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Ecology of Arctic Populations of Lake Trout, *Salvelinus namaycush*, Lake Whitefish, *Coregonus clupeaformis*, Arctic Char, *S. alpinus*, and Associated Species in Unexploited Lakes of the Canadian Northwest Territories

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The available data on the fish populations of 35 lakes in the Northwest Territories are examined. The lakes range in size from Great Bear Lake (31, 156 km^2) to Keyhole Lake (46 ha); they are situated between lat. 60 and 75° N, east from the Mackenzie River to the west coast of Hudson Bay. Lake trout (*Salvelinus namaycush*) and whitefish (*Coregonus clupeaformis*) form the main populations of the mainland lakes and together make up to 95% of the total catch. There is a trend toward increasing importance of whitefish with decreasing severity of conditions. Most populations show a uni, bi-, or trimodal length distribution; age distributions are unimodal. No change in these distributions was observed over a large number of years in certain lakes. These populations are considered to have reached a climax condition comparable with a vegetational climax, and are therefore in equilibrium with their environment. All incoming energy is ultimately used in respiration to support a high biomass of fish.

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L'auteur analyse les données disponibles sur les populations de poissons de 35 lacs des Territoires du Nord-Ouest. La superficie de ces lacs varie de celle du Grand lac de l'Ours (31 156 km^2) à celle du lac Keyhole (46 ha); ils sont situés entre les latitudes 60 et 75° N, et depuis l'est du fleuve Mackenzie jusqu'à la côte occidentale de la baie d'Hudson. Les populations de touladis (*Salvelinus namaycush*) et de grands corégones (*Coregonus clupeaformis*) prédominent dans les lacs de la terre ferme et constituent, à elles deux, jusqu'à 95% des prises totales. On observe une tendance à l'augmentation chez le grand corégone à mesure que les conditions deviennent moins sévères. La plupart des populations montrent une distribution bimodale ou trimodale des longueurs; la distribution des âges est unimodale. Dans certains lacs, il n'y a pas eu de changements dans ces distributions pendant plusieurs années. On considère ces populations comme ayant atteint un climax comparable à une végétation au stade climatique et étant donc en équilibre avec leur environnement. Tout l'apport d'énergie est utilisé en dernier lieu dans la respiration servant au maintien d'une biomasse élevée de poissons.

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THE Canadian Northwest Territories is one of the few remaining regions in the world where a large number of lakes exist unmodified by man's agency. These lakes are comparatively young having developed in isolation since the retreat of the last Pleistocene glaciation, 8,000–12,000 yr ago.

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The lakes in this arctic region vary enormously in size, from Great Bear and Great Slave lakes at over 30,000 km^2, through a vast number of intermediate size down to the myriads of small tundra lakes and ponds.

The winter climate common to all lakes is severe in intensity and duration; this is followed by a short summer which, at least on the mainland, is comparatively warm. In winter between 1 and 3 m of ice develop on the surface of the lakes and it is the rate of melting of this ice which greatly influences summer conditions; the interaction between climate and morphology of the individual lake gives rise to great differences in the internal environment. Great Bear Lake (66°N) retains its ice until the second half of July, nearly 6 wk after Keller Lake (64°N) becomes ice-free. Keller Lake may reach an isothermal condition at 13 C soon after the point of maximum heat intake in August (L. Johnson unpublished data), whereas Great Bear Lake circulates close to 4 C throughout most of the short summer (Johnson 1975a). In this respect Char Lake (75°N) is comparable with Great Bear Lake: it becomes ice-free slightly later than Great Bear Lake, circulating at 4 C when heat intake reaches a maximum (Schindler et al. 1974). Char Lake freezes in early September and Keller Lake in October, but Great Bear Lake is not completely ice-covered until the beginning of December. These lakes are among the more extreme in their response to climate; the majority of the lakes to be considered are intermediate in their regimes.

Except for the smallest ponds all the lakes in the region support fish populations; however, the fauna of any given lake is determined, not only by the opportunities for migration that have been available to each species (McPhail and Lindsey 1970), but also by the environment within that lake (Johnson 1975b).

Although primary productivity in arctic lakes is low (Kalff 1970; Kalff and Welch 1974) it is evidently sufficient to maintain relatively simple food webs leading to high standing crops of fish; the individual fish in these populations are, characteristically, of large size. As a result, the large standing crops of large fish have popularly given rise to the impression that these waters have considerable potential for exploitation; it is equally apparent that the low primary productivity is inadequate to support a high rate of harvest in the terminal parts of the food web.

Over the last 30 yr investigations, primarily directed at the assessment of fish stocks and their potential rates of exploitation, have yielded considerable information on northern lakes. It is the purpose of this paper to examine this material and to attempt some generalizations on the ecological processes involved, generalizations that in all probability can only be developed through consideration of unmodified systems.

Materials and Methods

The material for this paper was collected over a number of years by many people. In 1945 Miller and Kennedy (Miller 1947; Miller and Kennedy 1948; Kennedy 1949) carried out the first fishery surveys in northern Canadian lakes. Grainger (1953) started a study on Arctic char (*Salvelinus alpinus*) in the Sylvia Grinnell River and Frobisher Bay, Baffin Island, in 1948 that continued for 3 yr. This was followed by several years of intensive work by the Arctic Unit of the Fisheries Research Board (now the Arctic Biological Station of the Fisheries and Marine Service, Department of the Environment): in 1959 a survey of lakes in the barren grounds, that area of mainland Canada north of the tree line and west of Hudson Bay, was carried out by J. G. Hunter; Johnson (1964, 1972, 1973) investigated lakes in the arctic archipelago and northern mainland; and Johnson (1975a, b, c) carried out a study of Great Bear Lake between 1963 and 1965. A detailed study of Arctic char production in "Keyhole" Lake was made by Hunter (1970) between 1963 and 1967. In 1967, the Canadian section of the International Biological Programme established a research station at Char Lake, Cornwallis Island (Bigler 1972) which operated until 1973. In 1967 surveys of Nonacho and Kakisa lakes were carried out under my supervision. A survey of Lac la Martre was undertaken by Bond (1973) in 1972 in connection with a commercial fishery established there. Fiona Lake, Somerset Island, was reexamined by de March and Eddy (1976) in 1975. Monitoring of the sportfishing on Great Bear Lake was conducted by the Operations Directorate of the Fisheries and Marine Service (Falk et al. 1974). Test fishing results obtained by the Operations Directorate have been of much value.

More recently in 1973 a new study was initiated by the Freshwater Institute (Research Directorate, Fisheries and Marine Service, Department of the Environment) on the production of anadromous Arctic char at "Nauyuk" Lake on the Kent Peninsula, Northwest Territories. This program, under my supervision, embraces subsidiary studies on landlocked populations in "Little Nauyuk," "Gaviafaeces," and "Klondike" lakes and included return visits to Keyhole and Namaycush lakes in 1975.

With few exceptions the early collections of fish were made with standard gangs of nylon gillnets of graded mesh size. The standard gang consisted of the following mesh sizes (stretched measure): 1½ in. (38 mm), 2½ in. (62 mm), 3½ in. (89 mm), 4½ in. (114 mm), and 5½ in. (140 mm). These nets were set as a single gang wherever possible but were divided into two or more sets where this was not practical. In Great Bear Lake in 1964 and 1965 only 3½-, 4½-, and 5½-in. mesh nets were used as the smaller sizes had been almost completely unsuccessful in 1963; in Keyhole Lake the largest mesh used was 3½ in. and the smallest ¾ in., owing to the small size of the fish present. The nets used in test fishing were exclusively 4½- and 5½-in. mesh, the only legal sizes in the Northwest Territories.

In 1974 and 1975 two new experimental gillnets were introduced with great success, particularly for smaller fish; one net consisted of six panels, each 20 m long and 1.8 m deep, each panel being of a different mesh size (stretched measure): 20, 38, 66,

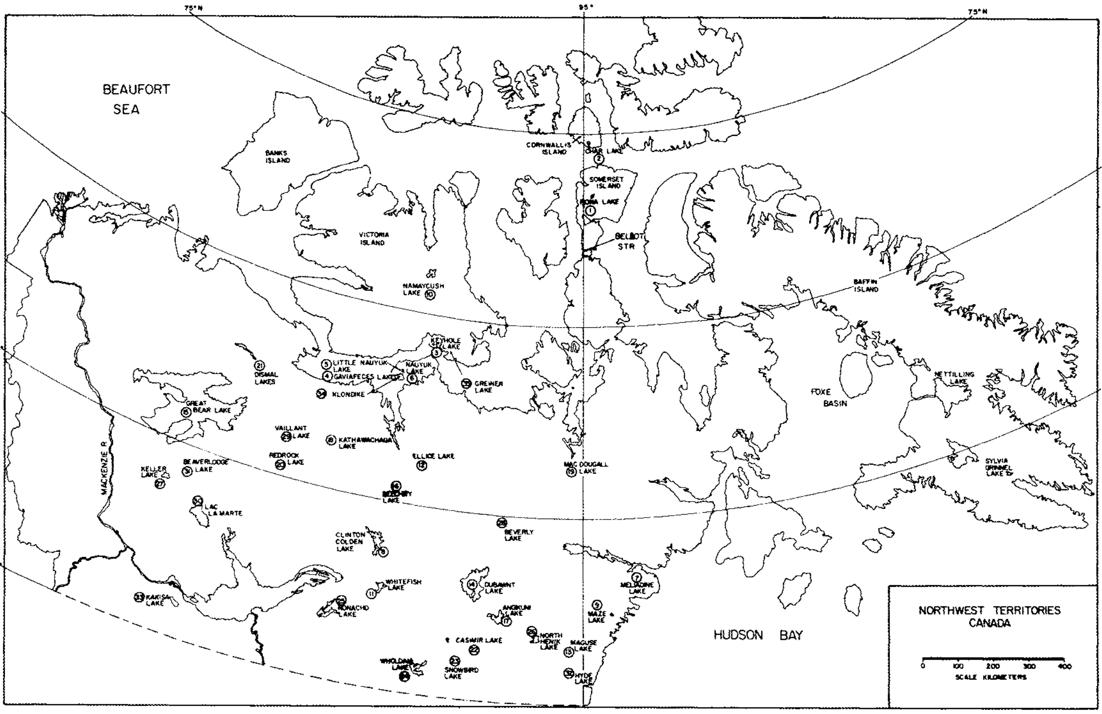


FIG. 1. Northwest Territories of Canada with the locations of the lakes referred to in the text.

90, 110, and 120 mm stretched measure. The second net was similar but with the following mesh sizes: 20, 25, 32, 38, 44, and 50 mm. The nets used prior to 1973 will be referred to as standard gangs and the two newer gillnets will be called experimental nets when fished simultaneously.

To supplement the experimental nets electrofishing has been used on an increasing scale owing to the recent development of functional battery operated equipment.

Some samples were occasionally taken using fish poison, notably the 1962 sample of Arctic char from Fiona Lake, Somerset Island. In Char Lake rod and line and fine-meshed trap net were both used extensively.

The most unbiased sample, and perhaps the most extensive, was taken at the Nauyuk Lake counting fence which was operated on both upstream and downstream migrations in 1974 and 1975. The information on this system was supplemented by use of experimental gillnets, trapnets, seines, and electrofishing gear.

Immediately after capture the fork length was measured in millimeters and the fish was weighed as accurately as possible, to the nearest gram for fish under 50 g, to the nearest 10 g for fish 50–1,000 g, and to the nearest 25 g for fish in excess of 1,000 g.

Scales from the region immediately below the posterior edge of the dorsal fin were taken for aging whitefish (*Coregonus clupeaformis*), lake trout (*S. amaycush*), and walleye (*Stizostedion vitreum vitreum*); the sagittal otolith was removed for aging lake trout and char.

Fish in northern waters are notably slow growing (Miller and Kennedy 1948; Grainger 1953; Johnson 1973; Falk et al. 1974) so that aging presents some difficulty. This is particularly so with fish over 25 yr of age. Good agreement was obtained between various samples taken in Great Bear Lake over a considerable number of years. Miller and Kennedy (1948) used scales, I used scales and otoliths, and Falk et al. used only otoliths. For fish up to 20–25 yr of age agreement was good between scales and otoliths, but in older fish otoliths tend to give higher values: these are probably closer to the truth. Johnston (1975b) obtained two tag returns from lake trout that had been at liberty for 8 and 9 yr respectively, following tagging; these fish were 627 and 953 mm at tagging and 635 and 959 mm on recapture. The small amount of growth, particularly by the larger fish, casts doubt on whether annuli are laid down in the otolith when there is essentially no growth in length. The possibility therefore exists that the age of very slow growing fish may be underestimated.

The lakes with which this paper is concerned are all north of the Northwest Territories boundary (60°N) and lie between the Mackenzie River in the west and Hudson Bay in the east. The most northerly example is Char Lake (75°N) on Cornwallis Island close to the present position of the North Magnetic Pole. Within this large study area the lakes vary in size from Great Bear Lake (31,152 km^2) and a depth of 445 m to Keyhole Lake (48.6 ha) and "Little Nauyuk" Lake (46 ha) with maximum depths of 16 and 6.5 m, respectively. In trophic status they all probably have a primary productivity level below the 100 $g \cdot cm^{-2} \cdot y^{-1}$ established by Vollenweider et al. (1974) as an arbitrary upper limit for carbon assimilation in an oligotrophic lake. However, large differences in primary and secondary productivity do occur between lakes, but these have yet to be measured directly.

The names of several of the lakes considered have not yet received official recognition; where this is so the name is put in quotation marks the first time it is used.

Great progress has been made over the last 25 yr in plant ecology through the examination of the differences in plant communities along lines of known environmental change, rather than the study of units of vegetation (Whittaker 1951, 1953, 1965, 1967; Curtis and McIntosh 1951; McIntosh 1967). A comparable approach seems appropriate to the analysis of populations across a large number of lakes where the species remain relatively constant although experiencing changing environmental conditions of climate, lake morphology, and nutrient supply.

Briefly the concept of gradients states that species existing along a line of environmental change do not have sharp boundaries at points which might correspond to well-defined physiological limits of tolerance. Each species appears to have a central mode or peak of maximum density which decreases gradually on either side; the curves appear to be binomial or Gaussian in form (Whittaker 1967; Brown and Curtis 1952).

As each species responds differently to the environmental variables vegetation is conceived as being primarily "a complex continuum of populations rather than a mosaic of discontinuous units" (Whittaker 1967). A plant community is a particular limited area in which there is no marked progressive change toward a different kind of vegetation, and the sum of the environmental factors, or as Billings (1952) prefers the gestalt of interrelated factors, that affect the community is its environmental complex.

The analysis of vegetation directed toward elucidating the effect of environmental variables, including that of associated species, is termed gradient analysis. This may be direct gradient analysis in which species are arranged and studied according to known magnitudes (or indices of position) along an environmental gradient that is the accepted basis of the study, or indirect gradient analysis in which the axis may or may not correspond to environmental gradients; but if they do correspond, the approach to these environmental gradients is indirect or inferential (Whittaker 1967).

