

Lake trout demographics in relation to burbot and coregonine populations in the Algonquin Highlands, Ontario

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Abstract The objective of the study was to test the hypothesis that lake trout populations change in relation to cisco, lake whitefish, round whitefish and burbot populations in lakes in the Algonquin Highlands region of Ontario. Lake trout population change is greatest where cisco and lake whitefish are present. Lake trout populations in lakes without either coregonine tend to have small adults and many juveniles. Where cisco or lake whitefish are present, adult lake trout are large, juvenile abundance is low, and the stock-recruit relationship appears to be uncoupled likely due to a larval bottleneck. Lake trout populations in these lakes may be sensitive to overfishing and recruitment failure. Lake trout populations do not appear to change in relation to round whitefish. There appears to be an indirect positive change on juvenile lake trout abundance through reductions in the density of benthic coregonines in the presence of large, hypolimnetic burbot.

Keywords Uncoupled recruitment · Larval bottleneck · Overfishing

Introduction

The lake trout, *Salvelinus namaycush*, is an important salmonine present in many northern lakes that may act as a keystone species and affect the structure of fish communities (Paine 1974; Trippel and Beamish 1993). Although many of the effects of lake trout on other species and the effect of angling on lake trout populations are known (Trippel and Beamish 1993; Olver et al. 2004), relatively little is known about how other species affect lake trout. In particular, juvenile lake trout ecology and population and community dynamics are poorly studied. In part, this is because over much of their range (including the study area) juvenile lake trout are benthic, scarce, and inhabit the deeper areas of lakes making quantitative sampling difficult. Evans et al. (1991) discussed physical and intraspecific factors such as cannibalism that may affect juvenile lake trout. Ciscos, *Coregonus artedii*, have been hypothesized to be a competitor of juvenile lake trout in north temperate lakes (Martin and Fry 1973; Trippel and Beamish 1989). In addition Hoff et al. (1997) and Carl (2000) found fish larvae in cisco stomachs. Lake whitefish, *C. clupeaformis*, diet studies have also found small fish consumed (Tohtz 1993; Doyon et al. 1998; Pothoven 2005). This suggests coregonines may have an impact on lake trout demographics through predation as well as competition.

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Several authors have suggested that burbot, *Lota lota*, a benthic piscivore, is a predator on lake trout (Martin 1940; Hackney 1973; Scott and Crossman 1973; Day 1983). For example, Day (1983) found a negative correlation between burbot and lake trout abundance in Lake Athapapuskow, Manitoba, while Carl (1992) found no correlation between lake trout and burbot population abundance or growth in Lake Opeongo, Ontario. However, Carl et al. (1990) indicated that the relative abundance of lake trout was lower in Ontario lakes in which burbot or coregonines, such as cisco and lake whitefish, were present compared to lakes in which these species were absent. Vander Zanden et al. (1999 and 2000) found smallmouth bass influenced lake trout trophic status indirectly through predation on common littoral or nearshore prey species.

Many oligotrophic lakes in the Algonquin Region of southern Ontario have simple offshore fish communities with one or two piscivorous and few to no planktivorous fish species. Burbot, cisco, lake whitefish, round whitefish, *Prosopium cylindraceum*, and lake trout constitute most of the biomass in the offshore habitat of these lakes beyond the littoral or nearshore area and therefore characterize the offshore fish communities in these lakes. For example Carl and McGuinness (2006) found that cisco made up 99% of the catch in floating gillnets in Lake Opeongo (one of the current study lakes) and in this study, the five species predominated in the catch of bottom set gillnets across all lakes. Therefore a comparative lakes study allows examination of changes in lake trout population parameters in relation to these predominant offshore species. The purpose of this study was to test the hypothesis that there is a relation between lake trout populations and cisco, lake whitefish, round whitefish, and burbot through changes in lake trout population size, structure, growth, and recruitment in a set of otherwise similar lakes. Response variables were the relative abundance, distribution, size, growth, and diet of lake trout.

Materials and methods

For this study, a factorial design was used with type of lake (open-water fish community composition) and depth strata (10–20, 20–30, and >30 m) as the two factors. A total of 20 lakes in the Algonquin Highlands of southern Ontario were chosen based on similar size,

water chemistry, and productivity (Table 1). Eighteen lakes were in a wilderness park (Algonquin) and only four lakes in the study had more than a dozen cottages on the shoreline. Angling effort was low, with only six lakes having public access roads to them. All lake sampling was conducted during July and August after a firm thermocline had formed. In a given year, each lake was sampled within a five day period. In each lake, 12 overnight bottom gill net sets were set in the hypolimnion as described in Carl and McGuinness (2006). Each net consisted of 19, 25, and 39 mm stretched bar mesh monofilament panels that were 15.2 m long and 2.4 m high.

Because maturity data from lakes in the area indicated that fish as small as 30 cm may be mature depending on the fish community in the lake (Evans et al. 1991), all lake trout under 30 cm were classified as juvenile or subadults to separate out size variation due to early maturity in some of the study lakes. For each gill net set, all lake trout 30 cm or larger were measured and released; all other fish were enumerated and put on ice. The vertical position of each lake trout in the gill net was recorded to the nearest 0.3 m. Otoliths removed from juvenile lake trout were aged by a single technician, following the methods of Casselman (1987). Stomachs were analyzed for content.

