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Distribution of Fish Species in Great Bear Lake, Northwest Territories, with Reference to Zooplankton, Benthic Invertebrates, and Environmental Conditions

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Benthic invertebrates in Great Bear Lake are most highly concentrated in the upper 20 m. Densities between 20 and 100 m are low; below 100 m only *Mysis relicta* and *Myoxocephalus quadricornis* exist at measurable densities. All benthic organisms exhibit a high degree of patchiness.

Lake trout, *Salvelinus namaycush*, and *M. quadricornis* are two species that inhabit the lake at all depths (3–400 m) and temperatures (13.2 C for *M. quadricornis* and 15 C for *S. namaycush*).

Whitefish, *Coregonus clupeaformis*, inhabit only the bays, seldom being caught in water over 20 m deep. The distribution of whitefish is considered to be restricted mainly by the density of benthic organisms.

Three species are confined to the periphery of the lake, *Stizostedion vitreum*, *Lota lota*, and *Catostomus catostomus*. Two species, *Couesius plumbeus* and *Percopsis omiscomaycus*, are present in the headwaters and Great Bear River but have not been able to establish themselves in Great Bear Lake. Extreme oligotrophy is considered to have had the effect of reducing species diversity.

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Les invertébrés benthiques du Grand lac de l'Ours se concentrent surtout dans les 20 m supérieurs. Entre 20 et 100 m, leur densité est faible; au-delà de 100 m, *Mysis relicta* et *Myoxocephalus quadricornis* sont présents à des densités mesurables. Tous les organismes benthiques ont une distribution très inégale.

Le touladi, *Salvelinus namaycush*, et *M. quadricornis* sont deux espèces qui se rencontrent à toutes profondeurs (entre 3 et 400 m) et températures (13.2 C pour *M. quadricornis* et 15 C pour *S. namaycush*).

Le grand corégone, *Coregonus clupeaformis*, ne fréquente que les baies et n'est que rarement capturé à des profondeurs dépassant 20 m. La densité des organismes benthiques serait le principal facteur limitatif de la distribution du grand corégone.

Trois espèces sont confinées à la périphérie du lac, *Stizostedion vitreum*, *Lota lota* et *Catostomus catostomus*. Deux espèces, *Couesius plumbeus* et *Percopsis omiscomaycus*, sont présentes à la tête des eaux et dans la Grande rivière de l'Ours, mais n'ont pu s'établir dans le Grand lac de l'Ours. On croit qu'une extrême oligotrophie est responsable du peu de diversité des espèces.

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NORTHERN lakes are among the few remaining natural resources that have not been subjected to modification by development or advancing technology. This is because of their isolation and the difficulty and expense encountered in reaching them. In the 1950s this situation began to change and since that time there has been an ever increasing demand on the aquatic resources of the north (Johnson 1975a).

In 1957 it was recognized by the Fisheries Research Board that more information on physical and biological components of northern lakes was required if these resources were to be managed on a satisfactory basis; of particular importance was Great Bear Lake where a growing angling industry faced an increasing demand from fishermen to open the lake for commercial purposes.

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More recently the possibility of hydroelectric development on the Great Bear River has been at issue (Crippen and Associates 1972). With the objective of obtaining more information about the fish stocks and their environment, investigations on Great Bear Lake were started in 1963. The initial part of the program was to explore the fish populations in detail with particular reference to the effect to limnological conditions on abundance and distribution.

Methods

The physical and chemical background of Great Bear Lake has been discussed by Johnson (1975b); to summarize: it is an extremely oligotrophic lake, essentially polar or cold monomictic in character (Hutchinson 1957), although set in a subarctic geographic region where other lakes are north-temperature dimictic in their circulation pattern. The great volume of the lake enables it to gain and lose vast quantities of heat with little temperature change. This perennially cold condition is superimposed on a relatively small catchment basin mostly of insoluble rock so that nutrient supply is very low. Only in the most sheltered portions of the lake do temperatures reach 15 C in summer.

In view of the large size and unknown nature of the bottom topography it was not possible to plan detailed sampling programs in advance. Stations were established at suitable locations and plankton hauls, bottom samples, gillnet sets, and limnological observations were made at one locality. Approximately 100 stations were occupied each year; at 35% of these a full set of observations was carried out..

In addition to the vessel, M.V. *Radium Gilbert* and limnological equipment previously described (Johnson 1975b), the principal fishing gear was gangs of graded gillnet of the following mesh sizes: 1½ inches (38 mm), 2½ inches (62 mm), 3½ inches (89 mm), 4½ inches (114 mm) and 5½ inches (140 mm); one 50-yard (45.7-m) panel of each mesh size constituted a gang. The mesh sizes 1½ inches and 2½ inches were not used in 1964 and 1965 owing to their lack of success in 1963. Nets were set on alternate nights between the middle of June and September 10, between 1600 and 1000. A unit of effort was 50 yards (45.7 m) of net set for 16 h. An attempt was made to sample all areas of the lake, but as the vessel's crew was limited to an 8-h working day more attention was given to waters in the vicinity of suitable harbors. Two gillnet sets were made in deep water, one in 400 m and the other in 200 m. In that both these sets were successful in catching fish the experiments were not repeated; the expenditure of time, effort, and equipment would not have been commensurate with the additional information obtained. An attempt was made to obtain at least one deep net set (>50 m) in each region investigated. The depth at each end of the net was sounded and surface and bottom temperatures measured using a reversing thermometer.

A small beam trawl or dredge with a mouth opening of 1 m and a bag with 1-mm^2 mesh size was used successfully down to 220 m. The trawl was allowed to reach the bottom and then towed for 5 min at 1 km/h. Abundances were determined on the basis of a swept area of 134 m^2. The trawl was not of the closing type so that there is some possibility that additional organisms were collected between the bottom and the surface (but not the reverse as the frame floated upright). The only organism likely to be affected was *Mysis relicta* which was occasionally taken in plankton hauls. Duplicate tows were carried out only when there was doubt about the efficient working of the equipment, but most localities were investigated on more than one occasion in the course of the 3 yr.

One of the greatest problems encountered was the extreme patchiness of results with little to indicate possible reasons. This condition has been noted in Lake Superior (Cook and Johnson 1974) and attributed to differing bottom types.

In addition to the beam trawl an otter trawl with a 4.9-m opening was occasionally used to a depth of 220 m.

Plankton samples were collected using a no. 20 mesh net (73 μm) attached to a 152-mm (6-inch) Clarke-Bumpus plankton sampler. Hauls were made at depths of 1, 5, 10, and 20 m; vertical hauls were taken in deep water. Collections were made on a regular basis in the waters off Port Radium in addition to the sampling at stations throughout the lake.