The first stage in the analysis of fish populations of northern lakes is based on the principles of indirect gradient analysis. The methods, in this context, are still in their formative state and before further progress can be made data must be collected with this specific purpose in mind. The same is true of direct gradient analysis; here, it is as yet uncertain as to which environmental variables, against which species could be arranged, might be most profitably measured. Only through trial will satisfactory methods emerge and until specific data is collected it will not be possible to apply the more sophisticated methods of ordination (Whittaker and Gauch 1973).

Use has been made of a further botanical concept, the importance value of a species. The importance value is "some expression of massiveness, conspicuous activity or interest of a species in a community" (Whittaker 1967). If the importance value for a given species is divided by the total of the same kind of importance value for all species in the sample the resulting value is the relative importance value. For fish species in a community the most readily obtained importance value is the percentage by weight of each species in a series of catches taken by one gear type within a single community.

Satisfactory importance values for fish communities are difficult to determine as controls on the effectiveness of the gear; the representativeness of the sample and the boundaries of the community are extremely difficult to determine except through the sampling process. However the adequacy of the sampling can be judged by the frequency and type of anomaly that occurs when the samples are analyzed on the basis of gradients.

The second stage of the analysis is an examination of the structure of individual populations within a community and the development of equilibrium within that community.

Results

GENERAL TRENDS

The general distribution of northern freshwater fishes has been given by McPhail and Lindsey (1970) much of whose material was obtained from the same collections as are discussed in this paper.

North of Viscount Melville Sound, Bellot Strait, and Davis Strait, the only fish species encountered is Arctic char (*Salvelinus alpinus*) with the exception of the two sticklebacks *Pungitius pungitius* and *Gasterosteus aculeatus* which occur in southern Baffin Island. Arctic char exist throughout lakes in the northern islands, either as anadromous populations making short feeding trips to the sea in summer, or, where uplift of the land has isolated the lakes from the sea, as landlocked populations. Migratory and nonmigratory char populations often exist together in the same water body; both types are known to be present at the northernmost limit of land in Lake Hazen (83°N), Ellesmere Island (Anon. 1959).

To the south of Viscount Melville Sound, lakes in Victoria Island have a more varied fish fauna; six additional species are encountered: lake trout (*S. namaycush*), lake whitefish (*C. clupeaformis*)

TABLE 1. Lakes supporting populations of Arctic char (*Salvelinus alpinus*) lake trout, (*S. namaycush*), and associated species of fish and macroinvertebrates in waters close to the Arctic Ocean. Figures in parentheses indicate associated groups of lakes.

		Species present								
Lake	Elevation (*m*)	*S. alpinus*	*S. namaycush*	*Coregonus autumnalis*	*C. sardinella*	*Myoxocephalus quadricornis*	*Gammarus lacustris*	*Gammaracanthus loricatus*	*Mesidothea entomon*	*Mysis relicta*
Fiona	150	X								
Char	30	X								
Keyhole (2)	30	X								
Gaviafaeces (1)	65	X								
Little Nauyuk (1)	30	X							X	X
Namaycush (2)	100		X	X	X					X
Klondike (1)	10		X		X	X	X			
Nauyuk (1)	10	X	X	X	X	X	X	X	X	X
Greiner (2)	26	X	X	X	X		X	X	X	X

and subsequently referred to in this paper simply as "whitefish," least cisco (*C. sardinella*), Arctic cisco (*C. autumnalis*), the fourhorn sculpin (*Myoxocephalus quadricornis*), and the ninespine stickleback (*P. pungitius*). Crossing to the northern mainland, lakes are found that contain in addition to the foregoing; burbot (*Lota lota*), northern pike (*Esox lucius*), round whitefish (*Prosopium cylindraceum*), broad whitefish (*C. nasus*), longnose sucker (*Catostomus catostomus*), and Arctic grayling (*Thymallus arcticus*); however, distribution is unpredictable for any given situation. Away from the coastline lake cisco (*Coregonus artedii*) replaces Arctic and least ciscos in lakes but not in major rivers.

In the drainage basin of Great Bear Lake and lakes further south three more species are added to the list: pickerel or walleye (*Stizostedion vitreum vitreum*), lake chub (*Couesius plumbeus*), and trout-perch (*Percopsis omiscomaycus*). In the Great Slave Lake basin the list increases considerably but the only additional species mentioned in this paper is the white sucker (*Catostomus commersoni*) which forms a considerable fraction of the total fish population in Kakisa Lake.

In the islands and along the mainland coast, species composition appears to be influenced by competitive exclusion particularly in lakes where there is no access to the sea. The number of fish species is reduced as is also the number of macroinvertebrate species considered to be marine-glacial relicts (Johnson 1962, 1964). Where there is access to the sea, char, lake trout, two species of cisco, and whitefish all exist together (Greiner, Nauyuk lakes) as well as the relict species: *Mysis relicta* (Mysidacea), *Mesidothea entomon* (Isopoda), and *Gammaracanthus loricatus* var. *aestuariorum* (Amphipoda); the freshwater amphipod *Gammarus lacustris* is sometimes present. Where the lake is isolated from the sea, either char or lake trout alone is present; usually, it is char which survive and appear to eliminate many of the invertebrate species in addition to the trout (Table 1). Where lake trout survive rather than char, at least one species of cisco is also found (Klondike and Namaycush lakes). Nauyuk, Little Nauyuk, Gaviafaeces, and Klondike lakes are all adjacent and it may be assumed that they all derived their faunas from the same species pool. Nauyuk Lake, which is the most recent to emerge from the sea, has eight species of fish present and three marine-glacial relict macroinvertebrates; the number of species declines with isolation from the sea until only char remain in Gaviafaeces Lake. A similar series exists between Greiner and Keyhole lakes in Victoria Island.

GRADIENTS

The great majority of lakes on the mainland have populations in which lake trout and white-

TABLE 2. Lakes of the Northwest Territories showing relative importance value of species present and the ratio of lake whitefish (*C. clupeaformis*) to lake trout (*S. namaycush*). Lakes with Arctic char (*S. alpinus*) indicated (X) but their relative contribution to the species cannot be calculated (for full explanation see text).

Lake	*S. alpinus*	*S. namaycush*	*C. clupeaformis*	*C. nasus*	*C. artedii*	*C. sardinella*	*C. autumnalis*	*Prosopium cylindraceum*	*Thymallus arcticus*	*Esox lucius*	*Catostomus commersoni*	*C. catostomus*	*Lota lota*	*Stizostedion vitreum*[a]	*Coregonus clupeaformis*: *Salvelinus namaycush*
Klondike		73.50				26.50									—
Meliadine	X	99.5					0.5								—
Maze	X	91.9					3.6	3.8	0.3				0.5		—
Clinton-Colden		89.32			2.93			3.17	4.56						—
Ellice		90.09	7.8					0.89	1.21						0.09
Whitefish		79.65	5.31		4.32			7.47	0.49			2.72			0.06
Namaycush		89.97	9.21			1.27	8.67								0.11
Kathawachaga	X	77.37	9.16				8.83	3.22	1.29						0.12
Nauyuk	X	54.39	8.1			7.5	29.9								0.15
Dubawnt		78.52	15.03		0.05			2.03	0.86			3.39	0.11		0.19
Angikuni 1958		70.21	17.01		1.03			9.62	0.40			1.54			0.24
Great Bear 1964		78.85	18.77							2.30		0.01		0.01	0.24
Maguse	X	56.61	13.59		3.51			4.48		0.35		21.44		20.01	0.24
Beechey		77.59	19.46					1.58	0.60			0.53	0.31		0.25
Great Bear 1963		75.32	20.71		0.69			0.80		2.41		0.06		0.01	0.27
Great Bear 1965		68.40	24.13		0.04			0.01	0.01	6.10		0.34		0.50	0.35
Redrock		63.87	33.93	0.34				1.17		0.46					0.53
Angikuni 1968		63.92	35.96						0.11						0.56
Casmir		60.32	34.75							4.92					0.58
Snowbird		58.02	35.55							6.43					0.61
Wholdaia		44.81	27.62							27.33	0.05	0.17			0.62
Dismal		51.84	34.36	5.05		0.49	8.34	0.42	0.11						0.66
Nonacho		53.26	41.82		0.01			0.03		3.98	0.13	0.63	0.12		0.79
MacDougall		50.83	42.07					3.81	2.80						0.83
North Henik		48.89	51.11												1.05
Keller		40.66	51.46					2.60	20.01	6.83		0.02	0.01	0.72	1.27
Beverly		39.99	51.45		0.34			0.56	0.11	7.44		0.09			1.29
Beaverlodge		31.41	49.85		20.01			20.01		18.66					1.59
Vaillant		35.47	59.68					0.48	2.03	1.48		20.01	0.79		1.68
La Martre 1972		29.17	60.19		20.01							10.64			2.06
La Martre 1959		29.25	63.51		20.01			0.96		5.54		0.71			2.17
Hyde		4.61	54.04		0.11			0.03		40.57		0.51	0.11		11.72
Kakisa 1946[b]			27.92		0.01					5.85	25.38	0.89		39.95	—
Kakisa 1968			14.09		0.01					24.32	21.61	1.26		38.71	—
Winnipeg[c]			69.46	—	0.2	—	—			1.3	0.67	—	—	27.43	—

[a] Combined total of walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) is given under *S. vitreum*. Not included is 0.94% of other species, mostly yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), etc.

[b] Data from Kennedy (1946).

[c] Data from Annual Report, Manitoba Department of Mines, Resources and Environmental Management (1972).

fish predominate (Table 2). Such lakes range from those in which lake trout are present without whitefish (e.g. Clinton-Colden Lake) through those in which both species coexist in approximately equal proportions (e.g. Snowbird, Wholdaia, Nonacho, and Keller lakes) to those in which whitefish are the most abundant (e.g. Beaverlodge and Hyde lakes).

Certain lakes are known in the more southerly part of the region in which walleye assume the greatest importance value (Kakisa Lake, also Lac Ste. Thérèse and others designated as "pickerel lakes" under the Northwest Territories Fishery Regulations, Anon. 1974). These pickerel lakes are turbid and shallow and, although they contain whitefish, they are devoid, in general, of lake trout. These lakes probably do not belong to the main lake trout–whitefish series but form a subseries of their own.

One limit of the lake trout–whitefish series is formed by those lakes which contain only lake trout; the other limit seems to be the large lakes, outside the Northwest Territories boundary, such as Southern Indian Lake (McTavish 1952; Ayles and Koshinsky 1975) or Lake Winnipeg (Hewson 1959, 1960) which are completely devoid of lake trout. The relative importance value of lake trout and whitefish in the lakes that lie between these extremes is plotted in Fig. 2. In the majority of cases the points fall close to the line that indicates that together they make up 95% of the total fish population; there is no clustering of values which might suggest an association of the two species in which constant proportions develop.

Lakes in which species other than lake trout or whitefish form a significant fraction of the population are readily identified by their position away from the 95% line; Hyde, Wholdaia and Beaverlodge lakes have high relative importance

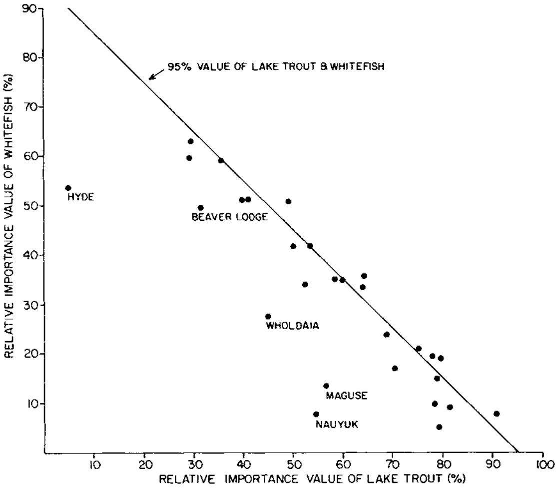


FIG. 2. The relationship between the importance values of lake trout, *Salvelinus namaycush*, and lake whitefish, *Coregonus clupeaformis*. The diagonal line represents the series of values of combined lake trout and whitefish which together equal 95% total catch by weight.

values for northern pike and Maguse is high in longnose suckers. It is not possible to incorporate anadromous Arctic char into such an ordering as the bulk of the population leaves the lake in summer, thus making it impossible to obtain true relative values. Dismal Lake is somewhat anomalous as large numbers of Arctic cisco were taken during sampling, but this high incidence is masked when abundance is considered in terms of importance value.

POPULATION STRUCTURE

By gillnets — The length-frequency distribution of the total catch of the standard gang and that from the individual mesh sizes have been plotted for each lake. A series of histograms was obtained that shows a remarkable degree of uniformity in the size of fish taken by each mesh size in each lake. The grouped results all show well-defined dome- or bell-shaped curves (Fig. 3–6). The modal size for each mesh within a given lake remains remarkably constant within a species, whether it be char, lake trout, or whitefish being considered, but the modal size between lakes for each species varies greatly.

For the experimental nets only total catches are plotted; these all produce bell-shaped curves but over a wide range of modal sizes. The catching ability of these nets at the small end of the scale is demonstrated by the results from Gaviafaeces Lake (Fig. 7), with a modal value between 100 and 120 mm and Little Nauyuk Lake with a well-defined mode at 220 mm (Fig. 7); the char from Keyhole Lake (1975) show a modal value of 314 mm and Lake Namaycush (1975) lake trout, the largest in the series, 693 mm. Little Nauyuk, Keyhole, and Namaycush lakes (Fig. 7) were also fished along the shoreline using electrofishing gear. Keyhole and Namaycush lakes were sampled previously in the early 1960s using a wide variety of gear.

From all the gillnet results the catch curve is either unimodal: Little Nauyuk, Fiona, and Gaviafaeces (char); or bimodal: Keyhole Lake (char), Namaycush Lake (lake trout), Vaillant Lake (whitefish) (Fig. 3), Lac la Martre (whitefish 1972, lake trout 1959, 1972) (Fig. 3), and Kathawachaga Lake (lake trout) (Fig. 4). The remainder shows only a single well-defined mode (Fig. 8 and 9) but the existence of a smaller mode is not precluded as the gear was not sufficiently effective to catch fish of a size below about 250 mm. In populations with a bimodal distribution the second mode may show up either to the right or left of the main peak. A subsidiary mode of very large lake trout can be observed in Lac la Martre in 1959 and 1972; this mode is noticeable in every mesh size. If the second mode is to the left of the main peak it tends to show up only in the smaller mesh sizes (e.g. Nonacho Lake, lake trout and whitefish, Fig. 3 and 4).

The mode varies considerably in the length at which it occurs within a species between lakes (Table 3, Fig. 3–10). Arctic char modes vary from 153 mm in Gaviafaeces Lake and 225 mm in Little Nauyuk Lake to 592 mm in Maguse Lake. Lake trout modes range from 486 mm in Vaillant Lake to 745 and 789 mm in Beaverlodge and Namaycush lakes, respectively. Whitefish are the most uniform species with modes from 426 mm in Beverly Lake to 549 mm in Redrock Lake. The mean size of whitefish in Ellice Lake is 633 mm. In the majority of lakes whitefish peaked at about 500 mm (e.g. Great Bear, Dismal, and Vaillant lakes).

The mean length of fish caught by each mesh size varies more than does the length at which the mode occurs. This seems to result from each mesh having a minimum size of fish which can be retained while showing no evidence for a maximum. This is demonstrated in Table 4 where the 1½-in. mesh captures the greatest size range whereas the 5½-in. mesh catches the smallest range of sizes. The 4½-in. net is the most efficient measured by the number of fish caught; the 1½ in. is the least efficient.