The field work was carried out in three consecutive years. A total of 16 lakes were sampled the first year. In the second year 13 lakes were resampled in addition to four new lakes. In the third year three lakes were sampled for the second time and five lakes were sampled for the third time (Table 1).

Statistical analysis

To test the hypothesis that the presence of burbot and coregonines impact lake trout populations, lakes were stratified into four categories. Type 1 lakes (lake trout only) had no burbot or coregonine present. Type 2 lakes (burbot) had burbot and lake trout but no lake whitefish or cisco present. Type 3 lakes (whitefish–cisco) had one or both of these species and lake trout. Type 4 lakes (coregonine–burbot) had lake trout, burbot, and up to three coregonines present. Lake trout biomass, fork length and catch per unit effort (CUE) data were not normally distributed. Biomass, fork length and catch per unit effort data for lake means, equally weighted for each depth strata, were \log_{10} transformed to normalize distributions (\log_{10} (bio-

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

Lake type	Area (ha)	Mean depth	TDS	Year sampled	Total species	Lake trout <30 cm		Lake trout >30 cm		All lake trout	
						FLEN	CUE	FLEN	CUE	FLEN	CUE
						Lake trout only lakes (Type 1)					
Cache	287	6.7	40.2	92,93	13	215	1.73	478	0.09	230	1.82
Louisa	489	17.0	23.8	92,93	9	197	4.54	418	2.88	284	7.42
Pen	379	9.2		92	9	173	2.92	315	0.08	177	3.00
Shirley	481	7.4	28.1	92	8	179	3.00	486	0.09	188	3.09
Source	271	8.0	23.2	92,93,94	9	200	4.97	379	1.56	243	6.53
Mean						192.8	3.43	415.2	0.94	224.4	4.37
Lake trout lakes with burbot present (Type 2)											
Big Porcupine	235	7.5	45.8	92,93	9	180	2.63	388	1.33	250	3.96
Butt	456	16.6	19.9	92	4	182	8.33	392	2.08	232	10.42
Rock (RW)	509	7.9	26.9	92,93	15	177	1.95	435	0.09	188	2.04
Two Rivers	292	15.4	52.4	92,93	13	190	0.46	410	0.38	289	0.83
Mean						182.2	3.34	406.3	0.97	239.8	4.31
Lake trout lakes with cisco and/or lake whitefish (Type 3)											
Biggar ^a (LH)	382	9.7	25.2	93, 94	11	216	1.24	450	4.84	403	6.08
Kioshkokwi ^a (LH,LW)	1127	12.5	46.2	93	14	192	0.17	487	1.67	460	1.83
St. Andrews ^a (LH,LW)	90	11.0	31.9	93,94	9	187	0.31	442	1.06	396	1.38
Mean						198.3	0.57	459.7	2.52	419.7	3.10
Lake trout lakes with coregonines and burbot (Type 4)											
Aylen (LW)	2,015	27.2	35.4	92,93	11	166	0.42	527	0.71	402	1.13
Booth (LH, LW,RW)	494	7.8	26.5	92,93,94	16	179	0.95	502	1.46	381	2.41
Burnt Island (LW)	854	10.8	52.9	92,93	11	204	0.30	559	1.70	505	2.00
Hogan ^a (LH, LW)	1303	6.7	30.1	93,94	15	204	1.00	571	4.46	509	5.46
La Muir (LW)	757	10.4	28.1	92,93	12	199	0.50	532	2.04	472	2.54
Opeongo ^b (LH,LW,RW)	1714	16.3	31.0	92,93,94	26	188	1.68	465	0.92	288	2.59
Smoke (LH,LW,RW)	607	16.2	27.5	92,93,94	10	191	0.77	519	0.97	379	1.74
Victoria (LH,LW,RW)	892	14.8	28.1	92,93,94	11	190	1.32	535	1.14	359	2.46
Mean						190.1	0.87	526.3	1.68	411.9	2.54

Lake trout catch per unit effort (fish per net night) and mean forklength (*FLEN*; mm) grouped by lake type. Initials in brackets after lake names stand for: *LH*=cisco, *LW*=lake whitefish and *RW*=round whitefish. The number of fish captured=12×number of years sampled×CUE.

^aMysis present

^bLake Opeongo is East Arm only, total fish species is high compared to other lakes because of intensive sampling.

mass+1), log₁₀ (fork length), log₁₀ (CUE+1)). Log₁₀ transformations of original CUE and fork length measurements did not normalize distributions. Therefore analyses listed below were done on ranked data, or using non-parametric methods for these two measures. Two-way analyses of variance (ANOVA; fixed effects treatment model) were performed on lake trout CUE with depth strata and lake type (presence/absence of burbot and coregonids) as the two main effects. Two-way ANOVAS from juvenile lake trout were performed on lake trout forklength data with age and species presence/absence as the two factors. One-way ANOVAS were performed on forklength to

compare lake type or species presence/absence. One way ANOVAs were also used to compare lake trout and total fish biomass across lake types. Least squares linear regression was used to see if lake trout CUE was related to coregonine density. To determine the stock/recruit relationship between juvenile lake trout CUE and adult lake trout CUE across the study lakes, a Beverton and Holt model was used:

$$R = \frac{aS}{b + S} e^{\epsilon}$$

where *R*=recruits, *S*=stock and *e^ε* is the lognormal error term.