Bottom samples were collected using a 152-mm (6-inch) Ekman dredge and a 0.1 m^2 Petersen dredge for deeper water; duplicate and often triplicate samples were collected. The typical offshore bottom mud of Great Bear Lake is a very heavy sticky yellowish-brown clay which is exceedingly difficult to sieve for bottom organisms. Only a coarse screen with an aperture of 0.25 mm could be used effectively within the imposed time constraints. Undoubtedly many of the smaller animals, particularly chironomid larvae, passed through the screen.

In 1965 an extensive tagging program on the lake trout (*Salvelinus namaycush*) was carried out in the east end of McTavish Arm, the area most heavily exploited by anglers. Trout were taken, using barbless hooks, by angling and by frequently tended gillnets; fish were measured for fork length and marked with a Petersen disc type tag. Three parties, one each in the north, center, and south of the Arm, applied 914 tags between the middle of June and the end of July.

Fish samples were examined in the field and the species weight, length, sex, and state of maturity were recorded. Scales or otoliths were taken for later age determination and stored in a dry state. Specimens of fish and bottom organisms were preserved and deposited with the National Museum, Ottawa.

Results

ZOOPLANKTON

Plankton hauls yielded a small number of crustacean species but showed uniformity both in species composition and total number of indi-

TABLE 1. Percentage occurrence of zooplankton in offshore waters of Great Bear Lake.

	McTavish Arm	Smith Arm	McVicar Arm	Dease Arm
	Aug. 2/65 0–350 m	Aug. 28/65 0–40 m	Aug. 26/65 0–97 m	July 30/64 0–50 m
	%	%	%	%
Limnocalanus macrurus				
Adults	0.5	4.5	9.3	5.7
Copepods	6.3			
Nauplii	2.1			
Senecella calanoides	2.0	0.03	1.1	0.4
Diaptomus sicilis				
Adults and copepodids	84.3	95.0	85.8	90.5
Nauplii	2.5	0.4		
Cyclops scutifer				
Adults and copepodids	1.9		4.6	3.4
Nauplii	0.04			
Daphnia middendorfiana		0.07		
Total no. individuals/m^2 ($\times 10^3$)	40	142	43	38

viduals. In the offshore waters only three species of copepods were collected; *Diaptomus sicilis* predominated at all stations (85–95%), with *Limnocalanus macrurus* and *Senecella calanoides* making up the balance. Table 1 gives representative samples for the main lake.

The number of adults of all species per square meter of surface area was calculated on the basis of a 50-m water column and a mean figure of 40×10^3 was obtained.

In the inshore waters there is an increase in plankton abundance in some of the bays (Good Hope Bay) (Table 2), but it is only at the south end of McVicar Arm that there is an appreciable increase in the number of species present; in fact the number approximately doubles from four to nine. The additional species are *Daphnia galeata mendotae*, *D. longispina hyalina* (*V. microcephala* ?), *Bosmina longirostris*, which is the most abundant of the additional species, and *Leptodora kindtii*.

The increase in species and number of individuals per unit volume in other inshore areas coincides with the marked elevation of temperature.

BENTHIC INVERTEBRATES

The main basin of Great Bear Lake has steep rocky shores along the eastern border; muddy bottoms in shallow water occur only at the extremities of the bays. Away from the Shield coastline in the larger bays (Hornby Bay, Good Hope Bay, Mackintosh Bay), there are extensive regions of flat sandy substratum in water depths of 3–20 m. Offshore the water shelves rapidly; the bottom mud is sticky yellow–brown clay. In McVicar Arm the eastern coast is shelving with a muddy bottom while on the side of Grizzly Bear Mountain the beaches are pure sand but drop off quickly into deep water.

In all parts of the lake it was only in the relatively shallow waters (<20 m) that there was an appreciable crop of invertebrates.

The greatest concentration of benthic forms was found in the upper 5 m, either associated with beds of algae in 3–5 m of water or in *Equisetum* beds in water less than 1 m deep.

The forms that were largely restricted to shallow water (<5 m deep) were: the amphipods *Hyalella azteca* and *Gammarus lacustris*, the gastropods, *Valvata cincera helicoidea*, *Gyraulus deflectus*, *Lymnaea elodes*, Trichoptera larvae, Ephemeroptera larvae, Coleoptera larvae, and Corixidae; Plecoptera larvae occurred along bouldery shorelines. Representatives of many of these groups could be found in a single dredge haul in the algal patches, in addition to the more abundant *Pontoporeia affinis*, *Mysis relicta* sphaeriids, oligochaetes, and chironomids.

Probably the most numerous organisms were chironomid larvae which were present at depths from 0 to 110 m. They reached their greatest abundance between 0 and 32 m but with only occasional individuals below this depth. Oligochaetes were most numerous in the upper 6 m; from 6 to 100 m numbers were very variable, ranging from one per 134 m^2 at 50 m to 6.4 per m^2 at 100 m.

Six species of sphaeriid clams were identified (Clarke 1973) in Great Bear Lake; *Sphaerium nitidum*, *Pisidium idahoenis*, *P. casertanum*, *P.*

TABLE 2. Percentage composition of zooplankton from inshore waters of Great Bear Lake.

	Northeast Dease	South Keith	Good Hope Bay	South McVicar
	Aug. 4/64	Aug. 15/64	Sept. 1/64	Aug. 24/64
Limnocalanus macrurus	6.5	3.2	.3	0.4
Senecella calanoides		0.1		
Epischura nevadensis		0.6		4.7
Diaptomus sicilis	68.1	93.6	97.4	51.0
Cyclops scutifer	3.6	2.5		
Cyclops vernalis	21.8			3.1
Cyclops sp. (copepodids)			2.3	16.6
Daphnia longispina hyalina var. *microcephala*				0.1
Bosmina longirostris				21.5
Leptodora kindtii			0	1.9
Daphnia sp. (?*middendorffiana*)			0.03	
Individuals/m^2 ($\times 10^3$)		268	471	

lilljeborgi, *p. nitidum*, and *P. conventus*. The highest abundance (all species combined) was found in water 1–5 m deep (400 per m^2) with 350 per m^2 between 5 and 10 m, and 200 per m^2 from 6 to 15 m, although individual densities reached 360 per m^2 at all depths to 15 m. Between 16 and 20 m numbers fell to 125 per m^2; below this depth collections became erratic and, where collected, numbers varied from 10 to 100 per m^2 with 85 per m^2 occurring at a depth of 100 m. None was encountered below this depth.

