

## Lake whitefish and lake herring population structure and niche in ten south-central Ontario lakes

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### Synopsis

This study compares simple fish communities of ten oligotrophic lakes in south-central Ontario. Species densities and population size structure vary significantly among these lake communities depending on fish species present beyond the littoral zone. Lake whitefish are fewer and larger in the presence of lake herring than in their absence. Diet analysis indicates that lake whitefish shift from feeding on both plankton and benthic prey when lake herring are absent to a primarily benthic feeding niche in the presence of lake herring. When benthic round whitefish are present, lake whitefish size and density decline and they move lower in the lake compared to round whitefish. Burbot are also fewer and larger in lakes with lake herring than in lakes without herring. Burbot, in turn, appear to influence the population structure of benthic coregonine species. Lower densities of benthic lake whitefish and round whitefish are found in lakes containing large benthic burbot than in lakes with either small burbot or where burbot are absent. Predation on the pelagic larvae of burbot and lake whitefish by planktivorous lake herring alters the size and age structure of these populations. As life history theory predicts, those species with poor larval survival appear to adopt a bet-hedging life history strategy of long-lived individuals as a reproductive reserve.

### Introduction

Understanding how aquatic ecosystems function is important for the effective management of fisheries and aquatic resources. Community and population theory and recent studies suggest that species interactions can significantly alter the structure of fish populations and communities (Nikolski 1969, Svardson 1976, Werner & Hall 1979, Carr et al. 2002, Townsend 2003). However, the effects of community interactions may be difficult to detect at the lake scale due to confounding factors such as lake size or water chemistry (Bar-

bour & Brown 1974, Harvey 1975), variability in population parameters such as growth and density when estimated from angler harvest data (Goddard et al. 1987) or low differentiation with simple presence-absence data (Jackson et al. 2001). A comparison of simple communities may allow examination of species interactions with a reasonable sampling effort (Tonn & Paszkowski 1986, Carl 2000). This study uses a comparative-lake approach to examine the interactions among three coregonines and burbot (*Lota lota*) in oligotrophic lakes in south-central Ontario. These four species, along with lake trout (*Salvelinus namaycush*),

constitute most of the biomass in these lakes beyond the littoral zone and, therefore, characterize the fish community in these lakes.

The lake whitefish (*Coregonus clupeaformis*) is a common species in these lakes which may adopt a pelagic or benthic feeding niche depending on conditions in the lake (Scott & Crossman 1973). Lake herring (*Coregonus artedii*) are pelagic while round whitefish (*Prosopium cylindraceum*) are benthic (Scott & Crossman 1973). The interactions among these species are not well known (Day 1983, Carl et al. 1990, Carl 1992a) and this paper tests the hypothesis that lake whitefish will shift feeding niches depending on the species present in the lakes. In addition, the influence of burbot, a benthic predator on the coregonine species in these lakes, will be examined.

## Methods

A total of ten lakes in the Algonquin Highlands of southern Ontario were chosen based on similar water chemistry, productivity and low to moderate

angling effort (Figure 1 and Table 1). Of these, eight were in a wilderness park (Algonquin Provincial Park) and only two lakes had more than a dozen shoreline cottages. All lake sampling was conducted during July and August after a firm thermocline had formed. Lakes were sampled in 1992–1994. One lake was sampled in one year, five lakes were sampled two years and four were sampled all three years.

Lakes were classified by the presence or absence of the four species studied. Of the ten lakes, three contained lake whitefish and burbot (whitefish–burbot lakes), three contained lake whitefish and herring (herring–whitefish lakes; one with burbot) and four contained lake whitefish and herring, round whitefish and burbot (coregonine–burbot lakes). All ten lakes contained lake trout.

Gill net sampling was used to estimate the relative abundance of lake herring, lake whitefish and round whitefish. In each lake for each year sampled, 12 overnight bottom gill net sets consisting of 19-, 25-, and 38-mm stretched bar mesh monofilament panels (15.2 m long and 2.4 m high) were made, with the middle panel size