The model parameters were estimated using non-linear regression after \log_e -transforming both sides of the equation ($\log(R) = \log(aS) - \log(b + S) + \varepsilon$). I report r^2 as the model sum of squares divided by the corrected total sum of squares. Two models were fitted: one for type 1 and 2 lakes; and one for type 3 and 4 lakes. The distributions of juvenile and adult lake trout positions in gillnets were compared among lake types using Kolmogorov–Smirnov tests.

In addition, Eloranta (1985) and Carl (1992) observed that burbot did not move into the hypolimnion until they reached a size greater than 25 cm and likely did not influence juvenile lake trout in these lakes. I therefore compared the density of juvenile lake trout in coregonine lakes with small or no burbot to lakes with mean burbot size greater than 30 cm to test for predation on juvenile lake trout by large, piscivorous burbot using a student t -test. The effect of round whitefish on juvenile lake trout CUE was evaluated by comparing lake mean CUE for Booth, Opeongo, Smoke and Victoria (round whitefish present) with Ayles, Burnt Island, LaMuir and Hogan (round whitefish absent) using a student t test.

Juvenile diet was investigated through examination of stomach weight, the number of items, and the number of taxa in a stomach. Two-way ANOVAs were performed on juvenile lake trout diet variables, with age and lake type as factors.

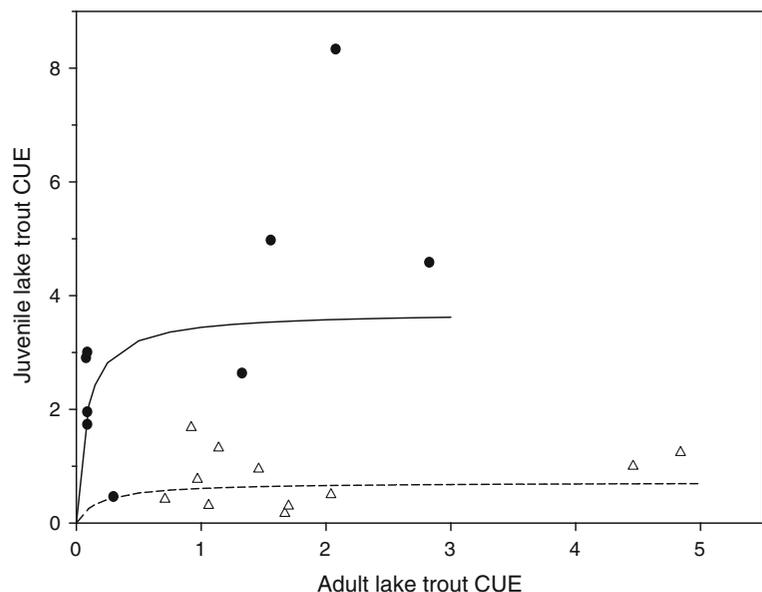
Results

Catch and biomass

The CUE of lake trout differed with lake type for both adults and juveniles ($P < 0.001$). Juvenile CUE was higher in type 1 and 2 lakes, whereas adult CUE was slightly higher in types 3 and 4 lakes (Table 1). The stock/recruit relationship for type 1 and 2 lakes explained 11% of the variation in juvenile lake trout CUE ($a = 3.716$ (1.629: standard error); $b = 0.080$ (0.107); $r^2 = 0.108$; Fig. 1). The relationship for type 3 and 4 lakes explained less than 1% of the juvenile lake trout CUE variation ($a = 0.718$ (0.421); $b = 0.180$ (0.844); $r^2 = 0.005$; Fig. 1). Juvenile and adult lake trout CUE's were not related to lake area ($r^2 = 0.12$, $P = 0.137$; $r^2 = 0.04$, $P = 0.408$: respectively (\log_{10} CUE+1)).

The juvenile lake trout CUE in Ayles, Burnt Island, LaMuir, (mean burbot length 245 mm) and Kioshkokwi, and St. Andrews (no burbot) was similar and averaged 0.34 fish/gillnet-night. In comparison, the juvenile lake trout CUE in Hogan, Booth, Opeongo, Smoke and Victoria lakes (burbot mean length 377 mm), was significantly greater at 1.14 fish/net-night ($P = 0.001$). The juvenile lake trout CUE in Booth, Opeongo, Smoke and Victoria (round whitefish present) was greater than the CUE in Ayles, Burnt Island, LaMuir and Hogan (round whitefish

Fig. 1 Relationship between juvenile and adult lake trout CUE with lake type 1 and 2 combined (solid circle – no cisco or lake whitefish) and 3 and 4 combined (open triangle – cisco and/or whitefish)



