

Effects of large lake trout (*Salvelinus namaycush*) on the dietary habits of small lake trout: a comparison of stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) and stomach content analyses

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Abstract We examined the effect of large (potentially piscivorous) lake trout (*Salvelinus namaycush*) on the dietary habits of small lake trout in an arctic lake. We hypothesized that large lake trout constrain the foraging of small lake trout, thus, in the absence of large lake trout, small lake trout will shift their diet from littoral to more abundant prey offshore. We tested this hypothesis using samples from a removal exper-

iment where all lake trout large enough to be susceptible to gill nets were removed from a small arctic Alaskan lake during 1988–1989. We examined size at age and conducted stomach content and stable isotope analyses of lake trout collected during removal (1988), early recovery (1990), and late recovery (1999) portions of the study. Lake trout grew more quickly following removal. All lake trout fed on a variety of prey, but stomach analyses provided little information on segregation of diet between size classes. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ analyses showed that small lake trout shifted their diet after large lake trout were removed, apparently toward more reliance on offshore zooplankton, which also implies a habitat shift to open water. Thus, we conclude that large lake trout are restricting the dietary habits of small lake trout, a restriction that was removed in an exploited population.

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Introduction

Many animals must balance the need to forage actively with the need to avoid predators (e.g., Anholt et al., 2000; Skalski & Gilliam, 2002). As a result, predators may affect the

foraging efficiency of prey by reducing their use of optimal habitats and/or relegating them to microhabitats that contain sub-optimal resources (Werner & Anholt, 1996; Biro et al., 2003). This reduction in foraging efficiency will often result in a reduction of prey fecundity and growth rates (Downes, 2001).

The trade-off between foraging efficiency and predation risk has been well documented in aquatic systems. For both large and small aquatic animals, predator avoidance can result in energetic costs to food-limited organisms (Sih, 1982; Werner et al., 1983), and food and predator distributions can determine individual growth, fecundity, and mortality rates (Werner & Gilliam, 1984). In streams, large fishes affect the spatial distribution of small fishes (Power, 1984; Power et al., 1985). In lakes, juvenile fish or small fish species are often restricted to sub-optimal habitats to avoid predation by larger fish (Johnson, 1972, 1976; Mittelbach, 1984; Byström et al., 2004).

In arctic lakes, juvenile lake trout are found in littoral areas despite the fact that there is greater food abundance offshore (McDonald et al., 1992). This habitat use is thought to reduce predation risk from adult lake trout and other piscivorous fish (Johnson, 1972, 1976; McDonald et al., 1992), similar to the pattern predicted for arctic char in Swedish lakes (Byström et al., 2004). Adult lake trout in arctic Alaskan lakes feed primarily on benthic invertebrates (O'Brien et al., 1979; Merrick et al., 1992; Sierzen et al. 2003), controlling invertebrate abundances and food web interactions (Hershey, 1990; Merrick et al., 1991; Hershey et al., 1999), although they also eat fish (Merrick et al., 1992), and affect the distribution of other fishes (Hanson et al., 1992; McDonald & Hershey, 1992). As a result of these effects, lake trout size distribution is typically skewed toward adult fish (Johnson, 1972, 1976; McDonald & Hershey, 1989). In the case of arctic fish, previous studies suggest that the large adult fish control recruitment by forcing juveniles into sub-optimal habitats, where foraging opportunities are reduced and growth is slow (see McDonald et al., 1992, 1996).

We hypothesized that in the absence of the predation risk imposed by large lake trout, small

lake trout would shift their diet to larger and more abundant invertebrates from offshore areas. To test this hypothesis, we examined samples from an experiment where by large lake trout were experimentally removed from an 8.5 ha arctic lake during 1988–1989. We used natural abundance of ^{15}N and ^{13}C and stomach content analysis to evaluate the diets of small and large lake trout from the experimental removal period, while the large lake trout were absent from the lake, and after the fish had returned to an approximation of their original size structure. Differences in the stomach contents, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ of small lake trout in the absence of large lake trout compared to when large lake trout were present would suggest habitat/foraging shifts resulting from change in the predation risk imposed by large lake trout.

Study site

Lake NE-12 is a small arctic lake (8.5 ha, $Z_{\text{max}} = 14$ m) 4 km north of the Toolik Lake Field Station on the North Slope of the Brooks Range in Alaska (Hanson et al., 1992). NE-12 is ultra-oligotrophic with an average chlorophyll concentration of 1.5 mg/l and a simple trophic structure. The fish community is comprised of lake trout (*Salvelinus namaycush*), arctic grayling (*Thymallus arcticus*), slimy sculpin (*Cottus cognatus*), and burbot (*Lota lota*).

Materials and methods

Field methods

Lake NE-12 was intensively gillnetted during the open water seasons of 1988 and 1989 to remove large lake trout. Removal was performed with experimental gillnets 38.1 m in length with 7.6 m panels ranging from 35 mm to 135 mm stretched mesh. Nets were checked every three days from late June to early August in 1988 and from late June to late August in 1989. Due to the small size of the lake, close interspersed of habitat types relative to net size, and irregular depth distribution along the shore, we did not feel we could reliably sample distinct habitats with the nets.

Rapid removal of large lake trout was also a higher priority in the study than sampling habitat distribution. Thus, nets were set perpendicular to shore with the smallest panels nearest the shore. In June 1990, the gillnet catch in 36 net nights contained no large lake trout (>350 mm), suggesting that virtually all large lake trout had been removed. Gillnetting was discontinued and the lake was considered to be in the recovery stage of the study. All fish that were removed were sacrificed. Otoliths were removed for age analysis, stomachs removed and stored in 95% ethanol for gut analysis, and mass and fork length recorded.