Larkin (1948) has discussed the distribution of *Pontoporeia* in Great Bear Lake. He found that the greatest abundance was encountered in the upper 17 m with densities between 1600 and 1800 per m^2; below 17 m numbers fell to 400 per m^2 and scarcely any were found below 60 m. The present collections confirm these findings but emphasize the great variation in density at any given depth. Densities up to 4000 per m^2 were found in patches of algae in only 3 m of water. In such circumstances *Gammarus* was about 25% as abundant as *Pontoporeia* but with its greater size probably made up about equal biomass. There was a rapid decline in numbers below 20 m; from 20 to 50 m, 50 to 500 per m^2 were encountered and this declined further at 100 m to one to two per m^2. Only one specimen (at 400 m) was taken at a depth greater than 100 m.

Mysis relicta was readily taken in Great Bear Lake using the small beam trawl. In contrast to other species there was an increase in the greatest observed density with depth down to 57 m (5 per m^2 at 3 m, 11 per m^2 at 13 m, and 22 per m^2 between 22 and 75 m). Down to 20 m high densities were associated with patches of green algae. Between 60 and 100 m densities were low (one to two per m^2), decreasing to one per 40 m^2 at 200 m, the greatest depth at which the species was taken. However, *Mysis* was found in *Myoxocephalus* stomachs, in turn taken from lake trout stomachs at 400 m.

In depths over 80 m in McTavish Arm and over 40 m in Dease Arm a species of *Hydra* was commonly found in bottom trawls.

Fish Species

The following species are listed by Miller (1947) but with the nomenclature adopted from McPhail and Lindsey (1970):

Salvelinus namaycush — lake trout
Coregonus clupeaformis — lake whitefish
Coregonus artedii — lake cisco
Esox lucius — northern pike
Thymallus arcticus — Arctic grayling
Prosopium cylindraceum — round whitefish
Stizostedion vitreum vitreum — yellow walleye
Lota lota — burbot or maria
Cottus cognatus — slimy sculpin
Pungitius pungitius — ninespine stickleback
Catostomus catostomus — longnose sucker

Miller records one trout-perch (*Percopsis omiscomaycus*) having been taken in the stomach of a northern pike, and Simpson (1843) indicates that inconnu (*Stenodus leucichthys*) was encountered at the north end of Dease Arm; neither species has subsequently been reported.

Occasional reports of chum salmon, *Oncorhynchus keta*, were recently verified by the capture and preservation of a specimen (D. H. Dowler personal communication) close to the Bear River outlet. Whether there is a spawning population of chum salmon in Great Bear Lake or whether the fish encountered there are strays from the regular small run of the Mackenzie River is not known.

TABLE 3. Catch and catch per unit effort (1 unit of effort = 50 yd [47 m] fishing for 16 h) of lake trout, *Salvelinus namaycush*, and lake whitefish, *Coregonus clupeaformis*, from Great Bear Lake in the years 1963, 1964, and 1965, for mesh sizes 4½ inches (114 mm) and 5½ inches (140 mm). Catch per unit effort (CPUE) calculated on only those nets catching fish. Also given is the percentage of the total catch of all other species.

Mesh size	Year	No. of sets	Total wt (*kg*)	CPUE (*kg*)
		Salvelinus namaycush		
4½	1963	23	493	21.4
	1964	37	930	25.1
	1965	22	578	26.3
	Total	82	2001	24.4
5½	1963	10	112	11.2
	1964	39	817	21.0
	1965	17	384	22.5
	Total	66	1313	19.8
		Coregonus clupeaformis		
4½	1963	7	99	14.1
	1964	16	245	15.3
	1965	11	115	10.5
	Total	34	459	13.5
5½	1963	7	69	9.9
	1964	15	141	9.4
	1965	12	165	13.8
	Total	34	375	11.0

Other species as percentage of total catch:

Stizostedion vitreum	4.07
Esox lucius	3.15
Catostomus catostomus	1.75
Thymallus arcticus	.68
Coregonus artedii	.28
Prosopium cylindraceum	.13

It seems that the latter is the more likely possibility since captures are infrequent despite continuous fishing by the native population close to the river at Fort Franklin.

The major addition to the species list provided by the present work is the bottom dwelling *Myoxocephalus quadricornis*, the fourhorn sculpin. This species is present in all regions and provides one of the major links in the food chain.

To avoid repetition the name whitefish is employed in this paper to refer to lake whitefish, *Coregonus clupeaformis*; *Prosopium cylindraceum* is referred to as round whitefish.

ECOLOGY OF THE FISH SPECIES

All fish species except *Myoxocephalus* were obtained by gillnetting, the only feasible method of capture; *Myoxocephalus* was obtained by trawling.

Gillnets were set in depths from 1 to 400 m in temperatures ranging from 2 to 15.5 C; a total of 236 sets were made comprising 10,856 m of net (Table 3). Catches per unit effort were high and uniform in each year. In 78% of all sets lake trout were caught, in 34% whitefish; only one net caught whitefish but no trout; 5% of all sets yielded only species other than trout or whitefish, mainly walleye and northern pike; 17% of sets failed to capture a single fish.

Lake trout — In the early part of the open-water season (mid-July to mid-August), before any definitive spawning congregation took place, lake trout varied greatly in their abundance (Fig. 1 and 2). At all depths a large number of apparently solitary fish were caught. At depths less than 80 m the lake trout became more abundant with catches of up to six fish per 47 m of net;

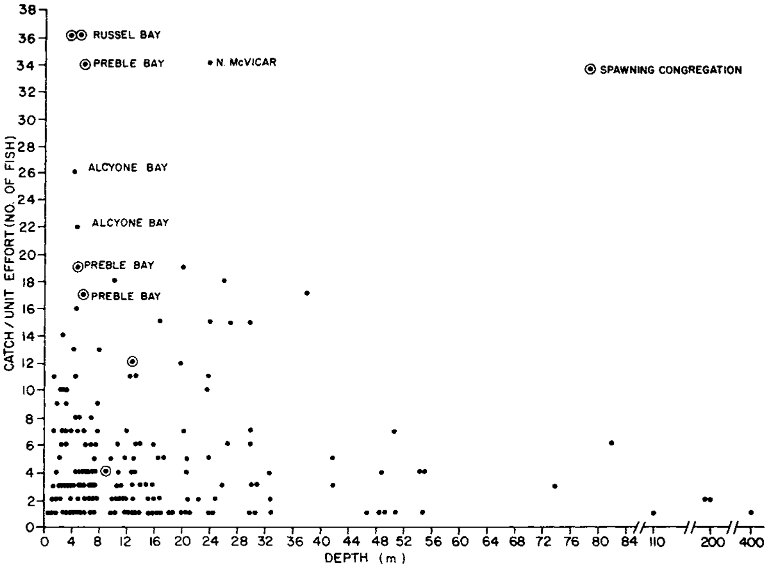

FIG. 1. The relationship between catch per unit effort (number of fish per 47 m of net set for 16 h) and depth of capture of lake trout, *Salvelinus namaycush*, in Great Bear Lake.

above 40 m catches up to 20 fish per net were taken and in depths less than 24 m catches of nonspawners rose to a maximum of 34 fish per net.