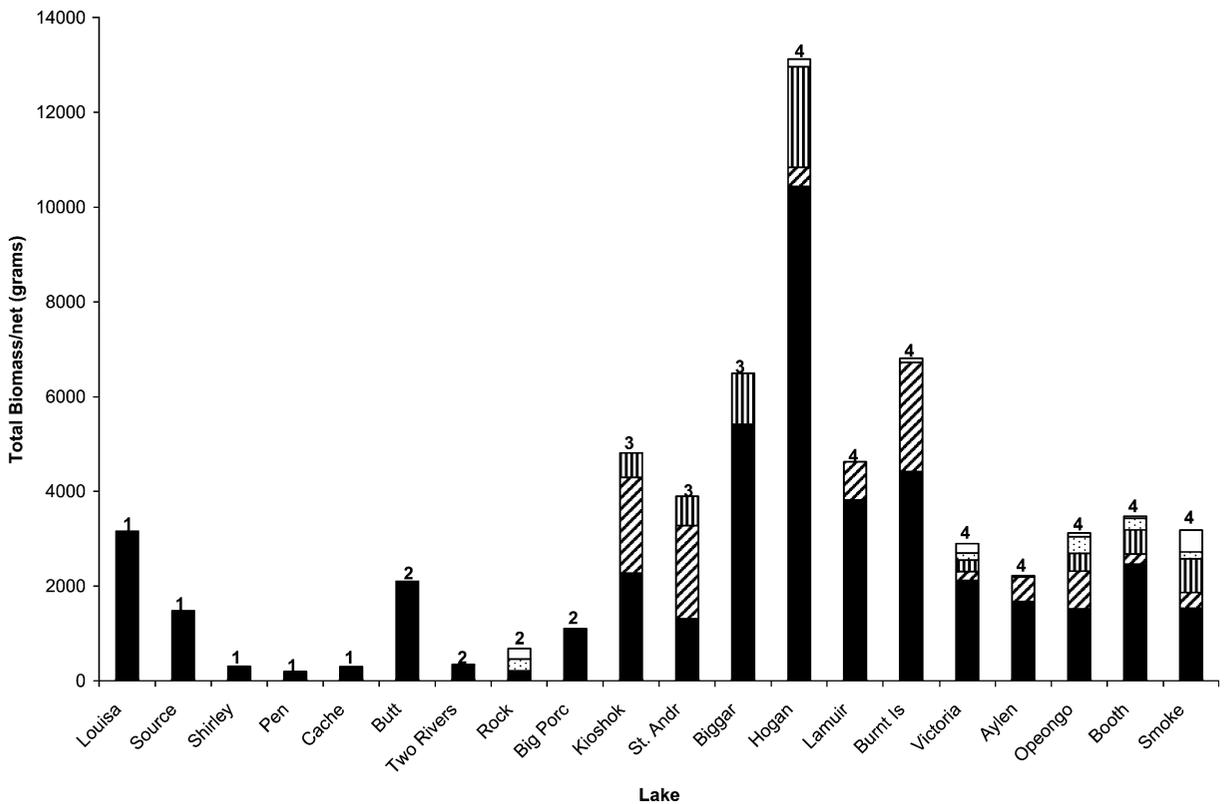


Fig. 2 Biomass (g per gillnet-night) for type 1 lakes (lake trout only), type 2 lakes (lake trout and burbot), type 3 lakes (cisco and/or whitefish) and type 4 lakes (coregonines and burbot).

Lake

Solid area=lake trout, Diagonal bars=lake whitefish, vertical bars=cisco, stippled area=round whitefish and clear area=burbot

absent) (1.18 and 0.56 fish/gillnet night respectively, $P=0.049$).

The relative biomass of lake trout (mean weight per fish (g)×number of fish per gillnet night) was significantly different among lake types (1,088 for lake trout only lakes, 930 for burbot lakes, 2,997 for whitefish–herring lakes and 3,497 for coregonine–burbot lakes; (g per gillnet-night) $P=0.020$; Fig. 2). The total fish relative biomass (g per gillnet night) also differed among lake types with 1,088, 1,056, 5,065 and 4,932 for lake types 1 through 4 respectively ($P=0.001$; Fig. 2). Lake trout relative biomass predominated in 17 of 20 study lakes (Fig. 2).

Size and growth

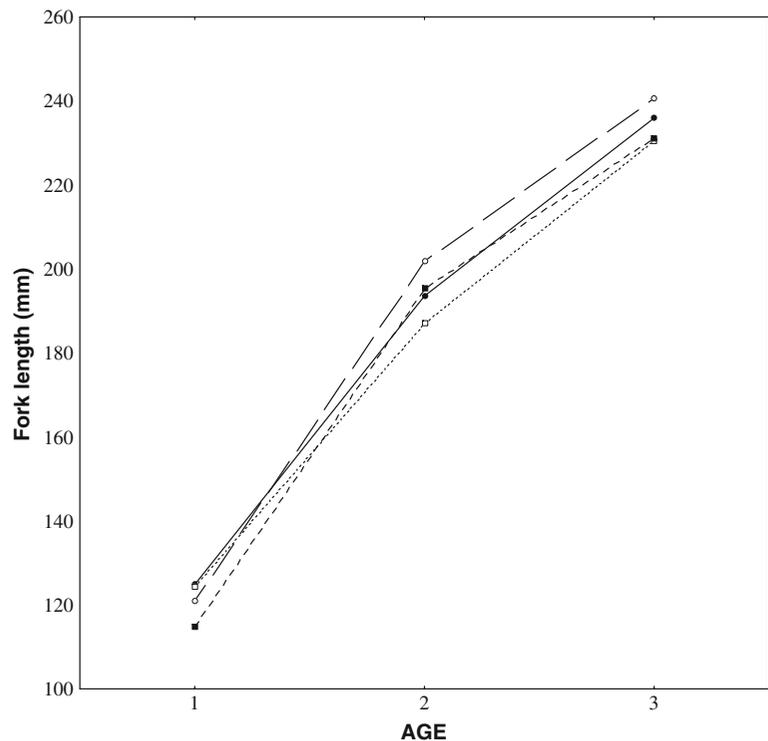
The overall mean size of lake trout differed significantly with lake type; fish in type 1 and 2 lakes were smaller than those in type 3 and 4 ($P<0.001$). This difference was driven primarily by adults, with the size of adult lake trout being significantly smaller in lakes

with no coregonines (415 and 406 mm for lake trout only and burbot lakes respectively) compared to lakes with herring and/or whitefish (460 and 526 mm for whitefish–herring and coregonine–burbot lakes respectively; $P<0.001$). Juvenile lake trout size at age was also significantly different among lake types but there were no consistent patterns across lake types (P (lake type) <0.001 ; Fig. 3).