Length at Age

A complete discussion of NE-12 lake trout growth history is outside of the scope of this paper (Lienesch et al. in revision). However, for the purposes of this paper, we present fork length as a function of fish age for lake trout sacrificed in 1988, 1990, and 1999. Age was determined from sagittal otoliths, which were mounted in epoxy. Transverse thin sections containing the nucleus were cut with a low-speed saw (Lienesch et al., 2005). Each thin section was ground with 600 grit wet/ dry sandpaper and polished with 0.03 μm aluminium oxide slurry. Annuli were counted at 100 \times magnification (Lienesch et al., 2005).

Stomach content analyses

We examined the stomach contents of 20 of the 35 lake trout from the removal period (1988), 28 lake trout from the first sampling year of the recovery period (late recovery, 1990), and 12 lake trout from after the lake had returned to an approximation of the original size distribution (1999) (Table 1, Fig. 1). The stomach contents of each fish were removed and initially sorted for larger prey items in a glass pan over a light box. Smaller prey items were then sorted using a stereoscope. All prey items were stored in 70% ethanol, identified to lowest taxonomic level possible, and counted. In some instances where zooplankton were too numerous to effectively count, the number of individuals was estimated by sub-sampling, using a sample splitter to randomly

split samples until approximately 100 individuals remained.

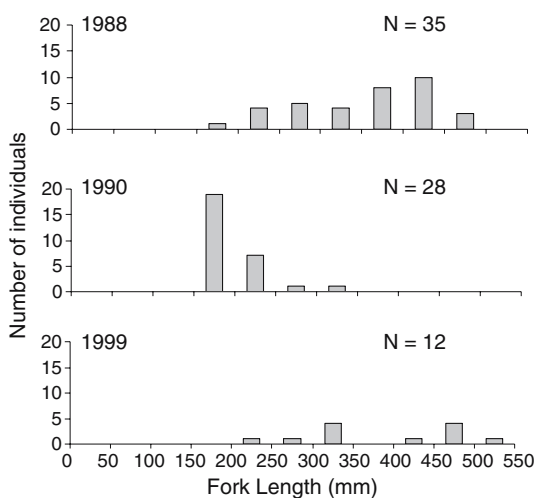
For the analysis, all prey items were grouped as zooplankton (*Daphnia middendorffiana*, *Daphnia longirimes*, *Heterocope septentrionalis*, and *Bosmina logirostris*), Trichoptera (primarily *Grensia*), fingernail clams (Sphaeriidae), snails (*Lymnaea elodes*, *Valvata lewisi*, and *Physa* sp.), chironomids, or fish. All zooplankton sampled are pelagic. Benthic invertebrates are distributed in both littoral and offshore benthic regions of the lake. Lake trout were separated into large (>350 mm FL) and small (<350 mm FL) size classes based on the approximate size when fish become sexually mature (McDonald & Hershey, 1989; Lienesch et al., unpublished data). These size categories effectively separated the samples into two groups based on the somewhat bimodal size distribution of 1988 and the distinctly bimodal distribution of 1999 (Fig. 1). The small size class also represents potential prey for large lake trout since lake trout are capable of consuming prey up to half their body size (Behnke, 2002). Due to a lack of normality and homoscedasticity in the data, no statistical analyses were conducted on gut content data.

Stable isotope analyses

Stomach muscle samples were removed from 21 large and 14 small lake trout harvested in 1988, 28 small lake trout from 1990, and 6 large and 6 small lake trout from 1999. Stomach muscle samples were dried at 60°C, frozen in liquid nitrogen, and pulverized with a mortar and pestle. For each sample, approximately 3–6 mg of the ground tissue was placed in a tin capsule and analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ by the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University. We obtained ethanol-preserved zooplankton from offshore zooplankton tows collected in 1990 and 1999, and ethanol-preserved *Lymnaea* and *Grensia* from stomach contents of fish in 1988 and 1999. We also collected zooplankton from offshore zooplankton tows during July 2001 and benthic macroinvertebrates during July 2003. Animals collected in 2003 were allowed to clear their guts overnight, and then prepared for isotope analyses. The prey

Table 1 The mean (\pm SE), median, and frequency of macroinvertebrates found in the stomachs of large and small lake trout (*Salvelinus namaycush*) from the removal (1988), early recovery (1990), and late recovery (1999) periods

	Year Size Class N	1988	1988	1990	1999	1999
		Small 8	Large 12	Small 28	Small 6	Large 6
Zooplankton	Mean (\pm SE)	212.0 (164.0)	75.0 (53.1)	0.47(0.4)	18.3 (15.4)	0.2 (0.2)
	Median	10.0	0	0	2.0	0
	Freq. (%)	62.5	41.7	6.7	66.7	16.7
Tricoptera	Mean (\pm SE)	3.4 (3.4)	13.92 (11.9)	1.3 (0.8)	33.3 (22.4)	64.0
	Median	0	0	0	12.0	0.5
	Freq. (%)	12.5	41.7	13.3	83.3	50.0
Lymnaea	Mean (\pm SE)	0	100 (40.7)	0	0	50.2 (25.1)
	Median	0	43.0	0	0	27.5
	Freq. (%)	0	75.0	0	0	100.0
<i>Valvata</i>	Mean (\pm SE)	0.1 (.1)	11.3 (7.0)	0	0	1.5 (0.7)
	Median	0	1.0	0	0	1.00
	Freq. (%)	0	58.3	0	0	66.7
Fingernail Clams	Mean (\pm SE)	1.0 (1.0)	15.42 (7.2)	0	0	7.17 (5.8)
	Median	0	1.00	0	0	2.0
	Freq. (%)	12.5	66.7	0	0	66.7
Chironomids	Mean (\pm SE)	80.5 (72.3)	4.33 (1.9)	17.6 (8.4)	79.00 (33.1)	17 (4.8)
	Median	2.0	1.0	0	79.0	18.0
	Freq. (%)	62.5	58.3	33.3	100.0	100.0
Chironid Pupae	Mean (\pm SE)	16.8 (10.4)	0.5 (0.3)	0.7 (0.6)	5.8 (4.3)	0.3 (0.2)
	Median	0	0	0	2.0	0
	Freq. (%)	37.5	25.0	6.7	66.7	33.3
Fish	Mean (\pm SE)	0.3 (0.2)	0.3 (.3)	0.03 (0.03)	0	0.3 (0.3)
	Median	0	0	0	0	0
	Freq. (%)	25.0	8.3	3.3	0	16.7