When all lakes, for which there is comparable information, are considered there is a high cor-

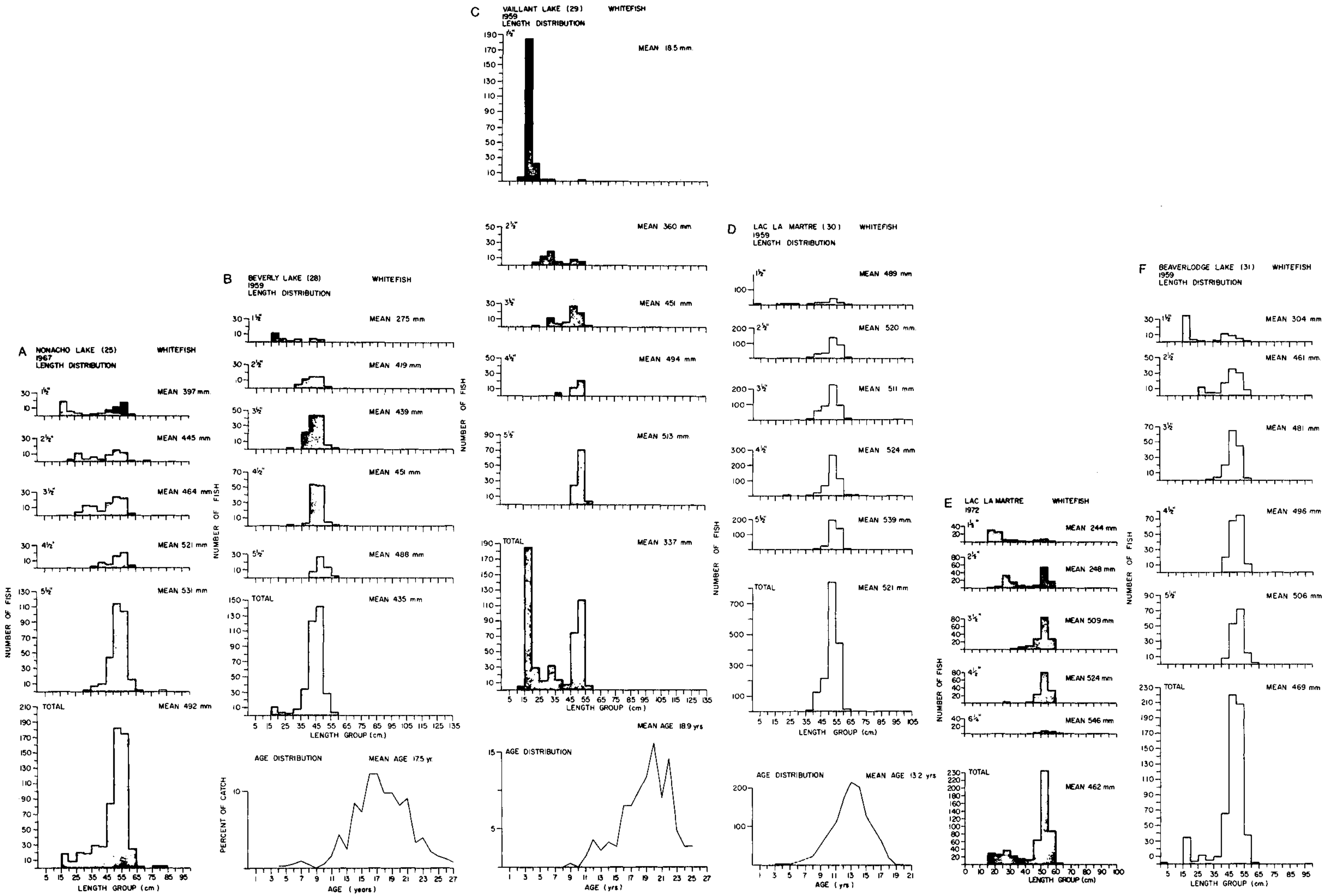


FIG. 3. Length-frequency distributions of lake whitefish, *C. clupeaformis*, by mesh size, with age-frequency distributions where available for the total catch from A, Nonacho Lake 1967; B, Beverly Lake 1959; C, Vaillant Lake 1959; D, Lac la Martre 1959; E, Lac la Martre 1972; and F, Beaverlodge Lake 1959. Data for Lac la Martre 1972 from Bond (1973).

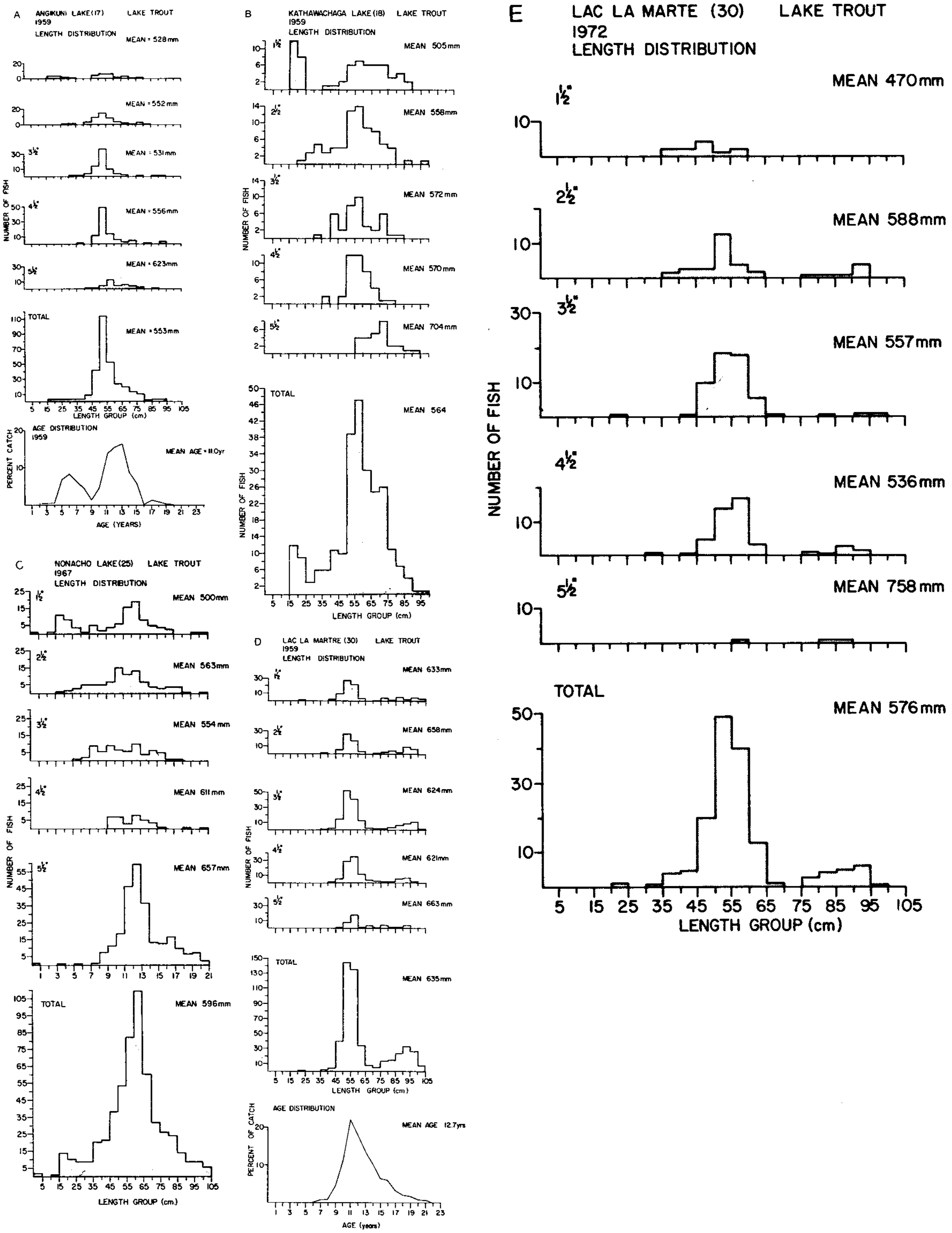


FIG. 4. Length-frequency distributions of lake trout, *S. namaycush*, by mesh size, with age-frequency distributions where available, for total catch from A, Angikuni Lake 1959; B, Kathawachaga Lake 1959; C, Nonacho Lake 1967; D, Lac la Martre 1959; and E, Lac la Martre 1972. Data for Lac la Martre 1972 from Bond (1973).

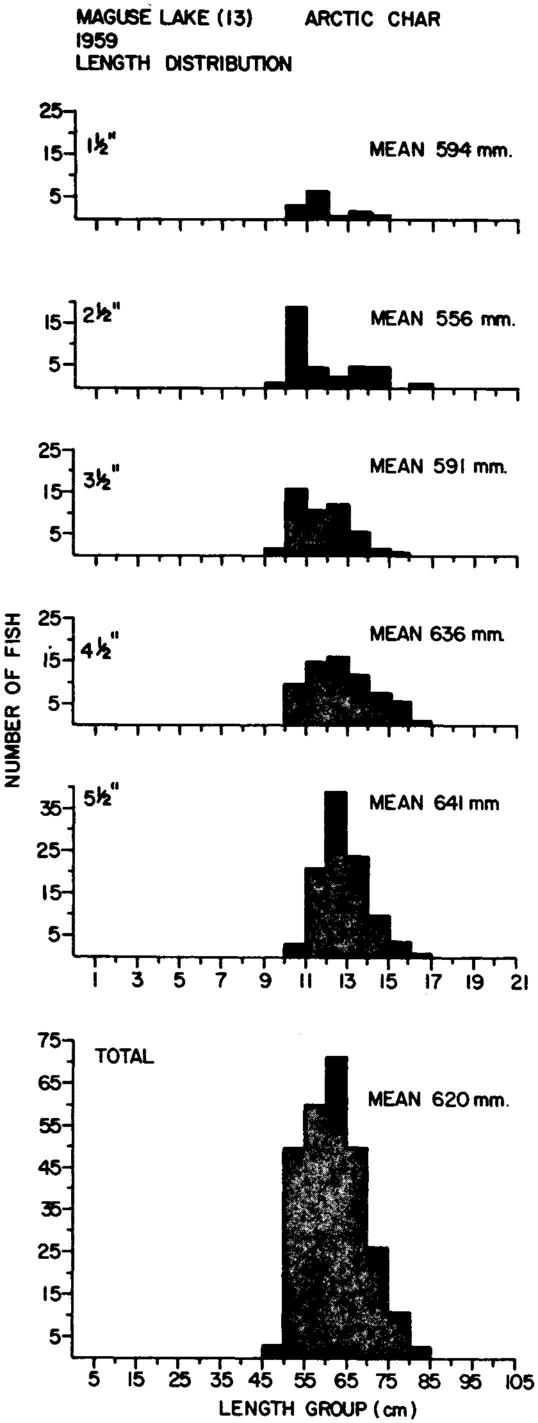


FIG. 5. Length-frequency distribution of Arctic char, *S. alpinus*, by mesh size, from Maguse Lake 1959.

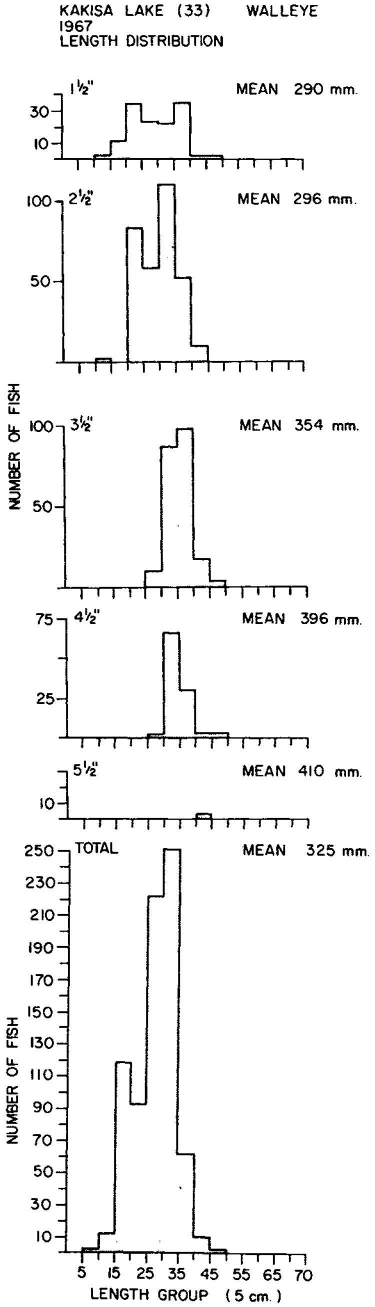


FIG. 6. Length-frequency distribution by mesh size of walleye from Kakisa Lake 1967.

relation (whitefish, $r = 0.94$; lake trout, $r = 0.87$) between the mean length of fish caught by the whole gang and the smallest mean length of fish caught by any individual mesh size (Fig. 10).

Usually the smallest mean size was taken in the 1½-in. mesh but this was not invariably the case. Stated briefly this means that the greater the mean length caught by the gang as a whole the greater the mean length caught in the smallest mesh size. The size taken in any mesh is therefore dependent upon the fish present and not wholly on the capacity of the net to "select" any particular size group. Any detectable selective effect is taking place within a lake; such may sometimes be observed in the slight shift of the mode toward the right as the size increases (e.g. whitefish: Beaverlodge, Nonacho lakes; lake trout: Lac la Martre, Kathawachaga lakes; Arctic char: Maguse Lake). The shift is small compared with the great differences in mesh size and also with the differences in modal size for the same mesh from different lakes.

This is not to deny the effect of mesh selection in certain circumstances (Kipling 1957; McCombie and Fry 1960; Regier and Robson 1966; Hambly 1975) but to negate the conclusion that the results obtained from northern lakes can be attributed to mesh selection. The wide differences in modal size in all three species amply demonstrate the ability of the gear to capture fish in a wide variety of sizes when they are in fact present. The capture of large numbers of whitefish in Vaillant Lake between 150 and 200 mm is of great significance in this connection.