Diet

The occurrence of fish in the diet of juvenile lake trout was extremely low in lake types 1, and 2 (<3.2%), moderately low in type 3 (11%) and highest in type 4 (29%) (Table 2). Diptera occurred in 58.6% and 62.0% of the lake trout only and burbot lakes lake trout stomachs, in 30.8% of coregonine–burbot stomachs, and in 33.3% of the whitefish–herring stomachs. The number of taxa per stomach did not differ among the lake types ($P=0.797$) or across fish aged 1 to 5 and ranged from 1.5 to 2.0 taxa per stomach ($P=0.989$).

Fig. 3 Juvenile lake trout size (mm) at age by lake type. Type 1 lakes – *solid circle*; type 2 lakes – *open square*; type 3 lakes – *open circle*; type 4 lakes – *solid square*



The mean stomach weight varied from 0.5 to 1.3 g but was not significantly different across lake types ($P=0.634$). There was a difference in stomach weight for juveniles of different ages ($P<0.001$), with older fish having heavier stomach weights. The mean number of items in each stomach differed with lake type ($P<$

Table 2 Juvenile lake trout frequency of occurrence of common food items, number of taxa in each stomach, stomach weight and number of items per stomach stratified by lake type

Item	Lake type			
	1	2	3	4
	Frequency of occurrence (%)			
Empty	5.9	1.5	–	10.3
Cladocera	11.6	12.9	5.6	8.2
Diptera	58.6	62.0	33.3	30.8
Ephemeroptera	9.1	7.6	–	15.8
Megaloptera	5.2	1.5	–	3.4
Fish	3.2	1.5	11.1	28.8
Number of stomachs	257	138	9	90
Number of taxa per stomach	1.6	1.9	2.0	1.5
Stomach weight (g)	1.1	0.5	1.3	0.9
Number of items per stomach*	139.8	143.9	9.3	11.1

* $P<0.01$

0.001) but not with age ($P=0.469$). Lake trout from whitefish herring and coregonine burbot lakes had the fewest items in their stomachs (Table 2).

Distribution

Adult catch was greater at shallower depths than deeper ($P=0.001$; Table 3). There was also a significant difference in the distribution of juvenile lake trout in relation to water depth strata across the four lake types ($P<0.001$; Table 3). However, there was an interaction effect between lake type and depth.

The frequency distribution of lake trout adult and juvenile position in the gillnet differed ($P<0.001$; Kolmogorov–Smirnov test). Nearly 80% of all juveniles were caught within 0.30 m of the net bottom while fewer than 40% of the adults were captured at the bottom of the net (Fig. 4). There was no difference in the distribution of juvenile lake trout in the presence or absence of coregonines ($P=0.998$). Adult lake trout were slightly higher, on average, above the bottom in the presence of coregonines (1.0 m) compared to their absence (0.8 m, $P<0.001$).

The size frequency distribution of lake trout captured in the gill nets was bimodal in all 3 mesh

Table 3 Relative frequency of adult and juvenile lake trout stratified by depth and lake type

Lake type	Depth					
	10–20 m		20–30 m		>30 m	
	Adult (%)	Juveniles (%)	Adult (%)	Juveniles (%)	Adult (%)	Juveniles (%)
1	61	33	13	38	26	29
2	73	29	18	39	9	32
3	66	43	22	52	12	5
4	55	32	33	43	12	25
Overall	63	34	22	43	15	23

sizes. The first mode rose sharply for each mesh size to twice the height of the second mode. The center of the first mode was ~90 mm in the 19 mm mesh net, ~140 mm in the 25 mm mesh net and ~200 mm in the 38 mm mesh net. The second mode was much wider than the first and centered in all three mesh sizes at ~450 mm.

Discussion

Trippel and Beamish (1989) found that lake trout growth was, in part, likely a function of growth efficiency from different food sources. Similarly, the results of this study strongly indicate that changes occur in lake trout population structure, including size, in relation to the presence of the four species in this study. The lake trout population changes were greatest in type 3 and 4 lakes with cisco and lake whitefish present. The lake trout size data show the overall mean size, an aspect of population structure, of lake trout is quite small in type 1 and 2 lakes and much larger in type three and four lakes. The larger size of prey in type 3 and 4 lakes appear to support larger lake trout (Kerr 1971). The juvenile growth data did not show such a clear pattern of differences in size relative to lake type. For example, fish in type 1 lakes are relatively large at age 1 but relatively small at age 2. This overlap is not surprising given similar productivity and presumably availability of