**Fig. 1** Fork length distribution of lake trout in Lake NE-12 captured in 1988 (removal period), 1990 (early recovery period), and 1999 (late recovery period)

items included the most dominant benthic macroinvertebrates and zooplankton. Although reports vary regarding the effect of various forms

of preservation on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, an experimental study conducted by Feuchtmayr & Grey (2003) indicates that ethanol-preserved zooplankton have $\delta^{15}\text{N}$ values which are slightly but not significantly enriched compared to samples that are processed immediately without preservation. It was also found that ethanol did not significantly alter $\delta^{13}\text{C}$ in zooplankton (Feuchtmayr & Grey, 2003). Since all fish and most invertebrate samples were preserved in ethanol, and across invertebrate taxa there was no general pattern of greater ^{15}N or ^{13}C enrichment of preserved versus unpreserved samples (see Results), we do not believe that the deviation in preservation methods for the 2001 and 2003 samples over the earlier samples affects interpretation of our results. In addition, there was no change in preservation method from 1988 to 1999, the interval when fish were collected for this study.

We used ANOVA with Tukey's HSD to compare $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of lake trout between size groups and years. We used Kruskal–Wallis

Rank Sum with Tukey's pairwise comparisons to compare $\delta^{15}\text{N}$ values between prey types and between sampling years for each prey type (JMP 2001). Kuskal–Wallis was used for these comparisons because the ANOVA assumption of homogeneity of variances could not be achieved through data transformation. We used linear regression to evaluate whether $\delta^{13}\text{C}$ of prey types changed temporally (JMP 2001). Due to a temporal change in $\delta^{13}\text{C}$ for some taxa (see Results), we did not make pairwise comparisons of $\delta^{13}\text{C}$ between sampling years. $\delta^{13}\text{C}$ data were $\ln(-x)$ transformed to homogenize variances.

We used linear regression to evaluate the change in $\delta^{15}\text{N}$ with increasing fork length of 1988 lake trout (SAS version 8.2, SAS Institute Inc. 1999–2000). We also conducted separate regression analyses of $\delta^{15}\text{N}$ versus fork length of fish from small and large categories.

Note that because we manipulated lake trout in only one lake, it could be argued that inferential statistics are inappropriate (see Hurlbert, 1984). However, we subscribe to the position of Oksanen (2001), who has argued that inferential statistics should be used to distinguish patterns caused by the manipulation from those caused by scatter in the population, regardless of whether an experiment is replicated, and that emphasis on replication often sacrifices examination of ecosystem level problems at appropriate temporal and spatial scales.

Results

Age and length distributions

Lake trout collected in 1988 ranged from 5 to 51 years in age (Fig. 2). In 1990, all lake trout fell into the small size category and we captured no fish older than 5 years (Figs. 1 and 2). Note that most of these fish (age 2+ and 3+) recruited during 1987 and 1988, and thus would have been present during the removal period, but would not have been large enough to have been captured by a gill net. In 1999, fish captured in gillnets ranged in age from 5 to 12 years. Fork lengths of the few 1–2 year old fish caught in 1990 were similar to that of the sole 5 year old fish caught in 1988.

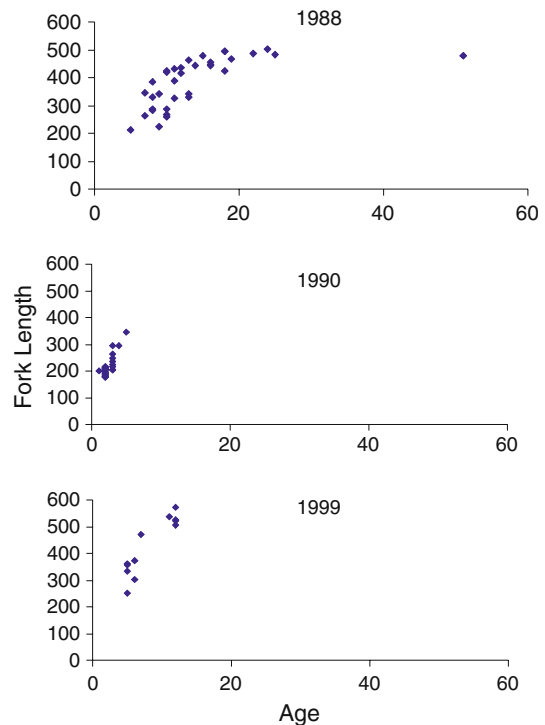


Fig. 2 Fork lengths at age of lake trout from 1988, 1990, and 1999

Fork lengths of 3 year old fish captured in 1990 broadly overlapped those of 5–10 year old fish captured in 1988 (Fig. 2). Fork length distribution of lake trout captured in 1999 was similar to that of fish captured in 1988 (Fig. 1). However, 1999 fish were considerably larger at a given age than 1988 fish (Fig. 2).