In only a few lakes were species other than char, lake trout, or whitefish taken in sufficient quantity to prepare length-frequency distributions. The northern pike of Beaverlodge Lake (Fig. 11) had a modal value between 700 and 750 mm; apart from this instance the other species were

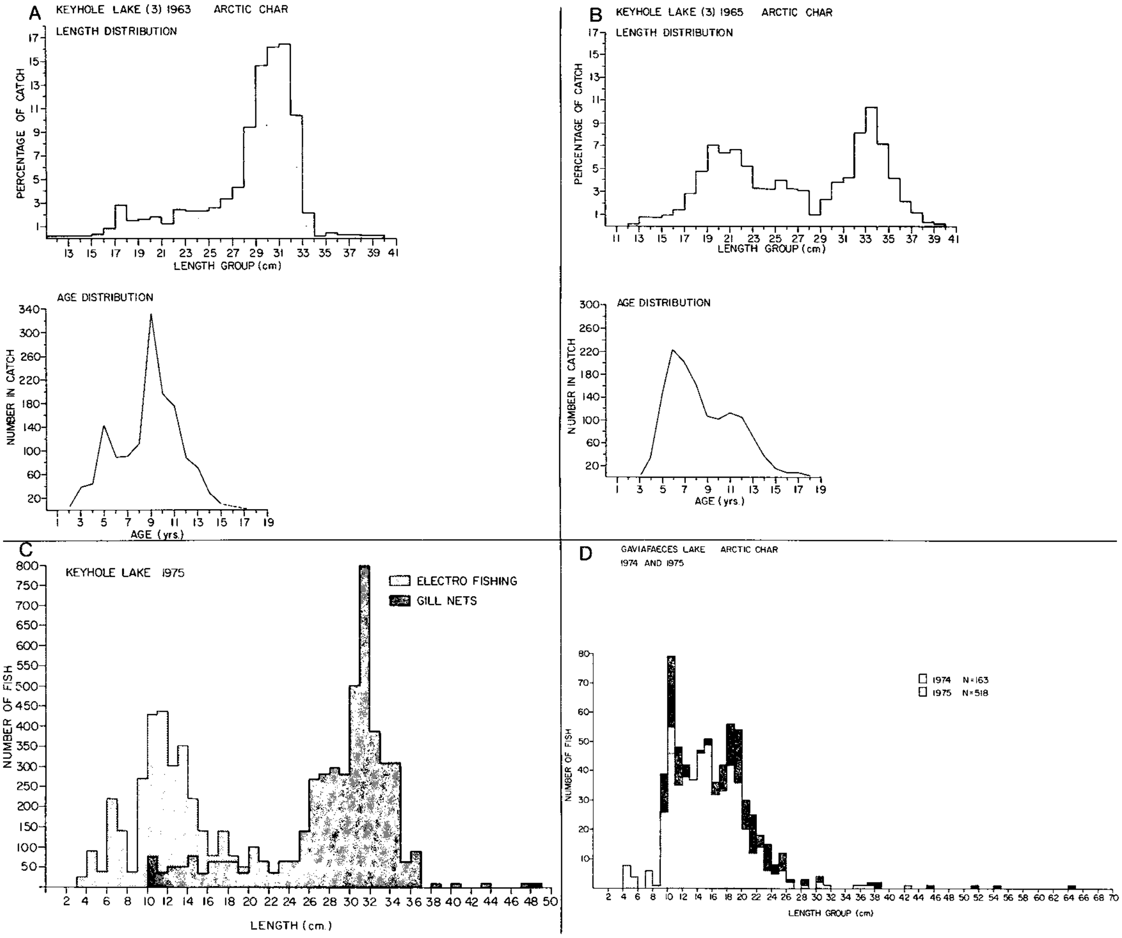


FIG. 7. Length-frequency distribution of Arctic char, *S. alpinus*, from A, Keyhole Lake 1962–63; B, Keyhole Lake 1965; C, Keyhole Lake 1975; D, Gaviafaeces Lake 1974 and 1975;

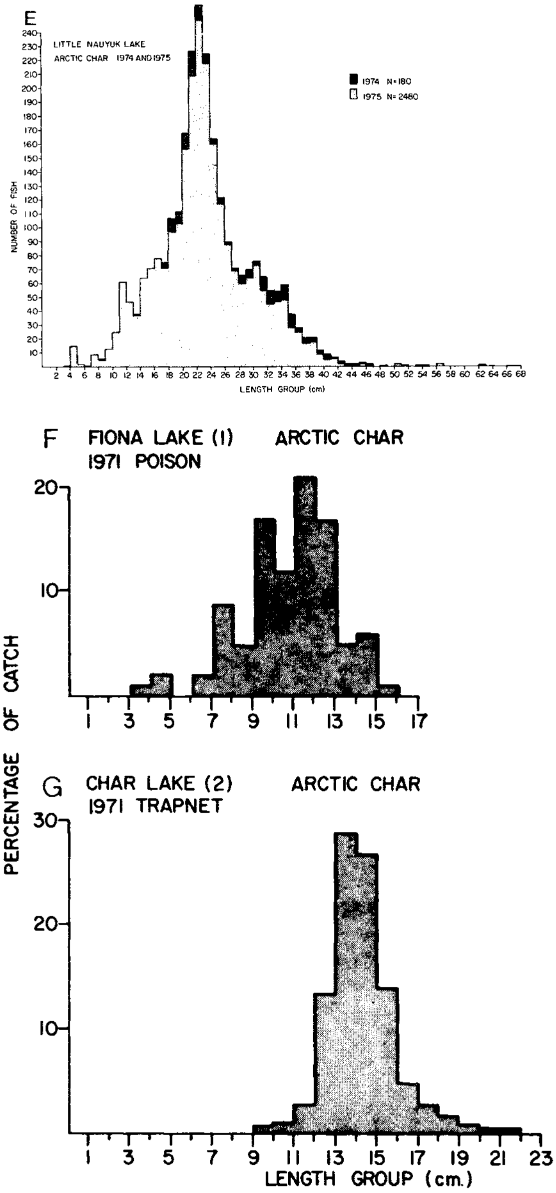


FIG. 7. E, Little Nauyuk Lake 1974 and 1975; F, Fiona Lake 1962; G, Char Lake 1971; and H, lake trout, *S. namaycush*, from Namaycush Lake. Figures for Keyhole Lake 1975 adjusted to the numbers taken in 1962–63. The two modes in Keyhole and Namaycush lakes are not expected to be in the proportions shown as the methods of capture were different.

of a much smaller size compared with the major populations. In Kakisa Lake (Fig. 6) the walleye had a modal size of about 300 mm, the Arctic ciscos of Dismal Lake, 250 mm, and the round whitefish of Whitefish Lake also 250 mm (Fig. 11).

The modal length of walleye from Kakisa Lake in 1967 is considerably smaller than that obtained by Kennedy (1962) in 1946 but the stock has been regularly fished commercially in the interval.

By methods other than gillnets — The Arctic char population of Nauyuk Lake has been sampled more intensively than that of any other northern lake; it probably ranks among the most intensively sampled of any fish population. The sampling was carried out by means of a counting fence established across the river down which the char migrate to the sea. The population has, to date, been observed over 2 yr (1974 and 1975); during this time seaward and return movements have been monitored. The entire seagoing population was counted through the fence during the upstream migrations in 1974 ($N = 10{,}960$) and 1975 ($N = 10{,}290$) and a high percentage weighed and measured. During the period when the greater part of the population was at sea (late July to early August) the lake was investigated for nonmigrating char; none above 200 mm in length were captured except for certain individuals moving farther up the system for spawning (Campbell and Johnson 1976).

The seaward migrating population shows two well-defined modes at 580 and 200 mm (Fig. 12). The char in the smaller mode migrated when the main run had completed its downstream movement, thus keeping the two groups separate in time (Johnson and Campbell 1975). At least two more size groups exist in fresh water, being too small to make the seaward migration; one of these groups is ephemeral made up of young-of-the-year. The various groups reflect the complex life history of this species.

Over the 2 yr of observation there has been no significant change in the population apart from that accounted for by fishing pressure. Tag returns of 70% show that a very low mortality is experienced in the sea. Growth rates over the summer migration period are exceedingly high particularly in view of sea temperatures below 4 C; a specific growth rate for weight of 1.1–1.5%/day (80–113% weight increase in 45–50 days) has been shown for tagged fish in the 250–300 mm size range, falling to about 0.7%/day for fish above 600 mm; however, much of this increase is lost over winter.

The char in Fiona Lake (Fig. 7) in Somerset Island were sampled with rotenone during a period of intense feeding on chironomid pupae which was taking place along the shoreline. Nets set for a short period in deeper water failed to catch any fish. All the poisoned fish were of a very small size, but one female of 130 mm was

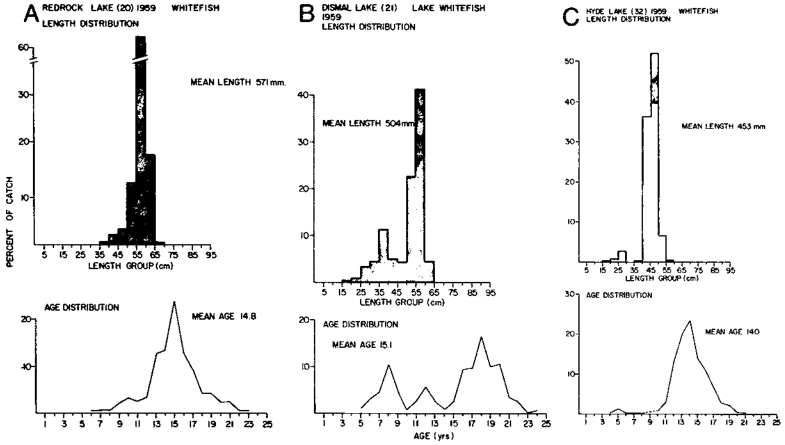


FIG. 8. Length-frequency distribution of lake whitefish, *C. clupeaformis*, all mesh sizes combined, from A, Redrock Lake 1969; B, Dismal Lake 1959; and C, Hyde Lake 1959.

found to contain 24 eggs. The lake was again visited in 1975 by de March and Eddy (1976) who set gillnets and caught several large fish (310–655 mm) but did not capture any small char, as the mesh was not sufficiently fine. The four largest fish were all found to be cannibals.

Char Lake on Cornwallis Island was sampled intensively with rod and line and a small-meshed trapnet (MacCallum 1972) (Fig. 7) as part of the International Biological Programme. A length-frequency distribution, with a well-defined mode at 130–144 mm was derived from the 2,700 char caught in the trapnet; angling yielded essentially the same results. There is an indication that a second mode at a much smaller length was present in that many small fish were observed along the shore (H. Welch personal communication).

Shape of the catch curve for age and length — An emergent character of the catch curves, for age and length, for whitefish and lake trout in Keller Lake was that they show a frequency close to that of a normal distribution curve (Johnson 1972). Many of the catch curves of other arctic lakes have a similar tendency; it is the objective of this section to examine the departure of the curve from the normal or Gaussian condition in terms of being more peaked (leptokurtic) or less peaked (platykurtic) (Croxton and Cowden 1965).

The results (Table 3) show an almost invariable occurrence of the leptokurtic condition in the catch curves for length. This indicates a high degree of clustering around the modal value. In some cases (e.g. whitefish, Redrock Lake, Fig. 8) the condition is extreme with 62% of the population falling in a 50-mm size-class (550–599 mm). Only two lake trout populations (Beaverlodge and MacDougall lakes) are less peaked than in a normal distribution; no whitefish samples were of this type.

The high degree of clustering around the modal value in the curves derived from the combined catches of the five different mesh sizes is of great significance in refuting the contention that the normal-shaped distribution can be ascribed to gillnet selection or to reduced vulnerability in length-groups below that of the modal value. The clustering around the same value is seen in all mesh sizes which, if reduced vulnerability is the reason, would imply that vulnerability is reduced at the same length irrespective of the mesh considered. One size of mesh might be highly selective for fish of a certain narrow size-group, but that five widely different mesh sizes should all be equally selective at the same size is not credible. The ability of the nets to catch small fish (over 250 mm) is shown in the results from Vaillant Lake and Dismal Lake. It is much more satisfactory to believe the results obtained and conclude that the nets are catching a reasonably representative sample of the population, at least in sizes over 250 mm, in the area where they are set.

The age-frequency distribution in the various populations has been examined in the same manner; in the majority of cases a normal or leptokurtic condition exists. The only significantly platykurtic distribution for age was found in the Arctic char from Sylvia Grinnell Lake (1948–51). This age distribution is for the fish actually

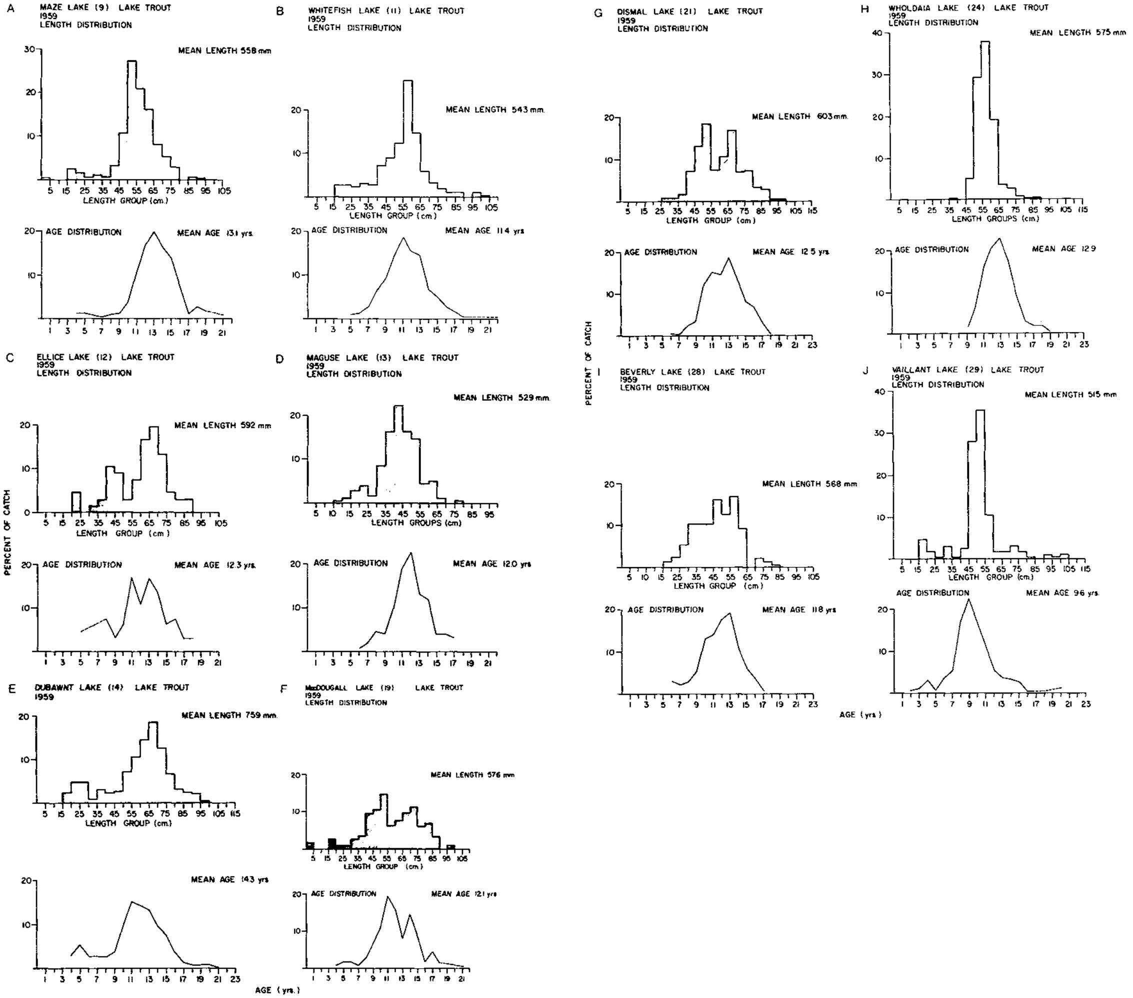


FIG. 9. Length-frequency distribution of lake trout, *S. namaycush*, all mesh sizes combined, from A, Maze Lake 1959; B, Whitefish Lake 1959; C, Ellice Lake 1959; D, Maguse Lake 1959; E, Dubawnt Lake 1959; F, MacDougall Lake 1959; G, Dismal Lake 1959; H, Wholdaia Lake 1959; I, Beverly Lake 1959; J, Vaillant Lake 1959.

caught and states nothing about the age of fish below the limit of vulnerability which is considered to be about 250 mm in the standard gang.