Nonspawning congregations could be identified by the absence of spawning fish; spawning congregations had a high proportion of ripening males even before the spawning act started. There was no suggestion that the nonspawning congregations were of small fish; one was of exceptional mean size (666 mm); 26 fish were caught in total and seven were over 900 mm.

There was little to indicate a definite preference for temperature among the nonspawning population. A wide range of catch per unit effort was observable over a considerable range of temperature although there was an indication that the greatest concentrations occurred between 4 and 9 C. It was apparent that there was no avoidance of the warmest waters of the lake (15.5 C) at the mouth of the Johnny Hoe River; either the trout are continuous residents in this area or they have had to pass through 20 km of water at a minimum temperature of 11.5 C.

Several authors have shown that lake trout tend to seek out the cooler part of the lake, below the thermocline if it should exist (Kennedy 1941; Martin 1952; Rawson 1961). In general lake trout seem to avoid waters over 12 C although Martin showed that they make feeding excursions into water of higher temperature above the thermocline. Ferguson (1958) lists 12 C as the laboratory determined preferendum but recognizes that it lies between 8 and 15.5 C when estimated from field observations. At the highest temperature encountered by the lake trout in Great Bear Lake (15.5 C) they are at their peak of physical activity, estimated by Gibson and Fry (1954) to be about 16 C. This is likely to increase the catch per unit effort relative to actual abundance in such warm waters, although maximum abundance of lake trout was not obtained at these temperatures.

Spawning concentrations, on the other hand, occurred only within a narrow range of depth and temperature. All spawning recorded took place between 5 and 13 m at temperatures between 4.5 and 6 C from August 18 to September 4.

Whether the deep-dwelling trout are permanent inhabitants of the region or whether they interchange with surface stocks has not been ascertained. The two specimens from the deepest part of the lake were examined by Khan and Qadri (1970) but they found no morphological differences which might indicate the development of a separate population comparable with the deep-living "ciscowets" of Lake Superior (Eschmeyer and Phillips 1965; Rahrer 1965; Khan and Qadri 1970). The general absence of suitable spawning shoals in deep water in Great Bear Lake tends to preclude the development of permanent stocks in these regions; it seems most likely that replenish-

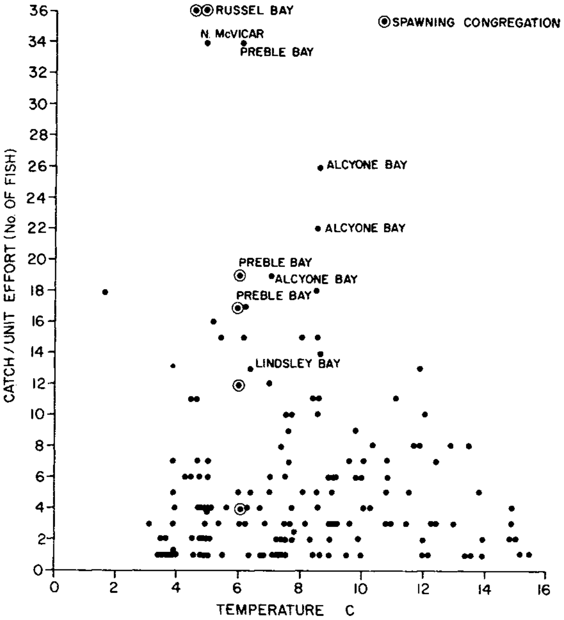

FIG. 2. The relationship between catch per unit effort (number of fish per 47 m of net set for 16 h) and temperature at the net for lake trout, *S. namaycush* in Great Bear Lake.

ment is from shallow water spawners. Lake trout and deepwater sculpin, their major prey below a depth of 200 m, are living in a zone of permanent darkness and constant temperature (Johnson 1975b).

Most trout taken in gillnets were in the size range 450–800 mm (Johnson 1973). As noted by Miller and Kennedy (1948a), the smaller sizes of fish were conspicuously absent. However, a number of isolated records are of interest. A small trout 50 mm in length and probably 1 yr old was taken in a trawl at a depth of 5.5 m in Preble Bay and a second one at 55 m in McVicar Arm. Four more of the same size and one of 105 mm were taken in a small stream entering Hornby Bay. No fish between 105 and 200 mm were captured. Similarly, Miller and Kennedy captured only one fish between 134 and 294 mm, and this from the stomach of a northern pike, but they took some under 100 mm long among rocks along the shore.

The youngest trout are apparently utilizing a variety of habitats: rocky shorelines, inflowing streams, and the deeper waters, all on the periphery of the area most intensively utilized by the adults. The most difficult problem is to elucidate the habitat of the intermediate-sized trout between 100 and 200 mm in length since not a single one was captured.

Movement of the adult trout was investigated by tagging fish in the areas subjected to the heaviest angling pressure. A total of 914 trout were tagged and 57 recoveries were made over the following 9 yr (Table 4). No general directional trend in movement is apparent nor is there any trend towards greater distance with time; some trout moved as much as 32 km (almost the greatest distance from the tagging site recorded) in the year they were tagged, while others were caught at the place of tagging 5 and 6 yr later. There was no indication that large fish (>700 mm) are sedentary while the smaller ones (<700 mm) travel; such a condition might be expected if there were a territory or home range being defended (Gerking 1959). All size-groups have some members that move and some that apparently do not. These results are comparable with those obtained by Keleher (1963) for lake trout of Great Slave Lake.

Analysis of stomach contents of the lake trout (Table 5) indicates a complete lack of specialization in feeding habits, and in general reflects more the site of capture than any specific food preference; this must not be overemphasized as all the species listed occur within the upper 10 m. The major item in the diet is the lake cisco, *Coregonus artedii*, which occurs more frequently than might be expected from net samples. Lake whitefish, *C. clupeaformis*, on the other hand, in spite of being the second most abundant species in gillnet captures occurs less frequently in trout stomachs than does trout itself. The higher than expected incidence of cisco and lower than expected whitefish incidence were also noted in Keller Lake (Johnson 1972).

The second most important foods are the cottids *Myoxocephalus quadricornis* and *Cottus cognatus*; trout from the deeper waters (which are underrepresented in the sample) fed almost exclusively on *Myoxocephalus*. There is a high incidence of cannibalism (2.8%) which is not common in other lake trout populations: Martin (1952) in a detailed study of trout in Algonquin Park, Ontario, did not record a single instance, nor was it recorded in Keller Lake by Johnson. Cannibalism is occurring in Great Bear Lake in a virtually undisturbed environment so there is reason to consider it may be part of the natural mechanism for population stabilization.