Stomach content analysis

Molluscs (*Lymnaea*, *Valvata*, and *Sphaeriidae*) were only collected from the stomachs of large lake trout (Table 1). All stomachs analyzed during the late recovery period contained chironomid larvae, and more fish had chironomid larvae in their stomachs at this time than earlier in the study. There were no clear patterns of abundance of zooplankton, Trichoptera, and chironomid pupae in lake trout stomachs. Stomachs of small lake trout captured in 1990 had relatively few prey compared to those from 1988 and 1999, but chironomids were the most abundant prey type.

Stable isotope analysis

Small lake trout from 1990, the early recovery period, were significantly ($P < 0.001$) depleted in ^{15}N ($\delta^{15}\text{N} = 8.00 \pm 0.08$; mean \pm SE) relative to small lake trout from both the removal ($\delta^{15}\text{N} = 8.84 \pm 0.25$) and late recovery ($\delta^{15}\text{N} = 9.10 \pm 0.28$) sampling periods (Table 2 a). However, the $\delta^{15}\text{N}$ value of the small lake trout from the early recovery period was not significantly different from the large lake trout collected during the removal and late recovery periods of the study, and large lake trout $\delta^{15}\text{N}$ did not differ significantly between removal and late recovery sampling periods (Table 2a).

All large lake trout from the removal period were significantly ($P < 0.001$) enriched in $\delta^{13}\text{C}$ ($\delta^{13}\text{C} = -24.60 \pm 0.26$; mean \pm SE) relative to all other lake trout in the study. Small lake trout from the early recovery ($\delta^{13}\text{C} = -29.60 \pm 0.18$) period were not significantly different in $\delta^{13}\text{C}$ compared to small lake trout collected during the late recovery ($\delta^{13}\text{C} = -29.79 \pm 1.00$) period. Both the small lake trout from the early and late recovery period were significantly different ($P < 0.001$) from small lake trout collected during the removal period ($\delta^{13}\text{C} = -26.95 \pm 0.39$). Large lake trout from the late recovery ($\delta^{13}\text{C} = -27.26 \pm 0.70$) period were not significantly different in $\delta^{13}\text{C}$ compared to small lake trout from the removal period. However the large lake trout from late recovery period were significantly different ($p = 0.002$) from small lake trout from both the early and late recovery periods (Table 2a).

A linear regression model using 1988 data showed that lake trout became more depleted in

$\delta^{15}\text{N}$ with increasing fork length ($P = .0004$, $R^2 = 0.32$):

$$\delta^{15}\text{N} = 10.51 - 0.006 \cdot \text{Fork Length}$$

However, linear regression also showed that there was no relationship between $\delta^{15}\text{N}$ and fork length ($P = 0.4993$; $R^2 = 0.039$) for small lake trout during the removal period. In contrast, large lake trout from the removal period showed a strong negative relationship between $\delta^{15}\text{N}$ and fork length ($P = 0.0007$, $R^2 = 0.459$; Fig. 3).

Invertebrate prey varied significantly in ^{15}N enrichment between groups. *Heterocope*, which are predatory copepods found in open water of many arctic lakes (e. g., O'Brien et al., 2004), were significantly more enriched than all other prey groups except for *Cyclops*, consistent with their status as predators (Table 2b). Chironomids were significantly more enriched than both *Grensia* and molluscs, which were similar to each other. $\delta^{15}\text{N}$ of *D. middendorffiana*, the dominant zooplankton present and the most common zooplankton in lake trout stomachs, was intermediate between chironomids and both *Grensia* and molluscs, and not significantly different than either (Table 2b). Within groups, *D. middendorffiana* $\delta^{15}\text{N}$ differed between years ($p < 0.02$, Table 3), but did not show a consistently declining or increasing temporal pattern. *Daphnia* $\delta^{15}\text{N}$ declined from 1990 to 1997, increased in 1999, then returning to approximately 1990 levels in 2001 (Table 3). *Lymnaea* $\delta^{15}\text{N}$ also differed significantly between years ($P < 0.004$). This difference was due to lower $\delta^{15}\text{N}$ in 2003, but no difference in $\delta^{15}\text{N}$ between 1990 and 1999, when lake trout were collected. The lower value in 2003 could have been due to

Table 2 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for small and large lake trout sampled from NE-12

Organism	Year	preservative	n	$\delta^{15}\text{N}$		$\delta^{13}\text{C}$	
				Mean	SE	Mean	SE
Lake trout							
Small lake trout	1988	ethanol	14	8.84 ^a	0.25	-26.95 ^b	0.39
	1990	ethanol	28	8.00 ^b	0.08	-29.60 ^c	0.18
	1999	ethanol	6	9.10 ^a	0.48	-29.79 ^c	1.00
Large lake trout	1988	ethanol	21	8.08 ^b	0.14	-24.60 ^a	0.26
	1999	ethanol	6	8.18 ^{ab}	0.51	-27.26 ^b	0.70

Matching letters indicate year and size classes of lake trout that were not significantly different using Tukey-Kramer HSD

