.5:1	3.5:1	2.0:1	5.2:1	2.0:1	5.8:1	3.9:1	2.5:1	5.8:1	9.4:1	4.6:1

[a] Number and percentage of dead and live eggs in the gravel computed from recovery of eggs in the spring from 1 m^2.

KURILE LAKE, KAMCHATKA (TABLE 90)

Most interesting data have recently been reported (Egorova, Krogius, Kurenkov, and Semko, 1961) on a long-term study of the natural propagation of sockeye salmon in the most productive and most extensive sockeye-producing area in Kamchatka, Kurile Lake, the source of the Ozernaya River (see Krokhin and Krogius, 1937b). Spawning of the multitudes of sockeye (0.5–4.2 million) takes place in the lake itself, in the tributary streams and in the upper part of the outlet river. The young remain in the lake usually for 2 or 3 years, during that period achieving about the same size as Cultus Lake seaward migrants (Krogius, 1961a, p. 133).

In view of this similarity in size of seaward migrants, the 10% figure for ocean survival, found for Cultus Lake (Foerster, 1936b), has been applied also to Kurile Lake sockeye (Krogius, 1961a, p. 140) in order to get from the published data (Table 90) some idea of the probable number of seaward migrants from Kurile Lake and the percentage survival to the seaward migrant stage, for comparison with other areas. Consequently, the percentage production of seaward-migrating smolts is rated as 10 times the percentage production of adults in Table 90 or an average, for all 15 years, of 2.9%. This would give, also, an average percentage survival, to the smolt stage, of 16% of "*live*" eggs and, of course, even higher for fry, presumably. All these calculated survival values are high, in comparison with the data for Lake Dalnee, but perhaps not too much out of line.

At Kurile Lake, as at Lake Dalnee (and presumably at all other spawning areas, also), mortalities at all stages, from egg deposition on, vary widely in severity. For some year-classes they are heavy at time of spawning, while in others, they are severe during incubation in the redds. Where heavy mortality occurs in both periods, e.g., 1945 and 1949, overall production is relatively very low. In both years, the spawnings were very intense.

For comparison with other areas, the production of smolts at Kurile Lake is taken as 2.9% of all eggs available for deposition.

KARYMAI SPRING, BOLSHAYA RIVER SYSTEM, KAMCHATKA (TABLE 91)

In this quite unusual situation the sockeye spawn in a region of outflowing ground water, where a wide lake-like but very shallow pool is formed (Semko, 1954a, p. 44). Upon emergence the fry scatter over a wide area of the adjacent stream and tarry for their year of freshwater residence in the backwater lagoons and shallow pools of the main river or its tributaries.

In some years emergence (hatch) of fry is quite high, e.g., 1943 and 1944, while in others it can be very low, e.g., 1947 and 1949. After emergence of the fry, predation by char and young coho takes place, varying from 86–70% in the 1943–45 year-classes to a low of 38–13% for 1947–49. During the year's residence in the spring, mortality varied from 99.5% (1947) to 80% (1949), the overall average amounting to 95%, mostly due to predation. Survival to the seaward-migrating stage is, on average, 0.7% of eggs deposited, with a range of variation of from 0.05 to 2.2%.

TABLE 91. Natural propagation of sockeye salmon at Karymai Springs, Bolshaya River, Kamchatka (from Semko, 1954a, tables 42 and 55).

	Year of spawning							
	1943	1944	1945	1946	1947	1948	1949	1950
No. of males	1,500	590	570	1,526	3,967	930	384	122
No. of females	1,500	580	640	1,525	3,966	930	384	120
Avg fecundity	4,500	4,668	4,552	4,834	5,165	5,136	4,829	4,633
Total egg deposition (*millions*)	6.75	2.71	2.86	7.42	18.88	4.78	1.85	0.56
Hatch of fry in redds (*millions*)	5.0	2.08	1.35	1.15	2.59	1.20	0.25	0.09
Per cent of egg deposition	73.6	76.5	47.0	15.5	13.7	25.1	13.5	16.3
Fry migrants (*millions*)	1.24	0.45	0.19	0.61	1.87	0.84	0.22	0.06
Per cent of egg deposition	18.4	16.8	2.5	8.2	9.9	18.7	11.8	10.7
Per cent of hatch in redds	29.0	22.6	13.8	53.0	72.1	74.4	87.3	65.8
No. of smolts	112,500	4,664	3,657	9,970	9,898	14,071	41,390	–
Per cent of egg deposition	1.7	0.17	0.13	0.14	0.05	0.29	2.2	–
Per cent of fry hatch	2.3	0.22	0.27	0.87	0.38	1.17	16.5	–
Per cent of fry migration	9.0	1.03	1.96	1.6	0.5	1.7	18.9	–

Karluk Lake, Alaska

No counts or estimates of the production of seaward migrants from the deposition of eggs by spawning sockeye each year are available for determination of the success of natural propagation in this very important sockeye-producing area. However, having established, from marking experiments, the probable ocean mortality of Karluk sockeye to be 78.45%, Barnaby (1944) makes a calculation of the mortality between the egg and seaward-migrating smolt stages. He finds it to be 99.55–99.10%, depending on whether the ratio of return from the sea per spawning individual be considered as 2:1 or 4:1. This mortality is exceptionally high, but of course the Karluk sockeye spend longer in the lake than those of other major areas: at the time of Barnaby's experiments (1926–32) the smolts consisted of age 2 and age 3 fish in about equal numbers, with a few of age 1 and age 4. Karymai Spring, a rather atypical sockeye region, also had a high egg-to-migrant mortality rate.

Wood River, Bristol Bay, Alaska (Table 92)

In many extensive sockeye spawning areas with large and fast-flowing outlet rivers it is impossible or impractical to construct counting weirs for complete enumeration of seaward migrants. As an alternative, fyke nets are operated at specific locations to get an estimate of the extent of the seaward migration each

TABLE 92. Natural propagation of sockeye salmon in the Wood River system, Alaska, with the relative abundance of smolts, based on fyke net catches, shown as an index only (from Burgner, 1958; FRI Annual Report, 1959).

	Year of spawning									
	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958
Escapement in thousands of fish	101	452	458	227	516	571	1,383	775	300	962
Per cent females	60.2	56.1	53.6	54.8	56.9	54.4	52.1	–	–	–
No. of females (*thousands*)	61	254	245	124	294	311	721	–	–	–
Egg deposition (*millions*)	242.2	1,003.3	989.8	479.9	1,217.2	1,166.3	2,718.2	–	–	–
Year of seaward migration	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960
Index of relative abundance of smolts[a]	10	100	296	439	222	327	166	231	61	223

[a] The year 1952 has been selected as the base year with a migration index of 100 (1950 spawning).

spring. Such estimates are of great practical value in ascertaining the relative size of the migration each year in order to predict the probable extent of the runs of returning adults in subsequent cycle years. In some cases they can serve, also, to give a reasonably accurate estimate of the number of migrants passing seaward.

In the Wood River this fyke-net sampling technique has been used (Koo, 1956; Burgner, MS, 1958; FRI, 1959, p. 8) to measure the relative abundance of smolt migrants and "the catches, when compared with those of previous years under similar conditions, are converted into a numerical value as the index" (FRI, 1959, p. 8). These are shown in Table 92 together with other pertinent data as abstracted from Burgner (MS, 1958). Each year's index includes, of course, both 1- and 2-year-old migrants. Prior to the migration of 1958 "the Age 1 smolts had constituted the vast majority of the smolt run in the Wood River system; Age 2 fish averaged about 10 per cent. In 1958, at least 35 per cent of the run was made up of Age 2 fish. These are part of the progeny of the large 1955 spawning escapement" (FRI, 1959, p. 8).

From the data available it is clear that the relation between escapement and resulting seaward migration "has been highly variable. The small escapement in 1952 produced a total of twice as many smolts as the large escapement in 1955 and 12 times as many per spawner" (FRI, 1959, p. 8).

Chapter 11. The marine phase of the sockeye's life cycle

This second period in the sockeye's life cycle is considered generally as commencing with the departure of the young seaward migrants from their freshwater nursery areas. Studies of ocean mortality are based on the return of adults from known or estimated seaward-migrating smolts and hence include whatever mortality occurs during the descent of the river. In many instances this descent may embrace hundreds of miles of river, e.g., from Babine Lake on the upper Skeena (Fig. 7), lakes of the upper Fraser (Fig. 6), Wood River system (Fig. 70), etc. while in others the distances may be short, e.g., from Port John, Lakelse (Fig. 7) and Cultus (Fig. 6). No information is available concerning the extent of the losses that may occur during this seaward migration nor the probable causes thereof. Naturally, it will vary quite appreciably from area to area depending on the hazards to be faced by the young fish—predators, pollution, exceedingly turbulent or rough stretches of river, waterfalls, etc.—and from year to year depending on the extent of the annual spring runoff, high or low water, etc. This remains as one phase of the problem still to be investigated.

TRANSFER FROM FRESH WATER TO SALT WATER: PHYSIOLOGICAL CHANGES INVOLVED

In the course of changing their freshwater environment to one in the ocean a quite profound change takes place in the physiological condition of the young sockeye. To a certain degree the necessary transformation or reorganization of body functions has already begun prior to migration, as intimated above (p. 294), especially a preference for salt water; but once in the highly saline water of the ocean, other adjustments must be made.

Since, under normal circumstances, the body fluids of fish are maintained at a concentration appreciably higher than that of fresh water they must be continually taking in water through the tissues by osmosis, mostly by means of the gills and oral membranes (V. S. Black, 1951, p. 174). They do not need to drink water. Any salts which are lost, either by way of the kidneys or in the faeces, are replaced by the taking up of chlorides by certain "chloride secreting" cells, these chlorides then being passed on to the tissues through the blood circulation. In the saltwater medium where the salt concentration is much greater than within the fish's body, the natural tendency would be for water to flow from the fish to its environment through osmosis. To maintain the water content within the fish, then, water must be imbibed. In so doing, the excess salts must be got rid of and this is done by the "chloride secreting" cells in the gills.

V. S. Black (1951) made tests with chum and coho salmon fry, transferring them, at 2 or 3 months after hatching, from fresh water to sea water with a salinity of 28–30‰. There was a rise in both density and chloride content within the body. The density increased from around 1.003 to 1.028 within 12 hr and then dropped to a level approaching that of the sea water (1.020) at about 24 hr. Body chlorides increased likewise for 12 hr but in the coho fry they continued to increase until death occurred while in the chum salmon they declined, returning to their normal level, or slightly above, within 36 hr, presumably due to the development and activity of "chloride secreting" cells which are not present, apparently, in coho fry but occur later at the yearling stage.

In tests conducted on sockeye seaward migrants in Kamchatka (Zaks and Sokolova, 1961), specimens, placed in sea water with a salinity of slightly over 20‰, showed an increase in the urine which became more evident with prolonged retention in the more saline environment. The osmotic pressure of the blood plasma increased as the salinity of the water increased but, as soon as the external medium had a higher salt content than the blood, the latter remained hypotonic, that is, maintained a lower chloride content. Such a condition is characteristic of marine fish, as is the increase in urine when salinity increases.

As Zaks and Sokolova (1961, p. 338) put it:

> "in general, the reaction of seaward migrants in a hypertonic medium can be expressed in the following manner. The first result of retention in salt water is the loss of water through the gills and the corresponding dehydration of the fish. It responds then as if it were naturally a marine fish, that is, it begins to drink water. The hypertonic liquid in the gut is readily absorbed by the blood and dilutes the plasma; the percentage of albumen is reduced causing a hydremia and simultaneously the osmotic pressure of the plasma increases. For marine fish the specific gravity of the plasma in similar cases, however, does not rise since the excess salt is excreted by the gills. It can be thought, then, that the excretory gill mechanism comes into operation in seaward migrating sockeye in consequence of which the osmotic pressure of the plasma does not increase to a level which endangers life."

One feature of importance here relates to the possibility of mortality arising during this change in environment, either by reason of too rapid an introduction into salt water or a breakdown in the appearance or functioning of the chloride-secreting cells which play, apparently, such a major role in maintaining the proper salt content of the body fluids. For example, Zaks and Sokolova (1961, p. 338) refer to a disturbance in coordination and a mass mortality occurring with a rise in salinity to around 25‰. Furthermore, tests conducted on seaward migrants which had been retained in fresh water for a period of 2 weeks prior to testing for adaptation to a high salinity environment indicated that these fish react to salt water quite differently from normal seaward migrants. Their reactions to a rise in the salinity of the surrounding water resembled those of freshwater fish. Somewhat similarly, Baggerman (1960, p. 302) found that sockeye yearlings retained in fresh water beyond their migration time "lost their preference for salt water and became indifferent with regard to salinities."

Whether these findings suggest the possibility of mass mortality of seaward migrating sockeye under adverse conditions is not clear. It seems highly unlikely that young sockeye in a river estuary would be thrust too suddenly into a too highly saline medium, although little is known of their speed of travel through the brackish water of river estuaries. Furthermore, seaward migrants must have a fairly wide limit of tolerance to salinity and be able to accommodate themselves satisfactorily to the conditions in which they find themselves. Nevertheless, the problem requires further study.

MIGRATION OF YOUNG SOCKEYE TO THE SEA

Little is known about the movement of the young sockeye from river estuary, through coastal water areas, to the open sea.

In beach seining operations carried out along the shores of the San Juan Islands, July 3 to August 8, 1950, Clemens (1951) captured large numbers of young pink, chum, and chinook salmon actively feeding, but no sockeye. Through these waters (Fig. 3) young sockeye from the Fraser River and other sockeye streams of the Strait of Georgia are presumed to pass en route to the Juan de Fuca Strait and the open Pacific. Clemens remarks (p. 12) that "possibly they had already passed through the channels or perhaps, being of larger size, they move farther offshore or in deeper water." He goes on to say that "once the fish arrive in Juan de Fuca Strait their transport to the open sea is facilitated by two circumstances: (1) during the period of heavy land drainage, which occurs in June, the outflow current is predominant in the upper waters and reaches a very high velocity at the height of the ebb tide; (2) the young fish tend to occupy the upper waters and are therefore almost continuously under the influence of the outgoing current."

In more northern British Columbia waters fishing operations (by small-mesh purse seines, beach seines, gill nets, tow-nets and equipment for fishing at night with lights) were conducted (Manzer, 1956a) during June–September, 1955, to discover the distribution and movement of young salmon after they left fresh water. In Chatham Sound, into which the Skeena and Nass rivers empty (Fig. 2), sockeye salmon were caught off the Skeena River mouth during the first 2 weeks in June in good number and were present also along the mainland beaches, as well as along a few scattered beaches on the west side of the Sound. During the next 2 weeks they were still present in these areas but less abundantly. By mid-July only single specimens were taken. None was captured after mid-July. Farther south, in Johnstone Strait (Fig. 76), migrants were taken relatively abundantly in late June and in July but by mid-August only moderate numbers were captured. Through this Strait pass young sockeye from streams of the British Columbia mainland, probably including some from the Fraser, and also fish from the northern section of the east coast of Vancouver Island, particularly Nimpkish River. In Queen Charlotte Strait young sockeye were caught in moderate numbers from mid-August to early September "but usually only over deep water around rocky islands offshore." Manzer con-

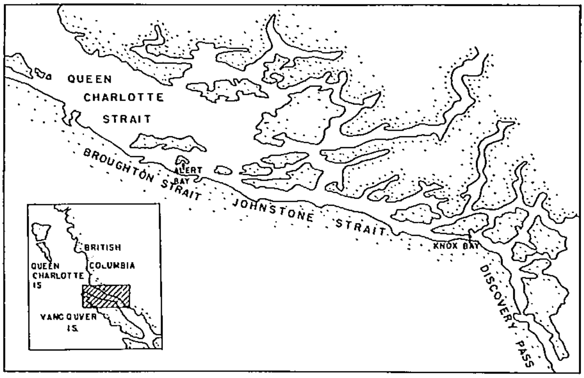

FIG. 76. Map of Johnstone Strait and Queen Charlotte Strait, British Columbia, and adjacent waters where young salmon were found. (From Manzer, 1956a.)

cludes that "such catches as were made in both areas suggest a similar movement and disappearance from inshore areas late in the summer" (Manzer, 1956a, p. 28).

The view heretofore generally accepted has been that, for our British Columbia sockeye populations, the ocean movement of young salmon is northwestward along the coast in the prevailing coastal current (Tully, 1942; Tully and Doe, MS, 1953; Doe, 1955). From each river system along the coast the young fish are added to this northward movement, arriving at length on the rich feeding grounds of the Alaska Gyral (Fig. 78). Whether they continue thereafter as a general mixed feeding population around the Gyral to the westward, or split off to remain as discrete racial aggregations moving about the North Pacific area wherever the food is abundant is not clear. Certainly, as recent distribution and tagging expeditions have revealed, the sockeye show a wide dispersion.

DISTRIBUTION OF SOCKEYE IN THE SEA

OCEANOGRAPHICAL CONDITIONS IN THE NORTH PACIFIC

In view of the importance of the North Pacific Ocean as a vast feeding ground for Pacific salmon, an understanding of its oceanographic features is of interest. It is of particular significance to know where the salmon are to be found from year to year, the conditions under which they live and the extent to which those features fluctuate which might have a bearing on their distribution and also on their well-being, i.e., their growth and survival.

Figure 77 shows the five "domains" into which the North Pacific Ocean has been divided on the basis of the temperature, salinity, and flow characteristics of the upper zone waters (60–275 m in depth) according to oceanographic researches for the International North Pacific Fisheries Commission (Dodimead et al., 1963,

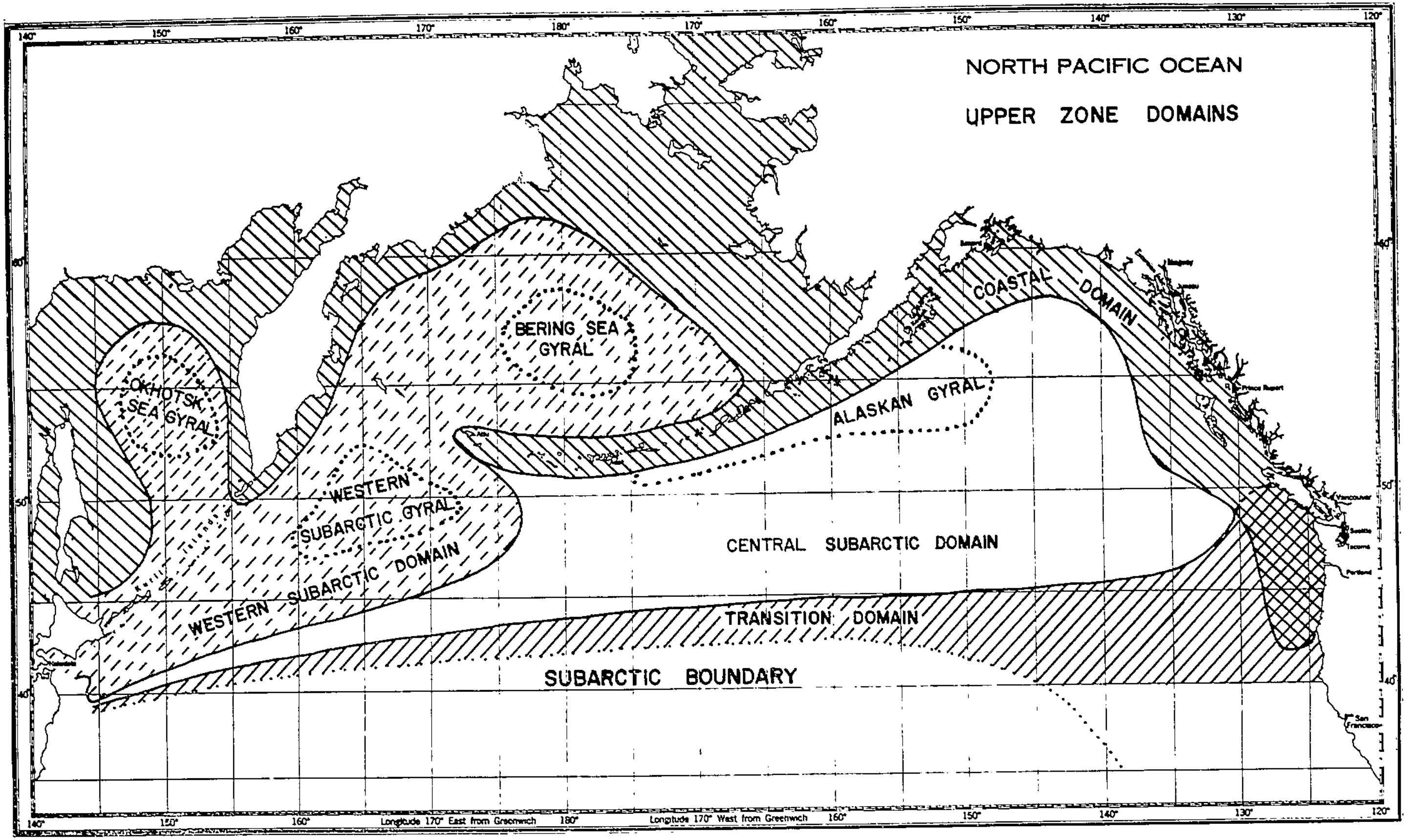

FIG. 77. Schematic diagram of upper zone domains of the North Pacific Ocean. (From Dodimead, Favorite, and Hirano, 1963, fig. 216.)

p. 4). These domains are (1) Western Subarctic, (2) Transitional, (3) Alaskan Stream, (4) Central Subarctic, and (5) Coastal. They have the following characteristic features:

1. Western Subarctic Domain: the temperature structure at all times exhibits a cold subsurface minimum at the bottom of the upper zone; depth—between 100 and 150 m; relatively high salinity water, generally between 33.0 and 33.2‰ in the surface waters of the Bering and Okotsk seas and slightly lower (32.6–33.0‰) in the remainder of the domain, while near the bottom of the upper zone the salinities vary between 33.0 and 33.4‰; temperatures less than 3.5 C at the bottom of the upper zone.
2. Transitional Domain, lying directly north of the subarctic boundary: flow principally zonal, except near the North American coast where it veers northward and southward; surface waters warm (warmer than 15 C in summer and 7 C in winter); relatively high salinity water—greater than 33.2‰ in surface strata and greater than 33.4‰ near the bottom of the upper zone, though east of 150°W dilution of these waters occurs; a subsurface minimum temperature at the bottom of the upper zone may be present; marked meridianal gradients of temperature and salinity occur.
3. Alaskan Stream Domain: associated with the relatively dilute warm water flowing out of the Gulf of Alaska westward along the southern side of the Aleutian Islands, beginning at about the longitude of Kodiak Island where the flow narrows and accelerates; coastal water also present but is modified by the considerable mixing due to the strong tidal currents along the Islands and through the passages; variations in the extent of the domain can be deduced from the distribution of surface water less than 32.6‰ and the relatively warm water in the vicinity of the Aleutian Islands.
4. Central Subarctic Domain, lying within the boundaries of the Western Subarctic, Transitional, Alaskan Stream, and Coastal domains: contains one cyclonic gyral, the Alaska Gyre; upper zone depth approximately 100 m except in Alaskan Gyre where it is approximately 75 m; salinity—32.4–32.8‰ in surface water and 33.2–33.4‰ near upper zone bottom.
5. Coastal Domain: marked variability of features from area to area because of local variations in runoff, heating and cooling, winds, tides, and advection; upwelling in many localities when the winds are suitable; the extent of this domain can be defined by the isohaline of 32.4‰ in the surface waters (at 10 m depth). In summer, when this surface lens of dilute water intrudes into the oceanic areas an overlap in the boundaries of this and other domains occurs.

Figure 78 shows the general surface current patterns which bear out closely the regional partition of the North Pacific area, as suggested by Dodimead et al., 1963. Yearly fluctuations in accordance with prevailing climatic conditions of course occur, but in general the current pattern is unchanged. Originating far to the westward, along the Asiatic Pacific coast, the warm Kuroshio current from the south meets the cold southward-moving Oyashio from the Bering Sea region and veers easterly across the Pacific as the "West Wind Drift." As this wide and slow-

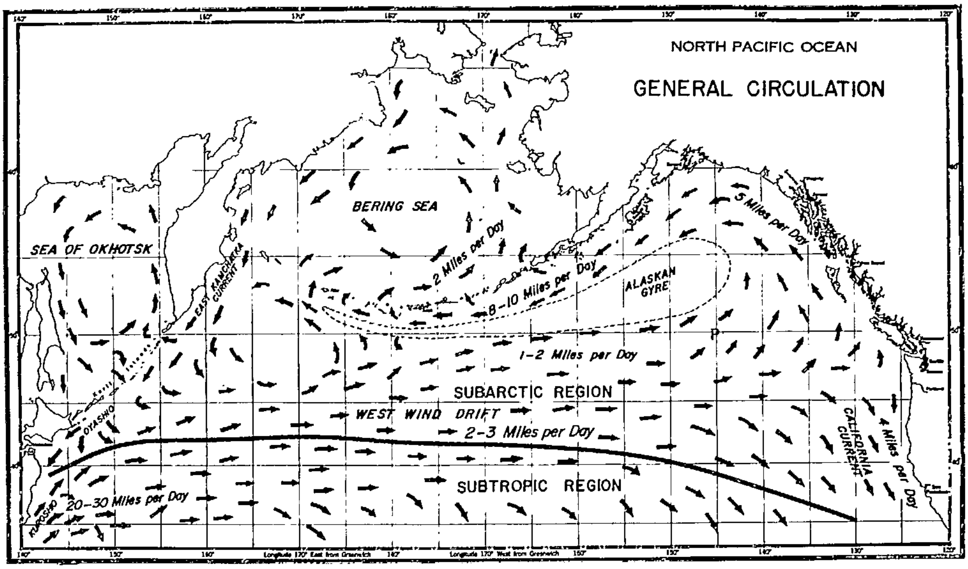

FIG. 78. General water circulation pattern, North Pacific Ocean. (From Dodimead, Favorite, and Hirano, 1963.)

moving current approaches the Pacific coast it divides (1) to northward proceeding along the British Columbia and southeast Alaska coasts into the Gulf of Alaska and (2) to the southward along the Pacific coast of the United States.

The North Pacific is the area of concern for Pacific salmon. The following characteristics of the region were brought to light by a synoptic survey made of the Pacific in 1955, under "Project Norpac," by 12 oceanographic agencies of Canada, United States, and Japan (Tully and Dodimead, 1956, p. 28).

> In summer a warm, homogeneous upper zone, 10 to 20 m in depth, is formed, with temperatures ranging from 10°C to 12°C (50°F to 54°F) and salinities low—less than 32.8‰ in the upper 60 to 100 m. This warm, low salinity stratum overlies the cold waters of the deep ocean whose temperature is very nearly constant, around 5°C, and salinity greater than 34‰.
>
> In winter the upper waters cool off appreciably, in the Gulf of Alaska decreasing to about 5°C (41°F), that is, close to those of the deeper ocean. Low salinities persist throughout the winter and 'unlike the temperature structure in these northern regions, is a permanent feature.' It is associated with the circulation of the water around the Gulf of Alaska and through the Bering Sea.

Analysis of data obtained from a weathership operating throughout the year at Ocean Station "P" (in the vicinity of 140°W 50°N) has shown (Dodimead, MS, 1960) that in the subarctic zone of the North Pacific the waters are virtually isothermal down to about 100 m at the end of the winter cooling period in late March. With the advent of the warmer weather in April a thermocline (a stratum with rapidly changing temperatures) is formed, above which lies a near isothermal layer which continues to warm up until the end of August and then cool off again (Fig.

