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Salmonid diet and the size, distribution, and density of benthic invertebrates in an arctic lake

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Abstract

Size selective predation on molluscs was apparent for lake trout (*Salvelinus namaycush*) and round whitefish (*Prosopium cylindraceum*), but not for arctic grayling (*Thymallus arcticus*), in the Toolik Lake region of arctic Alaska during the summer of 1986. Lake trout consumed significantly larger molluscs of all taxa than did round whitefish, and selected larger molluscs than were available on either rocky or soft-sediment habitats. Round whitefish were not size-selective on the snail *Lymnaea*, but were size-selective on the snail *Valvata* and on clams from the soft sediments. Round whitefish consumed fewer and smaller *Lymnaea* compared to lake trout. Because lake trout ate more *Lymnaea* and also tended to select larger, reproductive-sized individuals, this fish could potentially have a more detrimental impact on the *Lymnaea* population. Finally, differences in *Lymnaea* densities and size distributions between lakes with and without lake trout suggest that these fish may be responsible for the pattern of distribution, size, and density observed for *Lymnaea* in Toolik Lake and other area lakes.

Introduction

The effects of predation on the community structure of freshwater benthic epifaunal invertebrates is not well established. Existing evidence suggests that predation by fish may alter the relative abundance and species composition of some benthic communities (Crowder & Cooper, 1982; Gilinsky, 1984; Hershey, 1985), but not others (Thorp & Bergey, 1981a, b). Fish predation can influence density or standing crops of benthic macroinvertebrates (Crowder & Cooper, 1982; Hershey, 1985). Macan (1966) found that while trout predation led to decreased densities of a few benthic invertebrates, most species were unaffected.

It has been hypothesized that fish may influence benthic community composition by positively selecting larger invertebrates (Hall *et al.*, 1970; Crowder & Cooper, 1982). Werner & Hall (1977) demonstrated that size-selective predation is correlated with fitness in sunfish. In a growth efficiency model for piscivorous lake trout, Kerr (1971) suggested that size composition of the prey resource is a primary determinant of fish growth. In response to Kerr (1971), Konkle & Sprules (1986) asserted that lake trout must have access to increasingly larger food items, even when rare, to achieve large body size, and, if true, one may expect fish to select larger prey items. Selective predation by fish on benthic invertebrates also may be influenced by factors such as activity, exposure, and density of prey (Ware, 1973; Crowder & Cooper, 1982; Werner *et al.*, 1983; Gilinsky, 1984; Hershey, 1985). Shell morphology is reported to influence the vulnerability of snails to fish that crush shells (Vermeij & Covich, 1978; Stein *et al.*, 1984). Trout, however, ingest their prey whole, and large size is an important determinant in prey selection (Kerr, 1971; Ware, 1982, 1973; Konkle & Sprules, 1986).

Lake trout (lake charr, *Salvelinus namaycush*) are most commonly classified as piscivores but have a more diverse diet (e.g.; Martin, 1966; Johnson, 1972; Smith, 1972; Eddy & Underhill, 1974; O'Brien *et al.*, 1979; Konkle & Sprules, 1986). Prey availability appears to determine diet, and lake trout exploit almost any food that is found in abundance (Scott & Crossman, 1973). In arctic lakes, lake trout are typically viewed as a top predator and are reported to feed predominantly on fish (Johnson, 1976), including lake whitefish (*Coregonus clupeaformis*), lake cisco (*Coregonus artedii*), and slimy sculpin (*Cottus cognatus*).

Populations of lake trout in the Toolik Lake region of arctic Alaska show strong demersal foraging habits. Lakes in the Toolik area differ from many other lakes with lake trout populations since they lack a pelagic forage fish (Bendock & Burr, 1981). As juveniles, lake trout in Toolik Lake consume zooplankton and chironomids (Kettle & O'Brien, 1978; O'Brien *et al.*, 1979), but benthic prey, especially snails, dominate the adult lake trout diet (O'Brien *et al.*, 1979).