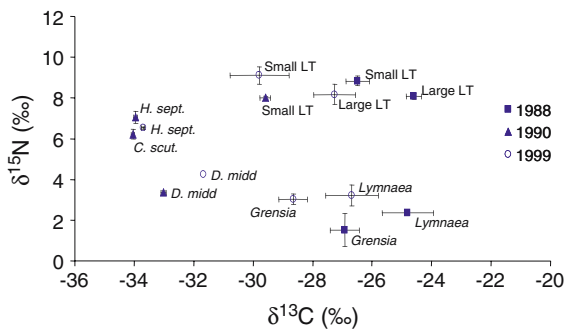


Fig. 3 Biplot of mean (\pm SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of small lake trout from 1988 (LT88S); large lake trout from 1988 (LT88L); small lake trout from 1990 (LT90S); small lake trout from 1999 (LT99S); large lake trout from 1999 (LT99L). Zooplankton include: *Heterocope septentrionalis* (H. sept.), *Cyclops scutifer* (C. scut.), *Daphnia middendorffiana* (D. midd.). Benthic macroinvertebrates include: snails (*Lymnaea elodes*, *Valvata*) and tricopteran (*Grensia praeterita*)

the fact that *Lymnaea* were collected from shore in 2003, whereas other *Lymnaea* were collected from large lake trout stomachs and could have

come from any benthic habitat in the lake. Preservation in ethanol on *Lymnaea* collected from the stomachs of the lake trout could also have influenced the $\delta^{15}\text{N}$ values (Feuchtmayr and Grey, 2003). However, since *Lymnaea* $\delta^{15}\text{N}$ did not differ between years that lake trout were sampled, the significantly lower $\delta^{15}\text{N}$ in 2003, has no affect on interpretation of the data. Other prey groups did not differ significantly between years in $\delta^{15}\text{N}$.

Invertebrate prey also varied significantly in ^{13}C enrichment between groups. All zooplankton (*Heterocope*, *Daphnia*, *Cyclops*) were significantly more depleted in ^{13}C ($P < 0.0001$) than all other macroinvertebrates. None of the zooplankton differed significantly from one another in $\delta^{13}\text{C}$. *Lymnaea* were not significantly different from *Grensia*, although there was a significant decline in *Lymnaea* ($P < 0.025$, $R^2 = 0.52$) and *Grensia* $\delta^{13}\text{C}$ from 1988 to 2003 ($P < 0.0008$, $R^2 = 0.41$).

Table 3 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for prey taxa used in this study Matching letters next to taxa designations indicate invertebrate taxa groups that did not differ significantly in $\delta^{15}\text{N}$ using Tukey-Kramer HSD, and matching letters next to means indicate means that did not differ significantly between years for a given taxon. A similar comparison was not made for $\delta^{13}\text{C}$ between taxa because $\delta^{13}\text{C}$ changed over time for the *Lymnaea* and *Grensia* (see text) but not zooplankton, and other taxa were only collected in 2003

Organism	Year	preservative	n	$\delta^{15}\text{N}$		$\delta^{13}\text{C}$	
				Mean	SE	Mean	SE
Molluscs^A							
<i>Lymnaea elodes</i>	1988	ethanol	5	2.43 ^a	0.39	-24.81	0.86
	1999	ethanol	5	3.09 ^a	0.65	-26.68	0.89
	2003	none	5	1.23 ^b	0.28	-27.66	0.24
<i>Physa</i>	2003	none	1	2.53	–	-29.54	–
	2003	none	1	2.05	–	-27.03	–
<i>Valvata lewisi</i>	2003	none	1	2.41	–	-33.12	–
Sphaeriidae							
Trichoptera (<i>Grensia</i>) ^A	1988	ethanol	6	1.52 ^a	0.82	-26.92	0.50
	1999	ethanol	6	3.03 ^a	0.25	-28.66	0.49
	2003	none	2	3.79 ^a	0.40	-29.93	0.60
Zooplankton							
<i>Daphnia middendorffiana</i> ^{AB}	1990	ethanol	3	3.35 ^{bcd}	0.12	-33.02	0.07
	1994	ethanol	3	2.77 ^{abc}	0.21	-33.33	0.91
	1995	ethanol	2	2.58 ^{abc}	0.08	-33.56	0.57
	1996	ethanol	1	2.27 ^{ab}	–	-33.09	–
	1997	ethanol	1	1.97 ^a	–	-32.55	–
	1999	ethanol	1	4.25 ^d	–	-31.68	–
	2001	none	2	3.52 ^{cd}	0.10	–	–
<i>Heterocope septentrionalis</i> ^C	1990 ^a	ethanol	3	7.06 ^a	0.53	-33.96	0.11
	1999 ^a	ethanol	3	6.53 ^a	0.10	-33.70	0.05
	2001 ^a	none	1	7.11 ^a	–	–	–
<i>Cyclops scutifer</i> ^{BC}	1990	Ethanol	2	6.22	0.24	-34.05	–
	1992	Ethanol	2	5.40	–	-33.55	–
	1994	Ethanol	2	5.25	–	-34.28	–
Chironomidae^B							
Chironomini							
Orthocladiinae	2003	none	1	4.47	0.28	-28.12	–
Protanypus saetheri	2003	none	1	4.64	–	-26.17	–
Protanypus saetheri	2003	none	1	5.29	–	-26.22	–