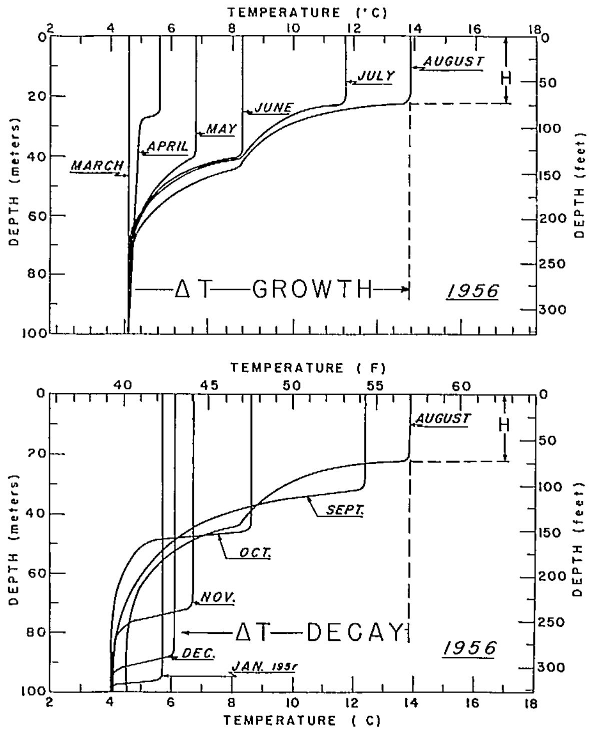

FIG. 79. Growth and decay of the thermocline at ocean station "P" (50°N lat, 145°W long). (From Dodimead, 1960, fig. 38.)

79). Below this there is the deep unwarmed body of water, maintaining the temperature and salinity characteristics of the previous winter structure.

On the western side of the Pacific much oceanographic work has also been done by Japanese and USSR scientists. That part of the western Pacific off the Commander Islands and east of Kamchatka has been given special attention (Burkov, 1960) because of its importance in salmon distribution. Burkov reports that:

> "on the basis of present understanding of the distribution of the water masses in the northwest Pacific, almost all of the Komandorsky-Kamchatka region lies within the limits of the so-called subarctic zone. Under the latter term is included all those more or less homogeneous water masses which have, vertically, a permanent pattern of conditions. In the present case the subarctic structure in the spring and summer season was made up of a surface water mass, cold and warm intermediate layers and a deepwater mass."

This subarctic zone in early spring extends south to around 40°N but with the approach of summer it shifts northeastward, close to the Aleutian Island chain. In Fig. 80 is shown the general temperature-salinity condition in such subarctic waters. Generally speaking, the cold intermediate stratum, indicated as occurring between 50 and 150 m, serves as the limit of vertical distribution. It is also of some sig-

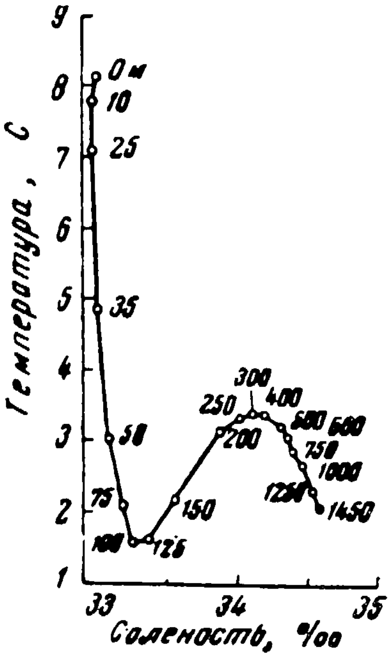

FIG. 80. A typical TS curve, characteristic of the subarctic structure in the Komandorsky-Kamchatka region. (From Burkov, 1960.)

nificance as perhaps influencing the abundance of salmon, since, as Burkov points out (1960, p. 170), at its southern boundary abundant supplies of plankton occur. These are thought to denote zones of divergence or upwelling of cold water, rich in essential nutrients. Similar conditions occur to the east, i.e., south of the Aleutian Islands, and to the southwest along the Kurile Island. Toward the northwest, however, i.e., toward the east Kamchatka coast, the biomass of zooplankton decreases.

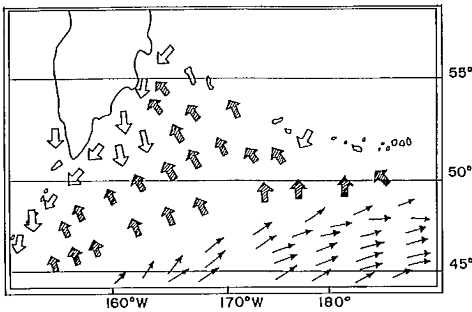

FIG. 81. A concept of the distribution and movement of water masses in the western North Pacific salmon area. Fine arrows—Kuroshio Current; broad, cross-hached arrows—Kuroshio Counter-current; broad, clear arrows—movement of cold water masses from Oyashio Current. (From Taguchi, 1955.)

Similarly Taguchi (1955) reports a broad northwestward water movement toward Kamchatka—a counter current of the Kuroshio flow—which in due course meets and mixes with the southwestward flowing cold Oyashio from the Bering Sea (Fig. 81). In the areas of mixing and divergence salmon are abundant. It is reported (Taguchi and Hirose, 1954) that the northwestward flowing current, the counter current, has, in the contact zone, a velocity of 0.5–1.0 mph while this westward-moving current south of the Aleutians has a speed of 2–4 mph.

HORIZONTAL DISTRIBUTION OF THE SOCKEYE

Where do Pacific salmon occur in the ocean? In what areas are they most abundant? What are the characteristics of the water (temperature, salinity, food constituents, etc.) in such areas? These topics have been the subject of intensive investigation over the last decade, participated in by the three nations of the International North Pacific Fisheries Commission—Canada, United States, and Japan—and independently by the USSR. A two-pronged attack has been made involving, on the one hand, oceanographic research to learn more about the North Pacific and its characteristic features in general and, on the other, extensive fishing operations to determine whether salmon are present, in what abundance, at what age, and under what environmental conditions.

Prior to 1955 fishing experience had already indicated (Tully and Dodimead, 1956, p. 32) that "salmon occur in all the coastal waters which have the same temperatures and salinity characteristics as the sub-Arctic waters in the Gulf of Alaska." They are found to tolerate, in the coastal areas, surface temperatures of from less than 5 C up to 20 C (41–68 F) and low salinities. Exploratory fishing operations since 1955 have served to confirm that, throughout the North Pacific, sockeye salmon are widely distributed across the whole ocean between 46 and 60°N lat., the main concentrations of them varying from year to year and throughout the summer season. No winter observations have yet been made. Catch records show that the fish, then in the spring of their 2nd year at sea, are first encountered in the more southerly regions of the subarctic zone and then presumably move northward and toward the coast, throughout the Gulf of Alaska, along the Aleutian Islands and off eastern Kamchatka (Margolis et al, 1966). Large numbers have been found moving to the westward along the south side of the Aleutian chain. By May of the third summer at sea many are again taken in the southern sections of their range, south of Kamchatka, south of the Aleutians and in the Gulf of Alaska, the maturing individuals subsequently moving northward separately and ahead of the immatures.

In the waters south of the Aleutian Islands chain a situation of considerable interest has been found (INPFC Annual Report for 1959, p. 89–90) in a region where upwelling of deep ocean water serves to bring vital nutrient substances to the surface stratum for intensive plankton production. North of this upwelling area lies the Aleutian Current flowing westward; south of it lies the eastward flowing extension of the Oyashio Current (Fig. 78).

Exploratory fishing in the area has revealed that immediately north and south of the northern edge of the eastward flowing current (set at 49°30′N) the catches of sockeye (and of chum salmon, too) at 49 and 50°N are notably less than at 48 and 51°N and even more striking is the difference in size, as indicated by length of the fish north and south of the 49°30′N division. As noted in fig. 23 and 24 of the INPFC Report for 1959 (p. 91) the catch records were as follows:

Lat (N)	52°	51°	50°	49°	48°
Along median 175°E					
No. of sockeye	25	40	17	28	35
Fork length (*cm*)	55.8	55.7	55.3	51.4	49.8
Along median 180°					
No. of sockeye	–	108	23	19	–
Fork length (*cm*)	–	54.8	55.0	44.6	–

These differences between the sockeye of the two regions, one with westward flowing water (north) and the other with eastward flow (south), suggest that, if subsequent analysis reveals these stocks of sockeye to be different, "the absence of any major difference in salinity or temperature values at the surface implies that the direction of the current or the identity of other constituents in the water, or both, may be important factors in the distribution of salmon in the region in early spring" (INPFC Annual Report for 1959, p. 90).

For western North Pacific regions the distribution has been generally outlined by Birman (1960). During the winter the salmon are congregated south of the Aleutians and east of the Kamchatka-Kurile Island coast, the various species having specific temperature limits, indicated (Birman, 1960, p. 157) as "sockeye—from 1.5° to 6°C, chums—from 1.5° to 10°C, pinks—from 3.5° to 8.5°C, coho—from 5.5° to 9°C." The sockeye appear to favour the coldest water. With the coming of spring, as the surface waters warm up, the whole mass of salmon shifts northward to the summer feeding areas and as the waters continue to warm up the distribution becomes wider and wider.

In August and September, at the time of maximum warming of the waters, the southern boundary of dispersion of the feeding sockeye is the surface isotherm of 12 C, while that for chums is 13.5–14 C. The position of this southern boundary shifts from year to year in accordance with the action of the Kurosio Current. In the zone of convergence of moderately cool and sub-tropical waters, where a surface temperature of 15–17 C was observed, no feeding salmon occurred. "In short," as Birman (1960, p. 158) summarizes it, "the salmon carried out in the sea, within the limits of the above-mentioned isotherms, seasonal migrations of approximately the same character as found among sardines, scombrids, anchovies and a number of other pelagic-feeding species in the Pacific. During spring and summer they occur in the north, extending into the northern regions of the Bering Sea and Okhotsk Sea but, with the approach of autumn and winter cooling, the fish which do not mature that season proceed back southward."

Early in August immature sockeye are concentrated in large numbers directly off the southeast coast of Kamchatka, the northern half of the Kurile Islands, and south of the Aleutian chain. At this time many of the maturing fish have moved shoreward and the proportions of immature fish in the catches increase. In August around 50% of the sockeye caught were immature.

DEPTH DISTRIBUTION OF THE SOCKEYE

The standard gear for exploratory fishing and in the Japanese deepsea fishery is a floating gill net of 20-ft (6.1-m) depth, so their catch records pertain to this surface stratum. But are the sockeye necessarily confined to this layer? May they not have a deeper distribution?

To provide information on this point, tests were conducted in 1957, 1959, and 1960 (INPFC, MS, 1958, p. 25; INPFC, MS, 1959, p. 35; Neave, 1960; Manzer, 1964). A 4.5-inch mesh nylon gill net, 40 ft (12.2 m) deep, was used, suspended from buoys by droplines of different length, so it could be set at any one of 5 depths down to 200 ft (61 m). Initial tests in 1957 in the southern part of the Gulf of Alaska indicated the presence of sockeye at depth, both in a 20–60 and a 40–80 ft stratum (6–18 and 12–24 m), though much less abundant there than near the surface (0–20 ft).

The 1959 test, made with nylon gill net of 4.5-inches stretched mesh, 400 fath (732 m) long and 40 ft (12.2 m) deep, was carried out at three stations, one located at or near 50°N, 135°W, one at 55°N, 150°W, and one intermediate between these two. These fishing stations had been selected because they represented three general areas where the temperature regimes and salmon abundance, at least in surface waters, varied markedly through the season. The sockeye catches are shown in Table 93.

TABLE 93. Relative numbers of sockeye, pink, and chum salmon caught in the Gulf of Alaska in 1959 at various depth intervals to 200 ft (61 m). Data are based on sunken gill-net catches at night, adjusted to 400 fath of gear per night (from INPFC Annual Rept. for 1959, p. 35).

Date	No. of sets	Depth interval (*ft*)	Sockeye		Pink		Chum	
			Avg catch	Per cent	Avg catch	Per cent	Avg catch	Per cent
May–June	3	0–40	8.7	68.4	1.3	30.3	0.7	10.1
	3	40–80	2.0	15.8	2.7	62.6	1.0	14.5
	3	80–120	1.0	7.9	1.3	7.1	1.7	24.6
	2	120–160	0.0	0.0	0.0	0.0	1.5	21.8
	1	160–200	1.0	7.9	0.0	0.0	2.0	29.0
Total:			12.7	100.0	4.3	100.0	6.9	100.0
July–Aug.	3	0–40	8.3	100.0	9.6	100.0	11.4	79.0
	3	40–80	0.0	0.0	0.0	0.0	3.0	21.0
	3	80–120	0.0	0.0	0.0	0.0	0.0	0.0
	2	120–160	0.0	0.0	0.0	0.0	0.0	0.0
	2	160–200	0.0	0.0	0.0	0.0	0.0	0.0
Total:			8.3	100.0	9.6	100.0	14.4	100.0

Again sockeye were captured at depth, i.e., below 20 ft (6.1 m), at least in the early part of the season, although not to the same extent as chum salmon. Bearing in mind the fact that gill nets are quite selective in the sizes of fish that are caught in them, any catch records are of limited value. They do, in this instance,

TABLE 94. Sockeye salmon catches at 55°N lat, 152°W long. in the northeast Pacific Ocean made by gill nets of 4.5 inches stretched mesh in 1960 (from Neave, 1960, table 1).

Date (1960)	Fishing time (*hr*)	Surface net		Deep net		
		Net length (*fath*)	No. of sockeye	Depth of net (*ft*)	Net length (*fath*)	No. of sockeye
Day sets						
May 17[a]	6.25	300	19	0–40	400	10
18[a]	5.00	300	4	40–80	400	3
19[a]	5.75	300	6	—Net lost—		
June 2	6.00	300	94	80–120	200	76
4	9.00	300	19	120–160	200	24
5	6.00	250	10	160–200	200	9
6	7.50	—Not set—		0–40	200	5
7	6.00	250	4	40–80	200	12
22	8.00	250	3	160–200	200	0
23	6.00	—Not set—		0–40	200	4
24	8.50	250	8	40–80	200	25
July 1	6.50	250	8	80–120	200	1
2	6.50	250	8	120–160	200	0
4	7.00	250	2	160–200	200	0
Total:			185			169
Night sets						
May 18[a]	11.00	300	14	0–40	400	15
19[a]	9.00	300	13	40–80	400	2
June 3	8.50	300	54	50–120	200	38
4	9.00	300	52	120–160	200	1
5	9.00	250	29	160–200	200	0
6	11.00	—Not set—		0–40	200	5
7	9.50	280	19	40–80	200	4
8	8.50	280	19	80–120	200	4
10	10.50	280	10	120–160	200	5
23	9.00	280	4	160–200	200	0
24	9.00	—Not set—		0–40	200	11
July 1	9.50	250	21	40–80	200	15
2	11.00	250	29	50–120	200	0
4	9.00	250	17	120–160	200	0
5	7.50	250	23	160–200	200	0
13	10.50	300	8	0–40[b]	200	8
Total:			312			108

[a] Position: 55°N lat, 155°W long.

[b] Mesh (3.25-inch) used (depth net only).

indicate, though, that catchable sockeye were present at depths down to 200 ft (61 m) in May and June, but in July and August they appeared to be limited to the upper 40 ft (12.2 m).

In 1960, a third test of vertical distribution was made, again in the Gulf of Alaska in an area 100–130 miles south of Kodiak Island, using the same type of gear as before. At the same time a conventional surface net was set, of 4.5-inch mesh, but only 20 ft (6.1 m) deep. Net sets were made both during the day and at night. The results, presented in Table 94, show (Neave, 1960) that during the early part of the season the sockeye occurred at all depths sampled, i.e., down to 200 ft (61 m). As Neave expresses it: "only a small fraction of the sockeye population was available to surface gill nets fishing by day at this time of year." Night sets during early summer indicated some upward movement (a diurnal shift) since no fish were taken in the lowest stratum fished and greater numbers were caught above 80 ft (24.4 m). In the later test fishing (June 22 to July 5) only one sockeye was caught below 80 ft (24.4 m) with again an indicated shift surfaceward by some of the fish at night.

By way of general summary of the vertical distribution data, Neave, (1960, p. 4) remarks that:

> "the results reported here bear considerable resemblance to findings reported by Japanese observers who experimented with echosounders on salmon fishing grounds in the western North Pacific (Hashimoto and Maniwa, 1956, 1959). They reported the presence of fish schools during the daytime in mid-July at depths of 20 to 40 metres, in close association with the scattering layer and with the thermocline. At night, some fish rose to the surface but others remained at the same level as in the daytime. The greatest depth at which fish schools were recorded was 60 metres—i.e., equivalent to the deepest fishing of the *Fort Ross*. The species involved in these Japanese observations could only be inferred from surface catches, which included sockeye, chum, pink and coho salmon."

The chief purpose in presenting this detailed information concerning the vertical distribution of sockeye is to bring out the possibility that operation of surface nets, as in commercial high-seas fishing and exploratory fishing studies, need not necessarily adequately nor accurately indicate the abundance nor general ocean dispersion of the fish, even of those sizes or ages which may be caught in the gill nets. The younger and smaller age-classes may well be below the depth ranges of surface-set gill nets (i.e., below 6–10 m). As Neave (1960, p. 4) further intimates "an obvious fact that emerges from the *Fort Ross* observations is that a majority of the sockeyes and chums caught (by day and by night and throughout the fishing season) were at levels below the reach of standard floating gill nets."

RATE OF TRAVEL OF SOCKEYE IN THE OCEAN

As determined by tagging and recovery of sockeye, information on the probable average rate of travel is available. For Bristol Bay sockeye such rates varied from 15 to 50 miles/day (Hartt, 1962, p. 57) with 30 miles/day given as "probably a fair average rate for mature red salmon during the last 40 days at sea." For sockeye on the Asiatic coast of the Pacific, a rate of 14 miles (12.3–12.5 naut. miles) was indicated. According to Sato (1938) it took about 40 days for the first school which contributes to the peak fishing in the Cape Kronotsk area to reach the Ozernaya River on the west coast of the Kamchatka Peninsula, some 500 naut. miles distant. This figure corresponded closely to a rate of 12.3 naut. miles obtained by data from previous tagging experiments.

Naturally any estimation of rate of travel obtained from tag recovery records must take into consideration a number of features. Calculations are based on the direct, shortest distance between the point of tagging and that of recovery and assume a continuous travel in the indicated direction. No account is taken of the direction and speed of flow of the ocean water.

Experiments conducted in an "exercising cage" (FRBC, 1961, p. 100–101) have indicated that "sockeye, averaging 21 inches total length, were able to swim at 2.5 ft per second [0.64m/sec] for at least 100 hours without rest of any sort. The threshold appears to be about 2.9 feet per second [0.88 m/sec] for uninjured or uninfected fish above which fatigue sets in rapidly." In one experiment three sockeye swam 235 miles during 6.2 days, at an average rate of 2.3 ft/sec (1.6 miles/hr, 0.70 m/sec). At this speed "the fish could recover from the stress of short periods of greater activity, occasioned by aggressive contests for territory within the cage."

The experimental rate of travel—38 miles/day—is close to the 30 mile/day average suggested by Hartt above. It corresponds closely, also, to the rate indicated by tagged sockeye recoveries made in 1961 and 1962 in Canadian taggings in the eastern North Pacific, according to Dr Ferris Neave (personal communication), for reasonably long ocean migrations. It might be considered, then, a good approximation of the rate of migratory travel of adult sockeye on pre-spawning migration in the ocean.

THE FOOD OF SALMON IN THE NORTH PACIFIC

EXAMINATION OF THE STOMACH CONTENTS OF SOCKEYE

It would seem only natural that the young sockeye, upon reaching their new marine habitat, should seek out the same type of food as that upon which they had subsisted during lake residence. This assumption was confirmed as long ago as 1908 (Chamberlain, 1907, p. 50–52), when the stomach contents of young sockeye captured in the coastal waters off Alert Bay in 1895, and off Alaska, 1894 and 1903, were found to contain pelagic copepods, amphipods, ostracods, crab larvae, and the like.*

More recent studies have substantiated and added to these findings. In stomachs of 98 young sockeye caught in coastal waters (see p. 328), the food was found to consist primarily of copepod crustaceans, with larvaceans (pelagic Tunicata–

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* An excellent reference, written in quite popular and exciting fashion, is "The open sea—its natural history: The world of plankton" by Sir Alister Hardy, 1958, 335 p., published by Collins, 14 St. James Place, London. It is profusely illustrated with figures and coloured plates of many of the ocean's plankton forms.

Oikopleura) ranking second (Manzer, MS, 1956b). Organisms of minor importance in these specimens were gastropods, ostracods, cirripedes, cumaceans, amphipods, euphausiids, decapods, and insects. In the Skeena River estuary, however, fish larvae, principally herring, were noted in some sockeye stomachs, thus indicating that the young sockeyes can be piscivorous to some degree. In Kamchatka waters (Avacha Gulf, through which the young sockeye from Lake Dalnee and other adjacent areas must pass) the chief food item in 100 stomachs examined was a marine cladoceran, *Podon*, but a number of other pelagic crustaceans also occurred, as well as small fish fry (Synkova, 1951).

All the evidence, admittedly limited in amount and geographical representation, indicates that pelagic plankton organisms constitute the main food of young sockeye during early life in the sea. There are suggestions that the young fish incline to be selective and favour certain organisms but the chances seem to vary according to size of fish and area inhabited at the time of capture. The food spectrum appears to be a relatively wide one. If the favoured food item is lacking, substitute organisms will be consumed. Yet the fact cannot be ignored that, in the early days of sea life, the quality and amount of food organisms available to the young fish may be highly critical and significant and the lack of suitable and favoured food organisms may lead to starvation and death. Thus, as in lakes when the fry first enter them, the synchronization of abundance of the right food items with the arrival of the young fish may be highly significant for the well-being of the young fish.

Sockeye in their 3rd year in Avacha Gulf were subsisting on essentially the same food as the adults (Synkova, 1951, p. 110). The contents of 15 stomachs indicated that with respect to frequency of occurrence and weight per stomach, the main food items were the euphausiid *Thysanoessa* and the hyperiid amphipod *Themisto*, although copepods (*Calanus tonsus, C. cristatus, Pseudocalanus sp.*) and crab larvae were also present in varying abundance. In a few cases, young fish made up a goodly share of the food. Squids occurred in 20% of the stomachs but made up only 0.5% in weight.

Adult sockeye during the summer in coastal areas had consumed mostly large plankton crustaceans, chiefly euphausiids (*Thysanoessa*), hyperiid amphipods (*Themisto*), and copepods (*Eucalanus elongatus, Calanus tonsus*, and *Metridia* sp.). In certain areas crab larvae were freely taken as well as squid and young fish.

On the high seas, during the summer season, pelagic crustaceans were overwhelmingly the favoured food, but there was considerable variation in area and stage of development or state of maturity. The findings from examination of 150 stomachs reported by Andrievskaya (1957) are summarized in Table 95 to show how feeding may fluctuate.

It was found that in the high-seas areas—Aleutians, Central, Commander—all the fish examined had eaten well; the stomachs were full. Empty stomachs were encountered only in the coastal areas. Andrievskaya (1957, p. 73) remarks that

> "the extent of the feeding of the fish at different stages of migration proved to vary markedly, being much lower in coastal areas than in regions more distant from Kamchatka. This decrease in feeding as they approach the coast seems to be the result not only of the scarcity of the larger plankton organisms in coastal water but also of the great concentration of salmon there.

No significant differences in extent of feeding had been noted among salmon in different stages of maturity when such fish were taken from the same area."

This suggested that "the extent of feeding during the foraging period is greater than during the spawning migration period because in the most distant regions the food supplies are more abundant."

TABLE 95. Stomach contents of sockeye taken on the high seas. The percentages represent the proportion of each organism in the total mass of food (from Andrievskaya, 1957).

Aleutian Islands region (south of Attu Island):
Copepods, 53%; euphausiids, 12%; hyperiid amphipods, 12%; pteropods, 12%; young fish, 11%.

Central region (central part of the triangle bounded by Cape Kamchatka, Attu Island, and Paramushu Strait):
Euphausiids, 42%; hyperiid amphipods, 34%; copepods, 11%; young fish, 9%; pteropods, 4%.

Commander Islands area:
Euphausiids, 60%; young fish, 28%; copepods, 13%; also young squids, crab larvae, pteropods, and insects.

Kamchatka Gulf:
Hyperiid amphipods, 55%; medusae, 29%; also small quantities of pteropods and euphausiids.

North Kurile Islands (off east coast of Shumshu and Paramushu islands):
Young fish (Alaska pollock), 31%; Larvacea (*Oikopleura* sp.), 22%; euphausiids and hyperiids, 18%; also small quantities of pteropods and copepods.

To emphasize the importance of plankton as a staple food and the extent to which it can be cropped by feeding fish, data for chum salmon, reported by Birman (1960, p. 161–162), may be cited (Table 96). In the second half of May, 1956, the biomass of the copepod *Calanus cristatus*, 100 miles off the Kamchatka coast,

TABLE 96. Stomach contents of chum salmon off Kamchatka. Data are from Birman (1960, p. 161), after Andrievskaya (1956).

	May–June		August	
Food component	No. of specimens	Per cent volume	No. of specimens	Per cent volume
Fish and fish larvae	4	2.05	4	52.38
Pteropods	2	17.03	1	5.95
Euphausiids	1	60.04	1	0.45
Hyperiid amphipods	4	9.27	4	6.16
Copepods	1	2.22	3	0.51
Squid	2	1.83	2	7.91
Polychaete worms	0	0	1	25.93
Miscellaneous	8	7.56	3	0.71
Index of stomach fullness (ppm)	35.7		17.0	

TABLE 97. Approximate frequency of occurrence (i.e., percentage of stomachs in which found) of food organisms in the stomachs of sockeye salmon containing identifiable remains, from the 1955 Japanese high seas fishery (from Allen, 1956a, p. 22).

Region[a]	Area	Date	No. of stomachs	Food organisms found in stomachs							
				Copepods	Euphausiids	Amphipods	Pteropods	Fish	Squids	Crustacean larvae	Shrimps
A	1	June 30	4	–	25	50	50	–	–	–	–
	2	July 10	13	–	–	70	–	–	10	85	–
	3	July 20	1	–	–	–	–	–	–	100	–
	4	July 20	2	–	–	–	–	–	–	100	–
	5	Aug. 10	14	–	15	95	–	10	15	15	–
	6	July 30	18	–	5	100	–	–	–	–	–
	7	June 30	7	–	15	45	15	–	30	45	15
B	8	July 27	20	20	10	100	15	–	15	–	–
	9	July 30	13	10	10	100	–	30	–	–	–
	10	July 14	10	–	–	100	10	–	–	10	–
	11	July 27	15	5	35	100	5	5	25	5	–
	12	Aug. 10	19	5	25	95	5	–	–	5	–
	13	July 13	9	–	10	100	35	–	–	–	–
C	14	June 1	10	100	80	60	–	–	10	–	10
	15	June 22	11	90	90	50	30	50	10	–	–
	16	June 1	10	50	70	20	10	10	–	–	–
	17	June 1	10	50	90	50	30	20	–	–	–
	18	June 22	20	70	75	15	45	15	–	–	–
	19	May 18	16	75	50	20	–	5	5	–	–
	20	May 18	17	70	55	20	35	45	–	–	–

[a] Region A—Okhotsk Sea off the west coast of Kamchatka. Areas 1 to 7.
Region B—North Pacific Ocean off the east coast of Kamchatka between 49.5°N and 53.5°N. Areas 8 to 13.
Region C—North Pacific Ocean from 165°E to 175°E and 48°N and 50°N. Areas 14 to 20.

was 100–110 mg/m^3, but by early September it had decreased to 8–10 mg/m^3, or about 90%. Studies conducted in 1957 off the Kamchatka coast south of Petropavlovsk revealed a reduction in *Calanus* biomass from 10,650 mg/m^3 in July to 3,160 mg/m^3 in September. It is conservatively estimated that for three species of copepods the overall decrease, June–September, amounted to around 24.2 metric tons/km^2 or 69 short tons/square mile. Similar data for consumption of other plankters were not available but it was found that, in the food of chum salmon, euphausiids dropped from 60% in May–June to but 0.45% in August. This drop in euphausiids had to be made up by an increase in diet-representation of fish and fish larvae, from 2 to 52% and of polychaete worms, from 0 to 26%. In fact, the whole change in the diet of the chums in these two periods is of interest, as shown in Table 96.