In the Toolik Lake region, populations of the pulmonate snail *Lymnaea elodes* are considerably less dense in lakes with lake trout in comparison to *Lymnaea* densities in lakes without these fish (Hershey, 1990). Round whitefish (*Prosopium cylindraceum*) and arctic grayling (*Thymallus arcticus*) commonly co-occur with lake trout in arctic lakes. Round whitefish forage almost exclusively on benthic invertebrates (Scott & Crossman, 1973) and prey on *Lymnaea*, as well as other common benthic invertebrates in Toolik Lake (O'Brien *et al.*, 1979). Grayling, although primarily planktivorous, also eat small benthic invertebrates in Toolik Lake (O'Brien *et al.*, 1979).

To evaluate the potential for lake trout to structure the benthic community of a lake which lacks a pelagic forage fish, we investigated the diet selectivity of lake trout in Toolik Lake. We compared lake trout diets to those of arctic grayling and round whitefish, which typically are not piscivorous. We examined size selectivity of these species by comparing the mean sizes of the dominant invertebrates in their diet with those available in Toolik Lake. The mean size of these invertebrates was also determined in five other area lakes; three contained no lake trout and two had lake trout present. In the two other lakes with lake trout, we also examined aspects of lake trout diet for which we had comparable data.

Study site

Toolik Lake is a small complex glacial kettle lake (148 ha) lying in an irregular basin in the northern foothills of the Brooks Range at 720 m elevation approximately 216 km south of Prudhoe Bay in arctic Alaska (Miller *et al.*, 1986). Toolik Lake has a maximum depth of 25 m, and a mean depth of approximately 7 m (McDonald *et al.*, 1982). It is ice-free from late June until late September or early October. Rocky shoals, which divide the lake into five basins and cover approximately 25% of the lake bottom, are scoured by ice each year. The remainder of the lake bottom is composed of soft sediments and is sparsely covered by diminutive macrophytes in some areas (Hershey, 1985).

The fish species present in Toolik Lake include lake trout (*Salvelinus namaycush*), round whitefish (*Prosopium cylindraceum*), arctic grayling (*Thymallus arcticus*), slimy sculpin (*Cottus cognatus*), and burbot (*Lota lota*) (O'Brien *et al.*, 1979; Bendock & Burr, 1981; McDonald *et al.*, 1982; Hershey & McDonald, 1985; Hershey, 1985). Other lakes in the Toolik area support some combination of these five species, but smaller lakes usually have fewer than five (Bendock & Burr, 1981). Our study sites also include nearby lakes S6, S7, and N2, which have grayling and sculpin, and Lake I8 and Itigaknit Lake, which have lake trout. Lake I8 supports all five species of fish; Itigaknit certainly has sculpin and grayling in addition to lake trout, but may also contain burbot and round whitefish.

Methods

A plastic sampling frame ($2\ m^2$) was used to assess relative densities and size distributions of *Lymnaea* in three lakes with and three lakes without lake trout. Sampling was conducted over unvegetated soft sediments in less than 1 m of water. Lakes S6 and S7 were sampled on 1 July 1986, lakes N1 and N2 on 9 July 1986, and lakes I8 and Toolik on 1 August 1986. All *Lymnaea* were collected, counted, measured with vernier calipers to the nearest 0.1 mm, and released in the area of capture. Mean density and size distributions for *Lymnaea* in lakes with trout and without trout were compared using a t-test for independent means. For this and all other statistical comparisons, means are reported ± 1 standard error, but variances were examined for homogeneity and transformed if necessary [using $\log_e (x + 1)$]. All statistical comparisons were regarded as significant if $p \leq 0.05$.

Salmonids for diet analysis were captured with a 30 m experimental gillnet and by angling. From June 13 until June 26, the gillnet was operated near the main inlet to Toolik Lake over soft sediments. After June 26, the gillnet was used on a variety of rocky shoals on the perimeter of Toolik's larger basins. A gillnet was set in Itigaknit Lake on 20–22 July 1986 (3 net days), and in Lake I8 on 13–15 August, 1986. Net depth ranged from approximately 2 to 8 m. Lake trout and grayling were also caught by angling in the same locations where gillnets were used.

Following capture, fish were weighed, measured, and sexed. Stomachs were then removed and preserved in ethanol. All prey items were enumerated. All molluscs were measured using a digitizing pad in conjunction with a dissecting microscope and camera lucida. *Lymnaea* were measured to the nearest 0.1 mm, and all other molluscs were measured to the nearest 0.01 mm.