Discussion

Lake trout are generalist feeders in arctic lakes throughout their life history. Stomach content analyses alone did not provide strong evidence for a diet shift between size classes, except that small lake trout ate few molluscs compared to large lake trout. A diet analysis approach often leads to equivocal results about intraspecific or interspecific relationships among fishes due to high variability in individual fish as well as the broad dietary habits of many fishes. In addition, stomach contents only reflect what a fish has eaten very recently, and may not represent long-term diet patterns or assimilation. Stomachs of the 1990 fishes generally had fewer prey items than those in other samples (Table 1). Because nets were fished only every 3 days, stomach contents would be expected to underestimate consumption, in general, and especially underestimate consumption of more digestible items, such as zooplankton. Also, stomachs were preserved in 95% ethanol because it is less toxic than formalin, but it is also less effective than formalin as a preservative. Thus, small prey, especially zooplankton, would not preserve as well as larger prey or those with hard body parts. One result that was clear from stomach content analyses was that large lake trout fed heavily on molluscs, primarily *Lymnaea*, which was the largest mollusc present, whereas small lake trout did not eat *Lymnaea* and rarely ate other molluscs. Since mollusc shells are relatively indigestible, they would have been present if the fish had been feeding on them. Thus, use of *Lymnaea* as a major prey item separates large lake trout from small lake trout, regardless of any habitat segregation that may occur.

Whereas stomach content analysis only reveals recent foraging history, stable isotope analysis integrates longer-term assimilation (e.g. Peterson & Fry, 1987; Vander Zanden & Rasmussen, 1999; Vander Zanden & Vadeboncoeur, 2002) and thus has the potential to provide more information on the effect of large lake trout on the diet of small lake trout than does stomach content analyses. In this case, significant $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ differences between small and large lake trout during 1988 indicate that they have significantly different

diets. Similarly, small lake trout had significantly different isotopic signatures in 1988 and 1990, indicating that a significant diet shift occurred between those years. These results support our hypothesis that large lake trout constrain the foraging of small lake trout. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data for prey items provide insight into the dietary basis for the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ shifts seen in small lake trout (Fig. 3).

$\delta^{15}\text{N}$ of prey types did not change in a consistent manner between years, and, thus, differences in $\delta^{15}\text{N}$ of small lake trout between years indicate a change in diet. The molluscs and the caddisfly *Grensia* had lower $\delta^{15}\text{N}$ than most other prey types and were abundant in the stomachs of large lake trout. Thus, the observed ^{15}N -depletion of large lake trout compared to small lake trout in 1988 and the significant decrease in $\delta^{15}\text{N}$ with increasing fork length for large lake trout from 1988 reflect the fact that large lake trout rely heavily on benthic macroinvertebrates whereas small lake trout do not. $\delta^{15}\text{N}$ of small lake trout from the removal period was variable but showed no relationship with fork length, indicating a variable diet unrelated to size (Fig. 4), and further illustrates that the size classes used reflect dietary differences between the fish. However, small lake trout from the early recovery period had $\delta^{15}\text{N}$ values very similar to large lake trout from removal and late recovery periods. It is very unlikely that these small lake trout could have achieved that $\delta^{15}\text{N}$ signature by adopting the same diet as large lake trout because we found no evidence that small lake trout ate molluscs during any of the sampling periods. Thus, they must have shifted toward other ^{15}N -depleted food sources, such as *D. middendorffiana*, which dominate offshore zooplankton in NE-12. If small lake trout moved offshore when large lake trout were removed, they very likely would have increased their consumption of *D. middendorffiana*, consistent with the propensity of fish to be size-selective on zooplankton (e.g., O'Brien et al., 2004), and also consistent with their $\delta^{15}\text{N}$ signature.

The pattern of *D. middendorffiana* $\delta^{15}\text{N}$ through time was variable, but the changes cannot be attributed to lake trout foraging, because we also observed a similar significantly higher $\delta^{15}\text{N}$ in

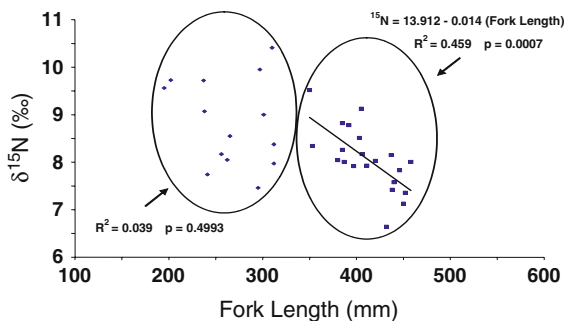


Fig. 4 Regression of lake trout $\delta^{15}\text{N}$ versus fork length for small (diamonds) and large (squares) lake trout captured in 1988

1999 *D. middendorffiana* than in 3 earlier years from nearby Lake NE-9B, which is fishless (Hershey & O'Brien, unpublished). Other potential prey types did not vary in $\delta^{15}\text{N}$ during the study period. The low $\delta^{15}\text{N}$ of *D. middendorffiana* in both 1988 and 1990, combined with the decrease in $\delta^{15}\text{N}$ of small lake trout, is consistent with an increase in the importance of *D. middendorffiana* in small lake trout diets. *H. septentrionalis* is also a large zooplankter that occurs in offshore areas of NE-12, but, as a predator (Luecke & O'Brien, 1983), it was more enriched in ^{15}N than most of the other potential prey types. However, previous studies indicate that *H. septentrionalis* is not very susceptible to lake trout predation (O'Brien et al., 2004), thus probably was less important in the diet of small lake trout than *D. middendorffiana*.

For both small and large lake trout, $\delta^{15}\text{N}$ values were enriched by $\sim 6\text{‰}$ relative to most potential prey except copepods and fish. Given that the limited data from stomach analyses consistently suggests that benthic invertebrates dominate the diet, the $\sim 6\text{‰}$ trophic shift is difficult to understand. However, the most likely explanation is that fish of all catchable sizes include some fish prey in their diets. A previous diet study of lake trout in Toolik Lake in the same region of arctic Alaska also found that benthic invertebrates were the dominant prey group but that 12% of lake trout stomachs contained fish remains (Merrick et al., 1992).