These findings show not only the change in diet between the May–June and August periods of feeding but also the decrease in food consumed, approximately 50%. This may be further evidence of an observation made by LeBrasseur (MS, 1959) that the feeding of salmon upon dense aggregations of food, i.e., on concentrations of plankton forms, must be much more advantageous than feeding upon the same density of food spread evenly over the same feeding area. It is much more common to have crustacean plankton develop in dense aggregations than fish or even squid.

From the Japanese high-seas fishery in 1955, the stomachs of 312 sockeye were available for study (Allen, 1956a). The results of examination are shown in Table 97 according to general area and date. Fishing began early in the season in Region C, south of the western tip of the Aleutian chain, and moved westward as the season progressed. In this region copepods and euphausiids were in greatest abundance, followed by amphipods. In Region B, further west and during July, amphipods, principally hyperiids, were the principal food item; in Region A, the Okhotsk Sea, the amphipods shared importance with other larval crustaceans, largely crab larvae.

Pteropods, fish (chiefly myctophids or lantern fish), and squid occurred frequently in all regions but were of minor importance by volume. The extent of feeding may perhaps be indicated by the volume of the stomach contents:

Region (See Table 97)	Per cent empty stomachs	Vol of stomach contents (*ml*)		
		Avg for all stomachs	Avg for stomachs with food	Max for a single stomach
A	49	6.1	12.8	25.0
B	27	15.9	19.5	54.0
C	13	16.2	18.2	100.0

Subsequent study (Allen, 1956b) of stomachs of sockeye from the Egegik, Copper, and Chignik rivers, Alaska, has shown that these fish had subsisted largely, also, on euphausiids. Gammarid amphipods, pteropods, fish, and squid were noted but were of minor importance. In 16 samples from the Gulf of Alaska, amphipods, crab larvae, fish, and squid were most abundant, pteropods and euphausiids being present in minor amounts.

For the northeastern Pacific off the British Columbia coast and in the Gulf of Alaska data are available from an examination of the stomach contents of 581 sockeye caught by two exploratory fishing vessels during May and June, 1958 (LeBrasseur, MS, 1959). The fishing stations occupied, the relative extent of feeding (food index, i.e., the quantity of food in the stomach expressed as a percentage of the fish weight and indicated by the diameter of the circles), and the major food constituents are shown in Fig. 82.

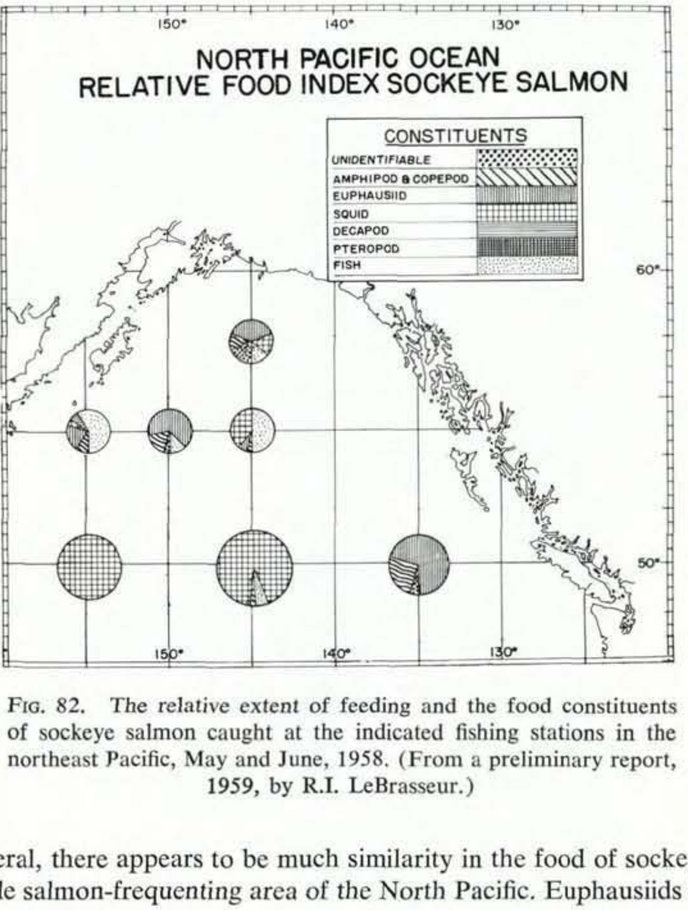

FIG. 82. The relative extent of feeding and the food constituents of sockeye salmon caught at the indicated fishing stations in the northeast Pacific, May and June, 1958. (From a preliminary report, 1959, by R.I. LeBrasseur.)

In general, there appears to be much similarity in the food of sockeye throughout the whole salmon-frequenting area of the North Pacific. Euphausiids and amphipods are a staple item of the diet although they make up varying proportions of the ration according to the region of capture. The great preponderance of squids in the diet in the northeastern Pacific and of fish (smelts and myctophids) in the Gulf of Alaska are rather striking features, but how general this is from year to year remains for further investigation to reveal. As LeBrasseur remarks: "If food is to be considered limiting in terms of survival on production of salmon, it may be most apparent further up the food chain, among fish and squid." Squids occupied a major role at two stations in the eastern Pacific. It will be interesting to determine the significance of squids in other years for which there are comparable data. Their absence may mean lower food indices; it certainly would if they were omitted from the 1958 observations or, more likely, it may bring about an alteration in the composition of the food and perhaps a slightly lower mean food index. The fish forming the bulk of the food index at coastal stations were, as might be expected, largely neritic forms. As such, their appearance at any offshore position undoubtedly varies annually, in turn affecting the food index at what seems to be a crucial growing period for salmon.

PLANKTON STUDIES IN THE NORTH PACIFIC

Since sockeye salmon throughout their period of ocean residence feed so heavily on various pelagic plankton forms, euphausiids, hyperiid amphipods, copepoda, clodocera, pteropods, Larvacea, and even squids, if these can be considered as plankton,* the distribution and abundance of the plankton in the ocean should be an integral part of any oceanographic study which is related to salmon in the sea. They have been given consideration in the International North Pacific Fisheries Commission studies but unfortunately not to the same extent as phases of physical oceanography. They have received considerable attention by USSR oceanographers, especially in the western Pacific.

While it would seem quite appropriate to refer briefly to the plankton studies thus far undertaken in the north Pacific, three facts must be kept in mind.

Firstly, the percentage composition of the plankton forms in the stomachs of salmon differs appreciably from the percentage occurrence in the plankton collected by plankton nets. In other words, the standard plankton nets do not adequately capture the larger plankters, the euphausiids and amphipods, etc., which are of prime concern to the feeding salmon. Several investigators have pointed this out (Allen, 1956c; Nakai and Honjo, 1954).

Secondly, in the use of standard plantkon nets, the significance of the catches depends primarily on the size of the mesh used and the purpose for which the plankton samples are taken. Thus, for example, with reference to collections made by the USSR oceanographic vessel *Vitiaz* in the Gulf of Alaska in 1958–59, comparison of results with those made earlier by Canadian investigators must take into account the fact that the latter used much coarser nylon gauze netting. The Canadian nets (termed a "standard Pacific Ocean net" of a mesh close to the USSR fine-meshed No. 150) seldom caught phytoplankton. Thus, in areas where phytoplankton "blooms" occurred, the Canadian plankton catches would indicate low plankton abundance whereas the USSR data would indicate very rich plankton crops. As the USSR investigators explain it (Beklemishev and Lubny-Gertsyk, 1959, p. 1271), "the principal difference between both types of charts (i.e., USSR and Canadian) is that in those areas where we found a biomass greater than 500 mg/m^3, the Canadians

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* Squids are dealt with by Hardy in his treatise on "The open sea—its natural history: The world of plankton" referred to in the footnote on p. 340.

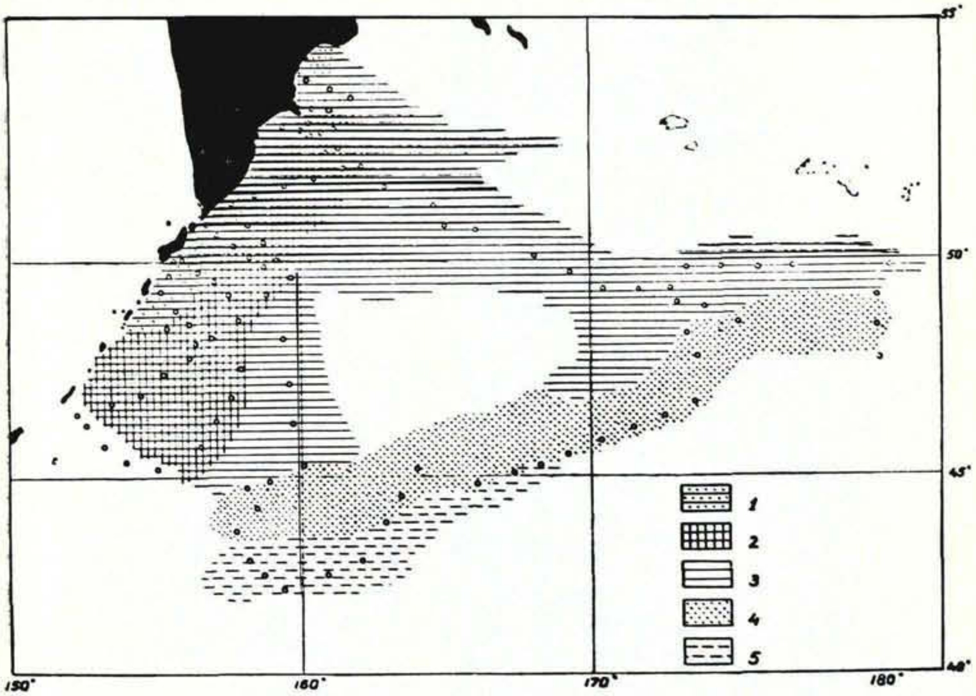

FIG. 83. Distribution of plankton complexes (August–September, 1956), western North Pacific: 1. intermediate-cold-water plankton with a mixture of neritic species; 2. plankton front of Oyashio; 3. intermediate-cold-water plankton; 4. plankton of the transition zone—"zone of mixing"; 5. warm-water plankton. (From Mednikov, 1958, fig. 1.)

reported less than 10 mg/m^3; one chart might be taken as representing exactly the opposite of the other." Or, as pointed out by Mednikov (1958, p. 76), "since collecting was done with small mesh nets, we have reliable data on the quantitative distribution only of the mesoplankton forms. Data on the distribution of the macroplankton—the hyperiid amphipods and euphausiids—is much less reliable. . . . In August–September, 1956, in order to catch the macroplankton, we were obliged occasionally to use a small-sized Peterson trawl."

Thirdly, because of the well-known tendency for most plankton Crustacea, as well as other forms, to migrate upward at night into the surface stratum, the time of day at which plankton samples are collected may affect very materially both the qualitative nature of the sample as well as the abundance of the various species. For example, Mednikov (1958, p. 85) notes that, in the stomachs of salmon, presumably feeding at or near the surface, the most important food form is the gammarid amphipod *Paracallisoma alkerta*, the upper limit of whose daytime distribution is 1000 m. The gammarid *Cyphocaris challengeri*, however, present in plankton samples down to 100 m, has not been found in salmon stomachs. The point at issue is that the time of plankton collection is exceedingly important if the plankton samples are to be considered as revealing the distribution and abundance of plankton

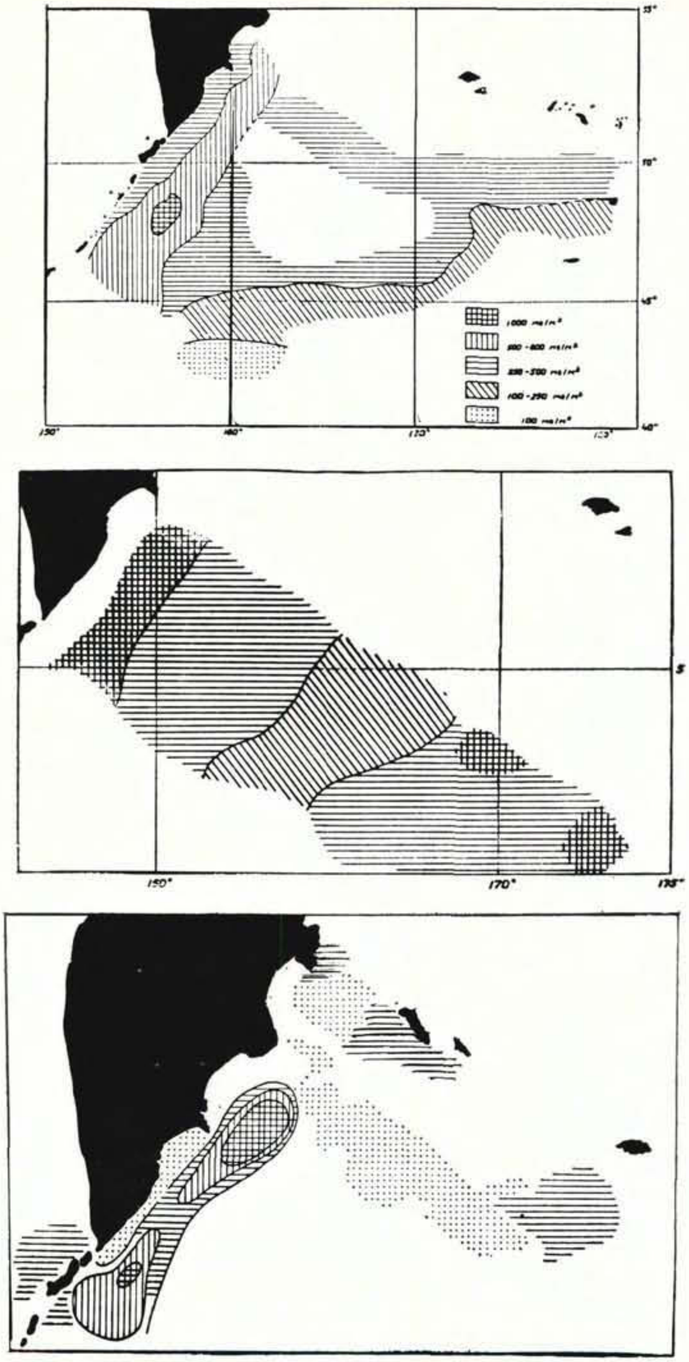

FIG. 84. Plankton biomass in the 50–0 m stratum of the western North Pacific: *top*—in August–September, 1956; *middle*—in May–June, 1956; *bottom*—in June–July, 1955. (From Mednikov, 1958, figs. 3, 4, 5.)

forms available to the salmon as food. So often the time of collection is not given and in many cases the tows are made during the day. The intensity of light during the day is likewise a factor.

Bearing these limitations in mind, the following data on plankton in the North Pacific may be briefly presented.

In Fig. 83 and 84 are shown charts of plankton distribution and abundance in the northwest Pacific (Mednikov, 1958) during the summers of 1955 and 1956. Along the coast and over the continental shelf the plankton supply in the surface stratum, 0–50 m, is limited (not greater than 500 mg/m^3) whereas immediately offshore, over the Kurile-Kamchatka Trench, it is appreciably richer—up to 1000 mg/m^3. Further out in the ocean plankton abundance decreases. Mednikov remarks (p. 78) that "the phenomenon of an increase in the biomass with distance from the coast and then a decrease has been noted by all investigators studying plankton in each area. They correctly associate this phenomenon with the vertical circulation features of the water in this region." It does not follow, however, that because the surface water plankton of warm-water areas is lower in quantity than that of colder water it is necessarily less in overall biomass. It may be merely a matter of some species sinking to lower strata. Furthermore, in warmer water the plankters may have a faster rate of development, a more rapid turnover.

During a cruise of the USSR oceanographic vessel *Vitiaz* in the northeast Pacific in 1958–59, plankton sampling showed a distribution and abundance as indicated in Fig. 85 (Beklemishev and Lubny-Gertsyk, 1959). The plankton samples were taken with standard Juday nets which catch both phytoplankton and zoo-

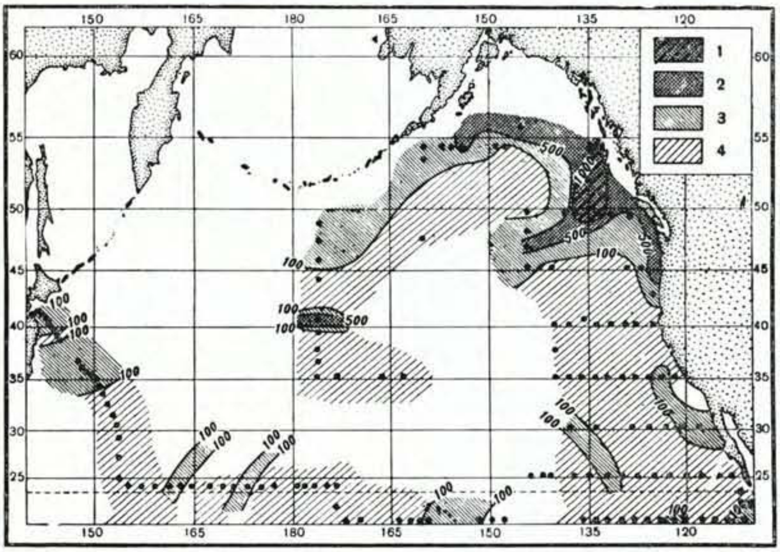

FIG. 85. Weight of wet seston in the northwest Pacific in 1958–59 in the 0–100 m stratum (mg/m^3). 1 = > 1000; 2 = 1000–500; 3 = 500–100; 4 = < 100 mg/m^3. Dots indicate stations where quantitative catches were made. (From Baklemishev and Lubny-Gertsyk, 1959, p. 1272.)

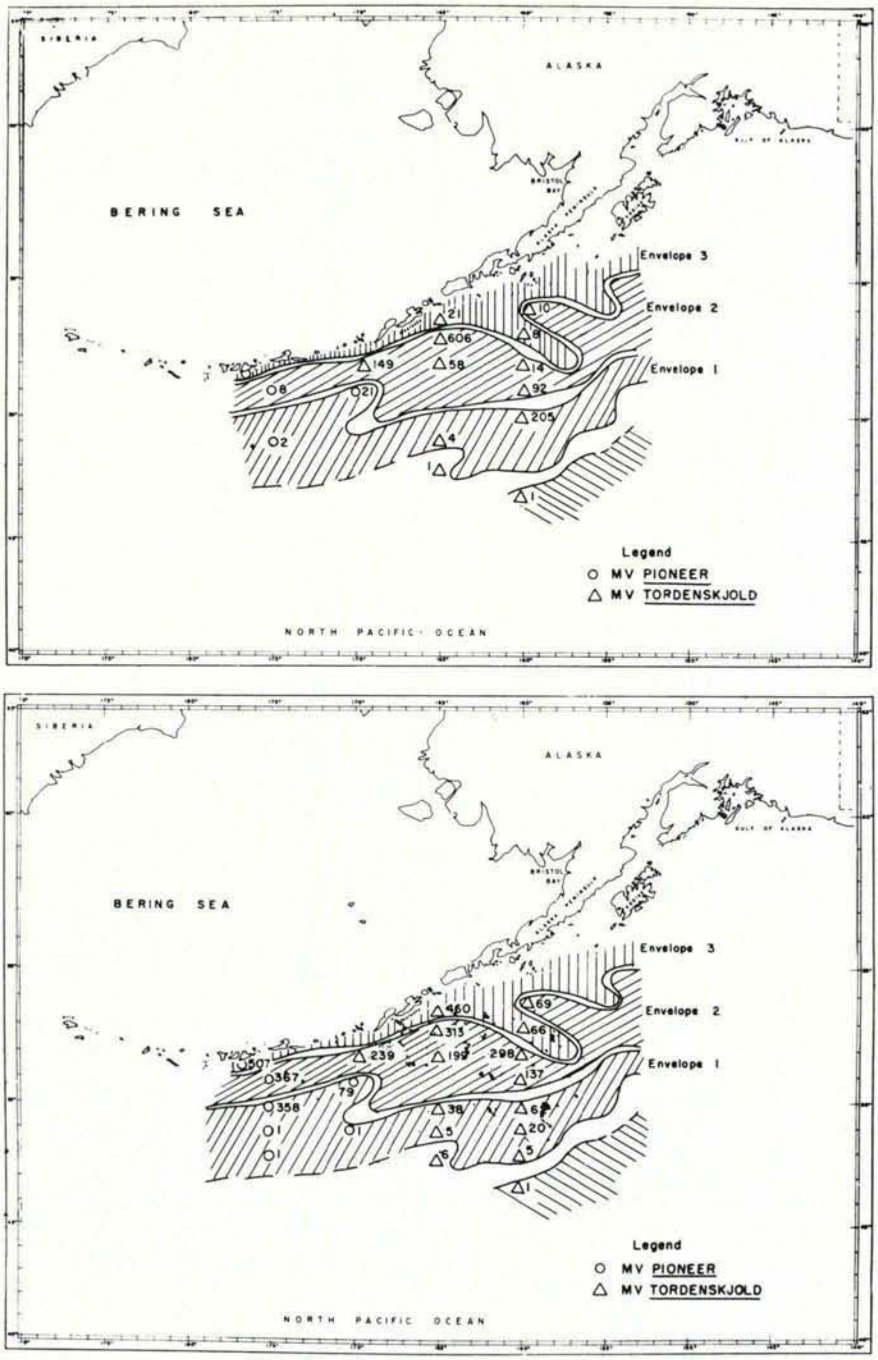

FIG. 86. The plankton catches, in wet weight in grams, of night-surface trawls of 15 min duration in August, 1959 (*bottom*), made south of the Aleutian Islands and the number of sockeye salmon caught in gill nets in the same period (*top*). (Data from INPFC Annual Report for 1960, 1961, p. 87.)

plankters. It is reported that an Isaacs-Kidd pelagic trawl and a fine-meshed surface trawl were also used but to what extent their catches contribute to the plankton picture as presented is not clear. It is indicated that the richest region, with a biomass of over 500 mg/m^3, occupied a wide band along the coast of Canada and in the Gulf of Alaska and was due to a great, active blooming of phytoplankton. Only in the vicinity of the Queen Charlotte Islands was the increase in biomass made up of zooplankton.

Data obtained for waters south of the Aleutian Islands (INPFC Annual Report for 1960, p. 84) are of interest. Isaacs-Kidd trawls were used; these sample principally the larger plankters. Collections were made after dark at a speed of 6 knots (11 km) for 15 min. The plankton catches, expressed as grams of wet weight, together with sockeye catches in the same regions, are shown in Fig. 86. Three areas are distinguished: coastal, westward-flowing water in Envelope 3; Oyashio, eastward-flowing water in Envelope 1; and in Envelope 2, an upwelling zone between the other two water masses. Although the limited number of samples and the errors inherent in plankton sampling, such as on patchiness and vertical migrations, preclude establishment of any precise relationships, it is intimated that there is

> "good evidence of a large standing crop of plankton in the region defined by Envelope 2 where sizeable red salmon catches were made. The low values near the Aleutians may possibly be explained by grazing or by high surface velocities and turbulence associated with the coastal current. The low values in the region defined by T-S envelope 1 are apparent, except for the value of 205 grams at 50°N, 165°W. It is interesting to note that at this Station the sample consisted mainly of the copepod *Calanus cristatus*, whereas at all the other locations the euphausid shrimps completely dominated the samples."

These observations demonstrate most effectively the value of this type of investigation in relating salmon distribution and abundance to the plankton food stocks.

Approximately 500 miles off the Canadian Pacific coast—at 50°N lat, 145°W long—is located Ocean Weather Station "P" (Fig. 78), occupied continuously by two Canadian ships that alternate every 6 weeks.

Station "P" lies within the North Pacific Subarctic water mass near the boundary region between the "mid-gulf" (i.e., with surface salinities higher than the surrounding offshore waters; Doe, 1955) and "offshore" (i.e., with surface salinities averaging about 32.6‰). It is far removed from the coastal zones with surface salinities less than 32.5‰. The Subarctic current enters the area from a westerly direction and diverges east of Station "P" as the south-flowing California Current and the northerly located counterclockwise Alaska Gyral (Fig. 78). The currents near Station "P" are slow, from 1 to 2 sea miles (1.85–3.7 km) per day.

Since August, 1956, one of these vessels has been equipped to carry out a quite detailed series of oceanographic observations, including plankton collections, made with a standard "NorPac" net of nylon netting of 0.33 mm aperture width. From a study of the plankton samples obtained August 1956 to January 1958 (McAllister, 1961) the plankton situation is as follows:

The seasonal cycle of surface zooplankton varied as shown in Fig. 87, with a low winter minimum, a summer maximum, a sharp decline in early autumn and a secondary maximum in December. In the upper 150-m stratum a similar seasonal cycle occurred but with somewhat lower concentrations. The seasonal cycle in vertical distribution is shown in Fig. 88. It is marked by two layers of high concentration separated by one of low plankton abundance. The shallow and deep layers of abundant plankton persisted through night and day in all seasons, thus suggesting that

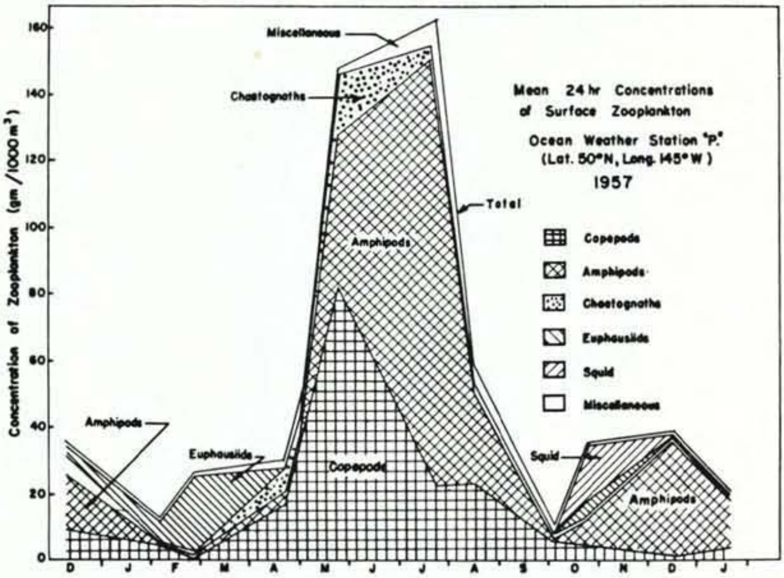

FIG. 87. Concentration and composition of surface zooplankton at station "P", northeastern Pacific. (From McAllister, 1961, fig. 17.)