Northern fish populations are of great age (Fig. 3–5, 7–9); the modal age of whitefish lies between 12.7 yr (Lac la Martre, Fig. 9), 17.0 yr (Great Bear Lake, Fig. 13), and 18.9 yr (Vaillant Lake, Fig. 3). The condition in Vaillant Lake is unusual in that there are two pronounced modes at lengths of 215 and 504 mm although only a single mode on the age-frequency distribution.

In lake trout, modal ages range from 11.8 yr (Beverly Lake, Fig. 9) to 18 yr (Great Bear Lake, Fig. 14); a mean age of 31 yr was obtained from Lake Namaycush (1962) although individual ages were so widely distributed as to give no indication of any clustering in spite of a well-defined modal value for length.

Sequential results from the same lake — Several lakes were sampled more than once, often after a lapse of many years. Great Bear Lake experienced three sampling periods over 30 yr, Angikuni Lake was fished in 1959 and 1969, Lac la Martre in 1959 and 1972, and Keller Lake in 1962 and briefly again in 1974. Keyhole Lake was fished heavily in 1962–1967 and revisited in 1975; Lake Namaycush was visited in 1962 and 1975.

TABLE 3. Populations of lake trout (*Salvelinus namaycush*), Arctic char (*S. alpinus*), and lake whitefish (*C. clupeaformis*) from lakes in the Northwest Territories, showing mean and modal length, mean and modal age and departure of population curve from a normal distribution. $*P < 0.005$; $**P < 0.01$.

Lake	Length (*mm*)			Age (*yr*)		
	Mean	Mode	Kurtosis	Mean	Mode	Kurtosis
			S. namaycush			
Maze	557 ± 112	534	Leptokurtic**	13.4 ± 2.11	13.5	Leptokurtic**
Ellice	596 ± 128	667	Normal	—	—	
Namaycush						
(1962)	775 ± 150	855				
(1975)	693 ± 133	765	Leptokurtic**	—	—	
Whitefish	543 ± 149	578	Leptokurtic*	11.4 ± 2.46	11.6	Leptokurtic**
Great Bear						
(1945)	562 ± 136	573	Normal	17.47	17.0	
(1963–65)	639 ± 117	636	Leptokurtic**	18.7 ± 4.14	17.95	
(1973)	664 ± 99	637	Leptokurtic**	24.75	20.0	
Dubawnt	649 ± 124	621	Normal	12.6 ± 2.39	12.9	Leptokurtic**
Kathawachaga	599 ± 126	566	Normal	13.1 ± 2.40	14.5	Normal
Angikuni (1959)	555 ± 113	527	Leptokurtic**	13.3 ± 2.04	13.1	Leptokurtic
Maguse	519 ± 112	525	Normal	12.0 ± 2.21	12.2	Normal
Nonacho	596 ± 161	618	Leptokurtic*	—	—	
Dismal	601 ± 132	593	Normal	12.5 ± 2.19	11.5	Normal
MacDougall	598 ± 155	517	Platykurtic*	12.1	11.7	Normal
Wholdaia	575 ± 76	565	Leptokurtic**	12.9 ± 1.82	13.3	Leptokurtic
Keller	579 ± 107	572	Leptokurtic**	16.2 ± 3.84	16.9	Leptokurtic
Berverly	569 ± 130	671	Normal	11.8 ± 2.30	13.6	Normal
Vaillant	512 ± 141	512	Leptokurtic**	9.6 ± 2.34	9.5	Leptokurtic**
Beaverlodge	765 ± 144	875	Platykurtic**	14.3 ± 2.51	14.3	Normal
La Martre						
250–749 mm	550 ± 53	547	Leptokurtic**	12.7 ± 2.8	11.75	Leptokurtic**
700–999 mm	895 ± 78	903	Normal			
Hyde	651 ± 19	649	Normal	14.2	14.3	—
			S. alpinus			
Fiona	107 ± 23	119	Normal			
Char	148 ± 17	149	Leptokurtic**			
Keyhole						
(1963)	289 ± 42	308	Leptokurtic**	8.8 ± 2.74	9.6	Leptokurtic**
(1975)						
30–220 mm	122 ± 40	111	Normal			
220–480 mm	306 ± 31	314	Normal			
Gaviafaeces	153 ± 48	—				
Little Nauyuk	231 ± 64	226	Normal			
Maguse	621 ± 73	618	Normal	9.9 ± 1.24	9.2	Leptokurtic**
Nauyuk	583 ± 122	602	Normal			
Sylvia Grinnell						
(1948–51)	526 ± 134	531	Platykurtic	14.41 ± 4.1	13.6	Platykurtic*
(1950)	517 ± 138	612	Normal			
			C. clupeaformis			
Great Bear	515 ± 69	531	Normal	16.9 ± 3.9	16.8	Normal
Redrock	569 ± 44	576	Leptokurtic**	14.8 ± 2.7	15.5	Leptokurtic*
Dismal	503 ± 99	566	Normal			
			(5–14 Yr)	9.9 ± 2.3	8.5	Normal
			(14–24 Yr)	18.3 ± 1.894	18.5	Normal
Wholdaia	422 ± 63	462	Leptokurtic**	—	—	—
Nonacho	495 ± 105	547	Leptokurtic**	—	—	—
Keller	562 ± 88	567	Leptokurtic**			
			(2–10 Yr)	5.6 ± 2.24	7.2	Normal
			(11–26 Yr)	18.4 ± 2.50	18.9	Normal
Beverly	446 ± 48	457	Leptokurtic*	17.3 ± 3.9	17.16	Normal
Vaillant						
100–450 mm	215 ± 70	176	Leptokurtic**	18.9 ± 3.2	20.4	Normal
400–600 mm	504 ± 80	514	Normal			
La Martre	522 ± 48	528	Leptokurtic**	13.2 ± 2.3	13.8	Leptokurtic*
Beaverlodge	492 ± 45	499	Leptokurtic**	—	—	—
Hyde	453 ± 49	463	Leptokurtic**	14.2 ± 1.93	14.3	Leptokurtic**

In 1945, Miller (1947) carried out the first survey of Great Bear Lake using cotton nets of 2½-, 3-, 4-, and 5-in. mesh sizes (stretched measure). The lake was sampled again by Johnson in 1963–65 (Johnson 1975b) and by Falk et al. (1974) who in 1973 obtained data from anglers' catch.

The age- and length-frequency distributions of lake trout from these three periods are shown in Fig. 13. There is little change in the distribution with time, for either age or length. Falk used otoliths exclusively for aging; these seem to give slightly higher readings up to 20 yr and considerably higher ages in older fish.

The change over the same period in the size of whitefish in Great Bear Lake is negligible (Fig. 14). This species is harvested by the native Indian domestic fishery in restricted areas so that the figures are for an essentially unexploited population.

Lac la Martre was sampled in 1959 during the survey of the barren grounds and again by Bond (1973) in 1972. Between 1969 and the start of the fishing season in 1972, it was estimated that

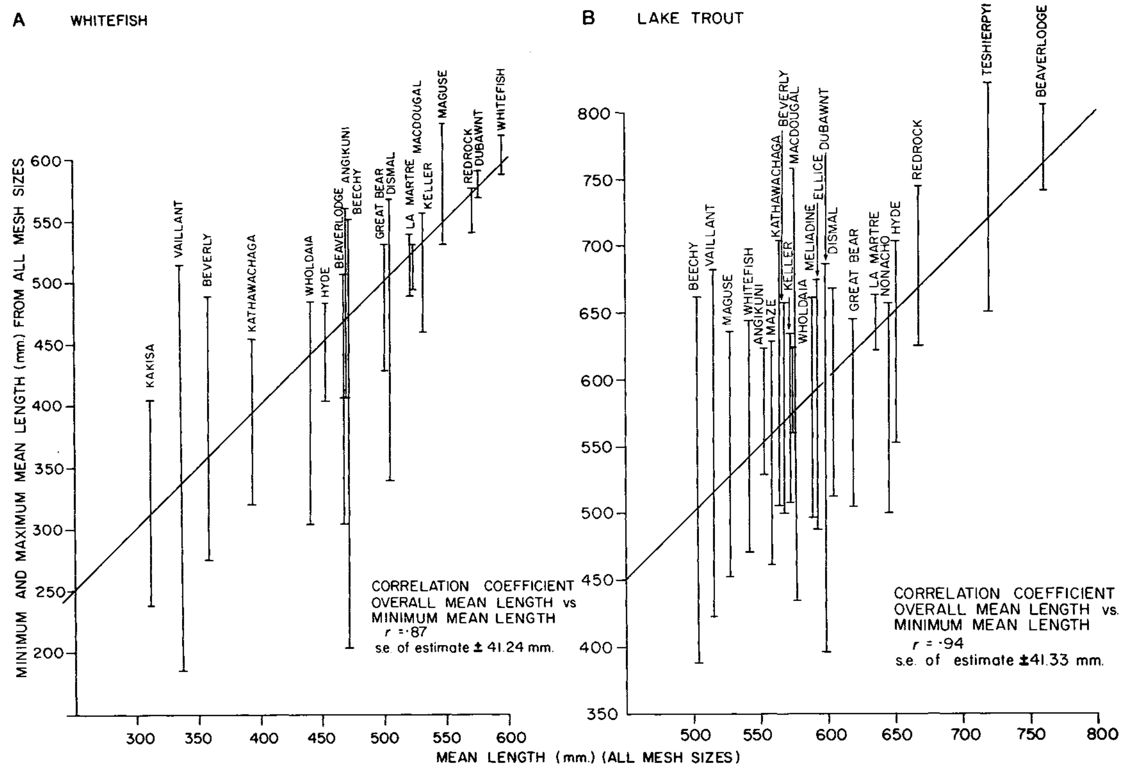


FIG. 10. Correlation between the mean length of fish caught in all mesh sizes and the smallest mean length of fish taken in any mesh size (usually 1½-in. mesh) for A, lake whitefish, *C. clupeaformis*, and B, lake trout, *S. namaycush*.

TABLE 4. Total number of fish caught by each mesh size for lake trout (*S. namaycush*) and lake whitefish (*C. clupeaformis*). Also score of number of length groups in which fish were caught, by mesh size (e.g. one set of a single mesh size capturing fish in five different 50-mm length groups scores 5). Data from Fisheries Research Board Barren Ground Survey 1959.

	Lake trout					Whitefish				
Mesh size (*in.*)	1½	2½	3½	4½	5½	1½	2½	3½	4½	5½
No. of length groups captured	251	249	218	199	201	109	107	97	89	85
No. of fish caught	695	921	1068	1229	889	594	1105	1535	1621	1370

681,000 kg of trout and whitefish was captured for a total removal of 3.8 kg per ha. The population has thus been subjected to some modification in the interval between samplings. Bond used a slightly different series of mesh sizes in Lac la Martre compared with those used in 1959; he substituted 6½-in. mesh for the 5½ in. previously employed; this was to conform with the practice of the local fishermen who can sell profitably only large whitefish. In spite of the relatively heavy fishery there is remarkably little difference in the length distributions of either whitefish or lake trout (Fig. 3 and 4). There is an increase in the numbers of small whitefish taken in the small mesh sizes in 1972 but this is not apparent for the lake trout; apart from this the shape of the distributions is identical in each one of the 2 yr.

The lake trout of Angikuni were sampled in

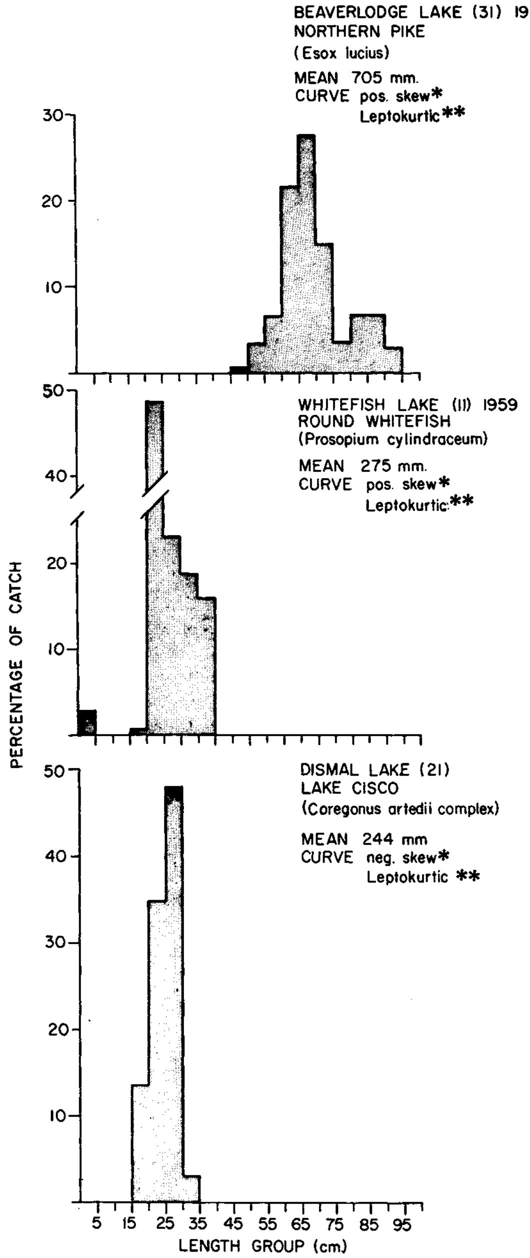


FIG. 11. Length-frequency distribution, all mesh sizes combined, for A, northern pike, *Esox lucius*, from Beaverlodge Lake 1959; B, round whitefish, *Prosopium cylindraceum*, from Whitefish Lake 1959; and C, lake cisco, *C. artedii*, from Dismal Lake 1959.

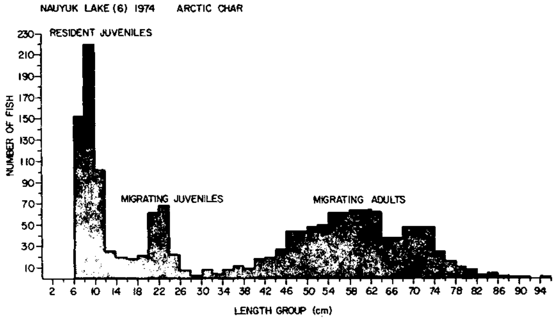


FIG. 12. Length-frequency distribution of Arctic char, *S. alpinus*, from Nauyuk Lake. Migrating adults and migrating juveniles taken at the counting fence on downstream run in 1974, resident juveniles taken during migration downstream from spawning lake in the same year.

1959 using standard gangs (Fig. 5) and again in 1968, using only 5½-in. mesh. The results of the 5½-in. mesh in 1959 are compared with those of 1969 in Fig. 15. The difference in the results of these samplings is small when it is recognized that the 5½-in. mesh is not the most efficient and captures the narrowest range of length groups (see section above); in fact, it is probably the worst mesh size for comparative purposes of all those employed.