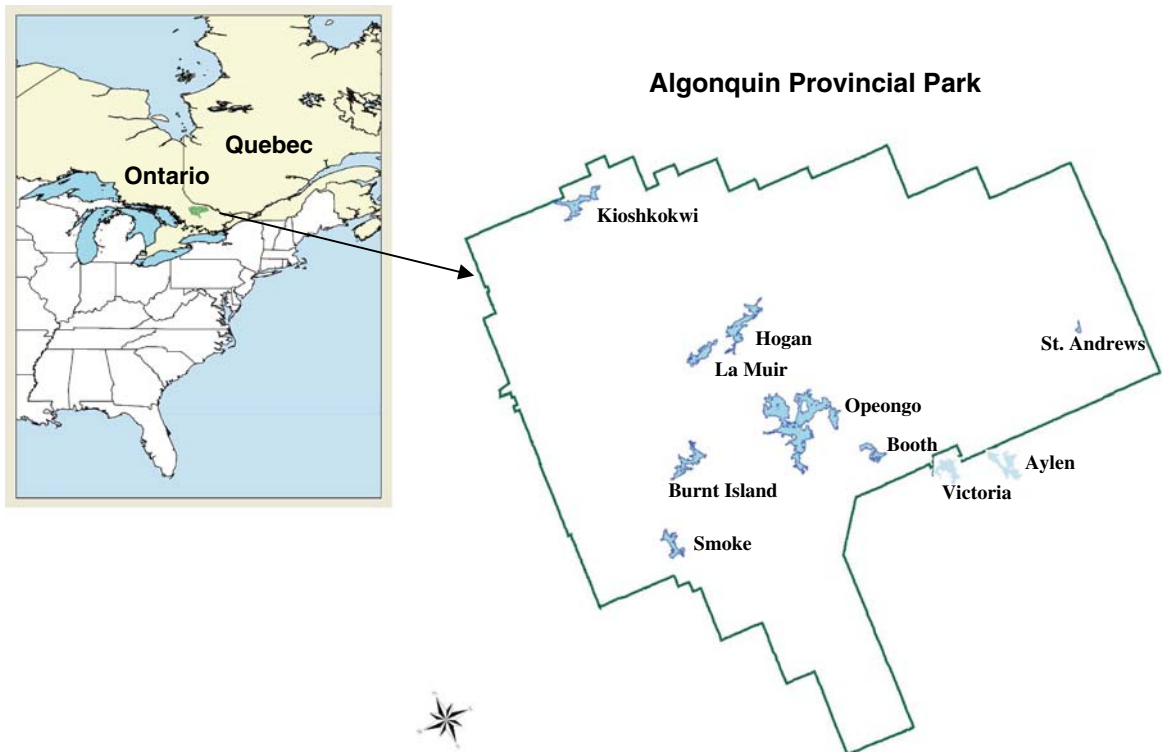


Figure 1. Map of Eastern North America with an inset of Algonquin Park and the ten study lakes.

randomly assigned. Three depth strata were sampled: 10–20 m, 20–30 m, and >30 m. Sites were chosen at random from each of the three depth strata, in proportion to the lake area within the strata, with a minimum of three net sets made per strata. Dissolved oxygen and water temperature were measured at each site before nets were set. Any site with dissolved oxygen readings below 4 ppm was rejected and another site was chosen to replace it.

Trap nets (1.8 m box size with 36–49 m leads) were set in lakes in which burbot were reported in Ontario Ministry of Natural Resources records to measure their relative abundance (Table 1). A total of nine trap net nights were fished in each of these lakes, with sites randomly chosen along the shoreline. Sampling sites were restricted to those in which the box of the trap net was 6 m deep because burbot are known to forage in deep water in the summer months (Carl 1995). All fish caught using both methods were measured and weighed, and stomachs were collected from the four species except burbot, which were released alive. Stomachs were weighed and contents assessed for number of items and number of taxa. Otoliths were removed and aged using the methods of Casselman (1987). Diet data were not analyzed for

round whitefish due to small sample size and burbot that were released alive.

### Statistical analyses

To detect differences among different combinations of species, analysis of variance (ANOVA) was performed. Pairwise comparisons were made with student *t*-tests. All catch per unit effort data (CUE; fish per net night) were transformed ( $\log_{10}(\text{CUE} + 1)$ ) before analysis. As a measure of somatic growth, size at age 3 was used for lake whitefish and size at age 2 for herring. As a measure of maximum size for lake herring, lake whitefish, and burbot, the mean of the ten longest fish for each lake type was used. Mean age of lake whitefish and herring were compared among lake types. The depth distribution of coregonines was estimated by lake type as the relative catch frequency at each of the three depth strata ((mean CUE for strata/sum of CUE's for 3 strata)×100).