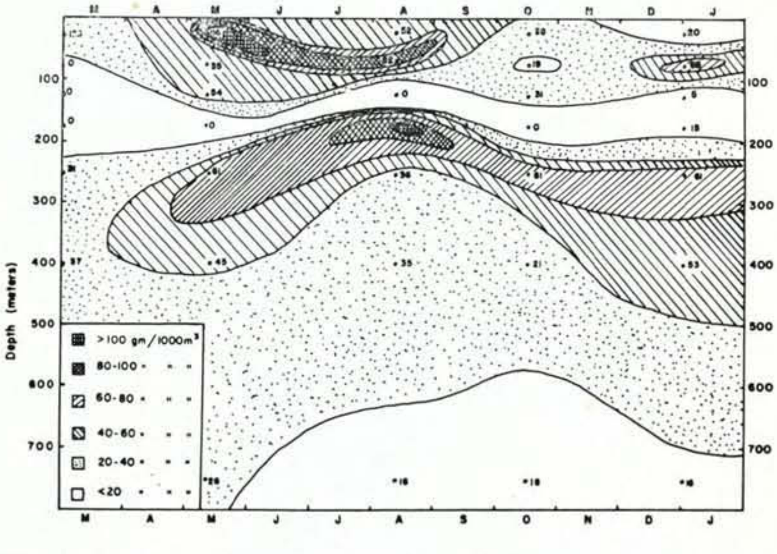

FIG. 88. The vertical distribution of zooplankton at station "P". (From McAllister, 1961, fig. 15.)

they are permanent features of the vertical distribution of the zooplankton in the northeast Pacific. As pointed out by McAllister (1961, p. 17):

> "the deeper layer of zooplankton exists in a stratum too dark for phytoplankton production. In addition, the density gradient in the halocline might, to a large extent, prevent dead organisms and detritus from reaching the lower layer of zooplankton. Thus, in order to obtain sufficient food the herbivorous zooplankton in the lower layer may have to migrate upwards periodically in order to graze in the productive upper layers. The carnivorous zooplankton could, of course, remain in the lower layer and prey on the migrating herbivores."

One further observation is pertinent. Available evidence indicates that the depth range through which fish may feed without restriction, so far as prevailing light intensity is concerned, is relatively constant throughout the daylight hours down to a depth of, say, 300 m but becomes sharply reduced at night. Near sunset and sunrise unrestricted feeding may be confined to only the upper few metres, where surface sampling has indicated that the plankton food is abundant. During the summer, the long days would permit protracted feeding but, in winter, the coincidence of short days with generally sparse zooplankton supplies would suggest that the plankton available may be less utilized than the concentrations alone would indicate. Thus "it seems not impossible that winters with very sparse zooplankton, heavy cloud cover and unusual turbidity could be critical periods for survival of young fish" (McAllister, 1961, p. 25).

GROWTH, AGE, AND MATURITY OF SOCKEYE IN THE SEA

Growth in the Sea

Several factors govern the rate of growth during ocean residence. These might be listed briefly as:

1. the amount of food (plankton principally) available,
2. the temperature conditions in the feeding areas—the warmer the waters (within limits) the faster the growth,
3. the degree of competition for food, i.e., the size of the feeding salmon population in general.

Naturally, the general condition of the fish also comes into the picture, but since there is no information available on that score, it must be assumed that they all enjoy a normal state of health.

Thus, fluctuations in growth are to be expected from year to year, resulting in different lengths and weights attained at maturity. An example of such changes in average length is given in Table 98 which shows the average lengths of males and females of the principal age-groups for the Skeena River, Rivers Inlet, and Nass River sockeye. Similar variations from year to year around a long-term average occur for all age-groups in all areas where there are sockeye runs, but there seems no need to illustrate them.

TABLE 98. Average lengths, in inches, of sockeye salmon of the principal age-groups from three British Columbia river systems, to show the variation in total growth during life, for the years 1942–56. M—male; F—female (from Foskett & Jenkinson, 1957).

	Skeena River				Rivers Inlet				Nass River	
	4_2		5_2		4_2		5_2		5_3	
	M	F	M	F	M	F	M	F	M	F
1942	22.6	22.3	25.2	24.3	21.9	21.3	25.0	23.8	24.9	24.3
1943	21.9	21.9	25.1	23.9	20.5	21.1	24.3	23.7	24.1	23.5
1944	22.4	21.7	24.8	23.9	21.1	21.0	23.5	23.3	24.8	23.8
1945	22.6	22.3	24.9	24.1	20.9	21.2	24.2	23.9	24.7	24.0
1946	22.7	22.0	25.4	24.3	20.6	21.1	25.1	24.1	24.9	23.9
1947	22.3	22.0	25.1	23.8	20.6	20.7	24.0	23.5	24.5	23.6
1948	23.0	22.3	25.3	24.1	21.4	21.3	25.2	24.2	25.0	24.1
1949	22.5	22.2	25.3	24.5	20.9	21.4	23.8	22.8	24.7	23.7
1950	22.8	22.3	25.7	24.4	21.1	20.8	25.2	24.2	24.5	23.7
1951	22.7	22.6	25.9	24.8	21.9	21.9	25.8	24.8	25.1	24.1
1952	23.3	22.6	25.8	24.7	21.5	21.5	26.0	25.0	24.8	23.9
1953	23.2	22.8	26.2	25.0	21.6	21.8	26.5	25.3	24.9	24.1
1954	22.2	22.4	26.6	25.2	22.0	21.6	26.1	25.1	25.3	24.5
1955	22.5	22.1	25.6	24.5	21.2	21.0	25.4	24.5	24.1	23.2
1956	23.6	22.9	26.1	24.9	21.5	21.5	25.3	24.3	24.3	23.6
Average:	22.7	22.3	25.5	24.4	21.2	21.3	25.0	24.2	24.7	23.9

How much growth the sockeye put on each year is of general interest. This can only be ascertained by back calculations, using the scale markings as the index. It is now well known and readily accepted that among sockeye the scales grow in fairly close correspondence with the length of the fish, and, therefore, the length of the radius of the scale from the first ring or circulus to the outer margin of the scale is indicative of the fish's growth (see Krogius, 1957). It has been found that the young fry lays down its first ring or circulus when around 38 mm (1.5 inches) in length (Foerster, 1929b). Therefore, the scale radius from first circulus to outer margin of the scale is proportional to the total length (tip of snout to centre of fork of tail) less 38 mm or 1.5 inches.

Since, on each scale, the "fast" summer growth (marked by relatively widely spaced circuli) and the "slow" winter growth (marked by closely packed circuli) can be distinguished (see Fig. 1), each year's growth increment can be computed by the distance between the outer edge of each "winter band" or "annulus." That is, the width of each annulus ("summer" and "winter" bands), expressed as a proportion of the total scale width—first circulus to outer margin—is equivalent to the length increment of that year, computed from the total length of the fish less 38 mm. A further breakdown into summer and winter growth increments can also be made (Krogius, 1960) (see Table 99).

TABLE 99. Average length increments (centimeters) per year of residence in lake and sea for Cultus (Foerster, MS), Dalnee (Krogius, 1960), and Karluk (Barnaby, MS, 1932) lakes, both sexes combined.

Area:	Cultus					Dalnee				Karluk				
Age-group:	3_2	4_2	5_2	5_3	6_3	4_2	5_2	5_3	6_3	4_3	5_3	6_3	5_4	6_4
First year in fresh water	9.6	10.5	10.2	6.1	6.4	12.8	12.9	10.3	10.4	6.9	6.7	7.5	5.7	6.8
Second year in fresh water	–	–	–	8.0	8.9	–	–	7.3	6.7	5.8	5.9	5.0	4.7	3.8
Third year in fresh water	–	–	–	–	–	–	–	–	–	–	–	–	3.8	4.5
First ocean summer	–	–	–	–	–	15.2	14.4	15.6	13.7	–	–	–	–	–
First ocean winter	–	–	–	–	–	3.8	3.4	3.6	3.3	–	–	–	–	–
First ocean year	25.8	21.3	21.0	23.3	19.5	19.0	17.8	19.2	17.0	24.3	20.0	19.5	23.9	22.0
Second ocean summer	–	–	–	–	–	11.6	8.9	10.0	7.7	–	–	–	–	–
Second ocean winter	–	–	–	–	–	3.5	2.8	3.8	2.7	–	–	–	–	–
Second ocean year	–	19.8	17.9	17.2	13.8	15.1	11.7	13.8	10.4	–	17.3	13.6	–	14.4
Third ocean summer	–	–	–	–	–	–	7.9	–	6.4	–	–	–	–	–
Third ocean winter	–	–	–	–	–	–	2.8	–	2.6	–	–	–	–	–
Third ocean year	–	–	10.4	–	9.2	–	10.7	–	9.0	–	–	10.3	–	–
Portion of last ocean year	14.6	7.4	5.5	6.6	3.5	6.6	4.7	5.2	4.1	14.4	6.5	6.3	13.2	5.1
Total average length:	50.0	59.0	65.0	61.2	61.3	53.5	57.8	55.8	57.6	51.4	56.4	62.0	51.3	56.6

In Table 99 are given the annual growth increments for sockeye of the principal age groups returning to Cultus Lake, British Columbia, to Lake Dalnee, Kamchatka, and to Karluk Lake, Alaska.

Extensive discussion of the differences in growth increments for the three widely separated areas for which comparative data are available hardly seems warranted, because of the differences in numbers of fish sampled and in the number of years for which data were obtained. However, it is readily apparent that there is a general consistency. In all areas the length increment in the second ocean year is appreciably less than that in the first, and that in the third ocean season is less again. Secondly, it is evident that, comparing fish of the same freshwater age, those that spend longer in the sea have had a slower growth in length. Finally, among sockeye that spend only 1 year and a few months in the sea (growth types 3_2, 4_3, and 5_4), growth during the second summer in the ocean is phenomenal, twice that of older age-classes. Most such fish are males, precociously maturing it is frequently said, and the great development during the final months in the sea would certainly indicate a remarkable growth rate.

There are also characteristic differences among the three areas. For example, Lake Dalnee sockeye are somewhat smaller, age for age, and the length increments per year during ocean residence are less, while those in freshwater are greater, than for Karluk or Cultus.

Age at Maturity

Among sockeye there is a vast range in the age at which individuals mature and return to the rivers for spawning. Taking, as a basis for discussion, the data obtained for the Karluk River, Alaska, over a long period of years (1922, 1924–49) and conveniently summarized by Rounsefell (1958a), the ages ranged all the way from 3 to 8 years. For each age-group, furthermore, there is a further breakdown according to period of residence in fresh water. Some went to sea shortly after hatching while others tarried in the lake until their 5th year. Similarly the period of time spent in the ocean varied from a few months to 4 years. In all, 21 age-groups are reported (Rounsefell, 1958a, p. 154) as shown in the following array; the number of years in which they occurred is also given, together with the percentage representation over the 27-year period:

Age-group:	3_1	3_2	3_3	4_1	4_2	4_3	4_4	5_1	5_2	5_3	5_4	5_5
Occurrence (years):	6	7	1	17	27	27	5	1	27	27	26	1
Percentage:	x	x	x	0.1	1.0	1.4	x	x	1.7	58.3	1.7	x

Age-group:	6_2	6_3	6_4	6_5	7_3	7_4	7_5	8_4	8_5
Occurrence (years):	7	27	27	14	18	27	21	12	14
Percentage:	x	16.9	15.4	x	x	2.7	0.3	x	x

x = less than 0.1% representation

Three growth types, 3_3, 5_1, and 5_5, occurred only once; eight others were of quite minor significance. The principal growth type is 5_3, making up over 50%, while the 6_3 and 6_4 groups are also well represented. In fact, it is said that the latter group (6_4) has increased greatly in importance in more recent years, and the fact that these sockeye have spent an additional year in the lake has suggested to some observers that growth conditions in the lake may have deteriorated substantially (see p. 269–270), resulting in the further delayed seaward migration.

In contrast to the 2-year-in-freshwater and 2- or 3-year-in-the-ocean (that is, 5_3 and 6_3) sockeye, characteristic of many Alaskan sockeye areas (and also the most northerly sockeye river in British Columbia, the Nass), the basic growth types among more southern sockeye rivers are those that spend 1 year in the lake and 2 or 3 years in the ocean (4_2 and 5_2). The long-term percentage representation for these areas is as follows, minor age-groups making up the remainder of the 100%.

River	3_2	4_2	5_2	5_3	6_3	Source
Fraser	1.3	75.3	15.0	4.2	0.5	Clemens, 1938, p. 35
Skeena	present	45.5	43.2	8.6	3.9	Foskett, 1956, p. 37, 41
Rivers Inlet	present	47.9	50.7	1.1	0.4	Foskett, 1956, p. 37, 41
Wood	20.5	72.1	–	5.2	–	FRI, 1962, p. 7

Records for the Wood River, Alaska, are added since this population of sockeye conforms to this same pattern of age-group representation, quite in contrast to most other Alaskan sockeye areas studied.

As suggested by Clemens (1935) for British Columbia waters and perhaps justifiably applied to all sockeye areas, maturity among sockeye salmon is usually reached in the 3rd year of sea life with the young fish spending 1 year in fresh water Shorter and longer periods spent in the ocean are the result of either precocious development or slower rates of growth and development; longer residence in fresh water appears to be due to slower early development or very late hatch or both. Shorter freshwater residence prevails only, it would appear, where sockeye spawn in streams without lakes or suitable rearing pool areas,* and even in such cases the sockeye must have developed an unusual conditioning with respect to highly saline water, if experiments at Port John, British Columbia, are any guide (see p. 8).

The age-groups may then be arranged in an array—

$$\begin{tikzcd}
5_1 & 6_2 \arrow[l] & 7_3 & 8_4 & \\
4_1 & 5_2 \arrow[l] \arrow[u] & 6_3 \arrow[u] & 7_4 \arrow[u] & 8_5 \\
3_1 & \boxed{4_2} \arrow[l] \arrow[u] \arrow[r] \arrow[d] & 5_3 \arrow[u] \arrow[r] \arrow[d] & 6_4 \arrow[u] \arrow[r] & 7_5 \arrow[u] \\
 & 3_2 \arrow[r] & 4_3 & &
\end{tikzcd}$$

with the 4_2 group as the focus and from which all other age-groups develop according to their rate of growth and other growth-limiting environmental factors. In Table 100 are given the average lengths for the various age-groups sampled in several widely dispersed areas. Inspection (even without weighting to minimize the effect of unusually high or low values when samples are few in number) shows that, for each series of age-groups having the same period in the ocean, the average lengths are of the same general order, size increasing appreciably with each additional year in the sea. Extra residence in fresh water has a much smaller effect on growth. Thus, if due weighting of the data were made in accordance with size of sample (not possible in all cases), there would be but little difference in average length among the 4_2, 5_3, 6_4, 7_5 series, for example, or among 4_1, 5_2, 6_3, 7_4, 8_5 individuals, but between these two series the difference would be substantial, representing an additional season in the sea. With each extra year in the ocean the increase in length per year diminishes appreciably, as might be expected. The older the fish, then, the smaller the length increment per year.

FACTORS INFLUENCING AGE OF MATURITY

Some 30 years ago Clemens (1935, p. 165) reported that it was impossible at that time to unravel the factors which bring about the great diversity in age of maturity. He remarked that "undoubtedly heredity, physiological constitution and

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* The situation in the sockeye spawning areas of the Kamchatka River is not too clearly understood.

TABLE 100. Average fork lengths in cm of sockeye salmon, according to age, group, and sex. M—male; F—female.

Age group	Sex	Fraser River[a]	Rivers Inlet[b]	Skeena River[b]	Nass River[b]	Karluk River[c]	Dalnee River[d]	Ozernaya River[e]	Bolshaya River[f]
3_1	M	–	–	50.8 (1)	54.6 (23)	59.2 (32)	–	–	–
	F	–	–	–	54.4 (7)	57.1 (19)	–	–	–
3_2	M	47.0	39.9 (6)	40.6 (21)	–	41.0 (1)	–	–	–
	F	47.2	–	–	–	–	–	–	–
3_3	M	–	–	–	–	30.0 (2)	–	–	–
4_1	M	–	63.5 (1)	62.7 (1)	63.5	63.3 (18)	–	–	59.6
	F	–	61.5 (2)	60.7 (5)	58.4	61.7 (36)	–	–	
4_2	M	60.0	54.6	58.2	60.2	60.0	53.7	–	53.4
	F	58.2	54.6	56.9	58.2	57.4	–	–	
4_3	M	–	–	45.7 (2)	39.4 (1)	51.1	–	–	–
	F	–	–	46.6 (1)	50.8 (1)	52.5 (18)	–	–	–
4_4	M	–	–	–	–	32.0	–	–	–
5_2	M	64.9	62.8	64.0	65.5	65.1	57.8	–	60.5
	F	62.0	61.0	61.7	62.5	63.6	–	–	
5_3	M	60.5	57.2 (23)	59.7	64.0	62.9	55.8	54.7	55.0
	F	58.3	57.9 (28)	57.7	61.7	60.0	–	53.4	
5_4	M	–	61.0	–	–	54.4	–	–	–
	F	–	–	–	–	52.0	–	–	–
5_5	M	–	–	–	–	34.0 (1)	–	–	–
6_2	M	–	–	66.5 (1)	72.4 (1)	–	–	–	64.2
	F	–	69.1 (2)	64.3 (1)	–	–	–	–	
6_3	M	65.2	64.8 (6)	64.3	68.6	63.2	57.6	60.9	61.0
	F	62.4	65.0 (13)	62.0	65.4	61.3	–	58.3	

(Continued.)

TABLE 100. (Concluded.)

Age group	Sex	Fraser River[a]	Rivers Inlet[b]	Skeena River[b]	Nass River[b]	Karluk River[c]	Dalnee River[d]	Ozernaya River[e]	Bolshaya River[f]
6_4	M	–	–	64.3 (1)	65.5 (1)	63.5	–	55.0	–
	F	–	–	59.7 (1)	63.8 (1)	60.3	–	53.5	–
6_5	M	–	–	–	–	53.4 (5)	–	–	–
7_3	M	–	–	–	73.7 (1)	–	–	63.3	–
	F	–	–	–	–	–	–	60.9	–
7_4	M	–	–	66.8 (1)	–	65.6 (19)	–	60.9	–
	F	–	–	64.3 (1)	72.4 (1)	61.8 (28)	–	58.4	–

[a] From Gilbert (1920–25), Clemens (1938).

[b] From Foskett (1956). Minor age-groups from Foskett (1952–56). For these, the numbers of individuals are indicated.

[c] From Gilbert and Rich (1927). Numbers of specimens of minor age-groups are indicated.

[d] From Krogius (1960). Males only were measured.

[e] From Egorova et al (1961).

[f] From Semko (1954a). Sexes combined.

environment all play a part." Very little more definite is our present understanding, though much pertinent information is now available.

For Kamchatka sockeye, extensive study (Krogius, 1960) has revealed that rate of growth appears to be a very important influencing factor. Commencing early in the first years of freshwater residence, at least among those populations that are reared in lakes, two types of sockeye occur, one faster growing (on the average), the other slower growing, both originating from the same spawning stock. The individuals of faster average growth migrate from the lake and proceed to sea a year ahead of their slower growing associates (4_2's vs. 5_3's at Lake Dalnee, Table 99). Then, in the ocean, a further division occurs for each of these groups, the faster growing individuals making up the 4_2 and 5_3 returning spawning runs, while the slower growing ones comprise the 5_2 and 6_3 runs (on the average—again there is much overlap in the size of the individual fish in each group).

During both 1st and 2nd years in the ocean the length increments for both 4_2 and 5_3 fish average greater than for the 5_2 and 6_3 groups, respectively, even during the winter periods when growth is always retarded. In the final summer in the sea, too, the average increase in length of the 4_2 and 5_3 individuals appreciably exceeds that of the 5_2 and 6_3 fish. The data obtained at Cultus Lake show the same differences. For the Ozernaya River, West Kamchatka (Krogius, 1960, p. 85), a similar division of the sockeye into fast and slow growing groups occurs, though in this case, since the migrants normally remain in the lake for at least 2 years, the fast growers are represented by the 5_3 and 6_4 groups and the slow ones by the 6_3's and 7_4's.

Thus, for any area where 1-year-in-lake and 2-year-in-lake sockeye normally occur, there will be derived from a spawning, say in the brood-year 1960, two groups of young—those which have a faster growth rate and which migrate seaward early in their 2nd year, in the spring of 1962, and those which have an appreciably slower rate of growth and which remain in the lake 2 years and pass seaward in the spring of 1963. During ocean residence each of these two groups will divide again into fast-growing and slow-growing populations. At some time in their ocean period of life these groups reform, as it were. The fast-growing yearlings of 1962 will return to spawn in their 4th year, 1964, along with (1) the slow-growing-in-lake 2 year olds of 1962 (brood year, 1959), (2) the fast-growing-in-lake but slow-growing-in-the-ocean yearlings of 1961 (brood year 1959) and (3) the slow-growing-in-lake and slow-growing-in-the-ocean 2-year olds of 1961 (brood year, 1958). Or, expressed another way, there will return in any 1 year, say 1964,

(1) the 4_2's of the 1960 brood year which migrated to sea in 1962
(2) the 5_3's of the 1959 brood year which migrated to sea in 1962
(3) the 5_2's of the 1959 brood year which migrated to sea in 1961
(4) the 6_3's of the 1958 brood year which migrated to sea in 1961 and,
(5) as precociously maturing individuals, principally males, the 3_2's of the 1961 brood year, which migrated to sea in 1963.

For areas where the young sockeye predominantly remain in the lake for 2 or 3 years, for example, Karluk Lake, Ozernaya River, the five principal age-groups comprising the spawning runs will be 1 year older, that is, 5_3, 6_4, 6_3, 7_4, and 4_3.

On the basis of extensive and illuminating studies of the growth rates of Lake Dalnee, Kamchatka, sockeye in both fresh water and in the sea, Krogius (1960, p. 86) concluded that the regrouping of the age-classes in the ocean occurs during the second summer in the ocean. By this time quite a marked difference in size prevails between the fast-growing individuals of both the 1-year-in-lake type which mature as 4_2's (43.6 cm) and the 2-year-in-lake which mature as 5_3's (46.8 cm), and the slow-growing fish of both lake resident types which mature as 5_2's (39.6 cm) and 6_3's (41.8 cm). For the fast-growing fish this second ocean summer is the one which precedes the year of return to fresh water; for the slow-growing fish it is the second of the three summers spent by them in the ocean.

THE SIGNIFICANCE OF CHANGES IN GROWTH PER YEAR

It is of importance scientifically, and perhaps also from the point of "management" and prediction, to determine whether, during the period spent in the ocean, the growth and well-being of the feeding sockeye is appreciably affected by the actual abundance of sockeye there and by the abundance of other species of Pacific salmon which may occupy the same feeding areas and compete for the available food. The only good evidence reported comes, again, from the USSR Kamchatka studies (Krogius, 1960).

For Lake Dalnee sockeye salmon, a remarkable periodicity occurs in the amount of growth put on each year in the ocean, particularly for the so-called "fast-growing" age-groups 4_2 and 5_3. For these age-groups, the fish in their 1st year in the ocean have a greater length increment in the even years (average of 19.9 cm) than in the odd (average of 18.3 cm). During their 2nd ocean year, length increase is greater in the odd year (15.4 cm) than in the even (13.3 cm). During their 3rd and final season in the sea (only the spring and early summer) the fish again put on more growth in the even year.

In seeking the cause of these regular periodic fluctuations in length increase, the effect of changes in abundance of the Lake Dalnee sockeye run themselves could be ruled out because no constant periodicity in these runs occurred. The only logical factor seemed to be the relationship of the pink salmon runs, which, in East Kamchatka areas, are heavy in the odd years and light in the even ones. It was pointed out (Krogius, 1960, p. 82) that in the odd years the young sockeye entering the sea would be met by large schools of pink salmon returning to spawn, whereas in the even years, the pinks would be fewer and competition for food less severe. This, then, could explain the 1st ocean year fluctuations in sockeye growth. In the 2nd year in the ocean, on the other hand, the sockeye of odd year broods would be associated, in the feeding areas presumably, with vast quantities of pinks in their 1st ocean year, hence food competition would be severe and growth correspondingly poor. In their 3rd year the sockeye would be mingling with, and the fast-growing ones (4_2 and 5_3) returning with, small runs of maturing pinks while the slow-growing sockeye (5_2 and 6_3), due to return to fresh water to spawn the following year, would be feeding with small populations of pinks.

Nevertheless, according to Krogius (1960, p. 82), "in spite of the simplicity and reasonableness of such an explanation of fluctuations in the sockeye's rate of growth, it cannot be adequately substantiated." In the first place, after 1943 the pink salmon runs to East Kamchatka Rivers declined, yet the periodic changes in sockeye growth continued. Secondly, the 5_2 and 6_3 age-groups showed no such marked periodic growth fluctuations, particularly in the 1st ocean year. Clarification of the causes of these periodic growth fluctuations in sockeye in the ocean must await further study.

With regard to the lack of evidence of periodic fluctuations in growth among individuals of the slower-growing 5_2 age-group in 1st and 2nd ocean years it is suggested (Krogius, 1960, p. 83) that these smaller, slower-growing fish, as they enter the ocean, may lag behind their larger fellow travellers and remain in regions where feeding conditions are less favourable. Here they will be joined, the next year, by the larger 2-year-old smolts of the 5_3 and 6_3 age-groups. Or, more probably, these fish may just have a slower growth because of their smaller size and be unable to compete as forcefully for their food, thus maintaining a smaller size, in both 1st and 2nd years in the sea, equivalent to or less than the 4_2 and 5_3 brood year individuals of the same age in the odd years when growth is slower.

Data from the Ozernaya River, West Kamchatka, tend to substantiate the Lake Dalnee findings not only with regard to periodic yearly fluctuations in annual length increase but also with respect to the influence of pink salmon feeding populations in the sea. The yearling length increments fluctuate periodically in all ocean years but more appreciably in some than in others. In some cases the alternate year variation is broken. This may be due (Krogius, 1960, p. 85) to inadequate sampling. Since the sockeye runs to the Ozernaya River are very large (3–7 million, including the commercial catch) and vary greatly from year to year, the variation in abundance of feeding sockeye in the sea may have itself a quite distinct bearing on yearly growth rates. No uniformity exists between the length increase fluctuations of the two age-groups (5_3 and 6_3) though they go to sea and reside there together but perhaps in quite different feeding areas. No explanations are given.

DIFFERENCES IN SIZE OF SMOLTS AT BABINE LAKE

Among Skeena River sockeye stocks there is considerable variation from year to year in the proportion of the run which returns in the 5th year (5_2) and in the 4th (4_2) (see p. 11), though the individuals are derived from the same seaward migration leaving the lake early in their 2nd year. Examination of the scales of the returning adults of these two age-groups has shown (T. H. Bilton, unpublished data) that the 5_2 individuals have fewer circuli within the 1st year scale annulus than the earlier-maturing 4_2's. Taking 12 circuli as a dividing line, 5_2 adults generally have fewer than 12 in the 1st year band while 4_2's usually have more. The widths of the 1st year zone on the scale differ in corresponding fashion. If the number of circuli to the first annulus, and the width (radius) of the 1st year zone, be indicative of growth increment (as is now well-authenticated by many investigators for many species of fish), then the 5_2 sockeye must be composed of the smaller seaward migrants, those with 12 or less circuli, whereas the 4_2's consist of the larger seaward migrants. Although the data shown in Table 99 do not show any appreciable smaller size for 5_2 sockeye than for 4_2's at Cultus Lake and Lake Dalnee during the 1st year, the records for Babine clearly show this to be true, so much so that prediction of the probable return of Babine sockeye as 4_2's and 5_2's seems feasible, a notable advance in prediction if it proves to be reasonably consistent.