Keller Lake was studied in 1962 (Johnson 1972) and again sampled briefly in 1974 (Table 5). The whitefish are remarkably constant in size between the time of the first sampling and the second fishing in 1974. The figures for the lake trout are not in such good agreement but they do not indicate any positive change when the small size of the sample in 1974 is considered.

Keyhole Lake was fished intensively by Hunter (1970) between 1961 and 1967; the greatest catches were in 1963 and 1965 and it was estimated that the equivalent of close to 100% of the initial stock was removed. The initial condition appears to be unimodal with a modal value of 308 mm (Fig. 7) but there is evidence that a smaller mode existed: Hunter in a personal communication states that "electrofishing in Keyhole Lake resulted in large catches of small to 20 cm fish." The initial fishing was sufficiently heavy to cause a change in the size and age structure. By 1965 the remnants of the initial population have grown slightly and may be observed in the right-hand peak in Fig. 7, while the left-hand peak consists of fish not showing in the earlier sample. These "new" fish are mainly in the 5- to 8-yr-old age-classes, while the 1963 peak at 9 yr old can be observed at the age of 11 yr in 1965. It is apparent that the "new" fish were present in the lake in 1962 as 2–5-yr-olds but too small to be taken by the gillnets. Thus, the reduction in the large population appears to have resulted in an upsurge of juveniles.

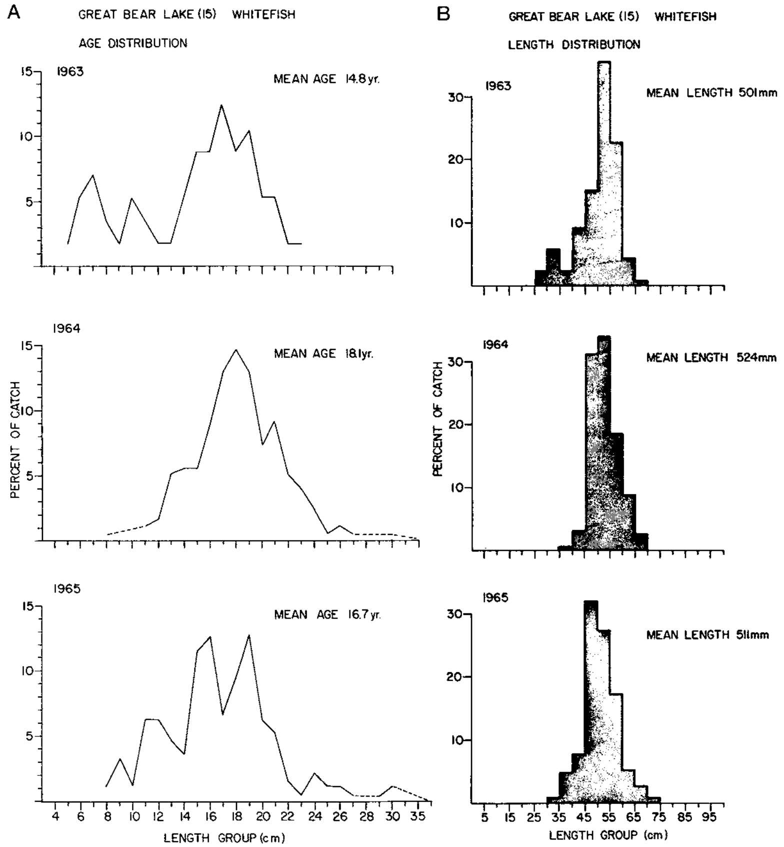


FIG. 13. Age- and length-frequency distributions of lake whitefish, *C. clupeaformis*, in Great Bear Lake for the years 1963–65, all mesh sizes combined.

Ten years later in 1975 (Fig. 7) the population has reverted to a condition very close to that of the original one; the char in the size range 170–250 mm have been eliminated as a significant group and two peaks have reestablished themselves with modal values at 111 and 314 mm. In addition to returning to a size structure very close to the original one the length–weight relationship is virtually unchanged:

1962–63 $\log W = 3.0236 \log L - 2.0461$
1975 $\log W = 2.95412 \log L - 1.9635$

Lake Namaycush was revisited in 1975 after a lapse of 13 yr (Fig. 7). Some differences in population structure can be observed, but in all probability these can be attributed to the sampling in 1962, which is now recognized as being unrepresentative. In this year only the shallow western end was sampled; no spawning fish were taken the majority being extremely large and probably senile. In 1975 the whole lake was explored more effectively and spawning fish in some number were captured; these were not in the largest size-groups. In both years the fish were extremely emaciated with heads of tremendous size. The length–weight ratio has remained virtually unchanged:

1962 $\log W = 2.62861 \log L - 3.95596$
1975 $\log W = 2.66830 \log L - 4.05757$

Relationship between age and size — In all northern populations it has been shown that there is a great range in age for fish of a given length (Grainger 1953; Miller and Kennedy 1948; Johnson 1972), and this condition has also been observed in other populations of considerable age, for example, the eel *Anguilla anguilla* of the English Lake District (Frost 1945). It is undoubtedly a widespread condition among fishes. In the populations at present being examined the majority of the fish occupy a relatively narrow length range, up to 60% falling within a single

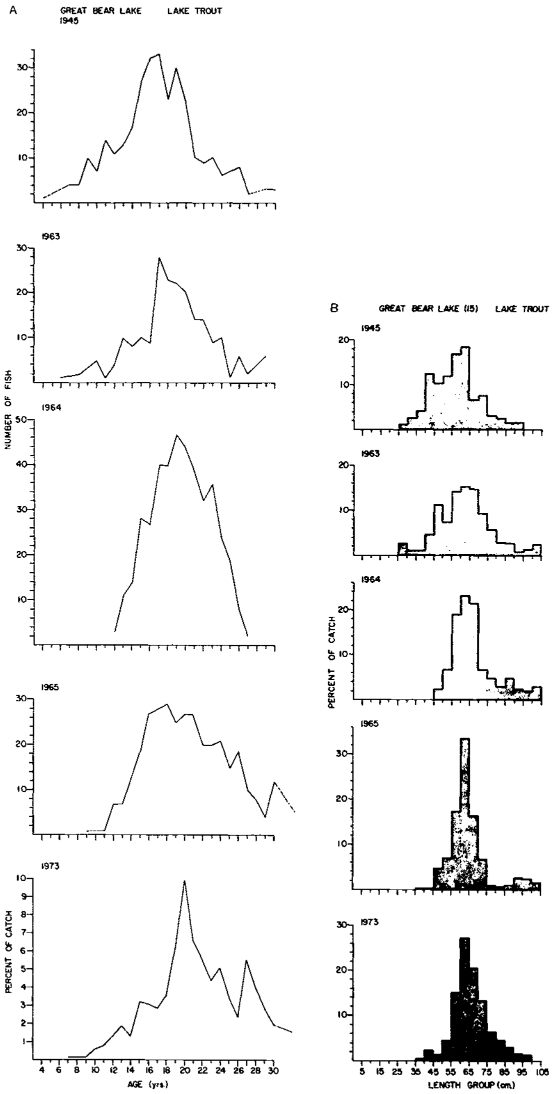


FIG. 14. Age- and length-frequency distributions of lake trout, *S. namaycush*, for the years 1945, 1963–65, and 1973. Data for 1945 from Miller and Kennedy (1948) and for 1973 from Falk et al. (1974); 1945 data from cotton nets, 1963–65 nylon nets, and 1973 from the sports fishery.

50-mm size-group; within such a length group ages may vary greatly. Obviously, the forces on the individual to achieve and retain a certain size are much greater than the tendency for the fish to increase regularly in length with time, i.e. there is little evidence for a regular growth pattern. Three examples, the whitefish of Beverly Lake (Fig. 16), the lake trout of Great Bear Lake (1963–65) (Fig. 17), and the lake trout of Lac la Martre (1959) (Fig. 4) will be considered.

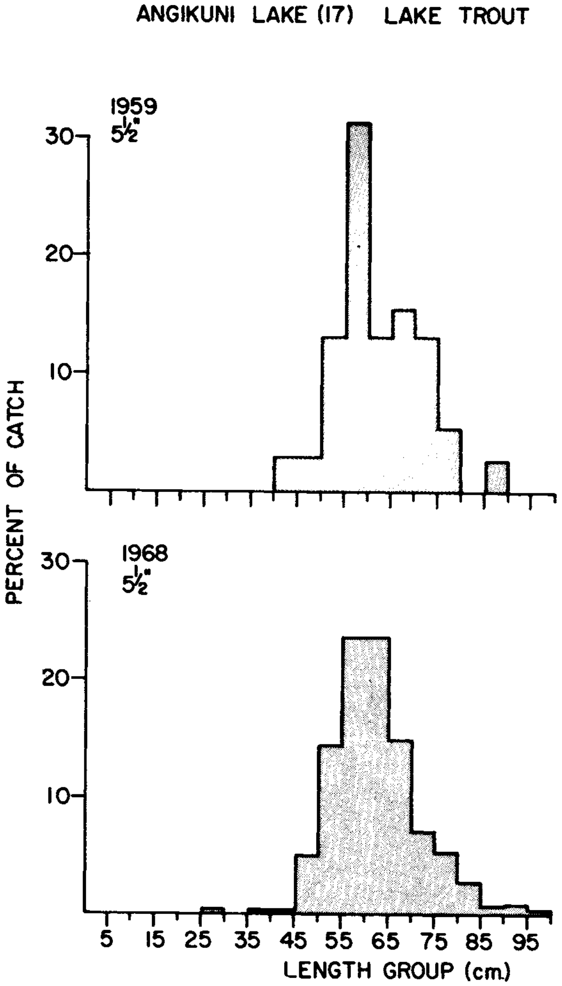


FIG. 15. Length-frequency distribution, for the 5½ in. mesh nets only, from Angikuni Lake in A, 1959 and B, 1968.

In Beverly Lake the most numerous whitefish length-group (400–499 mm) is composed of members between 6 and 26 yr of age; these ages embrace most of the sample (3–26 yr). The members of the 100-mm length-groups on either side of the most numerous group show no overlap in their ages (100–399 mm: 7–16 yr; 500–599 mm: 17–26 yr), but both these length-groups lie within the span of the 400–499-mm group. The trend to increasing length with age is thus only of a general nature.

The length frequency of lake trout from Great Bear Lake is plotted by individual age-classes in Fig. 17. There is some trend to increasing length with age up to 20 yr, but beyond this age there is no sign of general increase. The length distribu-

TABLE 5. Mean lengths (ML) of lake whitefish (*C. clupeaformis*) and lake trout (*S. namaycush*) captured in Keller Lake in 1962 and 1974.

	Whitefish				Lake trout			
	1962		1974		1962		1974	
Mesh size (*in.*)	ML (*mm*)	No.	ML (*mm*)	No.	ML (*mm*)	No.	ML (*mm*)	No.
1½	554	39	546	1	503	33	514	4
2½	528	187	540	3	555	143	511	3
3½	540	132	542	3	559	106	506	5
4½	543	135	575	6	579	154	522	4
5½	546	124	565	6	617	71	496	2
Combined	544	617	560	19	573	507	511	18

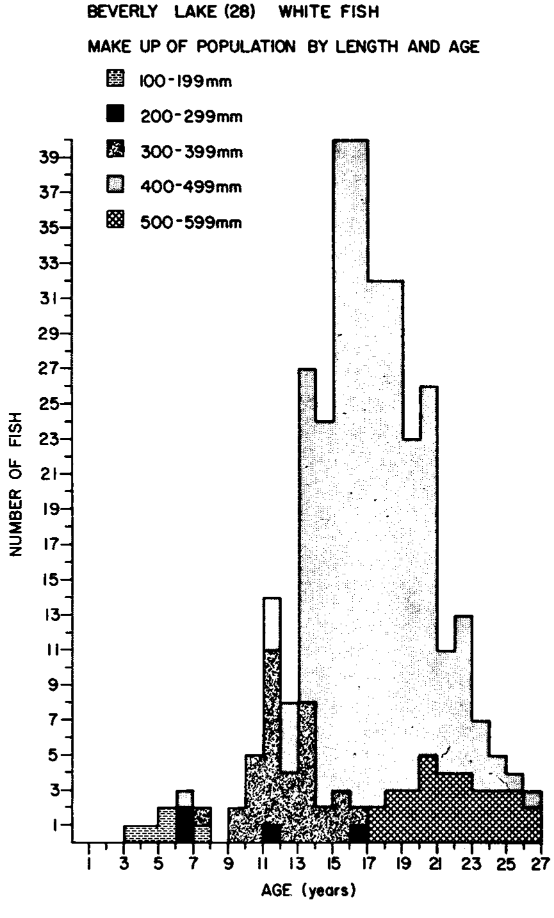


FIG. 16. The age-frequency distribution of lake whitefish, *C. clupeaformis*, in Beverly Lake 1959, by length groups. The relationship between age and length is general, the smallest fish being generally younger than the largest: the most numerous size-group 400–499 mm contains ages from 6 to 26 yr.

tion remains remarkably constant. This does not prevent certain individuals in any age-class from achieving a length greatly above the mean or conversely from lagging behind the mean class value at any age.

In Lac la Martre, the lake trout sampled in 1959 (Fig. 4) show one distinct group much larger than the majority. The fish in the more numerous smaller group are between 8 and 20 yr old with a modal value between 11 and 12 yr; the larger group is almost identical in age and is made up of 11–21-yr-olds. There is no bimodal structure to the age distribution. That the condition is not transient is shown by the appearance of the two distinct groups 13 yr later in 1972.

Discussion

SPECIES COMPOSITION AND ENVIRONMENTAL GRADIENTS

A well-marked gradient of increasing species diversity exists starting at northern Ellesmere Island (83°N) and moving south to the territorial boundary (60°N) and beyond; but there is also a gradient of increasing diversity from Baffin Island in the east to Victoria Island in the west. Such gradients are probably the result of an inextricable mixture of environmental conditions and accidents of distributional history; they are also based on a relatively small number of species.