Lake whitefish — *Coregonus clupeaformis*, lake whitefish, have a discontinuous distribution within Great Bear Lake (Fig. 3). They are confined to the bays and were never taken in regions exposed to open waters, even in the shallowest reaches.

TABLE 4. *Salvelinus namaycush*, distance travelled (in kilometers) and number of years at liberty following tagging in 1965. "O" indicates recapture at tagging site.

Year of recapture	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Years at liberty	0	1	2	3	4	5	6	7	8	9
Distance (*km*)	0	16.1	0	4.8	41.9	0	3.2	3.2	6.4	50.0
	0	9.7	8.0	3.2		4.8	0			
	0	8.0	8.0	8.0						
	5	1.6	16.1	6.4						
	0	8.0	71.6							
	1.6	6.4	40.3							
	1.6	9.7	8.0							
	16.1	0	6.4							
	32.2	8.0	3.2							
	35.4		0							
	0		25.8							
	11.3		12.9							
	6.41		14.5							
	8.0		0							
	9.7		19.3							
	6.4									
	0									
	0									
Total number recaptures	18	10	14	4	1	3	2	2	1	2
Mean distance (*km*)	7.4	7.6	11.3	5.6	41.8	2.4	1.6	3.2	6.4	37.0

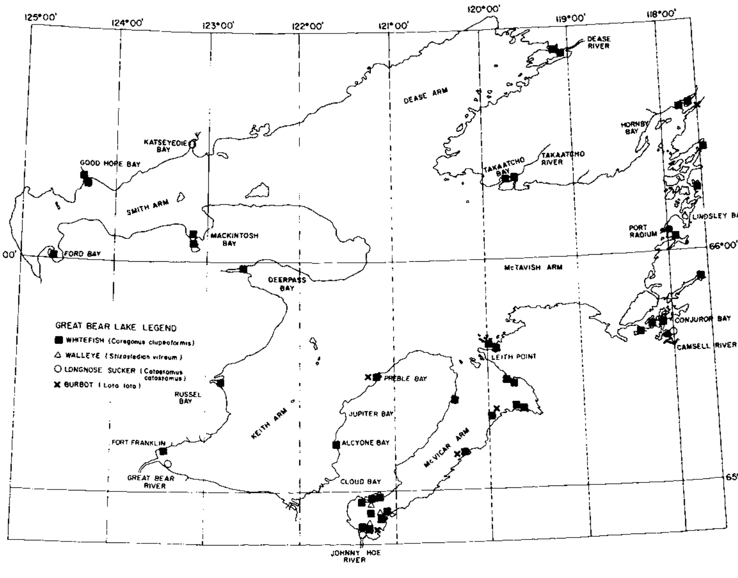

FIG. 3. The distribution of catches of lake whitefish, *Coregonus clupeaformis*, walleye, *Stizostedion vitreum vitreum*, longnose sucker, *Catostomus catostomus*, and burbot, *Lota lota*, in Great Bear Lake.

TABLE 5. Stomach contents of lake trout, *S. namaycush*, from Great Bear Lake. Gillnet samples taken in 1963, 1964, and 1965 in the open-water period mid-June to mid-September.

	Number[a]	% occurrence in those feeding
Fish		
Coregonus artedii	100	15.6
Unidentifiable cottids	25	3.9
Myoxocephalus quadricornis	20	3.1
Salvelinus namaycush	18	2.8
Cottus cognatus	16	2.5
Pungitius pungitius	11	1.7
Coregonus clupeaformis	11	1.7
Lota lota	6	0.9
Esox lucius	2	0.3
Thymallus arcticus	2	0.3
Prosopium cylindraceum	2	0.3
Unidentifiable remains	168	26.2
Eggs (mainly trout)	17	2.6
Invertebrates		
Mysis relicta	80	12.0
Gammarus lacustris	18	2.8
Pontoporeia affinis	17	2.6
Molluscs	15	2.3
Insects		
Chironomid nymphs	24	3.7
Hymenoptera	19	3.0
Beetles	14	2.2
Dipterous larvae	8	1.3
Corixids	7	1.1
Butterflies	2	0.3
Unspecified remains	25	3.9
Other		
Small mammals	1	
Frogs	1	
Plankton	2	
Nondigestible material (gravel)	23	

[a] Total number examined = 1079; number empty = 439 (40.7%); number feeding = 640 (59.3%).

Whitefish distribution in July and August represents normal summer feeding habitat because it is not until October that concentration for spawning takes place. It is at this time in the fall that they are heavily fished by the native population at the mouth of the Johnny Hoe River (Miller 1947).

The difference in environmental conditions between the bays and the open lake is more clearly defined in the main basin than in McVicar Arm; to emphasize this difference the catches per unit effort against depth and temperature have been plotted separately. In the main basin (Fig. 4 and 5) maximum catch per unit effort declines markedly with depth, but in McVicar Arm (Fig. 6 and 7) the decline with depth is not so regular, 10 fish per 47 m of net still being obtainable at a depth of 40 m. In both regions of the lake there is a strong tendency for maximum catches to be found at the highest temperatures; but high temperatures, in themselves, do not ensure high catches. Clearly bottom type and concentration of food organisms are overriding factors. The highest concentrations of whitefish are found on sandy bottoms where *Pontoporeia* (4000 per m^2) and sphaeriid clams (100 per m^2) reach maximum abundance. *Pontoporeia*, sphaeriids, and whitefish are all at low levels of abundance at 20 m and deeper.

Sphaeriid clams and other molluscs are by far the most important item in the whitefish diet (Table 6), followed closely by *Pontoporeia* and

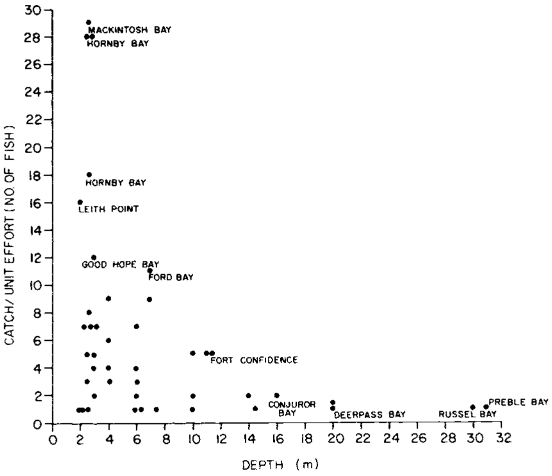

FIG. 4. The relationship between catch per unit effort (number of fish per 47 m of net set for 16 h) and depth of capture of whitefish, *C. clupeaformis* in the main basin of Great Bear Lake.