THE INFLUENCE OF HEREDITY ON AGE OF MATURITY

Reference has already been made to the fact that in four populations of young sockeye going to sea at the same age, for example, either early in 2nd year or early in 3rd year, some individuals remain in the ocean for only 2+ years before maturing and returning to spawn, for example, as 4_2's or 5_3's, respectively, while others spend 3+ years in the sea, returning to fresh water as 5_2's or 6_3's. Available evidence indicates that the latter age-groups have a slower growth in the ocean than the earlier-maturing groups, the 4_2's and 5_3's (Table 99 and text, p. 355). Data being obtained at Babine Lake suggest that the growth even during the 1+ year in fresh water may also be less, as indicated in the preceding section. Since it is of importance to know how many adults, from any known seaward migration of sockeye, may be expected to return from the ocean in specific years or at specific ages, it is necessary to know whether the factors governing their time of return, that is, their age, are mainly hereditary or primarily environmental, i.e., dependent on the feeding conditions which prevail in the nursery areas.

In the Skeena River stock both the 4_2 and 5_2 age-groups are well represented; the average for 32 years, 1917–48, was 47.7% 4_2's with a range of from 13 to 80%, and 39.6% 5_2's with a range of from 13 to 82% (Milne, 1955, p. 475). Statistical analysis of the catch data indicated "influences of both hereditary and environment on age at maturity and rate of survival" (Milne, 1955, p. 479). On the other hand, from a somewhat different treatment of the data on numbers of 4_2 and 5_2 sockeye caught on the Skeena River, 1912–54, and also in Rivers Inlet area for the same period, Godfrey (1958, p. 348) reported that "very definitely age at maturity in sockeye salmon is governed to a great extent by the inheritance of certain genetic components of the parents. Although some influence of environmental factors upon ages at maturity may exist, it remains to be proven definitely. The more important influences certainly appear to be heritable ones."

Examination of the year-to-year changes in average size—weight and length—of the two age-groups indicated that simultaneous increases or decreases occurred in successive years. Yet the similarity was less when sizes of sockeye of the *same brood year* were compared (these fish being caught a year apart) than when sizes of the fish *caught in the same year* (but from different brood years) were compared. This was taken to suggest that variations in the final size were determined principally by environmental factors operating during the last few months of ocean residence, rather than by any environmental influence during early freshwater or early ocean life. This, in turn, according to Godfrey (1958, p. 348):

> "would indicate that the age of maturing in sockeye salmon has already been determined at some early period in its life history, and is not directly dependent upon the growth experienced, and final size attained, during the last of the ocean phase. If this be so, it does not seem likely that maturity in sockeye salmon could be delayed for a year when growth in the current year has been slow (for example, that maturity in normally 4-year-old fish is postponed for a year so that they mature and return as 5-year-old fish)."

Even for the so-called "precociously maturing" 3_2 sockeye, which, in some areas at least, appear in abundance in the year preceding a "big" year, interesting data are available (Ricker, MS, 1959a). These fish, chiefly males, have been observed to have fast growth in the 1st ocean year and an exceptional growth during the final year (Table 99).

For the Adams River area of the upper Fraser system, the 3_2 males make up a fantastically high proportion of the spawning runs in the years preceding the "big" years (Table 101), normally over 90% of all spawners. Comparison of the representation of 3_2 males in the parent and progeny generations revealed a direct relationship which indicated (Ricker, MS, 1959a, p. 46) that the "observed difference between broods, in age of males at maturity, is strongly influenced by the age of their fathers." Females are normally of the older 4_2 and 5_2 age-classes (Table 101). The

TABLE 101. Age-class representation of sockeye in spawning runs to Adams River, upper Fraser system, 1945–61, as taken from Annual Reports of International Pacific Salmon Commission, 1946–62.

		Sex representation %			
		Males		Females	
Year	Estimated escapement	3_2	$4_2 + 5_2$	3_2[a]	$4_2 + 5_2$
1945	58,000	96.8	0.6	1.4	1.2
1946	1,835,000	0.0	36.4	–	63.6
1947	185,000	1.0	35.4	0.2	63.4
1948	12,600	13.5	16.5	3.4	66.6
1949	11,700	78.8	6.3	1.0	13.9
1950	848,000	2.3	50.7	–	47.0
1951	135,000	0.8	39.4	–	59.8
1952	8,700	29.5	27.3	–	43.2
1953	177,000	98.1	0.6	–	1.3
1954	1,532,800	0.2	44.5	–	55.3
1955	54,400	0.7	33.0	–	66.3
1956	7,500	9.2	30.8	–	60.0
1957	257,600	99.2	0.3	–	0.5
1958	2,736,800	0.3	48.2	–	51.5
1959	113,200	0.1	33.9	–	66.0
1960	2,200	0.4	28.3	–	71.3
1961	57,800	97.6	1.0	–	1.4

[a] No 3_2 females were recorded after 1949, though doubtless a few were present in most years.

"residual variability" in the data, according to Ricker, can be "ascribed to environmental influence, errors in population estimates, and variations in age or genetic makeup of the female parents" (Ricker, MS, 1959a, p. 46).

Just how the factors governing onset of maturity operate is not clear. If they be hereditary in nature, is it (1) through the rate of growth and the stimulation of the reproductive system by means of the appropriate physiological condition coming into play at a certain stage of development and growth,* or is it (2) quite independent of rate of growth but having growth rate as a coincident and closely related feature?

If environment be responsible, rate of growth would seem to be the most likely influencing factor.

From consideration of all the pertinent data presently available it would seem that both heredity and environment play important parts. The evidence for heredity (Godfrey, 1958; Ricker, MS, 1959a) is strong; that for environment not too clear. One weak point, raised by Godfrey (1958, p. 353), is whether, among sockeye, age

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* It is well known that development of the gonads is accompanied by changes in activity of the endocrine glands and a change in body metabolism.

at maturity can be advanced or retarded a year, as a result of faster or slower growth because of environmental conditions. The only evidence which might be applicable in this regard is provided by a transfer of kokanee ("landlocked sockeye") eggs from an interior area, Kootenay Lake, to Cultus Lake and the release of the reared yearlings (distinctively marked) in the outlet river of Cultus Lake (Foerster, 1947). No marked adults were obtained in the cycle 4th year, either in the commercial fishery or at Cultus Lake but in the following year a number were taken not only in the fishery but also at the lake, these fish being in their 5th year (5_2). Though there may be some doubt as to the proper identification of the marked fish returning to the lake, since the scales were too eroded to be used for age determination, there can be no doubt concerning the commercially caught individuals.

Thus, these specimens which normally mature in Kootenay Lake as 3-year-olds (Vernon, 1957) had, by reason of the change in environment and ocean residence, reached maturity only in their 5th year, 2 years later. It is suggested (Ricker, MS, 1959a, p. 47) that most of these fish might have begun to mature at sea in their 3rd or 4th year but that they might have gone too far out to sea to return to the Fraser River in time for spawning in those years, had spawned in some other area or had, perhaps, perished at sea. This suggestion can never be verified. It can only be said that some, at least, returned as 5_2's with normal age at maturity delayed by 2 years.

MORTALITY OF SOCKEYE IN THE OCEAN

TOTAL OCEAN MORTALITY

To arrive at some understanding of the natural mortality of sockeye salmon during the period that they are in the ocean has been the object of a number of investigations (Table 102). In order to be able to identify and enumerate the adult fish, returning from a known seaward migration of the young and occurring either in the commercial fishery or in the spawning escapement, some or all of the seaward migrating smolts were marked, by removal of certain fins, in certain areas, such as at Karluk (Barnaby, 1944), Cultus Lake (Foerster, 1936b), Port John (FRB data, 1948–56), and Babine Lake (Ricker, 1962). Data are available, also, from a number of other sockeye areas (Table 102) on the estimated return from the sea of adults surviving from estimated seaward migrations. No marking (i.e., removal of fins) was involved in these tests, thus making unnecessary any consideration of the adverse effects of the lack of the excised fins on the subsequent survival of the fish. It does, however, introduce certain errors inherent in estimating the numbers of smolts and returning adults, particularly those taken in the commercial fishery. Such errors are believed to be of little consequence.

In two marking experiments at Cultus Lake in which certain proportions only of the seaward migrants had been marked, calculation of the percentage return indicated that the return of marked fish was only 38% of the return of the unmarked. This suggested, then, a 62% differential mortality due to the marking and/or absence of the excised fins. Where return from the ocean is based on the return of

TABLE 102. Estimated percentage ocean mortality of sockeye salmon based on percentage return of adults from estimated seaward migration of smolts in the migration years indicated.

Area and years	No. of smolts	Age of smolts at time of migration	No. of adults recovered	Return (%)	Mortality (%)	References
Bare Lake						
1950–53	28,380	mostly 1+	1,394[a]	4.9	95.1	Nelson, 1959, p. 79
Chilko						
1948–55	63,002,000	mostly 1+	6,017,000[a]	9.6	90.4	Henry, 1961, p. 77
Karluk						
1929–33	169,836	2+	29,560[a,d]	17.4	82.6	Barnaby, 1944
1929–33	93,944	3+	24,142[a,d]	25.7	74.3	
Babine						
1946–48	300,500	mostly 1+	5,200–5,500[a,c]	1.8(4.7)	98.2(95.3)	Ricker, 1962, p. 556
1955–58	78,700,000	mostly 1+	3,601,000[a]	4.6	95.4	
Cultus						
1930–31	469,326	mostly 1+	16,653[a,c]	3.5(9.2)	96.5(90.8)	Foerster, 1936a
Port John						
1949	19,486	mostly 2+	651[b,c]	3.1(8.0)	96.9(92.0)	Unpublished FRB data
1948–56	149,242	mostly 2+	12,446[b]	8.4	91.6	
Dalnee						
1936–40	417,000	1+	148,800[b]	35.7	64.3	Krogius, 1948
1936–40	620,000	2+	274,900[b]	44.3	55.7	

[a] Estimated *total* adult return: includes counts or estimates of the pertinent commercial catch in coastal areas plus the escapement to the river.

[b] Includes returns to the river only—excluding fish caught commercially.

[c] Based on return of "marked" smolts. Extra mortality due to marking was estimated at Cultus to be 62% of the smolts marked; percentages in parentheses are adjusted on this basis, for Cultus and Babine. See Ricker (1962, p. 552) for an adjustment based on ratios of instantaneous mortality rates, which gives an average adjusted return of 7.3% for Cultus and 4.2% when applied to Babine.

[d] Based on return of "marked" smolts. Ricker (1962, p. 555) averaged the returns by years and obtained 19.3% return for 2+ smolts and 25.5% for 3+. The adjustment by instantaneous rates raises these figures to 27.4 and 34.2%, respectively.

marked fish, the actual returns should be increased by the factor 100/38 to give the probable return of normal fish. This has been done for Cultus Lake in Table 102 and applied also for the markings at Babine, 1946–48, and Port John, 1949. Although there is no direct evidence that the differential mortality among marked fish, established for Cultus Lake, would apply equally to these other two areas, the fact that the revised percentage return at Port John, 8.0%, coincides closely with the return obtained simply by calculating the return of unmarked adults 2 years later as a percentage of the smolt runs for the years 1948–56, namely 8.4%, suggests that the differential mortality may be much the same.

If this correction be accepted, it is found that for Cultus and Chilko lakes, the percentage return from the ocean agrees closely, 9.2 and 9.6%, respectively. If the

Babine returns, 4.7 and 4.6%, be revised to include both commercial catch and spawning escapement (considering the ratio of catch to escapement as 50:50), they will show as 9.4 and 9.2%, respectively. If the Port John return be increased slightly to include some catch* the percentage return might well approximate 9.0–9.5%. Thus, for British Columbia sockeye areas, the percentage ocean return would tend to approximate, say 10%, indicating an ocean mortality of 90%.

For Karluk and Dalnee areas, returns from the ocean are appreciably higher. In both areas the seaward migrants are much larger in size than in the other areas discussed. The larger the smolts, the higher is the ocean survival (Foerster, 1954a; Ricker, 1962). The Karluk data, embracing both commercial catch and escapement, indicate a general return of 21.4%, whereas the Dalnee returns, which include some but probably not all the commercial catch, are markedly higher, on average, about 33% (Krogius, MS, 1949). For the Karluk area no adjustment for differential mortality was made by Barnaby (1944), but Ricker (1962) computes a possible adjustment that brings the survival up to 30.8%. For Lake Dalnee, no marking is involved.

On the basis of the above evidence, therefore, ocean mortality, embracing that phase of the life history from the time of departure from the nursery lake to the time of return to the coastal area off the river mouth, amounts to around 10% for Canadian Pacific areas, 20–25% for Karluk, and 33–40% for Kamchatka.

In a discussion of the loss in total potential commercial yield from stocks of sockeye, when a high-seas fishery takes place, Ricker (1962) has used, for natural ocean mortality,** an average instantaneous mortality rate of 0.038 or 3.7% per month. He has demonstrated that when the smolts are small the mortality is greater than when they are large. Between Babine Lake smolts (82 mm avg length) and Karluk 3-year-old seaward migrants (143 mm avg length) there is a difference of 1.95 between their instantaneous mortality rates. This corresponds to an actual mortality of 86%. This, according to Ricker, (1962, p. 535), "can be taken as a first estimate of the loss which occurs while young Babine sockeye grow from 82 mm to 143 mm—a length increase which is accomplished in considerably less than a year. . . . The rest of the ocean mortality must then be distributed over the remaining 2 years or so, and must take 66% of the survivors." This latter percentage is the estimate of total mortality of Karluk 3-year-old smolts.*** Average total losses at sea vary from 95 to 64% or from 3.2 to 9.6% per month. In general, mortality was less when the smolt size was greater, as will be seen in Fig. 89. This figure admirably brings together all the available data on this important feature in sockeye salmon management or production.

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* The ratio of catch to escapement is unknown but in the 1948–52 marking experiment no recoveries were made in the fishery. No intensive search had been instituted, however.

** This includes "the interval from the departure of the smolts from their nursery lakes up to the time they are captured by coastal or river fisheries or return to the river" (Ricker, 1962, p. 533).

*** Ricker's calculations for ocean mortality (Ricker, 1962, table III) correspond closely to those in Table 102 above. Differences are due to the adjustment for marking mortality mentioned above, consideration of smolt size as well as period in the ocean, and different years' data in certain cases.

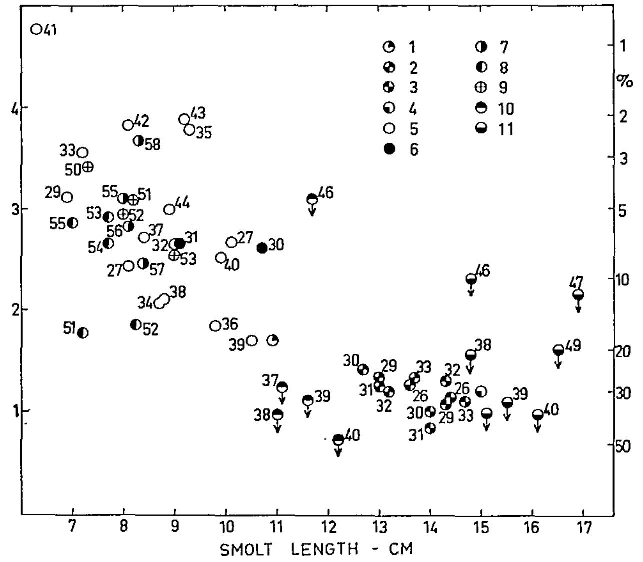

FIG. 89. 1—Karluk (1-freshwater smolts, 1926–33 average); 2—Karluk (2-freshwater smolts); 3—Karluk (3-freshwater smolts); 4—Karluk (4-freshwater smolts, 1926–33 average); 5 and 6—Cultus; 7—Babine; 8—Chilko; 9—Bare Lake; 10—Dalnee (1-freshwater smolts); 11—Dalnee (2-freshwater smolts). Estimates of instantaneous mortality rates (left-hand scale) for sockeye of six stocks. Corresponding percentage survival rates are shown at right. The year beside each point is the year of the smolt migration. The points for Karluk sockeye include an adjustment for mark mortality. The clear points for Cultus Lake are based on percentage return to the lake as spawning escapement (Foerster, 1954, table I) multiplied by the average factor 2.73 to adjust them to terms of total stock; the two black points are based on a complete enumeration of returning marked fish in the fishery and at the lake, adjusted for mark mortality. Lake Dalnee figures include some fishing mortality; the arrow pointing downward indicates that those points are all too high to be directly comparable with the rest. All other points represent natural mortality only (including mortality during downstream migration, and that during the upriver migration of fish which escaped the fishery), except that Bare Lake points may include a small amount of high-seas fishing mortality. (From Ricker, 1962, fig. 1.)

HIGH-SEAS MORTALITY

In an attempt to separate the ocean mortality, as discussed in the preceding section, into (1) that which occurs in coastal areas as the young sockeye go to sea, and return as maturing adults and (2) that which occurs during the years of ocean residence, Parker (1962) has treated the available data, summarized in Table 102, or variations of them, statistically to develop what he terms "a conceptual model" representing the natural marine mortality rate. He assumes a relatively high coastal mortality rate among the young salmon which varies appreciably according to the size of the migrants and the length of time they spend in coastal waters before reaching the open ocean; for the returning adults he recognizes that some extra mortality may occur, but he believes it to be of negligible significance.

For example, with reference to those areas where pertinent data are available, it is indicated that, assuming a standard open ocean mortality of 27% and an adult coastal mortality of 2%, the estimated magnitude of coastal mortality of young sockeye was calculated as (in per cent): Lake Dalnee—29; Karluk Lake—34; Port John—76; Chilko Lake—80; Cultus Lake—84; Bare Lake—88.

Parker (1962) remarks that Karluk sockeye, which enter the open sea almost immediately after leaving fresh water, are characterized by a relatively low juvenile mortality rate. At the other extreme, Cultus and Chilko sockeye enter the Strait of Georgia, an enclosed sea, and must travel more than 100 miles by most direct route to leave the coastal waters. Port John sockeye are intermediate in both juvenile mortality value and geographical situation while the Bare Lake sockeye would appear to present an exception to this generalization. In this case, however, the seaward migrants must negotiate a very shallow and exposed stream.

For open ocean natural mortality rates, the best available estimates are (in per cent): Lake Dalnee—29; Karluk Lake—23; Cultus Lake—37; Port John—32.

It is concluded, then, according to Parker, that open ocean mortality is relatively constant, of the order of magnitude of 27%.

HIGH-SEAS VERSUS COASTAL FISHING FOR SOCKEYE

Making use of (a) data available from Karluk and Cultus lakes on the growth of sockeye during ocean residence and (b) estimates of ocean mortality from several sources, Ricker (1962) has put together a most illuminating and revealing picture of the losses in yield of fish flesh when sockeye are caught (1) 13–16 months, and (2) 1–4 months prior to entrance into coastal areas where heretofore most fishing has been conducted. Only the commoner and most abundant age-groups are dealt with in detail—the 4_2's at Cultus, the 5_3's and 6_4's at Karluk.

For both areas growth appreciably exceeded the maximum mortality estimate during both the 2nd growth year in the ocean and that portion of their last year up to the time they reached coastal waters or the river mouth. For the former, the penultimate year in the sea, the estimated minimum increases varied from 67% (for Karluk 6_4's) to 138% (for Cultus 4_2's) or from 4.4 to 7.5% per month. For the final ocean year, the minimum estimates of monthly increase in bulk varied from 6.6% (for Cultus 4_2's) to 12.6% (for Karluk 5_3's).

Therefore, according to Ricker, if a coastal fishery exists that is capable of taking the optimum percentage of a sockeye stock, then, on the basis of the data presented and indicated above, *any* removal of fish *before* the end of their sea life will result in a loss of potential catch. The estimated losses, expressed as a percentage of potential yield of fish, may be tabulated as follows:

Stock and age-group	Capture on April 1 of the year prior to maturity[a]	Capture on July 1 of the year prior to maturity[b]	Capture in final year 1 month prior to reaching coastal waters	Capture in final year 4 months prior to reaching coastal waters
	(%)	(%)	(%)	(%)
Cultus 4_2	69	60	6.2	22.6
Karluk 5_3	72	65	11.2	37.6
Karluk 6_4	57	50	8.0	28.3

[a] For Cultus Lake fish the period of potential ocean growth lost is assumed to be 16.8 months, for Karluk fish, 16 months.

[b] The period of potential ocean growth lost is calculated as 0.7 of the preceding (April 1) column, for reasons outlined by Ricker (1962, p. 540).

For other age-groups of sockeye the data are less reliable because of limited information concerning growth rate. For what are generally called "precociously maturing" sockeye, that is, those of the 3_2 and 4_3 age-groups, ocean growth is substantially greater than for older fish (Table 99 and text, p. 355) and net increase (growth less natural mortality) is estimated, for Cultus Lake 3_2 males (Ricker, 1962, p. 541), to be around 2.5 times that of the 4_2 fish in their last growth year. Ricker concludes that "although 2-ocean sockeye would suffer a greater *percentage* loss from high-seas capture in the final growth year than 3-ocean fish, their small size and scarcity makes this a minor component of the total loss picture" (Ricker, 1962, p. 542).

For older sockeye, that is, those of the 5_2, 6_3 age-groups (i.e., 4-ocean type), growth every year appears to be somewhat less than for the 3-ocean fish of the same freshwater age (i.e., 4_2 and 5_3 age-groups). Therefore, estimates of the loss in yield by high-seas capture would also be less. It is concluded (Ricker, 1962, p. 542) that "on the whole, the yield from 4-ocean sockeye is likely to be reduced by high-seas fishing about as much as that from 3-ocean sockeye." Where fish of these age-groups are well represented, as on the Skeena and Wood rivers, at Rivers Inlet, etc., the potential losses resulting from too early capture at sea, which would amount to 60% of their weight if taken a year before maturity, 22% if taken 4 months prior to arrival in coastal waters or even 6% if taken but 1 month before reaching coastal fishing areas, merit serious consideration. More precise data pertaining to these age-groups are being collected and analyzed.

With reference to this whole subject of ocean mortality, an exceedingly important one in the matter of "managing" the salmon stocks and in predicting for industry and government the likely returns to be expected from known or estimated seaward migrations of young, the conclusions of Parker (1962) are of interest. He feels that "as a result of this study it is doubted that mortality rates can be more accurately defined by any repetition of the experiments and observations outlined" (and as referred to above). "A more definite approach designed to measure mortality directly during short intervals of times is needed, and experiments must be repeated often enough to describe annual variability." With this we sincerely concur. It presents an exciting challenge to future salmon researchers.

SUMMARY OF SOCKEYE MORTALITY IN ALL LIFE-HISTORY STAGES

Having reviewed all the pertinent data available to us concerning the several stages of the life cycle and having noted the extent of the losses that occur in each, consideration may be given again to the hypothetical mortality tabulation which had been initially prepared (see page 67) as a guide to indicate where and when the heavy losses took place in the life cycle of the fish. The original intention was, it may be recalled, to set up this hypothetical chart and, then, to revise it in accord with more precise data as obtained from specific investigations or observations. Having regard, however, for the magnitude of the variations which have been found to occur (chiefly as brought about by prevailing environmental conditions) it is questionable whether any real improvement in, or correction of, the hypothetical estimate can be justified. The tabulation is, therefore, reproduced again with appropriate notations, as follows:

	Mortality	Survivors
1. Initial potential egg deposition[1]		2,000,000
2. Loss during upriver adult migration—5%[2]	100,000	
Potential egg deposition reduced to:		1,900,000
3. Loss during spawning and incubation—50%[3]	950,000	
Resulting number of alevins hatched:		950,000
4. Loss during fry emergence and migration to lake—75%[4]	712,500	
Number of fry entering lake:		237,500
5. Mortality during lake residence—92%[5]	218,500	
Seaward migrants produced:		19,000
6. Natural mortality in ocean—90%[6]	17,100	
Adults returning from the sea:		1,900

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[1] Assuming a run of 1,000 sockeye, with the sexes equally represented; egg content of each female—4,000.

[2] Still a rather hypothetical figure, subject to great increase if and when severe obstructions or unusual climatic conditions occur—see p. 97.

[3] Includes wide variation in (a) eggs retained in females: 0.2–13.8%, p. 142; (b) losses in eggs and alevins: 1.7–99%, p. 148.

[4] In two studies the results were based on thread-marked fry. Mortality of these fry may have been greater than would prevail among normal fry (see text, p. 157). Range of mortality: 12.6–91%, p. 160.

[5] Again wide variations occur. Lake survival findings range from 3.6% in Midarm Lake to 84% in Port John Lake, p. 310, 311.

[6] Here only the British Columbia data (p. 365) have been used. If the survival rates for the large Karluk Lake and Lake Dalnee smolts were incorporated, they would not alter the final percentage adult return greatly, only from 90 to 85% (see p. 367).

The final return of 1900 adults represents a total survival from the initial egg deposition of 0.095% or, roughly, 0.1%. On the basis of the numbers of fish involved it represents a return of, roughly, two adults for each spawner.

Consideration of the mortality chart reveals that, for application to any specific river system or sockeye-producing area within a river system, important adjustments will be necessary. For example, it has been shown that at Karluk Lake, Alaska, the average return of sockeye (1.8 per spawner, Table 10) has been close to the hypothetical 1.9 shown in the chart. However, the losses during the fresh-water period of the life cycle are appreciably greater (p. 324) than the figures indicated on the chart. It follows that at some other stage of the life cycle, survival must be greater; and in fact during ocean residence (Table 102) it is 21.55%, much higher than the 10% shown on the chart.

Similarly, for the Fraser River (Table 7), the catch to escapement ratio, over 23 years, has been, on average, 1:0.33. This suggests, with no radical change in production occurring, a return of four adults for each spawner—double the ratio given in the chart. Therefore, there must, during some phase of the life cycle, be a greater survival than indicated on the chart.

Each river system, and perhaps each branch of it, will have ecological characteristics of its own which will cause it to vary, in efficiency of sockeye production, from the average here presented in the mortality chart. If within the area there is produced a substantial salmon fishery, sufficient to warrant scientific management, an appropriate mortality chart for it should be assembled in order to assess where the natural production is weak and where it might be advantageously improved.

Thus, as quoted earlier (p. xv) "hopes for continued abundance of salmon to support a flourishing industry and to maintain an important food resource seem to hinge on our ability to develop a sort of semi-cultivation of salmon" (Neave and Foerster, 1955, p. 437). If, (1) by ensuring an appropriately large and orderly movement of spawning sockeye upriver and on to the spawning beds, if (2) these latter can be assured a steady flow of good quality water and no interference from freshet or drought, and if (3) the depredations by predator fish, etc., on sockeye alevins and fry can be substantially reduced, the increase in sockeye production can be most appreciable. A 50% reduction of the rate of loss occurring at each stage between egg deposition and the entrance of the fry into the lake—items 2, 3, and 4 in the chart—would bring about a 440% increase in fry produced. To what extent a so much greater influx of fry into a lake would tax the feeding capacity of the lake would have to be considered. There are a number of ways in which this contingency could be successfully met. Again, the experiments conducted at Cultus Lake indicated that, by reduction of the numbers of predator fish in the lake, sockeye survival at this stage could be greatly increased. Any increase in lake survival means a greater recruitment of smolts to the ocean sockeye population. In the ocean the pastures are thought to be vast, both in extent and quantity of food. No limits to the productive capacity, so far as salmon are concerned, have been discovered. Thus, so far as we at present know, the greater the recruitment of smolts the greater the numbers of adult fish returning from the sea.

Chapter 12. The identification of stocks of sockeye salmon in the North Pacific Ocean

With the development in recent years (particularly since 1954) of a high-seas fishery for salmon by Japanese fishing fleets in the North Pacific region, attention became focussed on just what stocks of fish were thus being exploited. Prior to this extension of the salmon fishing grounds, by means of motherships and attendant catcher boats, fishing had been confined largely to coastal areas as the salmon moved in from the open ocean to ascend the rivers for spawning. To a large extent this coastal fishing could be associated with the spawning runs to adjacent river systems and the fishing operations thus regulated in order to assure a suitable escapement of spawners to the spawning grounds.