Diet breadth was assessed by presence or absence of each prey type and expressed in terms of percent occurrence for the fish population of interest. Lake trout and round whitefish diets from rocky shoal and river inlet habitats were compared to determine if fish diets varied by habitat. Large (>400 mm) and small lake trout (≤ 400 mm) from rocky shoals were compared to determine if fish size within a single habitat influenced diet breadth. Lake trout were assigned to small and large size classes based on data suggesting that fish <400 mm ate zooplankton more commonly than larger fish (O'Brien *et al.*, 1979). The size distribution of lake trout also showed a natural break at about 400 mm TL. These data were not evaluated statistically.

To determine whether relative abundances of prey items in fish diets varied among fish species, the mean number of each prey type was calculated for lake trout, round whitefish, and grayling. Comparison of means to determine minimum significant differences was done using Tukey's studentized range test (SAS User's Guide: Statistics, 1985). Because grayling consumed very few molluscs, they were not included in statistical comparisons for molluscan prey. Similarly, round whitefish and grayling were compared with respect to mean number of *Grensia* (caddisfly) consumed; lake trout and round whitefish were examined with respect to mean number of chironomids consumed; and comparison was made between lake trout and grayling with respect to mean number of zooplankton consumed.

To examine size selective predation on molluscs by lake trout and round whitefish in rocky (dominated by the snail *Lymnaea*) and soft-sediment (dominated by the snail *Valvata* and fingernail clams) habitats, mean mollusc size eaten was compared to the mean size available by t-tests for independent means. Round whitefish and lake trout were also compared with each other with regard to size of molluscs eaten using t-tests for independent means. To determine if larger fish selected larger molluscs, shell length was regressed on total fish length. A positive, significant slope would indicate that larger fish were selecting larger molluscs.

To determine if the lake trout sampled from Toolik Lake, Lake I8, and Itigaknit Lake possessed significantly different size distributions, mean total lengths were compared with Tukey's studentized range for minimum significant difference (SAS User's Guide: Statistics, 1985). To determine if lake trout in the three lakes were preying on molluscs of similar size, the mean sizes of mollusc selected by lake trout in each lake were compared in a two way ANOVA (Sokal & Rohlf, 1981). Because there was a significantly positive relationship between trout total length and the size of *Lymnaea* eaten in Toolik Lake (see Results), lake trout from Toolik Lake, Itigaknit Lake, and Lake I8 were divided into three matching size classes (320–399 mm, 400–479 mm, 480–559 mm). This allowed us to determine if fish of the same size class in different lakes selected the same size *Lymnaea*. A size class was added in addition to the size classes used in the Toolik Lake comparison because most of the Itigaknit lake trout were considerably larger than those in Toolik; it would not be appropriate to compare diet selection between fishes in different lakes if the fish were not of similar sizes. Mean *Lymnaea* size selected by lake trout in each lake for each size class was compared with Tukey's studentized range test for minimum significant differences (SAS User's Guide: Statistics, 1985).

Results

Nearshore *Lymnaea* density was 0.4 ± 0.4/m^2 (mean ± SE) in lakes containing lake trout compared to 8.9 ± 1.3/m^2 in lakes without lake trout; means were significantly different ($p < 0.001$, Fig. 1). The mean size of adult snails in troutless lakes (22.4 ± 0.5 mm) was significantly ($p < 0.02$) larger than the mean size from lakes with trout (18.0 ± 1.2 mm; Fig. 1).

Total length of lake trout caught in Toolik Lake was 423 ± 10 mm, with a maximum length of 607 mm. These lake trout fed heavily upon benthic organisms, especially molluscs (Table 1). The most commonly encountered organisms in trout stomachs were the snails *Lymnaea* (70% of lake trout sampled) and *Valvata* (58%) (Table 1). Other invertebrates in lake trout diets included chironomid larvae and pupae (50%), caddisflies (*Grensia*) (36%), several small fingernail clam species (32%), and zooplankton (30%) (Table 1). Fish were found in the stomachs of 27% of the lake trout sampled (Table 1).