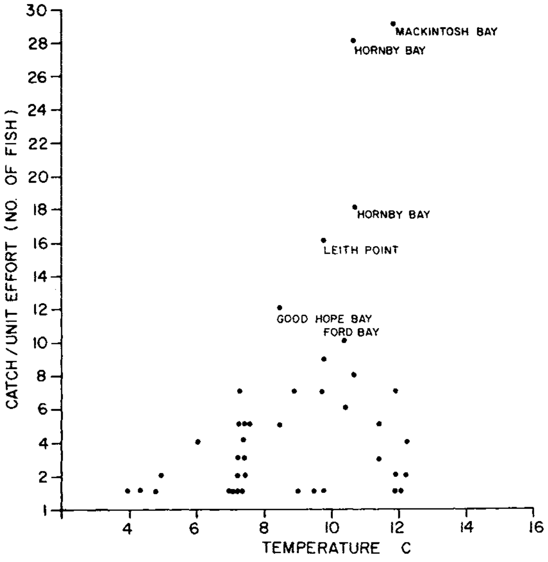

FIG. 5. The relationship between catch per unit effort (number of fish per 47 m of net set for 16 h) and temperature at the net for whitefish, *C. clupeaformis* in the main basin of Great Bear Lake.

Gammarus. Although *Pontoporeia* and *Sphaeridae* descend to a maximum depth of 100 m, it seems unlikely that they are in sufficient concentration to support whitefish populations.

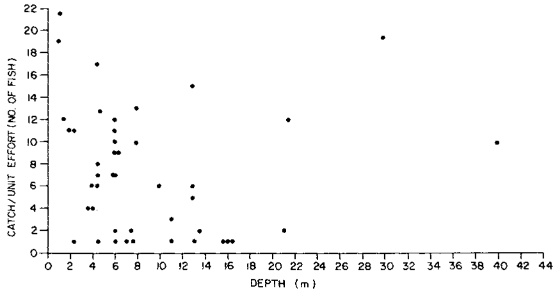

FIG. 6. The relationship between catch per unit effort (number of fish per 47 m of net set for 16 h) and depth of capture of whitefish, *C. clupeaformis* in McVicar Arm, Great Bear Lake.

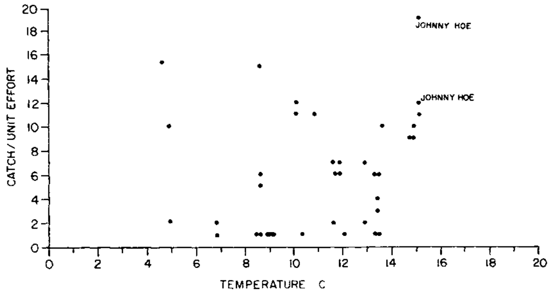

FIG. 7. The relationship between catch per unit effort (number of fish per 47 m of net set for 16 h) and temperature at the net for whitefish, *C. clupeaformis*, in McVicar Arm, Great Bear Lake.

The smallest whitefish occur along the deeper margin of the area occupied by adults. Two trawls yielded fish under 50 mm which were probably young of the year; 34 were collected in McVicar Arm at 31–37 m and 4.8 C, and nine in Deerpass Bay at 22 m and 6.2 C. No whitefish between 55 mm and 260 mm were taken by any method.

Fourhorn sculpin and slimy sculpin — In Great Bear Lake *Myoxocephalus* is the major converter of benthic organisms over the greater part of the lake bottom, and in turn serves as the most important food source of the deeper dwelling lake trout.

The fourhorn sculpin is the second species, with the lake trout, to occupy virtually the whole of the lake floor. The greatest depth at which *Myoxocephalus* was found was 220 m, the greatest depth at which trawling was practicable; however, specimens were found in stomachs of trout from 396 m. It was also taken by Rawson (1951) in an Ekman dredge at 461 m in Great Slave Lake, so it is reasonable to assume that *Myoxocephalus* exists in the very deepest water (446 m) of Great Bear Lake. Closer to shore the species was collected in a minimum water depth of 3 m. The maximum temperature at which it was cap-

TABLE 6. Stomach contents of lake whitefish, *C. clupeaformis*, gillnet samples taken in the years 1963, 1964, and 1965 during the open-water period mid-June to mid-September.

	Number[a]	% occurrence in those feeding
Fish		
Cottids	3	0.5
Pungitius pungitius	1	0.2
Unidentifiable	3	0.5
Invertebrates		
Sphaeriid clams	254	44.1
Other molluscs	139	24.1
Pontoporeia affinis	194	33.7
Gammarus lacustris	10	1.7
Unidentifiable amphipods	64	11.1
Mysis	15	2.6
Caddis larvae	16	2.8
Chironomids	51	8.9

[a] Total number examined = 709; number empty = 133 (18.8%); number feeding = 546 (81.2%).

tured was 13.2 C in 8 m of water at the southern end of McVicar Arm.

The density at which fourhorn sculpins occur is extremely variable (Fig. 8), but, it is apparent that there is no general trend of decreasing abundance down to a depth of 100 m. Densities ranged from one per 2 m^2 to one per 140 m^2. The ability of the sculpin to escape the trawl is probably not great, as its primary escape mechanism is to burrow in the mud where it would be susceptible to capture. The general distribution pattern is similar to that of its major prey *Mysis relicta.*

The habitat of *Cottus cognatus*, the slimy sculpin, is different from that of *Myoxocephalus quadricornis*; *Cottus* is largely restricted to the upper 3 m in Great Bear Lake, primarily along rocky shores, so there is very little overlap of the two species. Only once were they taken together in the same trawl; on this occasion *Myoxocephalus* was found in the highest temperature recorded for the species (13.2 C).

Walleye — In Great Bear Lake the walleye achieves its most northerly location as a lake inhabitant; farther north it occurs in the delta of the Mackenzie River where conditions are perhaps not truly representative of the latitude. In Great Bear the species is restricted to the almost circular basin at the southern end of McVicar Arm (Fig. 3). The area occupied has a diameter of 15 km and a maximum depth of 35 m; it is protected from the influx of cold bottom water from the more northerly part of the lake by a sill with a maximum depth of 20 m. This basin forms the largest mass of warm water within the whole lake; surface temperature at the center reached 13 C in summer with bottom temperature of 11 C. Secchi disc transparencies of 4 m were uniform in this region. There is no evidence that walleye exist elsewhere in the lake; the indication of the