As the high-seas fishery expanded, the runs of salmon returning to Kamchatka and Alaska rivers declined (Alperovich, 1957; Semko, 1958; Krogius, 1961b; Egorova et al., 1961). This led to the establishment of (1) negotiations between the USSR and Japan concerning the amount of salmon to be taken by the Japanese fishing fleets in the western North Pacific and (2) the International North Pacific Fisheries Commission by Canada, Japan, and the United States, for the conservation of the fisheries resources of the North Pacific Ocean. In both instances one fundamental requirement was to determine what stocks of salmon of Asiatic and American origin were present in the various regions of the North Pacific, what areas they frequented at various times of the year and whether these areas overlapped, i.e., where and when the Asian and American stocks intermingled.

Five methods have been used in an effort to identify the stocks of sockeye present in and caught in various sections of the North Pacific. These consisted of (1) tagging at sea and subsequent recovery in the coastal fisheries, (2) studies of the parasites of the fish, (3) morphological studies, (4) serological studies, and (5) scale studies.

TAGGING AT SEA AND SUBSEQUENT RECOVERY

Tagging involves the affixing of readily observable metal or plastic discs on the fish at time of capture in the fishing areas, the speedy release of the fish in good condition and the recapture of the tagged individuals again in the coastal fisheries or in the rivers. Special research vessels were usually assigned to the tagging work. Initially gill nets were used to capture the fish but it was difficult to obtain fish in good condition for tagging. Mortality of the tagged individuals was heavy. After due experimentation purse seining was adopted by United States investigators (Hartt, 1962), while the Japanese (INPFC, MS, 1958, p. 63; MS, 1959, p. 65; 1960, p. 63) and, later, the Canadians (INPFC, 1961, p. 29) used baited longlines quite effectively.

The high cost of purse seine operation and the difficulty in catching fish where the concentrations were low made it necessary to conduct purse seining in only those areas where salmon were abundant. Therefore, United States taggings were confined largely to the waters north and south of the Aleutian Islands, in the Gulf of Alaska, and in the Bering Sea. For Japanese and Canadian taggings, the ocean catches were much more widespread (INPFC Annual Reports, 1958–61).

It is only to be expected that, as the oceanographic conditions which influence the distribution of salmon vary from year to year and within each year, differences will show up in the tag returns from year to year depending on the ocean conditions prevailing and on the time of tagging. Thus, for United States taggings in 1956, 1957, and 1958 (reviewed by Hartt, 1962) in the vicinity of the Aleutian Islands, in which 2825 mature and 6457 immature sockeye were tagged, the recoveries of mature fish—182 in all or 6.4% (Hartt, 1962, table VIII)—indicated that sockeye, subsequently recaptured in Bristol Bay or obviously migrating there, had been encountered and tagged "as far west as experiments were conducted (173°E), although numbers tagged in the westermost were small" (Hartt, 1962, p. 90). Recovery of individuals caught and tagged as "immatures" one or two seasons prior to recapture revealed much the same ocean dispersion, although recoveries in 1957 of immatures tagged in 1956 were made as far west as 165°E long (Fig. 77 and 78). It appeared that in 1957 sockeye of Bristol Bay origin occurred further west than in other years, thus emphasizing that ocean distribution may vary quite appreciably from year to year, according to prevailing oceanographic conditions.

No data were obtained on the eastward dispersion of Asiatic sockeye. Hartt (1962, p. 90) remarks that "the presence of red salmon of Asian origin as far east as 180° was suggested, however, by the return of three fish from the high-seas fishery well to the west of the tagging locations." Furthermore, only one tag recovery was made east of 165°W and south of the Aleutian Island chain, namely at Chignik on the south side of the Alaska Peninsula (158°W). This suggested that sockeye produced in streams emptying into the Gulf of Alaska or along the west coast of North America do not occur in Aleutian waters. Limited tagging in the Gulf of Alaska showed the presence of Fraser and Skeena River sockeye as far west as 154° W, that is, in the western section of the Gulf.

Tagging work in 1959 and 1960 (INPFC, 1960, 1961) tended to confirm previous findings, as shown in Fig. 90, 91, 92, and 93. From the Gulf of Alaska, seven tagged sockeye were recovered in the Bristol Bay area (Naknek River) and one in Johnstone Strait, while in 1960, one sockeye tagged as an immature in 1958 south of Kodiak Island was returned from a cannery at Blaine, Washington, perhaps en route, when captured, to the Fraser River.

Taggings conducted by Japanese investigators (INPFC Annual Reports for 1956–60) in Aleutian waters have, in general, corroborated the United States results, namely, a movement of the fish to Bristol Bay areas. For taggings in the west-

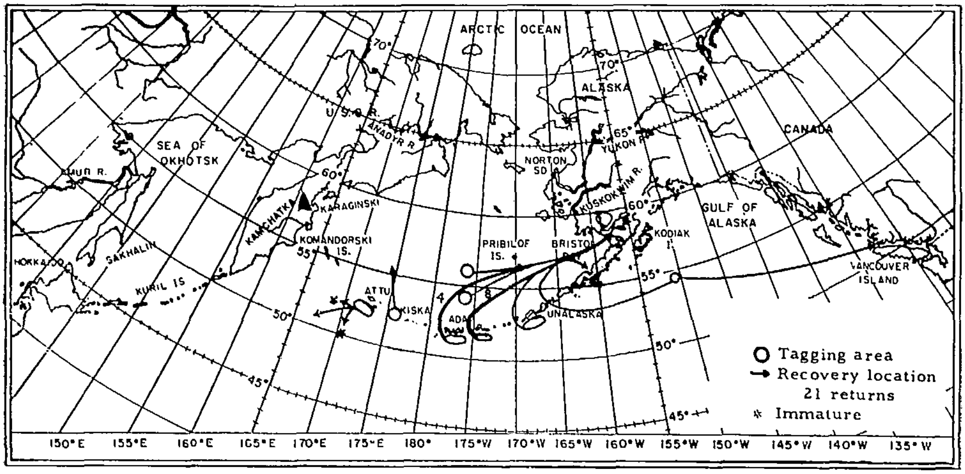

FIG. 90. Recovery distribution of sockeye salmon tagged in 1959 and recovered in 1959. (From INPFC, 1960, fig. 36.)

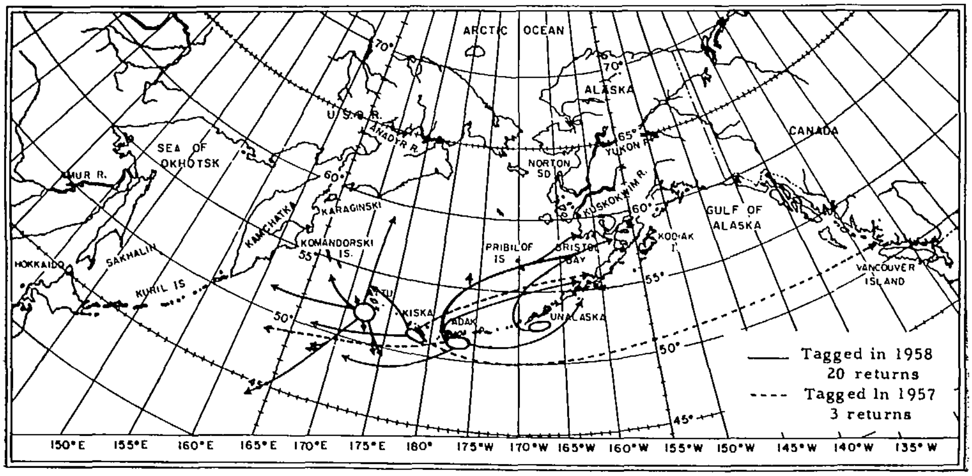

FIG. 91. Recovery distribution of sockeye salmon tagged in 1957 and 1958 and recovered in 1959. (From INPFC, 1960, fig. 37.)

ern North Pacific, off Kamchatka, returns have shown a general movement to the Kamchatka coast, even from as far to the east as 180°, south of Kiska Island.

Interesting results have attended tagging operations conducted by Canadian investigators in the eastern North Pacific where the work has been largely concentrated. In Fig. 94 is shown the general pattern of recoveries from the tagging in 1961 of 605 sockeye (INPFC, 1962, p. 29). Only 58 tags (9.6%) were returned —from coastal areas extending from southern British Columbia to Unimak Island and Bristol Bay, Alaska. It is remarked that:

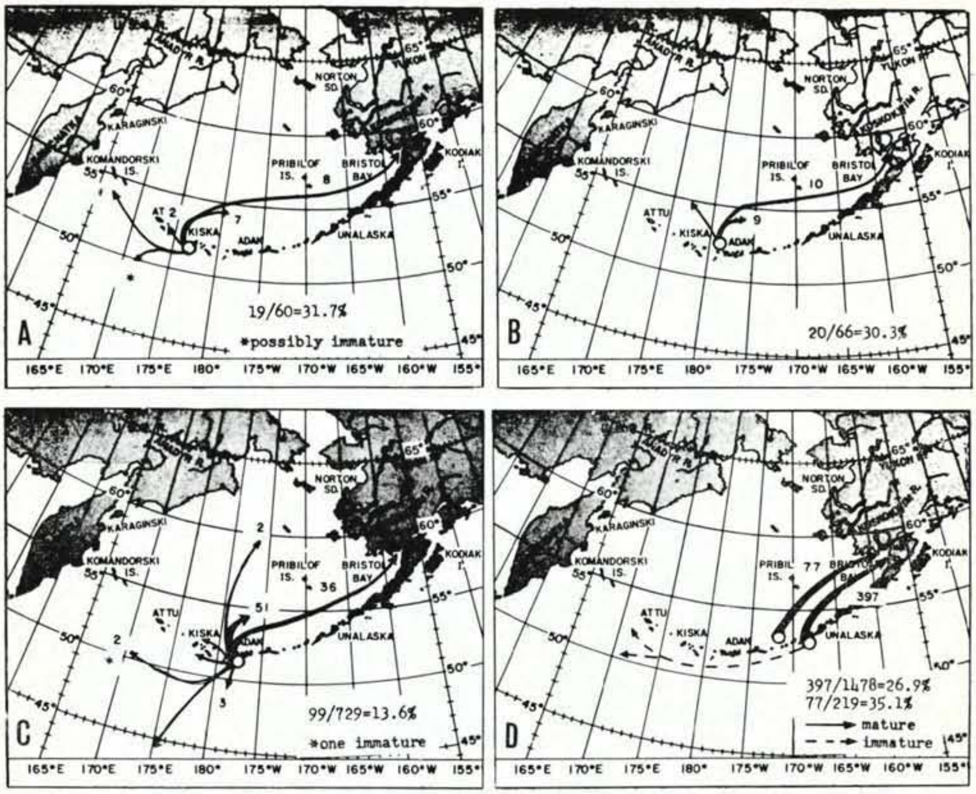

FIG. 92. Recovery distribution of sockeye salmon tagged and recovered in 1960 (A—tagged May 18-31; B—June 14-16; C—June 1-20; D—June 9-July 2). (From INPFC, 1961, fig. 34.)

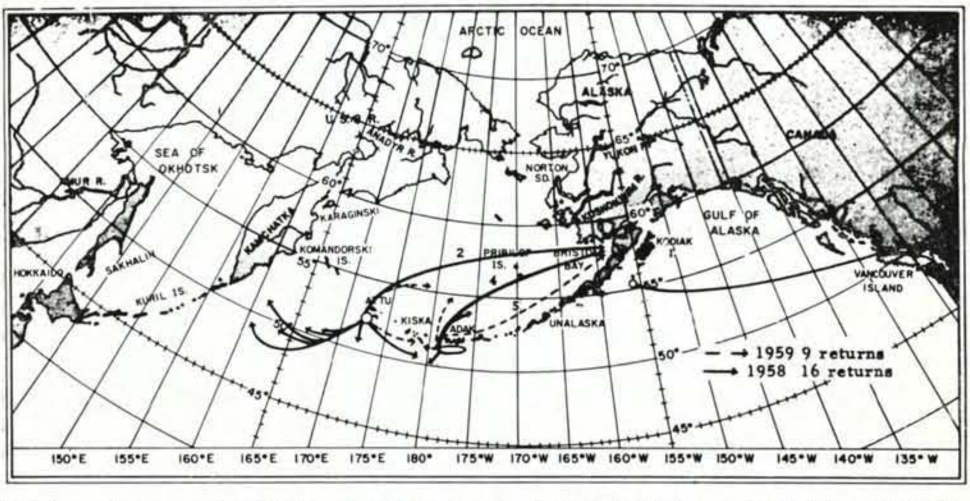

FIG. 93. Recovery distribution of sockeye salmon tagged in 1958 and 1959. (From INPFC, 1961, fig. 35.)

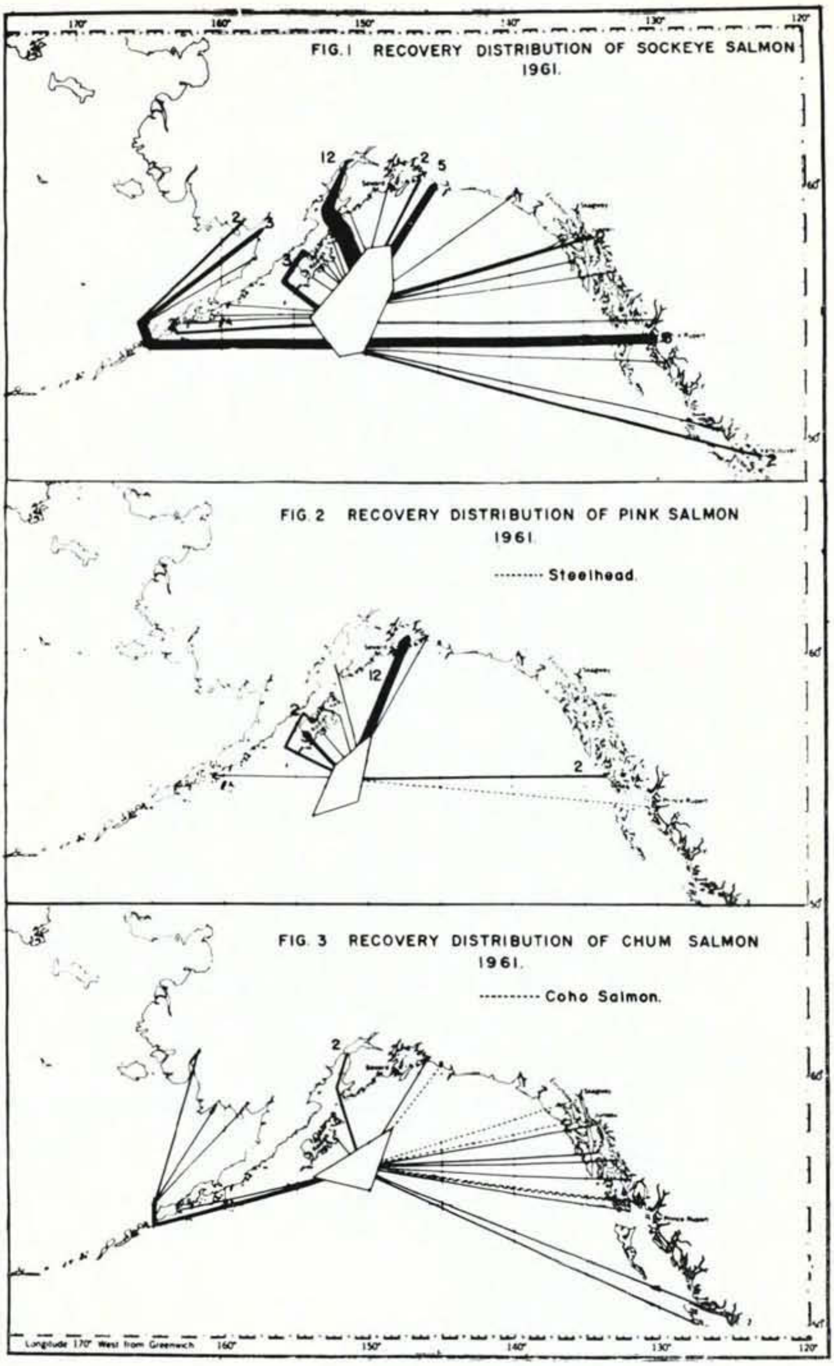

FIG. 1 RECOVERY DISTRIBUTION OF SOCKEYE SALMON 1961.

FIG. 2 RECOVERY DISTRIBUTION OF PINK SALMON 1961.

········· Steelhead.

FIG. 3 RECOVERY DISTRIBUTION OF CHUM SALMON 1961.

·········· Coho Salmon.

FIG. 94. The general pattern of recoveries of sockeye salmon tagged by the Canadian vessel *Fort Ross* in the area south and east of Kodiak Island in the Gulf of Alaska in 1961. (From INPFC, 1963, p. 29.)

> "although 11 tags (19% of the recoveries) were reported from Canadian waters, only three could be associated with the important sockeye runs to southern British Columbia. These three (one caught in the Johnstone Strait area and two found in tributaries of the lower Fraser River) were somewhat atypical for this region in that they were five years old. No recoveries were received from the Rivers Inlet and Smith Inlet fisheries which caught over a million sockeye in 1961. This suggests the possibility that the north-south distribution of British Columbia stocks is maintained to some degree in their high-seas distribution and that the Rivers Inlet and Fraser River sockeye in the Gulf of Alaska in 1961 were mainly south of Latitude 54°N."

The results of Canadian tagging operations in 1962 and 1963 have been discussed and are shown pictorially in fig. 25–34 of the Annual Report for 1963 of the International North Pacific Fisheries Commission (INPFC, 1964). The concentration of North American sockeye continues to be evident in the Gulf of Alaska. Sockeye salmon from more southerly rivers seem to be resident in the more southerly regions of the eastern North Pacific. More information is needed to substantiate this phenomenon. It seems fairly clear, though, that British Columbia sockeye salmon are to be found in the Gulf of Alaska area, in the rich feeding grounds associated with the Alaska Gyral (Fig. 78).

INTERNAL PARASITES

The possibility that internal parasites of sockeye salmon might constitute "natural markers" of the geographical origin of these fish, when caught in the open ocean, was early recognized by the scientists involved in the researches of the International North Pacific Fisheries Commission. Of more than 50 species of parasites found to occur in sockeye (INPFC Annual Report for 1956, p. 39–44), only two subsequently proved to be "useful indicators of the origin of some stocks of sockeye" (Margolis, 1963). These were *Triaenophorus crassus*, found in western Alaskan sockeye (particularly of Bristol Bay origin), and *Dacnitis truttae*, which occurs in some sockeye of Asian origin. Examination of thousands of sockeye caught on the high seas by the Japanese fishing fleet and by Japanese, United States, and Canadian research vessels, 1955–59, has shown (Fig. 95) the presence of *Triaenophorus*-infected sockeye as far west as 170°E while *Dacnitis*-infected Asian sockeye were taken as far east as 170°W.

MORPHOLOGICAL CHARACTERISTICS

Another method devised to identify at least the continental origin of sockeye captured on the high seas, if not the more precise river origin, was that initiated by United States scientists in which certain morphological characters could be examined and the differences analysed by the "discriminant function" method. This, according to Fukuhara et al., (1962, p. 20) is "one of the best methods of differentiating racial stocks and of describing their relation to one another."

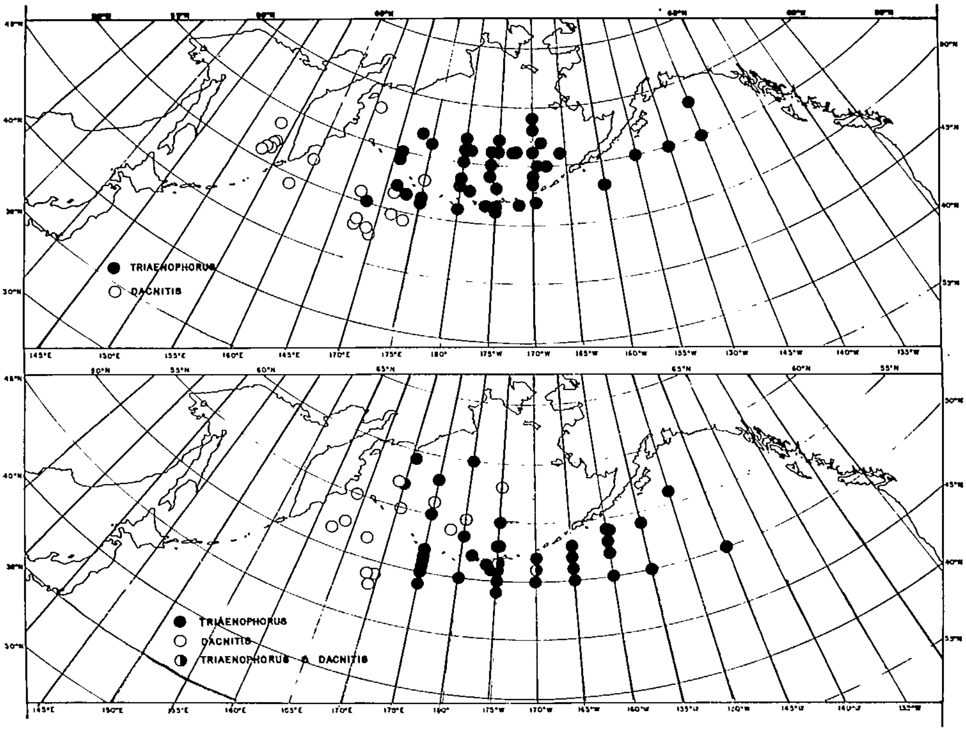

FIG. 95. High-seas locations of catch of *Triaenophorus*-infected and *Dacnitis*-infected sockeye salmon from 1955–59. *Upper chart*—maturing sockeye; *lower chart*—immature sockeye. (From Margolis, 1963, fig. 21.)

Seven morphological characters were used:

(1) the total number of scales along the lateral line,
(2) the total number of vertebrae,
(3) the position of the first complete haemal arch,
(4) the number of gill rakers on the ventral arms of the first left gill arch,
(5) the total number of gill rakers on the first left gill arch,
(6) the number of pectoral fin rays,
(7) the number of anal fin rays.

The extent to which differences in morphological characters can be used to distinguish populations depends primarily on the amount of information available concerning the sockeye of each river system or coastal areas and, secondly, on how wide and how prominent the differences are between them. There must be available, for proper differentiation between river stocks, sufficient material to indicate the natural variations in the several characters to be examined and to set up a usable average value. The more pronounced the differences between these average values the more readily the racial or stock identifications can be made.

Although pertinent data for separation of stocks were obtained from all major river areas of the North Pacific, the problem of separating North American and Asian stocks in the high-seas fishery appeared to concern principally those populations originating in the Bristol Bay and Kodiak Island areas, on the American side, and in the Kamchatka-Okhotsk Sea areas, on the Asian side. Therefore, sample fish from these two main areas were used as standards in the "discriminant function" analysis. On this basis, "in general, during June a substantial percentage (greater than 70 per cent per sample) of mature North American red salmon apparently occur on the high-seas as far west as longitude 178°E, this percentage diminishing to 43 and 27 as far west as 163°E. Mature southwestern Kamchatka red salmon dominated the samples as far east as longitude 175°E. From lack of samples between 175°E and 175°W, south of the Aleutians, no inference can be derived concerning the extent of the eastward distribution of southwestern Kamchatka red salmon" (Fukuhara et al., 1962, p. 50). It was pointed out that when samples from North American areas other than Bristol Bay, Kodiak Island, and Chignik River were classified, using this discriminant function, they would be more likely classified as Asian fish, since the probability of misclassification was very much greater with the Kamchatka-Okhotsk Sea standard than with the North American one.

SEROLOGICAL STUDIES

Early in the investigations of the International North Pacific Fisheries Commission the possibility of distinguishing races or stocks of sockeye by means of the difference in serological reactions of the sockeye's blood was given consideration by both United States and Japanese scientists. By using antisera absorption tests, promising results were obtained (INPFC Annual Report for 1957, p. 46, 66). Further study revealed that differences in the strength of reaction of the cells of individual sockeye with pig sera occurred which seemed to be genetically controlled (Ridgway, Cushing, and Small, MS, 1961) and that antiserum produced by injecting rabbits with sockeye salmon sera reacted with most (96.8%) of the samples of serum taken from sockeye of many North American streams quite differently to samples (92.1%) taken near Kamchatka (Ridgway, Klontz, and Matsumoto, 1959).

Nevertheless, even though blood group differences among Pacific salmon had been found (Ridgway and Klontz, 1960), which might serve as "markers of racial identity," difficulties in handling and storing blood samples taken from salmon caught on the high seas were encountered. For this reason, further study will be required on the possible effect of sampling, preservation, etc. (INPFC Annual Report, for 1960, p. 98).

In serological researches by Japanese biochemists (INPFC Annual Report for 1958, p. 61–63), three separate groups of samples were distinguished in sockeye taken from the western North Pacific and Bering Sea regions. Those samples "taken from south of the Aleutian Islands belong to a different origin from that of the samples from the Bering Sea and are more closely related to the samples from Kamchatka waters" (INPFC Annual Report for 1958, p. 63).

SCALE STUDIES

Early in his investigation of the sockeye salmon runs to British Columbia rivers, Gilbert had noted, in his scale studies, that "one of the most variable features is the size of the nuclear area itself and the number of rings it contains, both being roughly proportionate to the size of the yearling at the period of seaward migration" (Gilbert, 1915, p. 49). This variability he attributed to differences in growing conditions prevailing in the nursery lakes and, when scale samples became available from the more important individual spawning areas, it was possible to associate certain ring or circulus counts in the nuclear or freshwater area of the scales with certain nursery lakes, that is, with the contiguous spawning areas.

The possibility, then, of identifying certain stocks or races of sockeye within a river system by means of the 1st-year circulus counts was recognized and, for the Fraser River, this has been put into practice (Clutter and Whitesel, 1956). Since the number of circuli varies from year to year, in accord with growth conditions (amount of plankton, numbers of young sockeye in the feeding population), it is necessary to know, for identification of the adults each year, the range of variation and the average circulus count for the brood year seaward migration. This means that each year the seaward migration must be sampled and the numbers of circuli on the scales determined both for range of variation and average number. Careful study was made of various factors involved in selecting the most suitable scales for examination and how they should be read or measured. The following conclusions were reached:

(1) When scale samples are taken in the commercial fishery, about 200 samples of readable scales will suffice where only one spawning stock or race is present. If two or three stocks are present, the sampling should consist of 200 scales/day. If the run embraces a complex of stocks or races, around 400 scales are desirable.

(2) When samples are taken from a commercial fishery, due consideration should be given the possible selective action of the fishing gear.

(3) For age determination only, scales may be taken from any part of the adult fish's body. For racial studies and comparative growth analysis the scales from near the lateral line and in the zone below the dorsal and adipose fins are used. Actually, since 1952 *one* scale only has been taken, by the International Pacific Salmon Commission's scale samplers (Clutter and Whitesel, 1956, p. 48), from each fish, "selected from the diagonal scale column which extends backward and downward from the insertion (posterior) of the dorsal fin and on the second horizontal row above the lateral line." Where possible, the scale is taken from the left side of the fish, though no difference was found in sample scales taken on either right or left sides.

(4) When scales are taken from smolts, four scales are taken from the body area immediately posterior to the insertion (posterior) of the dorsal fin and in the first two rows above the lateral line. All four scales are examined and the most clearly impressed and regular scale is used (Clutter and Whitesel, 1956, p. 25).