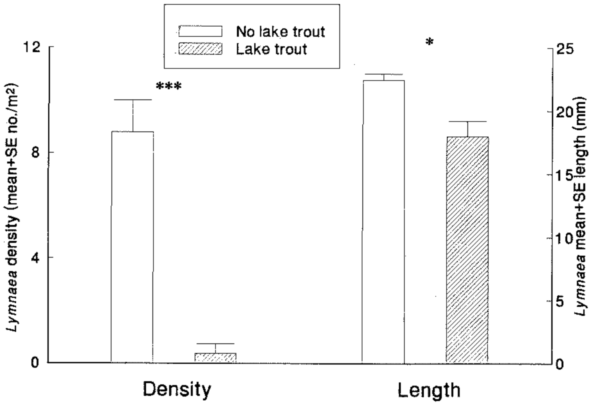

Fig. 1. Density and size distribution of *Lymnaea* at three sites in three lakes without lake trout and three lakes with lake trout. Asterisks indicate significant differences between lakes with and without lake trout (**, $p < 0.02$, $p < 0.001$).

Toolik Lake round whitefish total length was 428 ± 4 mm. These fish were strongly demersal, with molluscs being the dominant food group found in their stomachs (83%; Table 1).

Grayling in Toolik Lake were the least demersal fish considered. Grayling total length was 327 ± 29 mm. The dominant forage items found

Table 1. Percent occurrence of prey types in the stomachs of lake trout, round whitefish, and graying during the summer of 1986.

	Lake trout ($n = 74$)	Round whitefish ($n = 71$)	Grayling ($n = 10$)
Mollusca	79.7%	83.1%	70.0%
Lymnaea	70.3%	36.6%	10.0%
Valvata	58.1%	43.7%	60.0%
Sphaeriidae	32.4%	31.0%	0.0%
All fish	27.0%	0.0%	0.0%
slimy sculpin alone	12.2%	0.0%	0.0%
Chironomidae	50.0%	45.1%	30.0%
Trichoptera	36.5%	67.6%	50.0%
Zooplankton	29.7%	0.0%	70.0%
Terrestrial Insects	5.8%	1.4%	20.0%

in Toolik Lake grayling stomachs were zooplankton (70%), *Valvata* (60%), *Grensia* (50%), and chironomids (30%) (Table 1).

Some differences in diet breadth data for Toolik Lake were observed when fish of similar size (>400 mm), but different locality were compared. Lake trout captured over soft sediments near the lake's main inlet had more clams, fish, and chironomids, and fewer zooplankton in their stomachs than trout captured over rocky shoals (Table 2). Percent occurrence of *Lymnaea*, *Valvata*, and *Grensia* in lake trout stomach contents were similar between capture locations (Table 2). This comparison was not made for trout ≤400 mm as none were captured at the inlet gillnet sampling location. Whitefish diets were also slightly different by habitat (Table 2). Fish captured near Toolik Lake's main inlet contained more clams, chironomids, and trichopteran larvae and had less *Lymnaea*, than fish captured over shoals (Table 2). Percentage of whitefish consuming *Valvata* was similar in both areas.

Differences in diet breadth were apparent between large trout and small lake trout from the rocky shoal (Table 3). Larger fish more commonly preyed on molluscs, less commonly on *Grensia* and zooplankton than small fish. Large trout did not feed on sculpin at this sampling site (Table 3).

Lake trout in Toolik Lake ate significantly more *Lymnaea* than round whitefish and grayling, but round whitefish ate significantly more *Grensia* than lake trout and grayling (Table 4). *Valvata* consumption by lake trout was high but variable and did not differ significantly from consumption by whitefish (Table 4).

Table 2. Percent occurrence of prey types in the stomachs of large lake trout (>400 mm) and round whitefish (>379 mm) from two gillnetting sites in Toolik Lake.

	Shoal		Inlet	
	LT (*n* = 13)	RW (*n* = 25)	LT (*n* = 23)	RW (*n* = 38)
Mollusca	84.6%	84.0%	91.3%	82.6%
Lymnaea	76.9%	60.0%	78.3%	23.9%
Valvata	69.2%	44.0%	73.9%	43.5%
Sphaeriidae	30.8%	12.0%	47.8%	41.3%
All fish	0.0%	0.0%	52.2%	0.0%
Chironomidae	15.4%	8.0%	87.0%	65.2%
Trichoptera	30.8%	52.0%	26.1%	76.1%
Zooplankton	38.5%	0.0%	0.0%	0.0%

Table 3. Percent occurrence of prey types in the stomachs of large (>400 mm) and small (≤400 mm) lake trout gillnetted in Toolik Lake on a shoal.