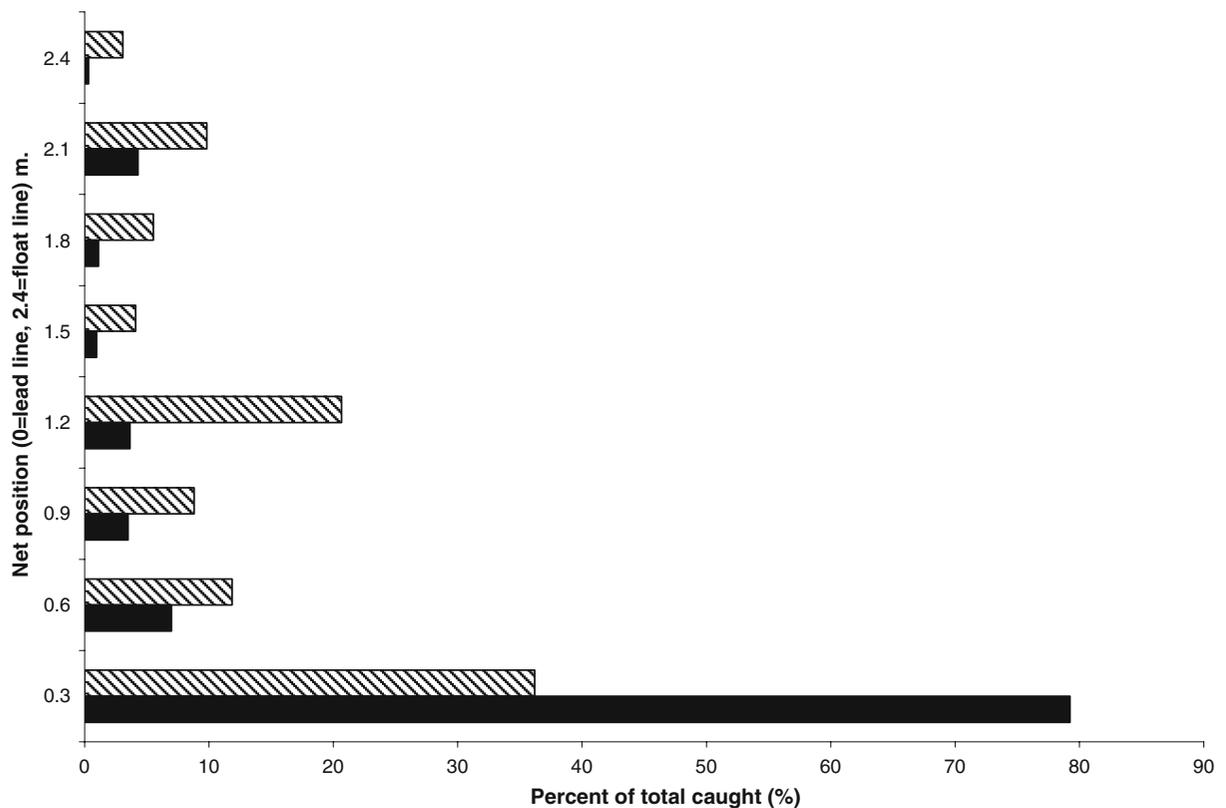


Fig. 4 The distribution of juvenile (<30 cm, solid bars) and adult (>30 cm, diagonal bars) lake trout position of capture in gillnets combined for all lakes

juvenile prey across the four lake types as opposed to much larger prey available for adults in type 3 and 4 lakes. The diet of adult lake trout that were live-released was not determined. However, juvenile lake trout diet differed slightly across lake types, with lake trout from type 1 and 2 lakes eating smaller items compared to type 4 lakes, where fish made up a significant part of the diet. Juvenile lake trout from type 3 and 4 lakes had the fewest items in their stomachs, suggesting an impact in coregonines lakes, but stomach weight was similar across lakes indicating ration size varied little.

There were significant differences in density of both adult and juvenile lake trout across lake types. Juvenile CUE varied little between type 1 and 2 lakes (high), and between type 3 and 4 lakes (low). Juvenile growth rates were similar in all lake types and there was no detectable difference in stomach weight of juveniles in any of the four lake types. This indicates food may be limiting juveniles in all lake types and suggests that intraspecific density had little impact on juvenile growth at these population levels. It would appear that juvenile lake trout may adjust to differences in fish species present through change in density rather than growth rates (McFadden and Cooper 1964), while adults may adjust to large prey in the coregonine lakes with increased size (Kerr 1971).

Juvenile lake trout abundance was similar whether round whitefish were present or absent. The four type 4 lakes with round whitefish also had large burbot present and had similar juvenile lake trout CUE to the fifth lake with large burbot (Hogan, juvenile lake trout CUE=1.0 fish/gillnet night) and no round whitefish. This indicates the higher juvenile numbers in these lakes are likely due to the presence of burbot. In addition, Rock Lake, a burbot only lake with round whitefish, had a juvenile lake trout CUE well within the range of type 1 and 2 lakes indicating little or no potential impact of round whitefish. Finally, Carl and McGuinness (2006) reported that over 80% of round whitefish in their study were captured between 10 and 20 m, whereas I found nearly two thirds of juvenile lake trout were captured below this depth.