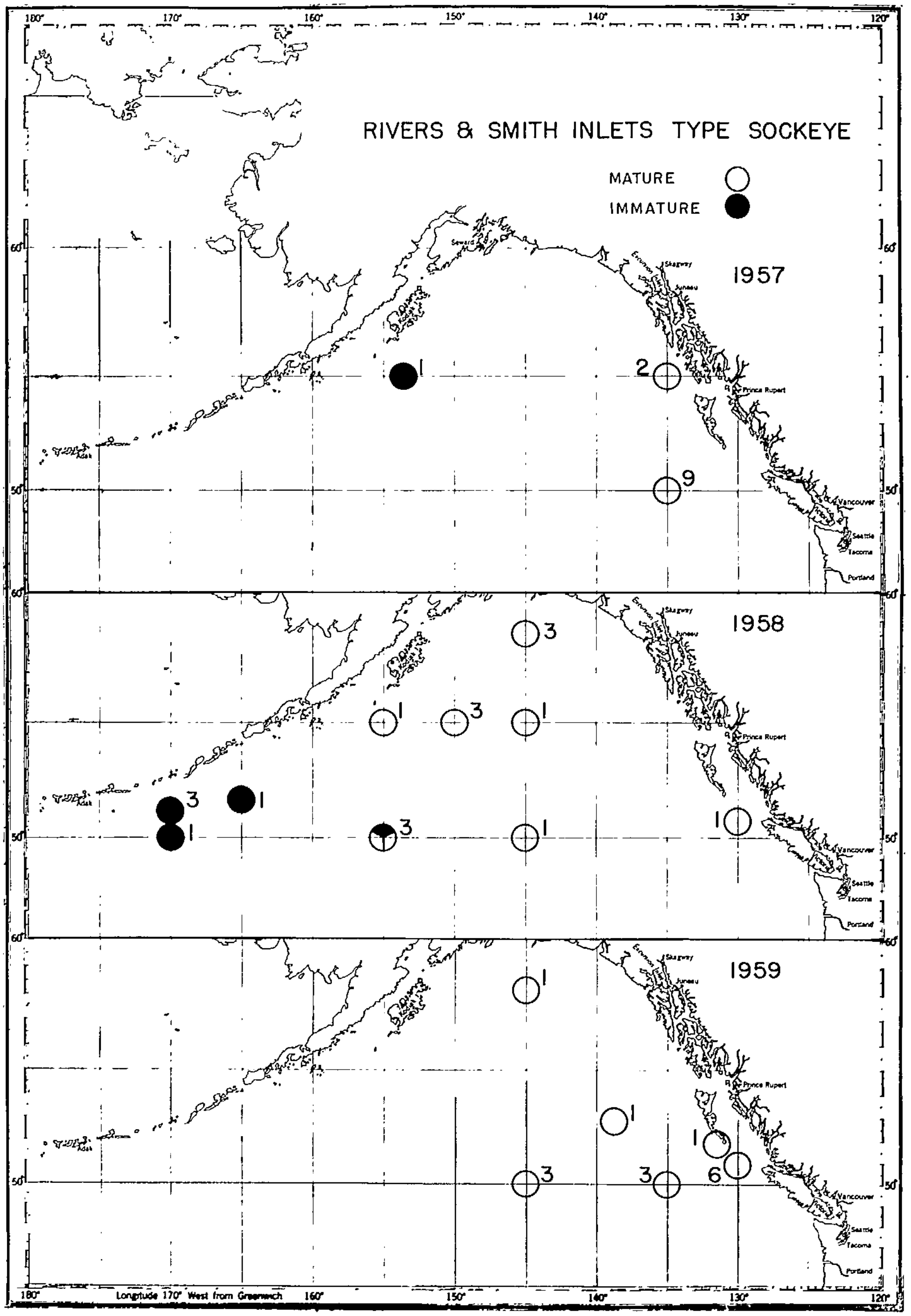

FIG. 96. Location and number of sockeye found to have had Rivers and Smith Inlet type scales when caught in the Gulf of Alaska in 1957, 1958, and 1959. (From INPFC, 1961, fig. 3, p. 32.)

(5) Enumeration of circuli and measurement of scale radius, scale diameter or scale area are all accurate in representing juvenile growth but, specifically, enumeration of circuli along the ventral 20° radial line of the scale is most efficacious. Radius measurement would, however, be more efficient in measuring sea growth (Clutter and Whitesel, 1956, p. 154) and avoid the somewhat tedious task of counting circuli.

(6) Modern techniques are, of course, now employed in preparing scales for study. Instead of the original scale being used, plastic impressions are now made, as outlined fully by Clutter and Whitesel (1956). This greatly facilitates handling and examination of the scale collections and, where necessary, extra impressions of scales can be made for study by other readers, as and when required.

All of these developments in collecting, mounting, and reading scales represent a notable advance in formulating "standards" whereby uniformity in techniques and in interpretation can be achieved. This becomes extremely important as the use of scales to measure comparative growth and to identify races or stocks becomes more general, is more widely accepted, and is adopted for purposes of (1) regulating the commercial fishing effort on particular populations or within a river system, as practised by the International Pacific Salmon Fisheries Commission on the Fraser River, or (2) identifying stocks of fish in the open ocean—a prime objective of the International North Pacific Fisheries Commission. It is of importance to each nation exploiting, in effective manner, stocks of sockeye throughout the North Pacific to know where the fish from their river systems go in the sea, how they are distributed, and where they tend to congregate during ocean residence.

Progress in tracing the distribution, on the high seas, of Asian and North American stocks is being made, as reported in the Annual Reports of the International North Pacific Fisheries Commission. More precise breakdown of the distribution of individual stocks must await further careful study of scale peculiarities and markings. To date an example of what may be achieved eventually is available from a study of the occurrence in the open ocean, of individuals from one area along the Canadian Pacific coast, the scales of which it has been possible to recognize, namely, Rivers Inlet, British Columbia. The distribution, as reported (INPFC, 1961, p. 32), is shown in Fig. 96.

Krogius (1958) began studies in 1955 to ascertain the practicability of identifying, in the ocean or on the spawning migration to the various Kamchatka rivers, the origin of the sockeye—that is, where they spawned and where they spent their early freshwater period of life. These studies embraced those stocks from the different spawning areas of the Kamchatka Peninsula, which were best known or which were of greatest significance in the propagation of the species (Krogius, 1958, p. 52). The criteria used were

(1) The number of circuli laid down each year in fresh water and in the sea. For the years in the ocean, the "summer" and "winter" circuli were counted separately.

(2) The size (radius) of the scale at the end of each "winter" band.

(3) The character of the circuli, that is, straight, crooked, broken, forked, etc.

(4) The shape of the scale, that is, oval or circular.

TABLE 103. Characteristics of sockeye scales (from Krogius, 1958, p. 54 & 55).

A. Zone of freshwater period of growth

No. of seasons spent in fresh water	Spawning area	Contour of circuli	No. of circuli			Characteristic features
			1-yr	2-yr	3-yr	
Less than one year	"Spring" sockeye (*azabachi*). Kamchatka, Paratunka, other rivers.	Regular[a] Wide	4–8	–	–	
One year	Kamchatka R.[a] Palana R.	Regular	10–16	–	–	Circuli narrow; the whole zone takes up 9–13% of the scale radius.
One year	Pylga R. (Apuka system)	Regular	10–16	–	–	Circuli narrow; the whole zone occupies 9–13% of the scale radius; many "winter" sclerites.
One year	Dalnee Lake	Regular	12–23	–	–	Circuli wide; whole zone occupies about 15–20% of scale radius.
One year	Bolshaya R.	Irregular[b]	5–10	–	–	Circuli narrow.
One year	Blizhnee Lake	Irregular	9–15	–	–	An accessory band of from 4–7 circuli in the centre of the scale.
Two years	Kamchatka R. Pylga R.	Regular	5–10	10–24	–	Circuli narrow; the whole zone making up 14–18% of the scale radius.
Two years	Dalnee Lake	Regular	6–23	10–24	–	Circuli wide; the whole zone—around 20–30% of scale radius.
Two years	Blizhnee Lake	Irregular	9–13	5–9	–	In the centre of the scale an accessory band of from 4–7 circuli.
Two years	Ozernaya R. Kykhtya R.	Irregular	5–8	9–13	–	Circuli wide; whole zone occupying around 40% of scale radius.
Three years	Dalnee Lake	Regular	5–15	5–15	5–15	Circuli wide; whole zone occupying around 40% of scale radius.
Three years	Kamchatka R.	Regular	5–8	5–8	5–8	Circuli narrow; whole zone occupying around 20% of scale radius.
Three years	Ozernaya R. Kykhtya R.	Irregular	5–8	5–8	5–8	Circuli narrow; whole zone occupying 17–20% of scale radius.

(Continued.)

TABLE 103. Characteristics of sockeye scales. (Concluded.)

B. Zone of ocean period of growth

Spawning area	Contour of circuli	No. of circuli 1 yr	No. of circuli 2 yr	Characteristic features	Shape of scale
Dalnee Lake	Regular	–	–	Usually not a clear boundary between "winter" and "summer" circuli.	Oval, elongated
Blizhnee Lake	Regular	10–20 zone small	7–10	Usually not a clear boundary between "winter" and "summer" circuli.	Circular
Kamchatka R.	Regular	10–20 zone small	10–18	"Winter" circuli clearly separated from "summer".	Oval, elongated
Pylga R. (Apuka R.) Paratunka R.	Regular	17–25 zone large	10–15	"Winter" circuli clearly separated from "summer."	Circular
Palana R.	Not irregular but split or fusing	10–18 zone small	5–16	Circuli not clear.	Oval
Bolshaya R.	Not irregular but split or fusing	16–23 zone large	–	2 or 3 narrow circuli, similar to an accessory band lying between the first "summer" and the clearly marked band of "winter" circuli.	Oval
Ozernaya R. Kykhtya R.	Irregular, discontinuous	14–19 zone small	7–17	"Winter" circuli clearly separated from "summer."	Circular

[a] The expression "Contour of circuli regular" means that the circuli have an equal, uniform spacing and are continuous, normal ovals.

[b] The expression "Contour of circuli irregular" means that the circuli are broken and crooked and the spacings are of irregular widths with crooked margins.

Although the early studies were considered insufficient for a complete understanding of the characteristic features of the scale pattern, they did serve to indicate the principal types of scale patterns, as indicated in Table 103. For general use it was proposed to prepare an atlas containing, in addition to the pertinent data as described above, photographs of the scales for all age-groups.

SUMMARY OF RACIAL "IDENTIFICATION" STUDIES

By two different but complementary methods, the dispersion of the many stocks of sockeye throughout the "salmon waters" of the North Pacific Ocean is being followed. By tagging, the fish are "marked" at certain locations in the ocean where they are captured in live condition by appropriate fishing gear and their subsequent movements or migration checked as they are recaptured either (1) still at sea, (2) moving toward coastal waters, (3) in coastal waters, or (4) in their natal spawning rivers. The activities of individual fish, then, can be readily followed and the routes of migration of specific ocean groups of sockeye back to their rivers of origin can be traced. A great many fish have to be tagged in order to assure a large enough recovery to reveal significant migration patterns. As reported by Hartt (1962, p. 56) for mature sockeye tagged in the Aleutian Islands area, 1956–58, tag recoveries ranged from 5.3% in 1956, to 7.8% in 1957, to 17.1% in 1958—an overall recovery of 10.1%. Approximately 90% of the tagged fish were retaken in the concentrated Bristol Bay fishery or in the adjacent streams.

The other procedure attempts to identify the individual sockeye at time and place of capture in the ocean. It is based on the recognition of particular features which denote the racial origin of the fish; these include morphological characteristics, blood serum constituents, scale nucleus pattern, or the place of rearing and early freshwater growth—such as the presence of particular internal parasites, scale pattern revealing growth rate. The racial origin of individual sockeye can, then, be ascertained no matter where and when the fish are caught. This is similar to the "marking" technique of earlier years (see p. 19) which is of very limited usefulness because of the relatively high mortality rate involved and the small number of fin combinations that can be removed.

Further refinement of salmon identification techniques is anticipated. The need for knowing the range of ocean distribution of the sockeye from individual river systems is urgent. Then one can assess the conditions which the fish must face and their effect on growth and survival. One may even devise a technique for assessing abundance, thus establishing an early index of the extent of coastal or river-estuary fishing upon each river stock.

Chapter 13. Artificial propagation and other management measures for sockeye

SOCKEYE HATCHERIES WITH SPECIAL REFERENCE TO THE CULTUS LAKE STUDIES

History of Sockeye Hatcheries in British Columbia

From quite early days in the history of the sockeye salmon fishery of British Columbia there was keen interest in and enthusiasm for artificial propagation as a ready means of improving upon nature's method of salmon production and of providing assurance against the adverse, destructive effects of commercial fishing. The evidence, at that time presented by fish culturists, seemed to indicate quite clearly that, by hand-stripping the ripe fish and rearing the eggs in hatcheries, a very high production of young fish could be assured whereas, in nature, losses were exceedingly high and hatch of fry very, very low.

In 1894 the first hatchery came into operation on the Fraser River, at New Westminster, sockeye eggs being brought down to it from collecting sites in lower Fraser tributaries. In succeeding years the number of hatcheries increased as follows, the date of establishment indicated in parenthesis:

Fraser River: Harrison Lake (1905), Pemberton (1906), Stuart Lake (1908), Cultus Lake (1916), Pitt Lake (1917);
Rivers Inlet: Owikeno Lake (1906);
Skeena River: Lakelse Lake (1903), Babine Lake (1908);
Vancouver Island, west coast: Anderson Lake (1911), Kennedy Lake (1911).

The egg-carrying capacities of these hatcheries varied but the extent of their operation may be judged from Table 104 which shows the egg collection for the 1918–32 period. All of these hatcheries were located in areas where good spawning runs of sockeye occurred. The spawners from which eggs were taken and fertilized for hatchery incubation represented, generally, only a part of the spawning run. The remainder, often much the major portion, was allowed to spawn naturally.

Despite these hatchery operations, no real, consistent benefit seemed to be evident. It was impossible to determine what effect the hatcheries had had in maintaining the runs or in increasing them, since so much natural spawning was also going on in the same areas, varying greatly in extent from year to year and fluctuating greatly in production of fry. The general consensus may be summarized in the words of the Royal Commission on British Columbia Fisheries of 1922:

TABLE 104. Sockeye salmon egg collections (in millions of eggs) made each year at each of the ten hatcheries operating in British Columbia during the 1918–32 period. Data extracted from Federal Department of Fisheries Annual Reports on Fish Culture.

	Fraser River						Skeena River		Vancouver Island		
Year	Pemberton Lake	Pitt Lake	Harrison Lake[a]	Cultus Lake[b]	Stuart Lake[c]	Rivers Inlet	Lakelse Lake	Babine Lake	Anderson Lake	Kennedy Lake	Total egg collection per year
1918	11.9	3.6	1.9	3.1	–	3.0	–	9.1	2.5	2.5	37.6
1919	30.7	3.9	7.5	10.5	7.4	11.5	–	17.1	9.1	9.0	106.7
1920	26.0	4.4	4.9	1.2	4.4	12.1	7.7	9.4	10.1	9.6	89.8
1921	26.0	2.7	0.7	4.3	5.5	18.4	4.3	11.6	10.0	1.9	85.4
1922	26.0	3.5	2.1	3.2	4.0	14.5	8.0	7.0	6.0	9.0	83.3
1923	30.6	3.4	15.3	5.2	–	15.4	10.2	8.4	8.5	5.3	102.3
1924	31.2	5.7	6.7	5.1	–	16.0	8.6	8.4	8.5	10.5	100.7
1925	40.4	5.3	–	–	–	18.7	11.2	7.2	8.5	8.7	100.0
1926	45.4	5.0	–	6.4	–	19.8	15.7	7.7	8.5	8.7	117.2
1927	37.0	5.2	3.9	–	–	20.6	3.5	12.8	8.6	3.3	94.9
1928	35.0	5.6	–	32.6	–	14.0	5.5	9.1	8.8	2.8	113.4
1929	18.0	5.3	0.2	11.1	–	20.0	8.2	7.8	8.5	7.5	86.6
1930	35.2	5.9	3.4	–	0.5	19.2	8.3	8.7	6.9	9.2	97.3
1931	20.4	2.7	–	39.4	–	20.0	6.3	7.8	6.2	5.2	108.0
1932	22.7	4.0	–	5.4	–	16.6	5.8	6.2	7.5	7.7	75.9

[a] In 1925, the Harrison Lake hatchery was found to require quite extensive repair. Operations were thus terminated, though some of the facilities were renovated in order that it might be used as an auxiliary eyeing station when required.

[b] From 1925 hatchery operation at Cultus Lake was incorporated into a study of the relative merits of natural and artificial propagation, referred to in p. 20–24 and in this section.

[c] Eggs for rearing in this upper Fraser River hatchery were collected at Babine Lake, Skeena River, and transferred for incubation and release of fry into the Stuart Lake system.

> "It was made quite evident to us that the old hatchery methods were of little commercial value. It was made equally plain that the retaining pond system which is still in the experimental stage and expensive by reason of the feeding of the fish, has, as yet, given no proof of its efficiency. . . . Consequently, we urge that before the service is extended, some definite experimental tests should be carried on for a series of years. We make the condition, however, that the operation be carried on and observations made directly under competent scientific supervision."

TESTS OF ARTIFICIAL PROPAGATION, I.E., HATCHERY OPERATION

In due course the Federal Department of Fisheries, through its scientific agency, the Biological Board of Canada (later to be called the Fisheries Research Board of Canada) set up a scientific programme for a study of the relative merits of natural propagation of sockeye salmon and the two methods of artificial propagation then being practised—(1) liberation of free-swimming fry and (2) planting of "eyed" eggs. Cultus Lake, a natural sockeye-producing area of the lower Fraser River system, was selected as the site of the tests because of its ready accessibility and its relatively small size whereby the necessary observations could be made and the hatchery operations conducted without too great difficulty and complication.

As fully reported elsewhere (Foerster, 1929b, 1936c, 1938a) all sockeye ascending to Cultus Lake were to be stopped at a weir located in Sweltzer Creek just below the lake. In years of natural spawning the fish would be counted through the weir and allowed to proceed to the lake. In years of artificial propagation, the fish would be held below the weir until mature and then stripped of eggs. All required data at time of spawning and during hatchery incubation would be collected. The numbers of eggs reared to the "eyed" stage and planted in streams tributary to the lake, or the numbers of fry hatched and released into the lake were estimated. The success or efficiency of each method of propagation was to be determined by the number of seaward migrants counted leaving the lake each year as fry, yearlings, or 2-year-olds, computed as a percentage of the total number of eggs contained in all female fish enumerated at the Sweltzer Creek weir. It had been the original intention to test each method of propagation alternately over a period of 12 years so that each method would be tested four times (once in each year of the 4-year cycle). Occurrence of a "big" year run every 4th year—1927, 1931, 1935—made it impossible to carry on artificial propagation in these years since it would involve greatly increased hatchery facilities. Therefore, the artificial propagation tests had to be rearranged accordingly and *not* include the "big" year. Furthermore, as the results of the experiments accumulated, it became quite evident that there was very little difference in efficiency between the various propagation methods. There seemed to be, therefore, little object in continuing the study after the second test of "eyed" egg planting—1933. Another phase of the problem revealed by the experiments, namely, the effect of predators in the lake in killing off the young sockeye (see p. 245), demanded early attention and was investigated.

In Table 105, the pertinent data obtained in the five tests of artificial (hatchery) propagation are set down. The following points warrant discussion:

(1) Mortality of females. The rigorous conditions laid down for the investigation tended to accentuate the losses in wasted eggs, due to the retention of all fish below the weir until "ripe." Under normal circumstances at Cultus Lake some of the early arriving fish would have been allowed to proceed to the lake to spawn naturally. This is undoubtedly the practice elsewhere, particularly where only a portion of the ascending spawning run is used for artificial propagation. Where the spawning weirs are located in streams above lakes and in the spawning rivers where the fish are in a more mature condition little retention may be necessary prior to stripping. However, a certain amount of retention has always been practised which undoubtedly causes mortality and loss of eggs. The point in question is the degree of such mortality and egg

TABLE 105. Details of three tests of artificial propagation with liberation of free-swimming fry, and two tests of artificial propagation with planting of "eyed" eggs, Cultus Lake, B.C.

	Fry liberation			"Eyed" egg planting	
	1926	1929	1932	1928	1933
No. of males	3,122	1,645	741	3,878	1,565
No. of females	1,949	3,437	1,518	11,461	1,906
Total eggs available ($\times 10^3$):	8,770	15,620	6,564	51,700	7,240
Females recovered dead	261	472	445	3,889	456
Egg loss involved ($\times 10^3$)	1,170	2,140	1,920	17,500	1,730
Eggs available for stripping ($\times 10^3$)	7,600	13,480	4,640	34,200	5,510
Per cent of total eggs available	86.8	86.3	70.7	66.1	76.1
Eggs not recovered in stripping ($\times 10^3$)	1,109	1,397	136	1,500	554
Eggs collected ($\times 10^3$)	6,487	12,079	4,504	32,657	4,955
Per cent of total eggs	74.0	77.3	68.6	63.2	68.4
Per cent of eggs for stripping	85.4	89.6	97.1	95.6	89.9
Losses of eggs in hatchery ($\times 10^3$)	571	2,435	506	488[c]	320
Per cent of loss during incubation	8.8	20.2	11.2	8.2	6.5
Total eggs or fry for distribution ($\times 10^3$):	5,916	9,644	3,998	5,497[c]	4,635
Per cent of total eggs	67.5	61.7	60.9	58.0	64.0
Per cent of eggs for stripping	77.9	71.5	86.2	87.8	84.1
Total eggs or fry distributed ($\times 10^3$):	5,916	9,093[b]	4,825[a]	2,650	4371.5
Seaward migrants					
Yearlings ($\times 10^3$)	336.2	349.9	121.7	38.6	242.5
2-year-olds ($\times 10^3$)	8.3	.2	13.8	5.2	2.2
Total ($\times 10^3$):	344.5	358.1	135.5	43.8	244.7
Migrants as percentage of:					
Total eggs	3.90	2.38	1.71	0.96	3.58
Eggs for stripping	4.54	2.76	2.42	1.45	4.71
Eggs or fry distributed	5.83	3.85	2.81	1.65	5.60

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[a] Additional fry were available for distribution. Percentages have been computed to account for this.

[b] Some eggs or fry were taken for other experiments. Percentages computed make allowance for this.

[c] The planting areas being limited, most of the eggs were transferred elsewhere and only 5,985,300 eggs were retained at Cultus Lake; percentages computed make allowance for this. Of the eggs held, only 2,650,000 were actually planted.

loss. In the present tests it varied from 13.2% of total eggs (in 1926) to 33.9% (in 1928), the average for the five tests being 22.8%. Losses of this kind or those due to trying to strip not fully mature females are seldom taken into account in ordinary hatchery practice.

(2) Incomplete stripping. Due to the incomplete removal of all eggs from the females and the stripping of not fully mature individuals, an appreciable wastage of eggs occurs. In the five tests made, such losses amounted to 14.6, 10.4, 2.9, 4.4, and 10.1%, respectively. It might be argued that the undue retention of the fish, as referred to in the preceding paragraph, might have caused higher losses in stripping but actually the data reveal that in those years, 1928 and 1932, when the mortality of females during retention was highest the losses due to incomplete stripping were the lowest.

In stripping the females a new technique had been initiated whereby the females were slit open and the eggs removed, rather than expressing the eggs by pressure applied by the hand along the ventral part of the fish from the anterior section of the fish toward the vent. This new method, termed the "incision" method, was supposed to assure the removal of all eggs. Tests conducted at Cultus Lake (Foerster, 1936d), showed that by "incision" around 12% more eggs were recovered than by the "expression" technique. In other words, even with adoption of the new procedure in stripping, the loss in unrecovered eggs may, in some instances, be quite appreciable.

(3) Incubation losses. During the period of incubation to the "eyed" stage, at which time the eggs were planted in prepared redds in streams tributary to the lake, the losses amounted to 5.2 and 4.4%, respectively, of total eggs, 7.8 and 5.8% of eggs available for stripping, or 8.2 and 6.5% of eggs actually collected. For the other three tests, that is, when the fry were hatched and reared to free-swimming stage prior to release into the lake, the hatchery losses amounted to:

(a) 6.5, 15.6, and 7.7% of total eggs;
(b) 7.5, 18.1, and 10.9% of eggs available for stripping;
(c) 8.8, 20.2, and 11.2% of eggs actually collected.

The circumstances which produced the unusually high loss in the hatchery in 1929 (second test) could not be isolated but in any season the variable effects of varying water flow and water temperature conditions in the hatchery troughs and of expertness in handling the eggs during incubation may be of considerable significance.

(4) Efficiency of artificial propagation in producing "eyed" eggs or free-swimming fry. The results of the five experiments, as shown in Table 105, reveal the hatchery production as follows:

Based on	"Eyed" eggs	Free-swimming fry
	(%)	(%)
Total eggs	61.0	63.7
Eggs available for stripping	86.0	78.5
Eggs collected	92.7	86.6

Of total eggs, the loss in artificial propagation amounts to around 40%; of eggs available for stripping, to 20%. The difference is the approximate measure of the wastage in eggs occurring through female sockeye dying during the retention and stripping period. How much of this loss should be considered a justifiable claim against artificial propagation is a matter of opinion. Losses during hatchery incubation total around 10%, higher, naturally, when the eggs are held for hatching and rearing to a free-swimming period.

(5) Production of seaward migrants. Heretofore, as intimated, consideration has been given, by fish culturists, primarily to the collection of eggs and the great success in producing "eyed" eggs or free-swimming fry. This high production has been compared to the alleged very poor

survival in natural spawning, though very little real evidence of the latter has been available. Not only has there been little effort to evaluate the results of natural production but there has been little effort to determine the success of artificial propagation in producing seaward migrants and thus of adult fish. It is necessary to determine (a) the comparable success or efficiency of natural propagation and (b) the extent of loss of hatchery-produced fish fry after liberation into the lake.

In Table 105, last line, are given the percentages of seaward migrants based on the actual numbers of (a) fry liberated into Cultus Lake or (b) "eyed" eggs planted. They amount to an average of approximately 4%. The losses in the lake thus presumably total 96%. When computed on the basis of total eggs or of eggs available for stripping, they amount to 97.5 and 96.8%, respectively, that is, a survival of but 2.5 and 3.2%, respectively.

EFFICIENCY OF ARTIFICIAL PROPAGATION IN COMPARISON WITH NATURAL PROPAGATION

For eight tests of natural propagation (Table 82, and p. 313), seaward migrations, based on total eggs contained in all females proceeding to the spawning grounds, of 1.0–4.2% occurred. For the five tests of artificial propagation, as noted in the preceding paragraph, the seaward migrant production amounted to from 1.0 to 3.6% of total eggs or 1.5 to 4.7% of eggs available for stripping. Having regard for the variations between each year's results it was found that statistically there is no significant difference between these percentages (Foerster, 1938a, p. 159). Therefore, it was concluded that "*artificial propagation exhibits no significantly increased efficiency, in point of seaward-migrating young sockeye, over natural spawning.*"

COST OF ARTIFICIAL PROPAGATION

It is obvious that hatcheries cannot be operated without some appreciable cost which must be taken into account in evaluating their overall practical value. Here again, it is not easy to get too accurate data from reports available but, as a rough guide, Table 106 may be of use, giving for certain British Columbia hatcheries the annual costs of operation, and, for an 11-year period, the average yearly egg collection, and the average operating cost per 1000 eggs. With a quite wide variation in cost per 1000 eggs of from $0.37 to $1.72, the average amounts to $0.96.