The small complement of species in a given situation in the arctic compared with that of a similar one in temperate or tropical conditions has long been recognized; it was on this account that Wallace (1878), and more recently Fischer (1960) and Dunbar (1960a, b; 1968) have suggested that, from an evolutionary point of view, arctic systems are immature. This thesis was

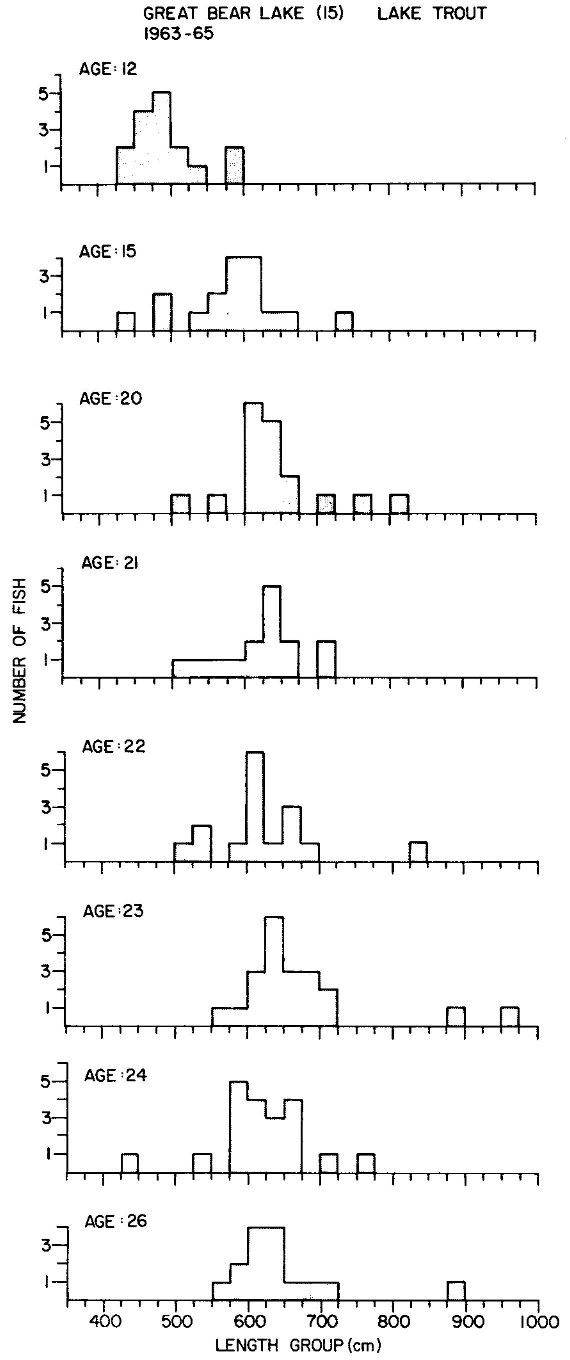


FIG. 17. Great Bear Lake, lake trout, *S. namaycush*, showing the gradual increase in modal length as age increases from 12 to 20 yr old. Beyond the age of 20 yr there is no increase in modal length.

rejected by Connell and Orias (1964) for lack of evidence and the problems entailed in obtaining confirmatory observations. It is questionable whether arctic systems have, in fact, had a short evolutionary history even though their existence in present locations is undoubtedly recent; there would seem to be no reason why they have not been able to migrate north and south in a manner similar to that suggested by Newell (1962) for more temperate biota.

A more fertile approach to understanding the individual species and the species interactions making up the total ecosystem is the study of gradients that can be more immediately related to environmental conditions. Vegetational analysis gradients have been shown to exist through time, leading to the equilibrium position of the climax (Tansley 1935, 1939; Whittaker 1953; Langford and Buell 1969) and space (Curtis and McIntosh 1951; Whittaker 1967). Species have been shown to change continuously in their abundance and growth form along lines of environmental change, changes in the status of individual species resulting in changes in the makeup of the communities. A climax is any well-marked enduring community which may persist indefinitely with relatively regular climatic conditions provided that there are no deterministic or organismic overtones as implied by Clements (1936).

Margalef (1968) equates maturity with diversity, a diverse system being more mature than one with fewer species. This, however, seems to be too broad a generalization, since mature forest may contain fewer species than the preceding successional stages (Whittaker and Woodwell 1972). Johnson (1975b) showed that fewer species existed in Great Bear Lake than in smaller lakes of comparable age within the same drainage basin. Low species diversity appeared to be the result of extreme environmental conditions. There also exist in the arctic, in regions of postglacial land uplift, at relatively low elevations above sea level, lakes that show less species diversity than lakes slightly below them and hence younger. Similarly two adjacent lakes at approximately the same elevation may each show a different species complex both of which appear to be derived from a condition that includes both sets. Little Nauyuk Lake (char dominated) and Klondike Lake (lake trout dominated) each have only a portion of the full species complement found in Nauyuk Lake (Table 1). Undoubtedly some species in each case have been eliminated by competition for the very short supply of resources; as in the forest climax a reduction of diversity is apparent compared with the earlier stages of succession. Given time each lake matures to reach a climax condition individual to that lake.

With the objective of examining the possible existence of gradients in fish populations, the relative importance values (percent catch composition by weight) of lake trout and whitefish were arranged in order of their relative magnitude (Table 2, Fig. 2). The results indicate that there are lakes where only lake trout are present (although invariably one species of cisco, *Coregonus artedii*, *C. autumnalis*, or *C. sardinella*, is present with the lake trout), through lakes where there are equal proportions of trout and whitefish to those lakes (mainly outside the region being considered) that contain, of the two species being considered, only whitefish. There is, in fact, a well-marked gradient of changing species composition.

The proportions of lake trout and whitefish show no clustering about a specific value; this is indicative of the independence of the two species and the formation of independent communities in each lake or region within a lake. This independence is confirmed by the largely independent food chains of the two species and the rather remarkable absence of whitefish in the trout diet (Johnson 1972, 1975b). Evidence obtained through the comparison of Great Bear and Great Slave lakes indicates that it is largely the density of benthic food organisms that limits summer distribution of whitefish, and not temperature or depth. In the southern portion of its range whitefish inhabit the warmer, more productive lakes that lake trout are apparently unable to tolerate. Lake trout, by contrast, are able to withstand extremes of great depth, no light, and low temperature.

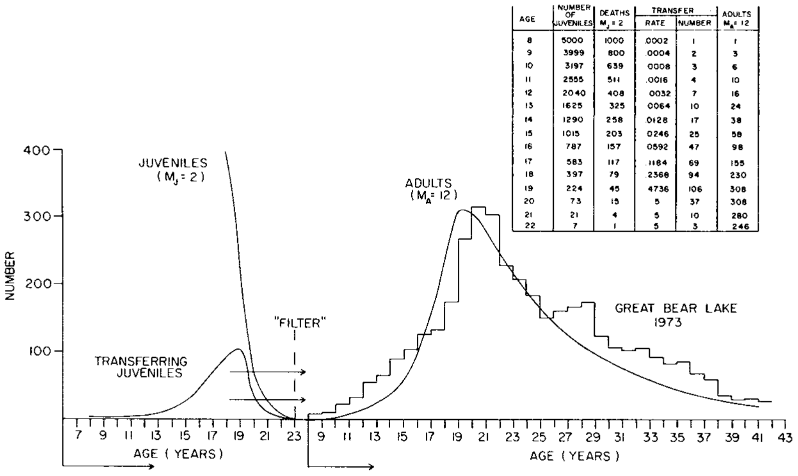
Whitefish and lake trout are terminal predators, each at the end of its respective food chain and each free of dependence on the other; both species eventually reach sufficient size to be entirely free from predation whatever the source. Both species live to a great age so that their populations reflect a "time-binding" character, or the embodiment in the population of the effect of past years' environments and interactions (Whittaker and Woodwell 1972). These fish populations thus appear to have the characteristics of the dominant species in a climax community. Whittaker and Woodwell contrasted forest and phytoplankton and concluded that it was difficult to apply the climax concept, as they had discussed it, to aquatic natural communities. In aquatic communities there may be a significant change of role between plant and animal so that fish in lakes dominate the structure of the community in a manner comparable with that of trees in the forest. This condition is not to be confused with the "biotic climax" of Tansley (1935), which is the term he applied to an arrested stage of succession, such as that maintained by grazing animals. In the aquatic situation it is a final stage of equilibrium, the so-called stable climax condition, which has been reached.

Equilibrium in Arctic Lakes

Since 1924 when Elton (1924) first showed that cyclical fluctuations occurred in the harvest of many northern Canadian fur-bearing animals, a considerable literature has developed (Elton 1934, 1942; Elton and Nicholson 1942; Vibe 1967) on animal cycles in the north. Cyclic fluctuations have become associated with the arctic; this has been reinforced by the conclusions of MacArthur (1955) that diversity leads to stability in tropical systems and hence, by contrast, arctic systems which are low in diversity are inherently unstable. More recently Krebs and Myers (1974) have shown that fluctuations in small mammal populations occur in many parts of the world irrespective of latitude. Clough (1972) has also reported the existence of a stable community of hutias (*Geocapromys ingrahami*) existing in a tropical island setting and having very low diversity of both plants and animals owing largely, to the low rainfall.

Johnson (1972, 1973) suggested that unexploited fish populations in northern lakes are constant in their age and size structure over long periods of time without any evidence of fluctuation, a conclusion also reached by Dunbar (1973) on the basis of work by Grainger (1953) and his own long arctic experience.

If arctic populations of fish show a steady state over long periods of time, is it possible to refer to them as being stable? The literature on this subject suffers from lack of differentiation between the terms "stable" and "being in an equilibrium condition." Margalef (1963, 1968) has suggested that the ratio of primary production to mean annual biomass (P:B ratio) is a measure of the stability of an ecosystem, and MacArthur (Leigh 1965) has pointed out that dimensionally this ratio is similar to the reciprocal of the mean life span: the smaller the P:B ratio (or 1/mean life span) the greater the stability. This index was developed for whole ecosystems, but by the same reasoning the relationship of the energy entering an individual species through its food supply in relation to the biomass of that species would be a measure of its stability. Hurd et al. (1971) developed a different measure of stability based on thermodynamic considerations,



AGE	NUMBER OF JUVENILES	DEATHS M_J = 2	TRANSFER		ADULTS M_A = 12
			RATE	NUMBER	
8	5000	1000	.0002	1	1
9	3999	800	.0004	2	3
10	3197	639	0008	3	6
11	2555	511	.0016	4	10
12	2040	408	0032	7	16
13	1625	325	0064	10	24
14	1290	258	.0128	17	38
15	1015	203	0246	25	58
16	787	157	0592	47	98
17	583	117	.1184	69	155
18	397	79	.2368	94	230
19	224	45	4736	106	308
20	73	15	5	37	308
21	21	4	5	10	280
22	7	1	5	3	246

FIG. 18. A possible mechanism whereby a constant modal age is maintained in the catchable portion of the population. Fish from a juvenile group are allowed to pass to the "establishment" as mortality in this group reduces pressures on the juveniles. Recruitment through the "filter" or suppressive mechanism of adult on juvenile is over a 15-yr span (from 8 to 23 yr); it is low at 8 yr and reaches a peak rate at 19 yr. The smooth curve represents the theoretical passage of a single year-class through time, and the histogram the actual age-frequency distribution of the angling catch in Great Bear Lake in 1973. Data for the angling catch from Falk et al. (1974) smoothed by 3s.

which requires that a stable system is one characterized by 1) the rapidity of the response to perturbation, 2) the amplitude of the deflection from the ground state, and 3) the rate at which the perturbation is damped.

Consideration of these definitions leads to the conclusion that the P:B ratio is an indication of the existence of a steady state, whereas application of the criteria of Hurd et al. provides information on the real stability of the system, or the force required to move the system from the equilibrium position. The P:B ratio is a measure of the persistence of the ecosystem in the face of the environmental conditions experienced over its lifetime; it provides no information on the stability unless information on the environmental conditions experienced is also given.

The invariably high mean age of the arctic fish populations sampled indicates the long-term existence of a state close to the equilibrium, or climax, condition. The fact that all populations appear to be in the same phase indicates that this condition exists indefinitely; if this were not the case it might be exepcted that fluctuations would be apparent in at least one or two lakes. The steady state is epitomized by Great Bear Lake where the rate of turnover in the adult population alone is 17.3 yr, and this does not include the period of 8–20 yr that these adults spend in the prerecruit phase (Fig. 18); these conditions have remained constant over 30 yr. In Lac la Martre conditions have remained constant over 12 yr, in Lake Namaycush over 13 yr, and in Angikuni over 10 yr; there is no evidence to indicate periodic fluctuations in these fish populations. Even in Vaillant Lake, the whitefish population, which by its size structure might be considered to be undergoing a recovery process, is shown by its age structure (mean age 18.9 h) to have been in this condition for a long time.

From a qualitative point of view primary production in arctic lakes is very low, being <8.5 g $C \cdot m^{-2} \cdot y^{-1}$ (Kalff 1970; Hobbie 1973), but total biomass is high. Hunter (1970) estimated the total biomass of char to be 48.8 kg/ha for Char Lake. Lac la Martre gave catches of 79 kg/100 m of net per 24 h and in the most favorable regions of Great Bear Lake 81 kg of trout and whitefish/100 m of net per day were obtained. Undoubtedly a very high biomass is present compared with primary production.

The only evidence for the magnitude of the forces inducing equilibrium is provided by Keyhole Lake. After a heavy fishery in 1962–63 and 1965 in which a large fraction of the initial population was removed, recovery was complete 10 yr later in 1975. Unfortunately, it is not known for how long prior to 1975 recovery had been achieved. The early stages of recovery (1965) are marked by an upsurge of juveniles present in the lake at the time of the initial fishery (as shown by their age); these fish in 1962 were presumably the equivalent of the fish in the left-hand mode of those captured in 1975. There appears to be little oscillation in numbers as the juveniles move forward to assume adult status. The recovery of Keyhole Lake is marked by a rapid response to a large perturbation and a high degree of damping as the ground state is regained, the essential characteristics of a stable population as defined by Hurd et al. (1971).

There is little doubt as to the essential stability of Keyhole Lake in the face of massive perturbation and its ability to regain and maintain an equilibrium position when extraneous perturbations are removed.

The second lake meriting careful scrutiny is Nauyuk Lake. There is no possibility here that the bimodal distribution of the seagoing population is caused by gillnet selection as all records were obtained at the counting fence. That the population is in equilibrium is demonstrated by the high percentage of tag returns and the virtually constant size of the population between the 2 yr.

The structure of the Nauyuk Lake char population is almost identical with that observed by Grainger (1953) in the Sylvia Grinnell system, Baffin Island.

Completely independent evidence for the ability of arctic ecosystems to maintain a steady state condition is provided by Rigler et al. (1974) who showed that the crustacean plankter *Limnocalanus macrurus* remained at quite constant numerical strength over a 4-yr study at Char Lake (75°N), Cornwallis Island.

From these considerations relatively simple systems can apparently exist in equilibrium and also exhibit a considerable degree of stability. This seems contrary to the conclusions of MacArthur (1955). Margalef (1968) considered that stable systems at low temperature might have existed at one point in the earth's history but that they were no longer present.

AGE AND LENGTH DISTRIBUTION OF A POPULATION IN EQUILIBRIUM

Frequency distributions of fishes in unexploited arctic lakes all show similar patterns of size and age; the characteristic form shows one or more bell-shaped curves that approach a Gaussian or normal distribution. A high degree of clustering around the modal value is characteristic for length but this is less marked for age. If these curves are truly representative of the populations from which they are drawn, how is it possible to reconcile them with the virtually static condition of the population? It will be shown that such a "standing wave" for length and age is in fact characteristic of a population limited by resources to a fixed establishment.

It has been known for some time that unexploited fish populations often show an extreme condition in which large numbers of old fish of uniform size exist. Baranov (1918) was first to discuss this condition; he provided the explanation that there was an accumulation of old fish whose growth decreased proportionally with age. Hart (1931) examined populations of whitefish from Shakespeare Island Lake which appeared to confirm these suggestions.