	Large Lake Trout (*n* = 13)	Small Lake Trout (*n* = 17)
Mollusca	90.9%	47.4%
Lymnaea	83.6%	36.8%
Valvata	67.3%	36.8%
Sphaeriidae	41.8%	5.3%
All fish	30.9%	15.8%
Slimy Sculpin alone	10.9%	15.8%
Aquatic Insects	69.1%	73.7%
Zooplankton	9.1%	89.5%

Lake trout consumed significantly larger *Lymnaea*, *Valvata*, and clams than did round whitefish in Toolik Lake (Fig. 2). Compared with molluscs available on the sediments (*Valvata* and clams) and rocks (*Lymnaea*), lake trout ate significantly larger *Lymnaea* (13.0 ± 0.2 mm vs. 5.6 ± 0.8 mm), *Valvata* (4.5 ± 0.04 mm vs. 2.9 ± 0.1 mm), and clams (5.2 ± 0.1 mm vs. 2.6 ± 0.1 mm) (Fig. 2).

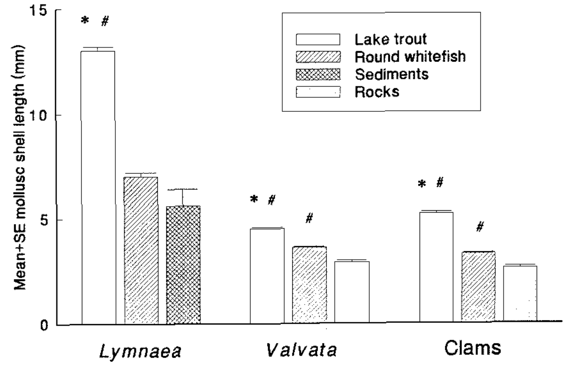

Fig. 2. Comparison of size of molluscs consumed by lake trout and round whitefish and sampled from substrates in Toolik Lake. Asterisks (*) indicate significant differences in sizes of molluscs consumed between lake trout and round whitefish. Pound symbols (#) indicate significant differences between the mean size mollusc of a given taxon eaten by the designated fish species and the mean size of that mollusc on the substrate.

Table 4. Mean (± SE) number of prey items in the stomachs of lake trout ($n = 74$), round whitefish ($n = 71$), and grayling ($n = 10$) from Toolik Lake. One asterisk indicates significant difference between indicated mean and lowest compared mean. Two asterisks indicate significant difference between indicated mean and both compared means ($p < 0.05$, Tukey's test).

Prey taxon	Lake trout	Round whitefish	Grayling
Lymnaea	**20.8 ± 3.9	6.4 ± 1.8	0.1 ± 0.1
Valvata	86.3 ± 69.3	40.5 ± 13.0	2.6 ± 1.0
Sphaeriidae	10.8 ± 4.5	13.1 ± 3.9	–
All fish	0.3 ± 0.07	–	–
Sculpin	0.2 ± 0.06	–	–
Trichoptera	3.2 ± 1.6	**27.8 ± 5.9	9.8 ± 4.5
Chironomidae	17.5 ± 4.5	12.3 ± 5.1	2.8 ± 2.2
Zooplankton	135.2 ± 49.7	–	298 ± 175.5

Round whitefish did not eat significantly larger *Lymnaea* (7.0 ± 0.2 mm vs. 5.6 ± 0.8 mm) than were sampled on Toolik Lake rocks, but did eat significantly larger *Valvata* (3.6 ± 0.05 mm vs. 2.9 ± 0.1 mm) and clams (3.3 ± 0.05 mm vs. 2.6 ± 0.1 mm) than were sampled on the sediments (Fig. 2).