Accepting this figure as a reasonable approximation, as well as the 3.2% survival to the seaward migrant stage (paragraph 2, above) and a 10% return of adults from the ocean (p. 371) the cost to produce one adult would be $0.30, capital not included. Whether this cost, having regard to the expenses involved in fishing, such as cost of vessel, gear, labour, etc., represents a fair and profitable investment, is a problem for economists.

RELATION OF HATCHERY PRODUCTION IN BRITISH COLUMBIA TO NATURAL SEEDING

Since artificial propagation had been introduced as a distinct improvement over natural spawning and as producing greater numbers of fish, it was of interest

TABLE 106. Approximate operating costs in dollars per year of six salmon hatcheries in British Columbia, average yearly egg collection, and average cost of rearing 1,000 eggs. (Of significance only as a rough guide to cost of artificial propagation. Capital costs of buildings, land, equipment, etc. not included.)

Year	Pemberton	Cultus	Pitt	Lakelse	Babine	Rivers Inlet
	($)	($)	($)	($)	($)	($)
1921	13,657	4,649	4,485	16,841	9,768	15,364
1922	14,606	5,051	4,461	12,139	8,436	13,656
1924	9,648	5,719	7,116	14,320	8,480	22,890
1925	14,062	–	5,605	13,172	9,347	15,746
1926	12,027	5,430	5,875	15,630	8,114	12,483
1927	12,986	–	5,997	15,630	7,183	12,717
1928	11,890	7,371	6,486	15,070	10,560	10,931
1929	9,765	7,334	7,144	10,969	9,214	12,333
1930	11,319	–	7,396	11,650	9,747	13,017
1931	9,413	12,619	6,502	12,540	9,645	11,398
1932	6,820	12,213	5,535	9,758	8,107	11,516
Avg yearly cost	11,472	7,548	6,055	13,429	8,964	13,824
Avg yearly egg collection ($\times 10^6$)	30.7	13.4	4.6	7.8	8.6	18.0
Avg cost per 1000 eggs	0.37	0.56	1.32	1.72	1.04	0.77

to determine how significant the hatchery operations in the three major sockeye-producing areas of British Columbia might be on production of sockeye in them.

To obtain a good estimate of the total natural spawning in any large river system during the 1918–32 period was difficult. However, let us assume, on the basis of evidence available, that (1) the number of sockeye escaping to the spawning grounds constituted one-quarter of the run, that is, was equivalent to one-third of the commercial canned pack, (2) that the fish averaged 12 to the case of canned sockeye, (3) that 50% of the escapement consisted of female fish, and (4) that the average egg content per female was 4000 eggs. Then for the 1918–32 period (Foerster, 1936c, p. 14), artificial propagation, carried on in the three river systems in question, in comparison with natural spawning represented:

River system	Estimated natural egg deposition (*in millions*)	Avg egg collection for hatcheries (*in millions*)	Egg collection as per cent of seeding
Fraser River	1145	45	4.0
Skeena River	778	16	2.1
Rivers Inlet	680	16	2.4

Thus, hatchery operations cannot be expected to alter appreciably the extent of the fishery or increase the sockeye stocks unless the benefits of artificial propagation are great, which they have been shown not to be.

CONCLUSIONS CONCERNING ARTIFICIAL PROPAGATION OF SOCKEYE SALMON

After due consideration of all factors involved in the problem it was the consensus of the Biological Board of Canada that "on the whole, it may reasonably be concluded that in an area such as Cultus Lake, where a natural run of sockeye occurs with a reasonable expectancy of successful spawning, artificial propagation, for purposes of continuing the run to that area, is unnecessary and, if producing any additional results over natural spawning, these would not appear to be in any way commensurate with the cost. This conclusion may not apply to areas where there is no reasonable expectation of successful natural propagation."*

FURTHER STUDIES OF ARTIFICIAL PROPAGATION PROPOSED

The findings of the Cultus Lake sockeye salmon propagation test, as outlined above, had application primarily to conditions as they were found at Cultus Lake and to other hatchery locations where similar conditions prevailed. It was recognized that Cultus Lake was not typical of more interior and more northerly hatchery locations, neither in climatic conditions nor in type of natural spawning ground. At Cultus Lake spawning took place chiefly in the gravelly inshore areas around the lake where seepage flow occurred; in other lakes spawning usually took place in the tributary streams. It was suggested, therefore, that the merits of hatchery operation in all other areas be investigated individually, having due regard for the prevailing local conditions.

To what extent differing conditions in other areas would alter the relative efficiencies of natural and artificial propagation was a matter of conjecture. Acting, however, on the fact that (1) artificial propagation involved such a small percentage of the eggs contained in the spawning escapements to any area and that (2) no clear evidence was available that hatcheries had achieved any beneficial results in any of the areas where they were located, the Federal Department of Fisheries closed down all hatcheries at the end of the 1935 season.

In no area, so far as can be determined at the present time, has the cessation of artificial propagation operations adversely affected the maintenance of the sockeye runs. The Lakelse Lake area may be one exception, but the situation there is so complicated by other changing circumstances that a much more systematic analysis of the situation would be required to bring out the salient facts.

It was further assumed that development of new techniques in hatchery operation, that is, in incubation and in release of fry, might well materially increase the efficiency of artificial propagation. Little research in this field had been conducted.** It seemed apparent that whatever advantages hatcheries might possess in incubating

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* Extract from the minutes of a Meeting of the Executive Committee of the Biological Board, held on November 9, 1935, as issued by the Honorary Secretary-Treasurer of the Board, Mr J. J. Cowie at Ottawa, Canada, February 4, 1936.

** Harvey and Cooper (1962) draw attention to the significance of the quality—in this case, degree of air saturation—of the water supplying a hatchery.

eggs and producing free-swimming fry, these were lost at the time of release of the fry into the lakes by reason of appreciably high mortality of the fry *after* their release. Heavy loss due to predation was thought to be a prime factor. The planting of "eyed" eggs in the gravel beds of tributary streams might well eliminate much of this loss of fry, it was felt. With a high percentage (88%) production of fry possible under reasonably good conditions (Foerster, 1935a) and with the fry emerging from the redds in a normal, natural manner, it was assumed that they would possess the characteristic inborn tendencies for self-preservation.

Tests had also been conducted at Cultus Lake on pond retention in order to determine the merits of releasing the young sockeye at a stage when they might more readily avoid predation and have a greater chance to survive the liberation into natural waters (see p. 308). The results (unpublished) indicated that the increased survival to the migrant stage of sockeye reared in ponds for different lengths of time more or less compensated for the extra cost of pond rearing, that is, for food, care, etc. Thus, the cost per yearling migrant would be approximately the same, that is, 3 cents (see p. 392), assuming no loss during pond retention. Having very clear evidence from Cultus Lake experiences (see p. 308) that a variety of epidemics may arise in the ponds and may quickly wipe out a large proportion, if not all, of the pond populations, this is a very serious hazard which can have a profound effect upon the success of pond retention and upon the economics of such procedure. Pond rearing of sockeye in the vast quantities required to be of any significance to the fishery would involve a gigantic rearing program. The dangers of infection and of mass mortality would be very great.

Finally, reference may be made again to the possibility of avoiding completely the various losses occurring during the one or more years of lake residence of young sockeye by transferring them directly from the stream where hatched to the ocean or to the estuarial waters of the river system. As pointed out on p. 8, experiments conducted over a 4-year period at Port John (FRBC, 1961, p. 99) provided very unfavourable results. Very few adults returned to the parent stream system.

According to Dr W. L. Calderwood, for many years an Inspector of Salmon Fisheries for Scotland, the benefits of artificial propagation, as compared with natural reproduction, must be measured, not by the output of the hatcheries nor by the fish so produced, but rather by the *difference* between such production and that otherwise provided by nature (Calderwood, 1924). From this point of view it is apparent that, as presently operated, hatchery production of sockeye salmon has been quite inconsequential. Nowhere has it been found to have increased a stock of sockeye. It is even debatable as to whether it has succeeded in maintaining a declining population.

General interest of fish culturists has been turned, then, to the possibility of improving conditions in nature which tend to limit or curtail production of the sockeye during the life cycle. The freshwater phases of the life history become of prime importance because they come more readily within the scope of man's control and influence. Reference has already been made (p. 154, 239) to the losses in streams and lakes due to predation on the young sockeye. The significance of predator control as a beneficial fish-cultural practice is discussed in the section to follow. The feasibility of using "barren" lakes as sockeye salmon producers has been considered. Tests have been made by the Alaska Department of Fisheries (ADF annual reports and Meehan, 1963), as outlined earlier (p. 312 and Table 88). The results for the first few years in Ruth Lake were quite promising but subsequent smolt production percentages fell most drastically. Further results from these experiments should be most illuminating, if the tests were continued.

Consideration is now being given to making available to the returning maturing adult sockeye additional spawning ground, particularly where it is thought that the area of spawning gravel, in relation to the lake area available for the rearing of the young fish, is unusually low. The Babine Lake area is thought to be of this type. At Fulton River and at Pinkut Creek—in this Bulletin referred to as 15 Mile Creek (Fig. 56)—extensive developments (1) to provide additional spawning areas and (2) to ensure complete water-flow control, thus avoiding the losses caused by drought and dessication or flooding and scouring-out, have been proposed. The cost is estimated to be from $4 to $5 million and could be phased over a 5-year period. An additional 100 million sockeye fry would be supplied to the main basin of the lake.* One can only applaud most warmly the enterprising viewpoint expressed in this preliminary report (p. 48): "Evidence at hand has indicated that a potential for increased sockeye production exists at Babine Lake and that this potential may be exploited by increasing the fry output into the Main Lake Region by the use of artificial aids. . . . Evaluation of development projects is necessary not only to measure the success of the projects but also to reveal the causes of success or failure. It is only in this way that full exploitation of the lake's potential can be achieved."

This principle of careful evaluation not only of the extra fry produced but of "the overall gain in adult production related to costs" is most essential and significant. If the results of the Babine developments are promising, one can foresee a great expansion of this type of "aid to natural propagation," as well as additional efforts to improve already available spawning grounds and make them more productive.**

CONTROL OF PREDATOR FISH POPULATIONS

The extent to which predator fishes in Cultus Lake were responsible for the heavy mortality (94%) of the sockeye fry during their residence in the lake has already been fully discussed (p. 310). As a result of the catching and removal of the 10,000 squawfish, 2300 trout, 935 char, and 730 coho (Table 55) from May 1935, to June 1938, it was apparent (Foerster and Ricker, 1941, p. 335)

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* "Proposed sockeye salmon development program for Babine Lake." A report prepared jointly by the technical staffs of the Department of Fisheries of Canada and the Fisheries Research Board of Canada, Vancouver, B.C., April, 1965, 53 p. (processed), 9 photographs, 14 figures.

** Cooper, A.C. 1965. The effect of transported stream sediment in the survival of sockeye and pink salmon eggs and alevin. Bull. XVIII, International Pacific Salmon Fisheries Commission, New Westminster, B.C., 71 p.

TABLE 107. Survival of young sockeye in Cultus Lake to the seaward migrant stage, before and after predator control. The last year for each method of propagation is after predator control had been in progress.

	Natural spawning	Artificial propagation			
Brood year	Eggs in females[a] ($\times 10^3$)	Fry liberated[b] ($\times 10^3$)	Eggs planted[b] ($\times 10^3$)	Total smolts ($\times 10^3$)	Survival (%)
1925	17,470	–	–	197.6	1.13
1926	–	5,916	–	344.5	5.83
1927	250,000	–	–	2,637.6	1.05
1928	–	–	2,650	43.8	1.64
1929	–	9,093	–	350.1	3.85
1930	24,900	–	–	788.0	3.16
1932	–	4,825	–	135.5	2.81
1933	–	–	4,372	244.7	5.60
1934	–	–	5,590	501.8	8.98
1935	40,000	–	–	3,125.0	7.81
1936	–	12,468	–	1,627.0	13.05

[a] These data, taken from Foerster and Ricker (1941), p. 328) do not conform exactly to those given in Table 82. The differences are slight.

[b] These data are also shown in Table 105.

"that squawfish more than 200 millimetres long have been decreased to about 1/10 of their original abundance, and char to about the same extent. Trout may have decreased somewhat but that is not certainly established; in any case they were very much less affected than squawfish or char. Coho show considerable variation in numbers due to variable spawning escapements, which obscures any effect the netting may have had."

The effect of this appreciable reduction in predators was of direct interest. As shown in Table 107 there was an appreciable increase in the survival rate of young sockeye, which occurred in all three methods of propagation tested, e.g., in natural spawning: from 1.13, 1.05, and 3.16 to 7.81%. Taking all methods into consideration the survival was increased three times or 300%, i.e., from an average, before predator control, of 3.13% (8 years) to an average, after predator control, of 9.95% (3 years). That this quite significant increase was indeed due to the removal of predators was substantiated by the facts that (1) no observable changes had taken place, within the lake, in the environmental or ecological conditions, and (2) survival increases applied to all three methods, suggesting that the factors of correlation must have acted on the fry in the lake. That the increase should be attributed primarily to decreased predation rather than to mere reduction of plankton food consumers was indicated by the fact that most of the predator fish removed were of large size consuming little plankton (though the trout might form a partial exception). Lake shiners, sticklebacks, and small squawfish consume plankton heavily. During the summer season, however, they are to be found chiefly in inshore waters, which the sockeye do not frequent.

COMMERCIAL VALUE OF PREDATOR CONTROL

It was of interest to compute the approximate commercial significance of the gains resulting from control of predators in the Cultus Lake escapement, based on the then-prevailing prices for sockeye and the 10% return from the sea as adults of seaward migrants (see p. 367).

The cost of the predator control work, 1935–38, was computed, approximately at $9,755 (Foerster and Ricker, 1941, p. 329). The value of the additional adults obtained (380,000), computed at their market value, was $190,000. The cost, then, of producing the extra adults amounted to 2.6 cents per adult.

However, according to Foerster and Ricker (1941, p. 330), "the operations to date will have considerable effect in improving survival for some years in the future, for two reasons. Even were control measures to be stopped, the predators would probably need two or more years to recover their former abundance and re-establish the former rate of predation; while the effects of the increase in salmon breeding stock upon future runs may extend for a much longer period. To estimate the magnitude of these future benefits is not easy, but they must be reckoned at least as great as those obtained to date. On this basis, the cost of control operations, per yearling saved (past and future) would be reduced to 0.13, or approximately $\frac{1}{8}$ of a cent." Assuming a 10% survival rate to the adult stage, the cost of the control work would approximate 1.3 cents per adult salmon added to the run. No matter which cost value is used, either 2.6 or 1.3 cents, it is substantially less than the cost of artificial propagation, 30 cents per adult (see p. 392).

INCREASE IN GROWTH OF SOCKEYE IN YEARS OF PREDATOR CONTROL

One very interesting and important result of the reduction of predator fishes in Cultus Lake was the marked increase in size of the sockeye at migration time. Average lengths and weights of migrants in the years from 1927 to 1937 are shown in Table 72, to which can be added the average weight of 7.2 g for the 1938 migration of 1,627,000 yearlings. The migrants of 1937 and 1938 were conspicuously larger, in relation to their numbers, than in pre-predator control years. Certainly no dwarfing in size occurred when the numbers were unusually large, as occurred in 1929 and 1933. The reason seems clear: with the greater survival rate due to fewer predators only about one-third as many fry were required to produce a given number of migrants, with a resulting much less severe competition for food. Thus, "It can be claimed therefore as a further very important advantage of the destruction of predaceous fish, that it will permit a much greater maximum population of sockeye to inhabit the lake than has been the case heretofore" (Foerster and Ricker, 1941, p. 332). As noted earlier (p. 266 and Fig. 66), in the years of predator control 40% of the total average yearly biomass production was converted into yearling sockeye, whereas, in pre-predator control years, only 12.6% of the average yearly production went into production of the yearling stock.

It is apparent, then, that the predator control measures applied at Cultus Lake resulted in:

(1) a greater efficiency of sockeye production from the standing crop of plankton in the lake,
(2) a greater survival of young sockeye in the lake,
(3) a greater survival of smolts and hence production of adults returning from the ocean, since a direct relationship has been indicated between size of seaward migrants and ocean survival as explained in the section which follows.

INFLUENCE OF SIZE OF SEAWARD MIGRANT ON PERCENTAGE RETURN OF ADULT SOCKEYE

Evidence was obtained, during Cultus Lake studies (Foerster, 1954a), that the larger the smolt, at the time of seaward migration, the higher the percentage return of adult fish. In other words, the larger the smolt the better the survival, presumably not only during downriver migration to the ocean but during the years of ocean residence. With an increase in average weight of smolts from 4 to 10 g, their mean percentage survival to adult stage was tripled.

The general significance of this relationship should not be minimized in endeavouring to achieve as large a return as possible of adult sockeye from a specific spawning, seeding, and smolt migration. Its importance deserves further study; its applicability to other sockeye-producing regions should be examined. If generally applicable, which would appear to be quite likely, then, any factors which might lead to a greater growth of sockeye during lake residence, hence to a larger size of smolt, should be looked upon most favourably and accepted as a highly beneficial and effective "management" technique or procedure.

Chapter 14. Interspecific crossbreeding of sockeye salmon

During every fishing season reports appear of the occurrence of Pacific salmon bearing unusual markings or showing peculiar features which suggest that they might be hybrids. Such reports always bring up the question as to whether such hybridization is possible, either (1) through the mating and spawning of two individuals of different species or (2) through the simultaneous spawning, in closely adjacent redds, of different species so that their sex products become mixed. Certainly such phenomena may conceivably occur in certain areas where and when pink and sockeye salmon or sockeye and chum salmon overlap in their spawning seasons. It may apply for other species, too, under unusual circumstances.

CULTUS LAKE EXPERIMENTS

During one season, 1927, the presence of all five species of *Oncorhynchus* at the Cultus Lake weirs in mature condition gave an excellent opportunity to test out the possibility of the various species interbreeding* and producing viable offspring. The success of such crossbreeding would tend, then, to indicate whether the occurrence of hybrids in nature is possible and whether the reports of fishermen re the capture of so-called hybrids can be substantiated. It might also serve as a first step in investigating the feasibility of deliberate crossbreeding measures to produce a more suitable Pacific salmon to meet new conditions.

Accordingly, on November 17, 1927, a male of each of the five species was used to fertilize the eggs of the other four species. The fertilized eggs were then placed in the hatchery for incubation. Observations were made throughout the whole period of development and during hatch. The free-swimming fry that resulted were retained in the hatchery troughs until July, 1928, when they were transferred to small rearing tanks.

The results of the cross-fertilizations (Foerster, 1935b) may be briefly given as follows:

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* Four of the species—sockeye, chum, coho, and pink—spawn quite commonly in Cultus Lake or its outlet stream, but the chinook, *O. tshawytscha*, occurs only rarely.

Male	Female	Remarks
Chinook	Sockeye	Excellent hatch of healthy fry.
	Coho	No hatch. Eggs died at the "eyed" stage.
	Chum	Moderate hatch of healthy fry.
	Pink	Moderate hatch of healthy fry.
Sockeye	Coho	Very poor. Only 3 fry from 1183 eggs.
	Chum	Good hatch of healthy fry.
	Pink	Moderate hatch.
	Chinook	Very poor. Only 1 fry from 762 eggs.
Coho	Pink	No hatch. Eggs died during incubation.
	Chum	Very poor. Only 5 fry from 965 eggs.
	Chinook	Very poor. Only 15 abnormal fry from 673 eggs.
	Sockeye	Only 50 weak alevins from 900 eggs.
Chum	Pink	Excellent hatch of healthy fry.
	Chinook	No hatch. Eggs died during early development.
	Sockeye	Good hatch of healthy fry.
	Coho	No fertile eggs recovered.
Pink	Chinook	Excellent hatch of healthy fry.
	Sockeye	Only 10 fry from 810 eggs.
	Coho	Moderate hatch. Fry abnormal.
	Chum	166 healthy fry from 1196 eggs.

When either parent was coho salmon, very few fry survived and in most cases these were quite abnormal; when the male fish was chinook salmon, successful crosses resulted with sockeye, pink, and chum eggs and healthy fry were produced; where chinook eggs were fertilized with milt from the males of the other species, only the cross with the pink salmon was successful. One fry only was obtained when sockeye milt was used, and with milt from a chum male complete failure resulted. The eggs were apparently fertilized but the exact stage of cessation of cell division could not be ascertained.

It was found that the sockeye milt will readily fertilize pink and chum eggs and produce viable fry. Sockeye eggs were fertilized successfully by chum milt but the fry were not as large as in the reciprocal cross. When sockeye eggs were treated with pink salmon milt, there appeared to be good fertilization and embryo development but the hatch was very poor. Many alevins were afflicted with "blue-sac" infection and those not so affected were thin and weak.

It was of interest, further, to determine whether the hybrids obtained from the crossbreeding tests were themselves fertile. The hybrids had been kept, as noted above, in small rearing tanks and in their 3rd year some of the male fish "ripened," namely, those of the chum-sockeye, sockeye-chum, chinook-sockeye, and sockeye-pink crosses (the male parent is named first). The milt from these males was used to fertilize eggs stripped from normal sea-run sockeye, and the eggs placed in the hatchery for incubation. Excellent hatches resulted in all groups. Therefore, the above named hybrids were fertile.

In the autumn of 1931 a number of the remaining hybrids reached maturity. Both males and females were taken in a ripened condition but, due to the earliness of the season, no suitably ripe eggs or milt from normal sockeye were available. Thus, the mature hybrids had to be interspawned, with results as indicated below, again the male parent of each hybrid being the first named:

Male	Female	Results
Chinook-sockeye	Chinook-chum	No fertilization. Eggs "blind."
Chinook-chum	Sockeye-pink	" " " "
Chum-sockeye	Chinook-chum	" " " "
Chinook-sockeye	Chum-pink	Good hatch.
Chum-sockeye	Chinook-chum	" "
Chum-sockeye	Sockeye-chum	" "
Chum-sockeye	Chum-pink	" "
Chum-sockeye	Chum-sockeye	" "

All that can be said about the above results is that, where fry were obtained, the parent hybrids were fertile; where no fry nor fertilized eggs resulted, it does not necessarily indicate infertility of either parent hybrid. The exact degree of "ripeness" of either eggs or milt, undiscernible to the eye of the stripper, may have been responsible. Further tests are required.

As far as sockeye salmon are concerned, it is apparent that reciprocal crossbreeding with both chum salmon and pink salmon produced healthy fry. Only for the sockeye-chum and chum-sockeye crosses, however, could it be clearly established that the hybrids were fertile.

HYBRIDIZATION STUDIES ELSEWHERE

According to Jordan (1906), certain hybridization experiments were conducted at Karluk, Alaska, early in the 1900s by J. A. Richardson. Apparently all five species of Pacific salmon were crossed but very few fry resulted. The crossbreeding of sockeye salmon (*O. nerka*) males with pink salmon (*O. gorbuscha*) females was superior to all others, thus suggesting a close relationship between these two species.

According to Andreeva (1954) experiments were carried out on the crossbreeding of sockeye and chum salmon at the Ushkov Hatchery on the Kamchatka River. The purpose was to obtain hybrids which (1) would be hardier than the sockeye, (2) would inherit the age at maturity and the body size of the chums, but (3) would have the excellent flavour, quality and fecundity of the sockeye. In 1948, for the first time in Kamchatka, viable fry were obtained from crossbreeding sockeye females and chum males. As the fry developed it was apparent that they possessed the hardiness and the growth rate of chum fry. Fully mature adult hybrids were observed in a number of areas by fish cultural personnel in 1952. One individual, a male 72 cm long and 4.4 kg in wt, was only 2 years old, i.e., it had matured at the same age as the very youngest chums, and 1 year younger than the youngest sockeye in the area. At Lake Azabach two mature female hybrids were reported, possibly of natural origin; one appeared to be a cross between a chum and a sockeye, the second had the features of sockeye and coho.

Again, in 1952, at the Ushkov Hatchery, a collection of 199,880 sockeye eggs, fertilized with chum salmon milt, was set down for incubation. A hatch of 194,176 fry resulted. However, no record can be found of the return from this liberation.

Much interest has developed in the USSR Far East, particularly in Sakhalin, in the hybridization of pink and chum salmon. The purpose is to obtain a fast-growing, large salmon maturing at an early age. Pavlov (1959) reports the successful production of fry from fertilizing pink salmon eggs with milt from autumn chum salmon. Poor results were obtained, however, from the pink-chum cross—that is, fertilizing chum salmon eggs with milt from pink salmon. The reciprocal cross was more successful, and from the Kalinin Hatchery, Sakhalin, commencing in 1953, some 300,000 chum-pink hybrid fry were released each year. Adult hybrids duly returned, chiefly as 2-year-olds, a characteristic which is considered as very important. In the number of eggs, their size and colour, the hybrids closely resembled their chum parents. In length and weight they were midway between pinks and chums but there were neither very small nor very large ones.

Kamyshnaya (MS, 1961), however, reports successful fertilization of chum salmon eggs with pink salmon milt at two hatcheries in Sakhalin. She remarks (p. 32) that "in analyzing the biological features of the hybrids in comparison with those of the original parent species, it is apparent that the female hybrids are much larger than the males and in both weight and fecundity they more closely resemble the chums. Male hybrids are larger than pink males. Age determinations showed that the male hybrids mature at 1+ years and the females at 2+." Thus, the hybrids exhibited faster growth, earlier maturity, and excellent edible qualities, factors of very great commercial importance.

These findings together served to corroborate earlier evidence of Smirnov (1953), in a study of the embryological development of reciprocal crosses of pink and chum salmon, that hybrid fry exhibited a shorter period of incubation, a more complete hatch and a much more rapid larval growth rate. In no Russian studies, thus far recorded, has the fertility of the hybrids been confirmed, however.

POSSIBILITIES OF SELECTIVE CROSSBREEDING OF SALMON

There are three important characters in which Pacific salmon differ—in age at maturity, in size, and in quality of flesh. If, by selective breeding, these features could be altered advantageously a more valuable commercial product would result. For example, the sockeye is reputed to be the most valuable species for canning purposes but it does not mature until in its 4th or 5th year. The pink salmon, of inferior quality when processed, matures in its 2nd year. Therefore, if, by interbreeding of these two species, either the age at maturity of the sockeye could be shortened without lowering the quality of the flesh or the quality of the pink salmon could be improved appreciably without changing its age at maturity, great benefit commercially would accrue. Or again, the chum salmon is much larger than the sockeye but its flesh is of lower quality when canned. Both mature at about the same age. If, by crossbreeding these two species, the size of the sockeye were increased without loss of quality or the quality of the flesh of the chums were improved without reduction in size, a superior strain of salmon would result.

The opinion, earlier expressed (Foerster, 1935b, p. 31), can only be reiterated: "such ideas may appear entirely impracticable and visionary, but the benefits derived from such practices in the field of agriculture—in plant and livestock breeding—cannot be gainsaid." As civilization spreads along our rivers, the use of increasing amounts of water will be used for other purposes, its quality will deteriorate, pollution will be intensified, and conditions for the natural propagation of salmon will become less and less favourable. It may therefore become necessary to develop, by selective crossbreeding, new varieties which will be able to thrive in the changed situations and contribute to a healthy fishery and provide a high-quality food product.

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It was most gratifying to learn, when preparation of this bulletin was first proposed, that the Fisheries Research Board of Canada concurred in the opinion that a general review of all that was known about sockeye salmon would be exceedingly useful since it would bring together under one cover, all—or at least all that was known to the writer—the facts concerning this species. At the same time it would reveal that which was still unknown and which yet had to be investigated. For those carrying forward researches into sockeye salmon or for those seeking pertinent information on specific phases whose opportunities to search the literature for facts may be limited either through lack of time or facilities, such a review bulletin should be quite helpful.

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