Diet was investigated by examining the number of taxa per stomach, the number of items per stomach, stomach weight and frequencies of individual taxa. Lake herring stomach weights and stomach contents were compared in herring–whitefish lakes and coregonine–burbot lakes using

Table 1. Physical characteristics, year sampled and fish species present of lakes sampled.

Waterbody	Area (ha)	Mean depth	TDS	MEI	Year sampled	Total fish species	Lake herring		Lake whitefish <sup>d</sup>		Burbot <sup>d</sup>	
							CUE	FLEN	CUE	FLEN	CUE	FLEN
Whitefish and burbot												
Aylen	2015	27.2	35.4	1.3	92, 93	11			6.5	172	1.00	276
Burnt Island	854	10.8	52.9	4.9	92, 93	11			41.5	164	1.36	247
La Muir	757	10.4	28.1	2.7	92, 93	12			13.5	168	1.22	213
Lake herring and lake whitefish												
Kioshkokwi <sup>a,b</sup>	1127	12.5	46.2	3.7	93	14	12.7	159	4.5	311		
St. Andrews <sup>b</sup>	90	11.0	31.9	2.9	93, 94	9	17.6	152	3.8	343		
Hogan <sup>b</sup>	1303	6.7	30.1	4.5	93, 94	15	37.2	171	0.8	357	0.91	379
Coregonines and burbot												
Booth	494	7.8	26.5	3.4	92, 93, 94	16	11.4	160	1.0	249	0.33	413
Opeongo <sup>c</sup>	1714	16.3	31.0	1.9	92, 93, 94	26	13.8	137	1.7	318	0.9	391
Smoke	607	16.2	27.5	1.7	92, 93, 94	10	15.3	166	2.3	215	0.55	415
Victoria	892	14.8	28.1	1.9	92, 93, 94	11	10.7	130	0.5	274	0.96	289

Lake herring, lake whitefish and burbot catch per unit effort and mean forklength (FLEN; mm) all grouped by lake type.

<sup>a</sup>Lake containing rainbow smelt (*Osmerus mordax*).

<sup>b</sup>*Mysis* present.

<sup>c</sup>Lake Opeongo is East Arm only, total species is high compared to other lakes because of intensive, long term sampling.

<sup>d</sup>Data from 8 of the 10 lakes were first reported in Carl (2000).

one-way ANOVAs on ranked data for all diet variables. One-way ANOVAs on ranked data were also used to compare lake whitefish stomach weight and diet between whitefish–burbot lakes and coregonine–burbot lakes.

## Results

### *CUE and size distributions*

#### *Lake herring*

Lake herring CUE varied from 10.7 to 37.2 fish per gill net night (Table 1), and was lower in coregonine–burbot lakes compared to herring–whitefish lakes (mean: 12.8 vs. 22.5 CUE;  $p=0.0001$ ). The size at age 2 was not different between the two lake types (mean: 155 and 153 mm;  $p=0.31$ ; Table 2). Maximum fork length was greater in herring–whitefish lakes (mean: 318 and 197 mm respectively;  $p=0.0001$ ; Table 2). The mean age of lake herring was greater in herring–whitefish lakes (2.9 years) compared to coregonine–burbot lakes (2.1 years;  $p=0.0001$ ). There were significantly more empty stomachs found in herring–whitefish lakes (mean: 66.3 and 11.3% of total) while the number of taxa, number of items and stomach weight were greater in coregonine–burbot lakes ( $p=0.0001$ ,  $p=0.001$ , and  $p=0.03$  respectively; Table 3). In general, cladocerans and copepods predominated in lake herring diets in all lakes. However in coregonine–burbot lakes, dip-tera were also common.

#### *Lake whitefish*

Lake whitefish CUE varied from 0.5 to 41.5 fish per net night (Table 1), and was highest in whitefish–burbot lakes (mean: 20.5 CUE;  $p=0.03$ ), lower in