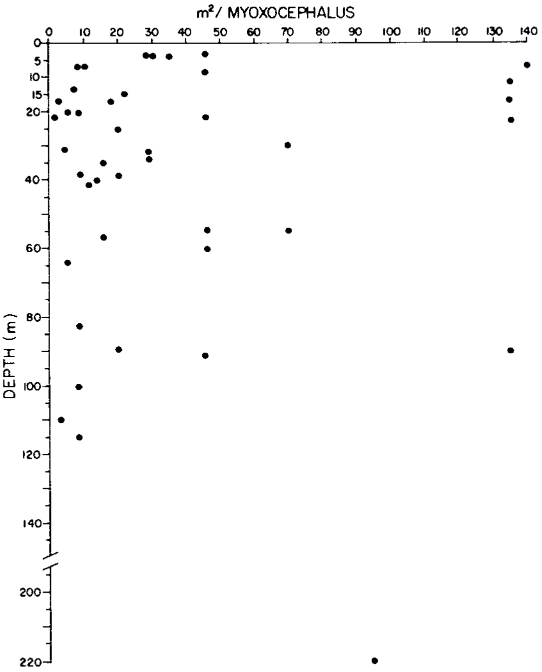

FIG. 8. The density of *Myoxocephalus quadricornis* (m^2 per individual) in Great Bear Lake, with respect to depth.

presence of walleye in the more northerly part of McVicar Arm given by McPhail and Lindsey (1970) should not be construed as indicating a specific record from this region (C. C. Lindsey personal communication).

Walleye is absent from the remainder of the lake and reappears only in the Great Bear River below the St. Charles rapids. It appears to be absent from the entire Camsell River although it is present in the Johnny Hoe system in Keller Lake (Johnson 1972) and Lac Ste Thérèse, the latter being designated a "pickerel (walleye) lake" in the Northwest Territories Fisheries Regulation (Anon. 1973). The temperature preferendum for walleye from field observations is given by Dendy (1948) and Hile and Juday (1941) as between 20.6 and 23.2 C, far above any temperatures recorded in Great Bear Lake. Scherer (1971) has indicated the importance of low light in the activity of walleye, and it is of interest that the southern portion of McVicar Arm has the lowest Secchi transparency of any area of the lake.

Burbot — Burbot, *Lota lota*, occurs infrequently in Great Bear Lake; it was never taken in gillnets during the present work nor during Miller's (1947) investigations. However, it is eaten by lake trout and was captured in a small inflowing stream in Hornby Bay. Miller records that one specimen was taken, presumably in shallow water, by being stabbed with a hunting knife.

The presence of a species in the stomach of its predator is not a completely reliable indicator of the habitat of the prey, but the small amount of movement on the part of lake trout in Great Bear Lake makes it possible to assess quite accurately the distribution of burbot (Fig. 3). Lake trout with burbot in the stomach were taken, with a single exception, in the warm shallow areas on the east side of McVicar Arm. The additional specimen was caught in Preble Bay on the east side of Keith Arm. All the burbot were less than 200 mm long.

The distribution pattern differs from that of walleye, in that burbot exists in widely dispersed locations throughout the lake, whereas walleye is restricted to a single area.

The small size of burbot is unusual, particularly when contrasted with the large size (604–832 mm) of specimens from the Great Bear River (Chang-Kue and Cameron 1975).

Little is known about the environmental requirements of burbot; it occurs in most northern lakes, occupying deep water in summer (Scott and Crossman 1973); in Great Slave Lake it is common at least to 100 m (Rawson 1951). McPhail and Lindsey (1970) report that burbot are quiescent in bright light but forage actively when the light is dimmed. Crossman et al. (1953) report a laboratory temperature preferendum of 21.2 C.

The high transparency of Great Bear Lake combined with lack of food supplies in the less well lit regions, coupled with 24 h of daylight in summer, is apparently inimical to the successful growth and development of this species.

Longnose sucker — This species has a distribution similar to that of burbot. It was collected only 3 times: once close to the outlet on the southern shore of Keith Arm, secondly at the northern extremity of Katsayedie Bay, a deep inlet on the northern shore of Smith Arm, and it was also quite abundant in the Camsell River (Fig. 3).

The longnose sucker ranges north of Great Bear Lake as far as the arctic coastline.

Other species — Little of significance can be added regarding the distribution of other species within Great Bear Lake. The lake ciscos in particular remain an enigma; they appear in some abundance in the bays of McTavish Arm prior to breakup of the main lake but are not caught in gillnets after this time. However, they occur regularly in the stomach contents of lake trout, and are caught throughout the summer in stakenets set by local inhabitants off Fort Franklin.

Round whitefish were collected very infrequently; too few were taken to allow their habitat to be characterized. Kennedy (1949) suggests that they prefer areas with a current, and more recently Chang-Kue and Cameron (1975) have collected many specimens in the tributaries of Great Bear River.

The growth and feeding of grayling in Great Bear was studied by Miller (1946); he reported the greatest concentration in the first 300–400 m of the Great Bear River. The river at this point flows with a strong current and maintains a temperature close to 8 C for much of the summer. Grayling are also found in lower concentrations in the mouths of the rivers originating on the Precambrian Shield and yet more infrequently along the more exposed coastlines where water temperatures are invariably below 10 C. Occasionally they were found in lake trout stomachs (0.2%).

Northern pike (Miller and Kennedy 1948b) and ninespine stickleback (*Pungitius pungitius*), are common in the warm shallow extremities of the bays in the vicinity of emergent or submerged vegetation.

Discussion

Great Bear Lake is oligotrophic in the extreme. In physical characteristics it is comparable with lakes of the arctic islands rather than those of the Canadian mainland (Johnson 1975b). The number of species of planktonic crustaceans is the lowest of any North American mainland lake (Patalas 1975), although not quite as low as Char Lake, Cornwallis island (Rigler et al. 1974) and Hazen Lake, Ellesmere Island (McLaren 1964) which each have a single species of copepod, *Limnocalanus macrurus* and *Cyclops scutifer*, respectively. However, the density of zooplankton in Char Lake which is between 23,000 and 48,000 stage V copepodites per square meter per year is quite comparable to the figure for standing crop of adult copepods in Great Bear Lake (40,000 m^{-2}).

Brylinsky and Mann (1973) have shown that on a global basis zooplankton production is better correlated with phytoplankton production than is benthic production. The low level of the zooplankton crop in Great Bear Lake may thus be taken as evidence of a low level of phytoplankton production.

The depth of the zone of maximum abundance of *Pontoporeia* appears to move downwards with decreasing oligotrophy, and *Mysis* is in all probability similarly affected. In the western basin of Great Slave Lake, Larkin (1948) found over 1000 *Pontoporeia* per square meter at depths between 50 and 100 m; at the same depth in the east arm the number was less than half (442 m^{-2}). *Mysis* was also present in the east arm at relatively high densities down to 280 m. In Lake Superior the profundal zone begins at about 70 m (Cook and Johnson 1974) and extends uniformly to the deepest points; this zone is dominated by *Pontoporeia*, and includes *Mysis relicta*, *Pisidium* sp., "*Chironomus*" sp., a number of oligochaetes, and a species of *Hydra*. In Great Bear Lake the zone of maximum abundance of *Pontoporeia* is between 0 and 20 m, in Great Slave Lake east arm 0–60 m, in Great Slave Lake west basin 50–100 m, and in Lake Superior 30–100 m.