Although $\delta^{13}\text{C}$ is often used to identify food sources in food web studies (Peterson & Fry, 1987), in this case, the $\delta^{13}\text{C}$ patterns must be

interpreted with caution because the benthic components of the lake food web became more ^{13}C depleted over the course of the study. A similar trend in another benthic invertebrate, *Stictochironomus rosenchoeldi*, was observed in another nearby lake which did not support lake trout (Hershey et al., 2005; Hershey et al. unpublished data), therefore the pattern was not due to the lake trout manipulation. The evaluation of the $\delta^{13}\text{C}$ shifts of consumers in regional lakes is beyond the scope of the current paper. However, the temporal shift does have implications for interpreting lake trout diet shifts in Lake NE-12. Large lake trout during the late recovery period were also depleted in ^{13}C compared to large lake trout in 1988. However, this cannot be attributed to a diet shift by lake trout because *Grensia* and *Lymnaea*, two of their major prey items, also became significantly more depleted in ^{13}C over time. Thus, the $\delta^{13}\text{C}$ shift over time for large lake trout simply reflects a temporal shift of their major diet items.

We hypothesized that small lake trout would shift their diet to include more offshore zooplankton. The $\delta^{13}\text{C}$ of offshore zooplankton did not decline over time as did benthic invertebrates. The $\delta^{13}\text{C}$ pattern observed in small lake trout is consistent with a change in their diet selection between removal and early recovery periods, but not consistent with a change toward benthic invertebrates. Small lake trout were depleted in ^{13}C by nearly 4‰ during the early recovery period compared to the removal period, a much larger change over only 2-years than would be expected if their food resource showed a temporal trend; $\delta^{13}\text{C}$ of *Grensia* and *Lymnaea* changed by $<2\text{‰}$ over 11 years. Thus, the observed $\delta^{13}\text{C}$ shift must have been due to a shift in prey selection by small lake trout. The only prey sampled that were sufficiently ^{13}C depleted to shift small lake trout toward more ^{13}C depleted values were offshore zooplankton, all of which were depleted in ^{13}C compared to all other prey. In addition, Hershey et al. (2006) have shown that all offshore invertebrates sampled from 20 lakes in the regions had lower $\delta^{13}\text{C}$ values than nearshore taxa. Thus, the observed $\delta^{13}\text{C}$ shift in small lake trout is also consistent with a shift toward inclusion of more offshore zooplankton in the diet, and not consis-

tent with feeding on nearshore taxa in general. The observation that large lake trout from the late recovery period had similar values to the small lake trout from the removal period can be attributed the $\delta^{13}\text{C}$ shift of prey for large lake trout over time, not any similarity in diet between large and small lake trout.

Finally, we did not observe a difference in $\delta^{13}\text{C}$ between small lake trout in early recovery versus late recovery periods. This suggests that habitat segregation had not fully recovered. $\delta^{15}\text{N}$ of small lake trout differed between 1990 and 1999, but $\delta^{15}\text{N}$ of *D. middendorffiana* differed by a similar magnitude (Fig. 3). Although the size of large lake trout did show recovery during the 11-year sampling interval, they had been growing very rapidly compared to those collected during the removal period, and the number of large lake trout present was still very low (Fig. 1). Thus, density of large lake trout may not have been sufficient to restrict the foraging of small lake trout.

Our study has shown that large and small lake trout in an arctic lake overlap broadly in diet, but nonetheless have isotopic signatures that indicate important differences in their diets. This latter result indicates that despite dietary overlap, the large and small fish derive much of their energy from distinct sources, most likely accomplished by habitat segregation. Large lake trout appear to restrict foraging by small lake trout, apparently by forcing them into less favorable, nearshore habitats. This has consequences for growth as indicated by the rapid growth of small lake trout after large lake trout were removed (Fig. 2). A similar effect was predicted for 1-yr old arctic char in Swedish mountain lakes (Byström et al., 2004). Another whole-lake experiment showed that age-0 rainbow trout were at risk of high mortality rates if increased foraging occurred in the presence of predators (Biro et al., 2003). These results provide insight into the mechanism by which large lake trout control recruitment into the adult population.