Baranov's reasoning is not, in itself, sufficient to explain the existence of what Ricker (1975) has termed the "dome-shaped" catch curve, which is a relatively symmetrical curve about a point where fish of a certain length are caught in greatest abundance and where frequency of capture declines on either side. There appear to be two possible explanations for the left-hand ascending limb of the curve. The first is that the fish are not fully vulnerable to the gear being employed and are, therefore, under represented in the catch in proportion to their actual abundance in the lake. This is the explanation usually invoked and has gained almost universal acceptance (Grainger 1953; Beverton and Holt 1957; Ricker 1975; Kennedy 1953). This explanation based on reduced vulnerability stems from the assumption that there is a mean size roughly correlated with age and that this growth pattern is relatively constant for a given water body. If growth is regular and year-class strength relatively uniform, then the numerical strength of each length-group will decrease as length increases, following a negative exponential function similar to that for mortality; catch curves for age and length will then be quite comparable. If year-classes are not numerically uniform then it might be expected that there would be numerous size-groups, which, owing to slightly different growth rates, would tend to become obscure, but that such discontinuities would show up in the catch curve for age. Neither condition provides a satisfactory explanation for the regularly ascending left-hand limb of the catch curves observed; ultimately, it is necessary to decide between an explanation involving reduced vulnerability or an explanation involving an irregular growth pattern.

The alternative explanation is that the catch curve is not an artifact of the sampling procedure but does represent the population in the lake over most of the lengths sampled. If it is assumed that the number of adult fish in a lake is constant, as appears to be the case from analysis of age and length, then recruitment must be controlled, most probably through a feedback mechanism that dampens fluctuations in year-class strength, if this occurs, and admits only such recruitment as is necessary to achieve equilibrium with mortality. In these circumstances it is necessary to postulate an increase in growth rate (not necessarily tied to a certain chronological age since recruitment occurs over a number of years) as soon as a fish moves into the phase of active recruitment.

There are several arguments that support the second alternative rather than the first. In the first place the modal size of fish in the catch curve varies from lake to lake in such a way as to require great changes in vulnerability to account for it. These changes in vulnerability would all have to move in concert for all the five different mesh sizes in the standard gang as shown in Fig. 3–5. It would be necessary to postulate that, using identical gear, lake trout smaller than 745 mm are not fully vulnerable in Beaverlodge Lake although fully vulnerable at 486 mm in Vaillant Lake. Similarly char become fully vulnerable at 150 mm in Gaviafaeces Lake, 220 mm in Little Nauyuk Lake, 320 in Keyhole Lake, while in Lake Namaycush, lake trout only become fully vulnerable at 765 mm.

The clustering of fish in the population curve around a certain length value, with this clustering being evident in all mesh sizes, makes it impossible to believe that these are samples from a population in which numbers decrease regularly with size, or that smaller sizes are not showing up because of reduced vulnerability at least above 250 mm for the standard gang or 100 mm for the experimental nets.

The counting fence at Nauyuk Lake does not have the assumed disadvantage of selectivity but the population of seagoing fish shows a well-defined bimodal structure.

If the samples described are representative of the populations from which they are drawn and these populations are in a steady state or climax condition, it is necessary for full understanding to provide a mechanism for population control through a feedback system and then to describe a model of the manner in which the system works.

THE FEEDBACK SYSTEM

In a forest climax young trees are suppressed by the exclusion of light at lower levels through the formation of a closed canopy; this canopy is a property of the assemblage of dominant trees but not the individuals. In a comparable manner it is suggested that corporate action of the adult portion of the dominant fish population maintains the juvenile mode in a peripheral position through some suppressive force.

The evidence for suppression is to be found in the bimodal structure of the populations from Keyhole, Namaycush, and Nauyuk lakes. In the first two lakes juveniles were found mainly along shorelines and tributary streams; in Nauyuk Lake the juvenile mode moved seaward only after the completion of the main adult run (Johnson and Campbell 1975). In Little Nauyuk and Gaviafaeces lakes, possibly also in Fiona Lake, the juvenile mode appears to be suppressed entirely apart from an ephemeral mode that would exist for a brief time after hatching. Cannibalism may play some part in the suppressive process; de March reports (personal communication) that most of the large char taken in Fiona Lake in 1975 had small char in their stomachs; Johnson (1975a) reported 2.8% cannibalism in lake trout in Great Bear Lake; however, it is felt that this is not the main mechanism, as cannibalism has not been observed in the majority of char or lake trout populations and never in whitefish. The restriction of juveniles to the periphery would tend to increase predation by birds when the population rose above the available niche space, the "nook-an-cranny" effect of Smith (1972).

When mortality in the established population reduces its ability to maintain juveniles in the peripheral zone, opportunities are created for the smaller fish to move forward, go through a period of rapid growth, and achieve establishment status. This process has the characteristics of an electronic filter in reducing "noise" or, here, recruits in excess of those necessary for replacement. Such a mechanism would tend to favor vigor as well as opportunity in a manner exactly comparable to the openings provided to seedlings or saplings in a forest; when a break in the canopy occurs, recruits move forward to occupy the space available.

The high degree of clustering around the modal size, although this size may be achieved over a wide span of ages, indicates that growth of individuals does not increase regularly with time. A plateau may be reached early or late in life, from which time onward size may remain stationary for a period; this is well illustrated by Beverly Lake whitefish (Fig. 16), Great Bear Lake trout (Fig. 17), and the direct observation of tagged lake trout in Great Bear Lake that did not grow appreciably over an 8–10-yr interval. These examples not only indicate nonuniform growth rates, but the existence of certain constraints on size, as if individuals represent nodes of equipotential in superimposed fields of force, one of the fields of force being the interaction between individuals.

A closely parallel condition has been observed in the predatory fish populations of Lake Tanganyika (Coulter 1970); data collected during purse-seining in the offshore waters for the small clupeid fishes *Limnothrissa miodon* and *Stolothrissa tangenicae* are remarkably similar to those from northern lakes. Three of the predator species *Lates mariae*, *L. microlepis*, and *L. angustifrons* are all shown to have a high degree of clustering around the modal value in the unexploited state: *L. mariae* has a modal length of about 600 mm, *L. microlepis* 700 mm, and *L. angustifrons* about 750 mm. Smaller modes of these species are found along the littoral regions of the lake at lengths between 50 and 180 mm. Coulter considers that, especially for *L. microlepis* and *L. angustifrons*, the catch curves for the pelagic populations represent the actual size distributions fairly closely. Aging was not possible as no check marks occur in tropical fishes.

MODEL OF A FISH POPULATION IN EQUILIBRIUM

A model of a fish population in a steady state has been developed for the Great Bear Lake lake trout population (Fig. 18). There is a wide range of ages in the juvenile mode, only the descending limb of which is shown. A given year-class will reach the earliest age at which it is possible for young trout to make the transference (age 8 yr in the model) to the establishment. As size of some individuals increases with time additional juveniles make the transference at successive ages until a peak rate at transfer is achieved (age 19 in the model); the rate of increase in the probability of any fish making the transference has been considered to be exponential until a maximum transfer rate of 0.5 occurs at the age of 20 yr; by this time numbers in the juvenile phase of the year-class have declined to a very low number, although at peak abundance in the adult phase. The juvenile segment becomes extinct at the age of 23 yr. The adult phase accumulates a given age-class up to the age when it reaches 20 yr after which mortality in the adults is greater than recruitment so that numbers begin to decline. Mortality rates of 20 and 12% have been applied annually to the juvenile and adult groups, respectively.

This model provides a close fit to the actual population data from Great Bear Lake as given by Falk et al. (1974). In the model Falk's results are shown in the histogram, while the computed results are shown in the smooth curve. The model does not violate, in any way, the "law" of mortality which requires that the number in an age-class must always decrease with time. It is only in the adult mode where numbers in a given year-class do appear to increase, but here only a fraction of the total existing year-class is represented. Growth calculated from adult catches will give a biased view of the growth of the year-class as a whole, since only the fastest growers will be included.

This model may be contrasted with that developed by Coale (1972) for a human population in equilibrium. In Coale's model birth rate is in balance with death rate but there is no feedback mechanism to control birth rate in the face of changing death rate. Such a model would have no built-in stability with which to resist perturbation; fluctuations in birth rate would be reflected through the population, while changes in death rate would reduce or augment the adult population. Coale's model does emphasize the present human dilemma but does not meet the constraints on fish populations that have reached the limit of the finite resources available to them.

There are two aspects to the feedback model that seem to be most satisfactory from an ecological viewpoint, particularly in conditions where resources are scarce. In the first place it is much more efficient as the majority of the energy entering a species in a steady state is directed to maintaining a large number of large adults, rather than toward the production of a large number of prerecruits which would, in effect, serve merely as energy gatherers for predators of other species, i.e. the greater part of the mortality takes place when the fish are small (even if quite old). The second feature is the great ability of the system described to absorb year-to-year fluctuations in year-class strength; if the juvenile population is depleted through several years of poor hatching or early development, it is quickly refurbished with the advent of a good year. The juvenile group is a reservoir from which recruits are drawn as necessary.

FEEDBACK MODEL IN OTHER BIOLOGICAL SITUATIONS

If the model described has validity in arctic lakes then it might be expected to be found in circumstances which are to a degree comparable. Reference has been made to similarities between the dominant fish species and dominant forest trees. It is here that one might expect to find the closest comparison in size and age structure.

It is difficult to find examples of truly untouched forest on which the necessary measurements have been taken; Jones (1945) gives examples of size composition by stem diameter for European forests and McIntosh (1972) and Buell and Carlton (1951) for North America. Jones, who doubts the existence of truly virgin forests in Europe, unmodified by fire, animal grazing, or cutting stresses the fact that stems of small diameter are often rare in a climax forest so that judged by the uniformity of trunk size the stands appear to be evenly aged.

Many forests, with little diversity in the species making up the canopy, have achieved an equilibrium condition, stable over many thousands of years in the face of the natural perturbations they have had to withstand. This stability may have been manifested through an annual climatic cycle of great variation as in the Douglas fir (*Pseudotsuga menziesii*) forests of the Pacific coast of Canada and the northern part of the United States.

The bell-shaped age and size structure of populations in the equilibrium condition, far from being unusual, is what might be expected when the four following conditions are fulfilled: 1) a fixed establishment; 2) entry not fixed at a specific age but occurring over a spread of years; 3) potential recruits exceed those accepted; 4) numbers in the establishment are sufficient to ensure a reasonably constant mortality, and hence, recruitment.

These conditions are frequently encountered in human social groupings such as in certain legislative bodies (e.g. Canadian Senate or British House of Lords where group renewal does not depend on election at fixed intervals), professional sports teams, and other social groups with a fixed establishment. In these circumstances age and size (length or weight) will follow nearly Gaussian distributions and these will remain constant with time.

IMPLICATIONS FOR FISHERIES MANAGEMENT

The existence of a gradient in the ratio of the relative importance value of lake trout and whitefish in a community emphasizes the need for conducting fisheries or other surveys in the field of aquatic biology through examination of environmental gradients. Surveys should be planned with the existence of gradients in mind. The nature of the gradient to be explored will depend on the circumstances of the survey but gradients may be found within lakes, through changing elevation, or across geological boundaries; latitudinal gradients are likely to be less profitable. As Whittaker (1967) maintains "gradient analysis has changed the concept of vegetation as much as research on the genetic basis of variation and evolution has changed the concept of plant species." Gradients in lake populations may be more difficult to explore and analyze than plant communities, but certainly the rewards could be as great.

Recognition of the fact that the dominant fish populations in northern lakes are in a steady state or climax condition implies the existence of a degree of homeostasis and therefore, according to Tansley (1935) and Baker (1966), a degree of organization. This organization can be discerned in the shape of the length and age distributions and in the clustering around a modal length value. The independence of each organizational unit (or lake) is shown by the different modal sizes and ages and in the proportion of each species present.

Any fishing pressure on a climax condition will tend to reduce the level of organization by increasing the energy flux through the system and producing a concomitant loss of equilibrium. With increasing pressure the system is strained to the point where the dominants can no longer exert any form of corporate control so that oscillations, triggered perhaps by small changes in the environment, are set up. A single species of fish, as in the char of Keyhole Lake, will return rapidly to the equilibrium position, whereas a more complex system will have many alternative pathways through which the energy can move. Therefore, the chances are greater for oscillations to develop before equilibrium is reestablished (May 1973). In Canadian freshwater fisheries it is usually the dominant species that are sought after; it is therefore essential to think in terms of sustained populations rather than sustained yields.

A singular characteristic of the dominant species has been shown to be that, in the final prerecruit stage, it must control its own recruitment. If the dominance is destroyed, what is the effect on the juvenile groups? Can they out-compete subordinate species without some form of parental presence, albeit of a repressive nature, or do they require a parental "canopy" for their proper survival? Production may be limited by the failure of the juvenile group to reestablish itself following initial replacement of a harvested population. The "fishing-up" process attempts to speed up the energy flow through the system and maintain a regular succession of ages and sizes through the fishery, but in Great Slave Lake, in spite of high initial abundance, lake trout were virtually eliminated from the Western Basin with no signs of a upsurge of small young fish (Keleher 1972). Evidently lake trout have evolved toward low replacement rates or K-selection (MacArthur 1972) to such an extent that they can only maintain a large biomass at an extremely low turnover rate. Char and whitefish have undoubtedly a much greater resilience to harvesting, and there is little doubt that the now decimated char populations of Greiner and Sylvia Grinnell lakes would recover rapidly if cropping were suspended. Traditionally the Eskimo fished char on an intermittent basis, moving to a new system when the run being fished was reduced to a low level of harvest, returning to the original fishery only after a lapse of several years. Rotational fishing of a slow-growing climax population seems to have much to commend it.

If the desired goal of lake fisheries management is the regulation and maintenance of a fishable population of large fish, then it is essential to determine the status of fish in the intermediate size range. In the bi- or multiple-modal model there will be a relatively small group of fish of this size, fast-growing and probably feeding voraciously and hence quite vulnerable; it is upon these fish that adult replacement will depend and it is essential that they be given maximum protection. If, on the other hand, the theory in which numbers decrease with size is valid then this intermediate group will be relatively abundant and will need little protection. Every effort should be made in any management program to ascertain the status of the postrecruits and to protect them accordingly.

The turnover time of a population will also provide most useful information on the state of a fishery. The turnover time ($\bar{T}$) is, in effect, the reciprocal of the P : B ratio and may be calculated:

$$\bar{T} = \frac{1}{N} \sum_{i_{\min}}^{i_{\max}} (T_i)(f_i)$$

where T_i = age of animal; f_i = number of animals in age class i; and $i_{\min}$ and $i_{\max}$ are the maximum and minimum ages in the catch. Changes in turnover time, being relative, will be less influenced by aging error than absolute values.

It will be seen from the foregoing that fish populations in lakes have evolved under different conditions from those in the sea. Lakes with their finite bounds have contained the incoming energy and evolved toward the establishment of dominance and the maintenance of the steady state, while the oceans with their fish populations living in a state of continuous instability (Longhurst et al. 1972) have had to solve a different set of environmental equations. Results from one set of circumstances should only be transferred to the other with a degree of caution.

Although it is arctic lakes that have been considered in this paper they do not appear to be greatly different in type or in species complex (apart from the presence of Arctic char) from those farther south. Most Canadian lakes east of the Rocky Mountains were originally dominated by whitefish and/or lake trout and, if the early reports are to be believed these species were present in great abundance and were of uniform size. Most populations have failed to withstand heavy exploitation. Perhaps management authorities and fishery scientists have been influenced too greatly by brilliant mathematical analyses and paid too little attention to the underlying ecology and the understanding of ecological processes which are often too variable and too complex to be satisfactorily represented mathematically.

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