lake herring–whitefish lakes (3.0 CUE;  $p=0.001$ ) and lowest in coregonine–burbot lakes (mean: 1.4 CUE vs. 3.0 for lake herring–whitefish lakes;  $p=0.024$ ). The size at age 3 was lowest in whitefish–burbot lakes (FLEN = 194 mm;  $p=0.0001$ ; Table 2) and similar in the other two lake types (225 and 231 mm, respectively). Maximum size was significantly lower at 280 mm in whitefish–burbot lakes ( $p=0.0001$ ) compared to herring–whitefish lakes and coregonine–burbot lakes (413 and 451 mm, respectively; Table 2). Mean age was lowest in whitefish–burbot lakes (2.4 years) intermediate in coregonine–burbot lakes (5.1 years) and highest in herring–whitefish lakes (7.2 years;  $p=0.0001$ ). The frequency of empty stomachs was similar for the two lake types with enough data to examine (19.7% for whitefish–burbot lakes and 16.9% for coregonine–burbot lakes). There were significantly fewer taxa per stomach for whitefish–burbot lakes compared to coregonine–burbot lakes (Table 3;  $p=0.0001$ ) and stomach weight was also lower ( $p=0.0001$ ). Stomachs from whitefish–burbot lakes held more items compared to coregonine–burbot lakes ( $p=0.004$ ) (Table 4).

#### *Round whitefish*

Round whitefish were found only in coregonine–burbot lakes. The CUE varied from 0.4 to 0.9 fish per net night and mean fork length varied from 245 to 289 mm. Mean length at age 3 was 220 mm and maximum forklength was 357 mm.

#### *Burbot*

Burbot CUE (fish per trapnet night) was lower in coregonine–burbot lakes (0.68 CUE) compared to whitefish–burbot lakes (1.19 CUE;  $p=0.06$ ; Table 1). The mean length of burbot in coregonine–burbot lakes (377 mm) was significantly

Table 2. Lake herring, lake whitefish and burbot lake type means for catch per unit effort (CUE), fork length (FLEN, mm), size at age (mm) 2 (herring) or 3 (whitefish) and maximum size (mm).

Species	Lake type	CUE	FLEN	Size at age	Max. size	Comment
Lake herring	Herring–Whitefish	22.5	161	155	318	Small, numerous
	Coregonine–Burbot	12.8	148	153	197	Small, less abundant
Lake whitefish	Whitefish–Burbot	20.5	168	194	280	Small, numerous
	Herring–Whitefish	3.0	337	225	413	Large, less abundant
	Coregonine–Burbot	1.4	272	231	451	Large, less abundant
Burbot	Whitefish–Burbot	1.19	245	<sup>a</sup>	366	Small, abundant
	Coregonine–Burbot	0.68	377	<sup>a</sup>	583	Larger, less abundant

<sup>a</sup>Live released.

Table 3. Lake herring and lake whitefish number of taxa per stomach, stomach weight, number of items per stomach and frequency of occurrence (%) of common food items, stratified by lake type.

Lake type	No. of stomachs	No. of taxa <sup>a</sup>	No. of Weight <sup>a</sup>	No. of items <sup>b</sup>	Empty stomach	Cladocera	Copepoda	Diptera	Hydracar	Unknown insect	Ephemeroptera	Worms
Lake herring												
Herring-Whitefish	169	0.6	0.05	3.9	66	28	27	0	1.2			
Coregonine-Burbot	284	1.93	0.21	16.9	11	60	36	31	1.1			
Lake whitefish												
Whitefish-Burbot	137	1.1	0.2	85.0	20	53	0	39	0	3	2	0
Coregonine-Burbot	71	1.7	0.5	25.2	17	24	0	59	0	0	11	6

<sup>a</sup> $p < 0.01$  for both herring and whitefish.

<sup>b</sup> $p < 0.03$  for herring and  $p < 0.01$  for whitefish.

larger than in whitefish-burbot lakes (245 mm;  $p = 0.0001$ ). The maximum size of burbot in coregonine-burbot lakes (583 mm) was significantly larger than in whitefish-burbot lakes (366 mm;  $p = 0.01$ ) (Table 5).

#### Net distribution

The lake herring distribution, as measured with bottom gill nets, was similar among the two lake types with over 60% caught in 10–20 m depth strata. Lake whitefish distribution appeared to differ depending on whether other coregonines were present or not. About 60% were captured in the 10–20 m depth strata in lakes without other coregonines compared to 46% when herring were present and only 40% when round whitefish were present as well. Over 80% of the round whitefish were captured in the 10–20 m depth strata and none below 30 m depth.