Based on regression analyses of prey and fish length, larger lake trout selected significantly larger *Lymnaea* ($Y = 0.014X + 6.49$, $n = 395$, $p < 0.001$) and clams ($Y = 0.004X + 3.08$, $n = 0.036$, $p = 0.036$), but not larger *Valvata* ($Y = 0.001X + 4.224$, $n = 403$, $p = 0.335$) with increasing total length. However, round whitefish total length was not related to prey size selection for any of these prey items (*Lymnaea*: $Y = -0.002X + 7.95$, $n = 179$, $p = 0.777$; *Valvata*: $Y = 0.001X + 3.32$, $n = 436$, $p = 0.60$; $Y = -0.004X + 4.97$, $n = 252$, $p = 0.051$).

Table 5. Percent occurrence of prey types in the diets of lake trout from three area lakes.

	Toolik Lake ($n = 74$)	Lake I8 ($n = 11$)	Itigaknit Lake ($n = 14$)
Mollusca	79.7%	72.7%	92.9%
Lymnaea	71.6%	45.4%	78.6%
Valvata	59.5%	72.7%	50.0%
Sphaeriidae	32.4%	36.4%	42.9%
All fish	27.0%	27.3%	0.0%
Slimy Sculpin	12.2%	27.3%	0.0%
Chironomidae	50.0%	36.4%	35.7%
Limnephilidae	36.5%	27.3%	14.3%
Zooplankton	29.7%	27.3%	0.0%

The total length of lake trout sampled from Itigaknit Lake (541 ± 12 mm) was significantly larger than from Toolik Lake (423 ± 10 mm) and Lake I8 (427 ± 35 mm). Of the lake trout captured in these lakes, 73% ate at least one species of mollusc (Table 5). Lake trout captured in Itigaknit Lake differed from trout of Toolik and I8 in that they did not have fish or zooplankton in their stomachs (Table 5). All lake trout captured in Itigaknit Lake were in the large size class. These fish ate significantly larger *Lymnaea* (21.04 ± 0.6 mm) than similar-sized lake trout from Toolik Lake (13.9 ± 0.3 mm) and Lake I8 (11.5 ± 0.5 mm). Mean *Lymnaea* shell lengths selected by trout from I8 and Toolik lakes did not differ significantly for any fish size class. *Valvata* selected by lake trout in Toolik Lake (4.5 ± 0.04 mm), I8 (4.1 ± 0.1 mm), and Itigaknit Lake (4.0 ± 0.1 mm) were of similar size. Clams selected by lake trout in Itigaknit Lake were significantly smaller (3.6 ± 0.1 mm) than clams eaten by trout in Toolik Lake (5.2 ± 0.1 mm) and Lake I8 (4.9 ± 0.2 mm).

Discussion

The summer diets of lake trout, round whitefish, and grayling in Toolik Lake suggest different predatory roles for these species: lake trout had more diverse diets than round whitefish, and arctic grayling had a much weaker demersal orientation than either of the other fishes. Differences in diet breadth between lake trout and round whitefish were associated with *Lymnaea* and Trichoptera (predominantly the larvae of *Grensia* sp.). This was largely due to increased use of caddisfly larvae and reduced use of *Lymnaea* by round whitefish in the inlet during June. The differences observed in percent of lake trout and round whitefish consuming chironomids between the two gillnet locations may be explained by the large chironomid emergence which was observed near the inlet in late June during the sampling period. There are major differences in relative abundances of benthos on rocks (Cuker, 1983) and soft sediments (Hershey, 1985; Hanson *et al.*, this issue). Higher densities of sphaeriid clams are found in the dense macrophyte beds near the inlet than on the rocky shoal (Hershey, pers. obs.). Thus, the relatively high percent occurrence of clams in the diets of both lake trout and whitefish in the inlet habitat when compared to the rocky shoal site may be due to availability.

In considering size-selective predation on *Lymnaea* by round whitefish and lake trout, it is important to note that multiple year classes of *Lymnaea* are present throughout the year in Toolik Lake and that reproductive size for *Lymnaea* is approximately 15.0 mm (Hershey, 1990). Lake trout consume significantly more and larger *Lymnaea* than round whitefish. Because only lake trout consume *Lymnaea* of reproductive size, the potential for lake trout to have a significant impact on the *Lymnaea* population in Toolik Lake is greater than for round whitefish. This size selectivity by lake trout on *Lymnaea* was observed for all sizes of lake trout, with larger fish selecting increasingly larger *Lymnaea*. We suggest that the reduction in the number of reproductively-sized *Lymnaea* due to lake trout predation is sufficient to cause the observed differences in *Lymnaea* populations between lakes with and without lake trout (see Merrick *et al.*, 1991).