The relationship of adult and juvenile CUE indicates that there are significant differences in recruitment as well as size structure and density in the different lake types. Type 1 and 2 lakes group together as do type 3 and 4 lakes. Type 1 and 2 lakes show a familiar stock-recruit relationship with a dome shaped curve. Type 3

and 4 lakes show no such relationship. It is unlikely that behavioural differences led to a difference in juvenile lake trout catchability among the lake types that would have changed the stock-recruit relationship. There was no difference in the height above the bottom at which juvenile lake trout were caught in gillnets in lakes with and without coregonines, suggesting similar foraging strategies. In addition, Davis et al. (1997) made visual counts of juvenile lake trout using a remotely operated vehicle in 1993 in two of my lakes (Source (type 1 lake) and Opeongo (type 4 lake)) and found a ratio (5.0 to 1) of juvenile lake trout CUE that was very similar to the 1993 gillnet data for the same lakes (5.4 to 1) from this study. This indicates that catchability was similar for juvenile lake trout across lake types. It is possible adult lake trout behaviour may have changed in the presence of coregonines and led to a change in catchability. Adults were caught slightly higher in the gillnet in the presence of lake whitefish and herring (1.0 m) compared to where they were absent (0.8 m). Perhaps large lake trout were pursuing coregonines into the nets, leading to increased catchability of larger lake trout compared to the prevalent small-bodied adults in lake trout only and burbot lakes. In counterpoint, the maximum catch frequency of the largest mesh net (38 mm) was ~200 mm, thus smaller trout were much more likely to be captured than larger trout in all lakes. It is not known if these two effects balance each other; however, other studies have found that total lake trout numbers are usually higher where small-bodied lake trout are present (Carl et al. 1990). As well, although presumed low, angling may have affected lake trout numbers, particularly larger fish found in type 3 and 4 lakes. However if adult numbers were reduced by angling there would still be little or no effect on recruitment as juvenile CUE was low in all type 3 and 4 lakes (Fig. 1).

The poor relationship between adult and juvenile lake trout CUE in type 3 and 4 lakes suggests that a survival bottleneck associated with coregonines may occur in the early life history of lake trout. Carl and McGuinness (2006) found pelagic coregonine stomachs contained benthic items indicating the potential for direct interaction with juvenile lake trout. The mechanism could be competition between benthic juvenile lake trout and coregonines or coregonine predation on lake trout at the egg or larval stage. Juvenile lake trout had similar growth regardless of species present, indicating competition was unlikely. Video images

taken by Davis et al. (1997) showed subyearling lake trout in study lakes often resting on essentially featureless substrate in the hypolimnion shortly after they had emerged from spawning shoals. These fish would likely be vulnerable to predation by coregonines foraging on benthos. In support Carl (2000) found that 6% of cisco contained an average of 11 fish larvae in Lake Opeongo gillnetting while Hoff et al. (1997) also found fish in Lake Superior cisco diet. Three studies found small fish in lake whitefish diet (Tohtz 1993; Doyon et al. 1998; Pothoven 2005). Another potential factor is cannibalism. Evans et al. (1991) suggested cannibalism particularly with large adults. This study was not designed to measure cannibalism and it could impact recruitment, however the lack of a relationship in type 3 and 4 lakes between juvenile and adult lake trout with large lake trout present and the positive relationship in type 1 and 2 lakes with smaller fish suggests any effect of cannibalism was small. In further support of coregonines effect on recruitment, Carl and McGuinness (2006) showed a coregonines effect on recruitment in other species suggesting that lake whitefish and cisco may also impact lake trout populations. Early predation may therefore be a mechanism, along with cannibalism, driving lake trout recruitment in the coregonine lakes. It is interesting to note that rainbow smelt, *Osmerus mordax*, were present in only one lake (Kioshkokwi) and that this lake had the lowest number of juvenile lake trout among the study lakes. Possibly, rainbow smelt contribute to the putative larval bottleneck as postulated for cisco and whitefish.

I could detect no negative change in lake trout population parameters in relation to burbot being present in a lake. Lake trout CUE and size structure were similar in type 1 and 2 lakes with and without burbot. Carl and McGuinness (2006) found burbot in lakes without coregonines or with only lake whitefish present were quite small and most often in the littoral area rather than in the hypolimnion with small lake trout. The small mouth gape and different habitats used suggest that burbot predation on lake trout was negligible in these lakes. Burbot may have had an indirect and, surprisingly, positive effect on juvenile lake trout due to a possible interaction between burbot and coregonines. In lakes with coregonines present, burbot were large and hypolimnetic (Carl 2000) and the densities of benthic coregonines were reduced compared to lakes without burbot (Carl and McGuinness 2006). Juvenile lake trout CUE in lakes with one or more coregonines

was three times higher in the presence of large burbot compared to lake trout in coregonine lakes where burbot were absent or small. It would appear that the indirect effect of reduced benthic coregonine abundance in the presence of large, hypolimnetic burbot may lead to increased densities of juvenile lake trout and may overshadow any possible predation by burbot on juvenile lake trout.

Biggar Lake was exceptional in regard to juvenile lake trout CUE. Although it grouped with the lakes with coregonines and large burbot in terms of intermediate juvenile lake trout CUE, burbot were absent, cisco densities were higher and average size lower (52.1 fish/gillnet night; mean forklength 132 mm, unpublished data) than any coregonine lake reported by Carl and McGuinness (2006). It may be that the putative bottleneck extends beyond lake trout emergence into the first summer. In Biggar Lake, the bottleneck window is shorter because subyearling lake trout reach a size beyond the small cisco earlier. In other lakes with larger coregonines, juvenile lake trout CUE is lower because subyearling lake trout may be vulnerable to predation longer due to the larger size of coregonines. For example Hoff et al. (1997) found large cisco over 40 cm eating prey 50–70 mm in length.