#### Discussion

We were able to test hypotheses related to community interactions by using lakes with similar characteristics (Table 1) as observational units and removing these potential sources of variance in population parameters. However, lake area varied from 90 to 2015 ha and fish species present varied from 9 to 26. Lake area was not correlated with fish species present ( $p = 0.165$ ) and therefore likely had little influence on population parameters measured in the study. In regards to fish species present, the Harkness Laboratory of Fisheries Research is located on Lake Opeongo and intensive sampling likely contributed to the 26 species present. The other nine lakes ranged from 9 to 16 species present, most of which are found in the littoral zone. In addition, Carl (2000) found over 99% of the fish captured in Lake Opeongo in floating gillnets set offshore were lake herring. Similarly, we found species other than the coregonines, burbot and lake trout rare in our nets. This indicates, as with lake area, that species present, outside of those examined in this study, did not have a major influence on the results of this study.

Lake whitefish were smaller at age 3, younger in overall mean age and had higher densities in lakes where they were the only coregonine. They also fed

Table 4. Lake herring frequency of occurrence of common food items, number of taxa per stomach, stomach weight and number of items per stomach stratified by lake herring–whitefish lakes and coregonine–burbot lakes.

Item	Frequency of occurrence (%)	
	Lake Herring–Lake Whitefish lakes	Coregonine–Burbot lakes
Empty stomach	66.3	11.3
Cladocera	28.4	59.8
Copepoda	27.2	35.9
Diptera	0	31.3
Hydracar	1.2	1.1
Number of stomachs	169	284
Number of taxa per stomach <sup>a</sup>	0.6	1.93
Stomach weight (g) <sup>a</sup>	0.05	0.21
Number of items per stomach <sup>b</sup>	3.9	16.9

<sup>a</sup> $p < 0.01$ .

<sup>b</sup> $p < 0.03$ .

Table 5. Lake whitefish frequency of occurrence of common food items, number of taxa per stomach, stomach weight and number of items per stomach.

Item	Frequency of occurrence (%)	
	Whitefish–Burbot lakes	Coregonine–Burbot lakes
Empty stomach	19.7	16.9
Cladocera	53.3	23.9
Diptera	39.4	59.1
Unknown insect	2.9	0
Ephemeroptera	2.2	11.3
Worms	0	5.6
Number of stomachs	137	71
Number of taxa per stomach <sup>a</sup>	1.1	1.7
Stomach weight (g) <sup>a</sup>	0.2	0.5
Number of items per stomach <sup>a</sup>	85.0	25.2

Stratified by whitefish–burbot lakes and coregonine–burbot lakes.

<sup>a</sup> $p < 0.01$ .

predominantly on pelagic prey and occurred at shallower depths in these lakes. These are all characteristics of the pelagic lake herring. In lakes with lake herring present, lake whitefish size increased, density declined, mean age increased, and fish moved downslope and fed more on benthic items. When round whitefish were also present, density and size declined, which again suggests that lake whitefish shift from pelagic to benthic feeding in response to lake herring, then decline in

numbers and mean size in response to the round whitefish, a fish specialized for benthic feeding. The depth distribution of lake whitefish appeared to shift even deeper in the presence of round whitefish presumably to avoid round whitefish concentrated in the 10–20 m depth strata. This shift was likely a behavioral adjustment to the presence of efficient competitors (Romare & Hansson 2003). Thus there is strong evidence for accepting the hypothesis that lake whitefish shift

niches due to competition with pelagic lake herring and benthic round whitefish.

It is not likely that burbot predation is a significant factor in the whitefish–burbot lakes. Burbot are so small as to make preying on pelagic whitefish unlikely due to mouth gape limitations. As well, burbot < 28 cm are usually present in the littoral zone rather than in the main body of the lake (Carl 1992a). Both factors make it highly unlikely that burbot have a significant predatory effect on whitefish in this lake type. In support of this, the densities of lake whitefish in these lakes are as high as the density of lake herring in two lake whitefish–lake herring lakes (Kioshkokwi & St. Andrews). The results from Hogan Lake are particularly important because it is the only herring–whitefish lake with large benthic burbot present. This lake had the highest density of pelagic lake herring of all the lakes and one of the lowest densities of benthic lake whitefish. This suggests that large, benthic burbot influenced benthic lake whitefish, most likely through predation, but did not appear to have a large effect on pelagic lake herring. In the final lake grouping both benthic coregonines exhibited low densities similar to those in Hogan Lake in the presence of large hypolemmetic burbot. Thus it appears that although planktivorous lake herring may influence the structure of the burbot population through a negative effect on larval burbot survival (Carl 2000), the few adult burbot that remain affect the structure of benthic lake whitefish and, presumably, round whitefish populations. Given that these burbot did not appear to seriously affect pelagic coregonines (whitefish–burbot lakes and Hogan Lake), it would appear that lake herring numbers are lower due to the presence of round whitefish in coregonine–burbot lakes. One probable mechanism is egg predation. Scott & Crossman (1973) list several studies that suggest round whitefish prey on other species' eggs and it is quite possible that this mechanism leads to reduced density of lake herring in lakes with round whitefish. Unfortunately, we did not sample round whitefish when coregonine eggs were present and, therefore, have no direct evidence of egg predation. It is also not possible to detect the effect of lake herring or whitefish on round whitefish because round whitefish were present in only one set of lakes with both species. Carl (2000) found that