Although lake trout and round whitefish selected significantly larger *Valvata* and clams than occurred in benthic samples from Toolik Lake, regression analysis showed that the size of *Valvata* did not significantly increase with increasing fish size. Lake trout did appear to select larger clams with increasing fish size. However, the slope of the regression line for trout predation on clams ($m = 0.004$) was shallow, indicating only a very slight tendency for larger lake trout to select larger clams.

The mean size of *Valvata* preyed on by lake trout was smaller than the reproductive size for *Valvata* (5.0 mm; Hershey, 1990) but closer to the reproductive size than the mean size preyed on by round whitefish. Thus, whitefish have little potential to control *Valvata* population density, but trout may exert some influence. However, Hershey (1990) has shown that *Valvata* are competitively inferior to *Lymnaea* and were only abundant on soft sediments when *Lymnaea* density was very low (as in Toolik Lake). Thus competition rather than predation is likely a more important mechanism limiting *Valvata* population density. Reproductive size for the sphaeriid clams in Toolik Lake has not been determined.

Lake trout's selection of larger *Valvata* or sphaeriid clams with increasing fish size was very small, but they did choose a significantly larger mean size for each prey type than round whitefish. Therefore, we hypothesize that selectivity for large *Valvata* and clams is a function of the lake trout's inability to detect or capture small molluscs. Round whitefish with their small subterminal mouth and stronger demersal orientation (Scott & Crossman, 1973) may be more effective predators on the smaller prey. Conversely, the failure of round whitefish to eat large *Lymnaea* is probably due to gape limitation.

Lake trout captured in Itigaknit Lake were significantly larger than trout captured in Toolik Lake and Lake I8; this may be due to reduced angling because of its more remote location. Toolik Lake and Lake I8 are both located in close proximity to the Dalton Highway and receive moderate fishing pressure during the summer. Other mechanisms which could contribute to fish size, such as higher lake productivity, have not been evaluated, although comparative data which do exist suggest that at least Toolik and I8 are similarly unproductive (M. C. Miller, Univ. of Cincinnati, pers. comm.). Diet breadth of the lake trout in these three lakes appears to be very similar, with the only differences found in the lack of sculpin and zooplankton in the diets of lake trout from Itigaknit. The absence of zooplankton was likely due to the lack of small lake trout in the sample; the absence of sculpin may reflect the small sample size (n = 14). Lake trout in the 480–559 mm size class in Itigaknit Lake ate significantly larger *Lymnaea* than trout of the same size class in Toolik Lake and Lake I8. This may be related to the amount of available refuge for *Lymnaea* associated with a particular lake. Itigaknit Lake, in addition to reduced angling pressure, also has a complex morphometry and extensive beds of well-developed submerged macrophytes (Hershey, pers. obs.) which may provide more refuge for *Lymnaea* and increase their changes of attaining a larger size. Lake trout size differences between lakes may also be due to larger prey items available in Itigaknit Lake. Toolik Lake and Lake I8, with less well-developed macrophyte beds relative to total lake area, may not provide *Lymnaea* with as much opportunity to grow as large as in Itigaknit Lake.

Conclusion

Size-selective predation on molluscs by lake trout and round whitefish was apparent during the summer of 1986. Lake trout consumed more and larger *Lymnaea* than did round whitefish; their tendency to select individuals of reproductive size suggests greater potential for lake trout to affect *Lymnaea* populations. Predation on *Valvata* and probably sphaeriid clams by both fish species appeared to be a function of availability on the sediments without regard to fish size. Finally, the pattern of distribution of *Lymnaea* across Toolik Lake rocky and soft-sediment habitats, coupled with the size and density distribution of *Lymnaea* in lakes with and without lake trout, is consistent with the hypothesis that lake trout determine *Lymnaea* distribution and abundance in lakes of the Toolik area.

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