Evans and Olver (1995), in an analysis of inland lake trout lakes, also suggested that egg or larval predators were interfering with establishment of lake trout populations in inland lakes, while Gunn et al. (1987) reported an inverse relationship between biomass of stocked juvenile lake trout and biomass of hypolimnetic fish species. Again these all suggest a potential bottleneck occurring in the early life stages of lake trout in the presence of offshore fish species.

Martin (1966) suggested that lakes with small-bodied adult lake trout that were primarily non-piscivorous, such as in lake trout-only and burbot lakes, had larger total numbers of lake trout than large-bodied piscivorous populations. The total CUE data from this study support that finding but indicate that lake trout biomass is much lower in these lakes, in the benthic habitat where lake trout often are found, because of the much greater weight of larger fish in type 3 and 4 lakes. This study was not designed to measure the influence of lake trout on other species. However, lake trout made up over 50% of the relative biomass in bottom set gillnets in 17 out of 20 lakes.

Lake trout may adopt a bet-hedging life history strategy of delayed maturation in whitefish-cisco and

coregonine-burbot lakes (Carl 2000). If this is the case, large piscivorous lake trout would predominate, recruitment would be low or sporadic and adult biomass high with a sufficient reproductive reserve to maintain recruitment with a serious bottleneck. Lake trout-coregonine communities are common and clearly lake trout persist in the face of the putative coregonine bottleneck. One of my study lakes, Opeongo, has three coregonines and burbot present. This lake has had an angler fishery and continuous creel survey since 1936. During this time the lake trout population has maintained itself in the face of this regulated fishery (Shuter et al. 1987; Carl et al. 1991).

However, if adult lake trout are ‘fished down’ by anglers or commercial harvest in a lake, the lake trout population may not be able to keep these coregonines in check (Trippel and Beamish 1993) or have a large enough reproductive reserve. It may be difficult for a lake trout population with few large adults to recover after overfishing with a large coregonine population able to maintain pressure on lake trout recruitment processes. Thus, these lakes may be very sensitive to collapse caused by overfishing and subsequent lake trout recruitment failure vis a vis Walters and Kitchell (2001) and Post et al. (2002).

Evans and Willox (1991) noted that juveniles inhabited deeper benthic areas than adults likely due to cannibalism. I found that adults preferred shallower depths across all lake types and were captured higher in

the net than juveniles (Table 3 and Fig. 4), while juveniles avoided the 10–20 m strata in all four lake types. Vander Zanden et al. (2000) found only 2 of 228 lake trout likely cannibalistic. One was from Lake Louisa (type 1 study lake), the second from a lake with coregonines. Thus if cannibalism is a factor in juvenile depth distribution, smaller adults generally found in type 1 and 2 lakes appear to trigger it as in type 3 and 4 lakes. This premise is also supported by the very similar proportion of age 1–3 lake trout captured in type 1 and 2 lakes compared to type 3 and 4 lakes (type 1 and 2 lakes; 21% age 1, 56% age 2 and 23% age 3: type 3 and 4 lakes; 22% age 1, 53% age 2 and 25% age 3). If large lake trout were preying heavily on juveniles (particularly larger juveniles) then one would expect lower proportions of age 2 and 3 lake trout in type 3 and 4 lakes compared to lake types 1 and 2. Thus cannibalism is likely not a major structuring factor in these lakes.

In pooling the results from this study and my earlier work, there appear to be important species interactions occurring in these lakes (Carl 2000; Carl and McGuiness 2006). Among the five species studied, lakes with cisco present saw the largest changes in fish community structure with a recruitment bottleneck in five major species and a consequent shift in adult size and abundance in four of the five species (Table 4). There were fewer changes in lakes with lake whitefish with recruitment bottlenecks in lake trout and longnose sucker, *Catostomus catostomus*. Round whitefish

Table 4 The impacts of cisco, lake whitefish, round whitefish and burbot on lake trout, cisco, lake whitefish, burbot, white sucker (*Catostomus commersoni*) and longnose sucker

		Impact on:				
Species	Lake trout	Cisco	Lake Whitefish	Burbot	White sucker	Longnose sucker
Cisco	Recruitment bottleneck, adults – large	–	Recruitment bottleneck; shift to benthic niche, adults large, low density	Recruitment bottleneck; adults large, low density	Reduced adult abundance	Recruitment bottleneck
Lake Whitefish	Recruitment bottleneck, adults – large	No apparent effect	–	No apparent effect	No apparent effect	Reduced recruitment
Round Whitefish	No apparent effect	Could not determine	Could not determine	Could not determine	Could not determine	Could not determine
Burbot	Increased juvenile density in presence of benthic coregonine	No apparent effect	Reduced densities of benthic whitefish	–	Could not determine	Could not determine

Results are from Carl 2000, Carl and McGuiness (2006) and present study

appear to have no detectable impact on lake trout, while burbot positively influence juvenile lake trout abundance by suppressing benthic coregonines (Table 4). It is clear one simple model does not fit all lakes. Fishery managers need to look at the fish community to determine the impact on various key characteristics of species of interest.

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