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References

- Anholt, B. R., E. E. Werner & D. K. Skelly, 2000. Effect of food and predators on the activity of four larval ranid frogs. *Ecology* 81: 3509–3521.
- Behnke, R. J., 2002. Trout and Salmon of North America. The Free Press, New York NY.
- Biro, P. A., J. R. Post & E. A. Parkinson, 2003. From individuals to populations: prey fish risk-taking mediates mortality in whole-system experiments. *Ecology* 84: 2419–2431.
- Byström, P., J. Andersson, L. Persson & A. M. De Roos, 2004. Size-dependent resource limitation and foraging-predation risk trade-offs: growth and habitat use in young arctic char. *Oikos* 104: 109–121.
- Downes, S., 2001. Trading heat and food for safety: costs of predator avoidance in a lizard. *Ecology* 82: 2870–2881.
- Feuchtmayr, H. & J. Grey, 2003. Effect of preparation and preservation procedures on carbon and nitrogen stable isotope determinations from zooplankton. *Rapid Communications in Mass Spectrometry* 17: 2605–2610.
- Hanson, K. I., A. E. Hershey & M. E. McDonald, 1992. A comparison of slimy sculpin (*Cottus cognatus*) populations in arctic lakes with and without piscivorous predators. *Hydrobiologia* 240: 189–201.
- Hershey, A. E., 1990. Snail populations in arctic lakes: competition mediated by predation? *Oecologia* 82: 26–32.
- Hershey, A. E., G. Gettel, M. E. McDonald, M. C. Miller, H. Mooers, W. J. O'Brien, J. Pastor, C. Richards & J. A. Schuldt, 1999. A geomorphic-trophic model for landscape control of trophic structure in arctic lakes. *BioScience* 49: 887–897.
- Hershey, A. E., W. J. O'Brien, K. Fortino, M. D. Keyse, E. Binkley, P. W. Lienesch, M. E. McDonald, C. Luecke, & S. C. Whalen, 2005. Long-term changes in $\delta^{13}\text{C}$ in DOC-based benthic food webs in arctic lakes. 53rd Annual Meeting of the North American Benthological Society.
- Hershey, A. E., S. Beaty, K. Fortino, S. Kelly, M. Keyse, C. Luecke, W. J. O'Brien & S. C. Whalen, 2006. Stable isotope signatures of benthic invertebrates in arctic lakes indicate limited coupling to pelagic production. *Limnology and Oceanography* 51: 177–188.
- Hurlbert, S. H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211.
- Johnson, L., 1972. Keller Lake: characteristics of a culturally unstressed salmonid community. *Journal of Fisheries Research Board of Canada* 29: 731–740.
- Johnson, L., 1976. Ecology of arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus*

- onus clupeiformis*, arctic char, *S. alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories. Journal of Fisheries Research Board of Canada 33: 2459–2488.
- Lienesch, P. W., M. E. McDonald, A. E. Hershey, W. J. O'Brien & N. D. Bettez, 2005. Effects of whole-lake experimental fertilization on lake trout in a small oligotrophic arctic lake. Hydrobiologia 548(1): 51–66.
- Luecke, C. & W. J. O'Brien, 1983. The effect of *H. septentrionalis* predation on zooplankton communities in arctic ponds. Limnology and Oceanography 28: 367–377.
- McDonald, M. E. & A. E. Hershey, 1989. Size structure of a lake trout population in an arctic lake: influence of angling and implications for fish community structure. Canadian Journal of Fisheries and Aquatic Sciences 46: 2153–2156.
- McDonald, M. E. & A. E. Hershey, 1992. Shifts in abundance and growth of slimy sculpin in response to changes in the predator population in an arctic Alaskan Lake. Hydrobiologia 240: 219–223.
- McDonald, M. E., A. E. Hershey, & W. J. O'Brien, 1992. Cost of predation avoidance in young-of-year lake trout (*Salvelinus namaycush*): Growth differential in sub-optimal habitats. Hydrobiologia 240: 213–218.
- McDonald, M. E., A. E. Hershey & M. C. Miller, 1996. Global warming impacts on lake trout in arctic lakes. Limnology and Oceanography 41: 1102–1108.
- Merrick, G. W., A. E. Hershey & M. E. McDonald, 1991. Lake trout control of snail density and size distribution in an arctic lake. Journal of Fisheries and Aquatic Sciences 48: 498–502.
- Merrick, G. W., A. E. Hershey & M. E. McDonald, 1992. Salmonid diet and the distribution, size, and density of invertebrates in an arctic lake. Hydrobiologia 240: 225–233.
- Mittlebach, G. G., 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65: 499–513.
- O'Brien, W. J., C. Buchanan & J. F. Haney, 1979. Arctic zooplankton community structure: Exceptions to some general rules. Arctic 32: 237–247.
- O'Brien, W. J., M. Barfield, N. D. Bettez, G. M. Gettel, A. E. Hershey, M. E. McDonald, M. C. Miller, H. Mooers, J. Pastor, C. Richards & J. Schuldt, 2004. Physical, chemical and biotic impacts on arctic zooplankton communities and diversity. Limnology and Oceanography 49: 1250–1261.
- Oksanen, L., 2001. Logic of experiments in ecology: is pseudoreplication a pseudoissue? Oikos 94: 27–38.
- Peterson, B. J. & B. Fry, 1987. Stable isotopes in ecosystem studies. Annual Reviews in Ecology and Systematics 18: 293–320.
- Power, M. E., 1984. Depth distributions of armored catfish: predator induced resource avoidance? Ecology 65: 523–528.
- Power, M. E., W. J. Matthews & A. J. Stewart, 1985. Grazing minnows, piscivorous bass, and stream algae – dynamics of a strong interaction. Ecology 66: 1448–1456.
- Sierzen, M. E., M. E. McDonald & D. A. Jensen, 2003. Benthos as the basis for arctic lake food webs. Aquatic Ecology 37: 437–445.
- Sih, A., 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmani*. Ecology 63: 786–796.
- Skalski, G. T. & J. F. Gilliam 2002. Feeding under predation hazard: testing models of adaptive behavior with stream fish. American Naturalist 160: 158–172.
- VanderZanden, M. J. & J. B. Rasmussen, 1999. Primary consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the trophic position of aquatic consumers. Ecology 80: 1395–1404.
- VanderZanden, M. J. & Y. Vadeboncoeur, 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology 83: 2152–2161.
- Werner, E. E. & B. R. Anholt, 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. Ecology 77: 157–169.
- Werner, E. E. & J. F. Gilliam, 1984. The ontogenic niche and species interactions in size-structured populations. Annual Reviews in Ecology and Systematics 15: 393–425.
- Werner, E. E., J. F. Gilliam, D. J. Hall & G. G. Mittlebach, 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540–1548.