lake whitefish appear to impact suckers (*Catostomus* spp.) but not burbot in oligotrophic lakes. Unfortunately, the effects of lake whitefish on lake herring could not be evaluated here because all herring lakes had lake whitefish. Further study is required to see whether whitefish, when present, do in fact affect lake herring.

*Mysis* (*Mysis relicta*) have a potentially confounding effect on fish community interactions in these lakes, as *Mysis* were present in the two lakes without burbot and only in one lake with burbot. Other authors have shown that *Mysis* can positively influence lake herring growth (Trippel & Beamish 1993). Although lake herring densities were greater in lakes without burbot and with *Mysis*, *Mysis* were not a part of lake herring or lake whitefish diet in lakes without burbot. Furthermore, lake herring diet data showed a classic intraspecific density response. In the herring–whitefish lakes where density of herring was almost two times that of herring in the coregonine–burbot lakes, lake herring had far more empty stomachs, fewer taxa per stomach and lower stomach weight. This indicates that food was limited and not what was expected if *Mysis* was a major food source for coregonines. This food limitation may have been caused by high densities of herring or presence of *Mysis* that are better competitors for zooplankton (Langeland et al. 1991). Therefore, it would appear there was no positive effect of *Mysis* in lakes without burbot. Lake whitefish also did not appear to be affected by *Mysis*. Although benthic lake whitefish in herring–whitefish lakes were larger and more numerous in the presence of *Mysis*, *Mysis* were not detected in whitefish diet, which strongly suggests no influence of *Mysis* on lake whitefish growth and density. Again, the likely factors in this lake type were the presence of pelagic lake herring and the absence of benthic round whitefish. Thus, a significant factor influencing benthic coregonine density in these lakes appeared to be influenced by the presence of coregonines and burbot.

Nikolski (1969) suggested that fish populations experiencing variable recruitment show a life history strategy favoring very few juveniles and old, large-bodied adults. Age-specific predation and massive mortality of young fish shifts populations of surviving fish to old, large-bodied individuals which mature late and delay spawning (Gadgil &

Bossert 1970, Law 1979, Stearns 1980). Delayed maturation in an environment of variable or poor recruitment allows a species to have a reproductive reserve on hand. Carl (1992b) found that some grayling (*Thymallus arcticus*) adults delay spawning so that the population has a reproductive reserve available to counteract frequent year class failures. The present study and Carl (2000) show that small-bodied lake herring impact lake whitefish and burbot, likely through competition with lake whitefish and herring predation on larvae of both species. These species adopt a bet-hedging life history strategy of delayed maturation. Lake whitefish were significantly younger, more numerous and smaller and the burbot population density was higher and adults smaller in the absence of lake herring and their drastic effect on whitefish and burbot recruitment. In addition, using an age-length graph for Lake Opeongo, one of the study lakes from Carl (1992a), indicated that burbot were much older as well as larger in the presence of lake herring, a larval predator (Carl 2000). This supports the delayed maturity hypothesis of life history theory.

Through a comparative approach and analysis of population structures, we have been able to characterize some of the interactions among fish species within these simple communities. It is apparent that the presence of lake herring, lake whitefish and burbot heavily impacted the fish community structure of these lakes through competition and predation. Lake herring and whitefish play a dominant role in recruitment and size structure of fish populations with pelagic larvae (Carl 2000). Species subject to this egg or larval predation appear to accommodate it by shifting life history strategies. Burbot predation on benthic coregonines reduces densities in these lakes. Effective management of aquatic ecosystems and fisheries should take fish community interactions into account when determining harvest levels of fish. Drastic reduction of large predators such as burbot may shift community dynamics and favor other species in the lake.

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