Vollenweider (1974) gives the estimated rate of fixation of carbon by phytoplankton photosynthesis in Lake Superior at 50 g C m^{-2} yr^{-1}; this places Lake Superior well below his limit of oligotrophy (100 g C m^{-2} yr^{-1}). In Char Lake, the most oligotrophic lake studied, Kalff and Welch (1974) estimate total photosynthesis at 21.1 g C m^{-2} yr^{-1}, of which only 20% or 4.1 g C m^{-2} yr^{-1} is planktonic. From the work of Welch and Kalff (1974) it seems that benthic production in Char Lake extends to 20 m. No figures for carbon fixation in the east arm of Great Slave Lake are available, but on the basis of the bottom fauna it is apparent that the order of increasing oligotrophy is: 1) Lake Superior, 2) Great Slave Lake east arm, 3) Great Bear Lake, 4) Char Lake. Carbon fixation by phytoplankton in Great Bear Lake is thus between 4.1 and 50 g C m^{-2} yr^{-1}, possibly close to 4.1 g C m^{-2} yr^{-1}; this may be only 20% of total photosynthesis, the remainder taking place on the bottom.

It is not possible to assess the role of plankton in the feeding of fishes in Great Bear Lake since the species most dependent upon plankton, *Coregonus artedii*, was taken infrequently. However, the frequency of *C. artedii* in lake trout stomachs in the shallow waters indicates considerable indirect dependence of the lake trout on the plankton. Lake trout in Great Bear Lake have not developed the ability to feed directly on the plankton as Martin (1966) showed occurs in some Algonquin Park lakes; it is possible that plankton is too sparse in Great Bear Lake for this type of feeding to be profitable.

Benthic invertebrates are of great importance in Great Bear Lake in the support of both lake trout and whitefish populations, but their main zone of production is limited to the littoral 20 m; whitefish are found only infrequently below 20 m. Whitefish appear to be restricted to this zone by their food supply, since in the western basin of Great Slave Lake where *Pontoporeia* is abundant between 50 and 100 m (Larkin 1948), whitefish are common down to 75 m (Rawson 1951). At 75 m water temperatures between June and September rise above 4.0 C only for a short period in August (Rawson 1950), temperatures which would be experienced in Great Bear Lake at the same depth. Approximately 13% of the surface area of the lake is less than 20 m deep, of which about half may be considered whitefish ground.

Within the upper 20 m lake trout are equally abundant as whitefish, but lake trout have the ability to penetrate the greatest depths. In the profundal zone below 20 m the food chain seems to be straight:

(Detritus) → *Mysis* → *Myoxocephalus* → *Salvelinus namaycush*.

The young of all species are conspicuously absent; in those cases where young of either lake trout or whitefish were encountered they were of small size and limited to the periphery of the area occupied by the adults; fish of intermediate size (50–150 mm) were very rare. On the other hand, adult whitefish and lake trout were abundant in the more favorable areas and yielded high overall catches per unit effort. The dynamics of such populations is considered further by Johnson (1975c).

It is possible to arrange the fish species in order of their adaptation to extreme oligotrophy. Lake trout and *Myoxocephalus* are undoubtedly able to utilize all regions of the lake; both occur in surface waters but *Myoxocephalus* was not found in the upper 3 m. Whitefish are abundant in bays but absent from areas affected by the main lake circulation. Lake cisco, too, is abundant along the littoral regions in spring but difficult to catch thereafter. Next is a group well adapted to northern conditions whose habitat is normally in river mouths or the lake margin: ninespine stickleback, northern pike, slimy sculpin, grayling, and round whitefish. These are followed by two species that are barely able to maintain a position in Great Bear Lake: burbot and longnose sucker. These seven species are all distributed in lakes to the north of Great Bear Lake and along the Mackenzie River. It seems they arrived as the original inhabitants of Glacial Lake McConnell.

The walleye appears to have invaded from the south and to have been prevented from moving beyond the most southerly part of Great Bear Lake by environmental conditions. Water temperature and transparency are undoubtedly factors in determining its distribution, but the one unique characteristic of its range in Great Bear Lake is the early beginning of the warmwater season, provided by a northerly flowing river system with few lakes. In this respect the Johnny Hoe is comparable with the Mackenzie River where walleye are also present. In the Camsell River, with its large numbers of lakes and slow warming in spring, walleye are absent.

Chum salmon and perhaps inconnu invade the Great Bear River, but appear unable to maintain populations.

Two species, lake chub (*Couesius plumbeus*) and trout-perch (*Percopsis omiscomaycus*) live in the Camsell or the Johnny Hoe rivers and are thus free to invade Great Bear Lake. Also, they are both present in the Great Bear River, lake chub above and trout-perch below the St. Charles Rapids, the main obstacle between the Mackenzie River and the Great Bear drainage. In spite of this distribution they have been unable to establish themselves in Great Bear Lake, although normally they form lake-dwelling populations.

MacArthur and Wilson (1967) have shown that island faunas tend to increase in the number of species present with the size of island; if a lake may be considered the aquatic equivalent of an island then it might, a priori, be expected that species number would tend to increase with size of lake within a given region. Keller Lake is an order of magnitude smaller but has more species than Great Bear Lake.

Margalef (1964) has argued that species diversity increases with increasing oligotrophy.

In a recent paper Patalas (1975) has shown that in 14 North American great lakes there is a strong trend for the number of species of crustacean plankton to increase with increasing temperature and mean depth up to a certain temperature; above this temperature species number is reduced although the trend to increasing diversity with increasing mean depth is maintained. This indicates that, from low epilimnion temperatures, species number increases with increasing temperature and increasing length of time that the temperature is maintained (since greater mean depth implies a slower rate of heating and cooling and therefore a longer growing period for a given epilimnion temperature); from high epilimnion temperatures species diversity decreases with increasing temperature.

In considering trends in species diversity, much therefore seems to depend on the set of lakes under discussion. Great Bear Lake has the lowest number of crustacean plankton species of any of the lakes discussed by Patalas so that any amelioration of temperature conditions would tend to result in increased diversity. Similarly a decrease in oligotrophy in Great Bear Lake would be likely to lead to an increase in the fish species present.

These conclusions strongly indicate that the low number of species present in some arctic lakes is due to environmental or competitive exclusion rather than, as Dunbar (1968) suggests, due to ecosystem immaturity.

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