University of Alberta

Influence of fish competitors on Lake Trout trophic ecology in sub-arctic lakes

by

Mark Francis Hulsman

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Science
in
Ecology

Department of Biological Sciences

Fall 2012
Edmonton, Alberta

Abstract

Competition for prey is known to narrow the trophic niche width of freshwater fishes. Upon release from interspecific competition, the niche variation hypothesis (NVH) predicts that population niche width will expand via increased inter-individual variation in resource use. I compared the trophic ecology, growth, and body condition of Lake Trout (*Salvelinus namaycush*) in sub-arctic lakes that varied in their competitive regime. Stable isotope analyses indicated that population trophic niche width and inter-individual variation were smaller in lakes with fewer competitors, a pattern inconsistent with the NVH. Further analyses revealed that these patterns were likely due to foraging shifts, as trout consumed primarily littoral resources in lakes with multiple competitors vs. primarily pelagic zooplankton in lakes with one competitor; growth did not differ between lake-types, but populations in the latter lakes were in better body condition. Findings highlight the potential sensitivity of northern Lake Trout populations to colonizing fish species.

Acknowledgments

I am extremely grateful for the opportunities, valuable guidance, and support that my advisors, Drs. Bill Tonn and Kim Howland, have given me. I learned a lot over the last few years and had fun doing it. In addition, I owe a big thank you to my graduate committee. R. Vinebrooke's questions and advice during meetings helped to shape my research, and A. Derocher's willingness to sub in late in the game was much appreciated.

I was lucky to work in the field with fellow ICECAPers B. Lunn, O. Yu, A.B.M. Baki, A.J. Chapelsky, G. Courtice, C. Cahill, A. Erwin, and K. Larsen, as well as with Lake Trout anglers extraordinaire, J. Hanisch and F. Noddin. Thanks for the long hours, laughs, and friendship. I would also like to acknowledge the staff of the Environment Department at Diavik Diamond Mine, Inc. for their help with field logistics and in familiarizing me with life at an industrial mine site. In the lab, L. Witschi, A.J. Chapelsky, S. Widen, and F. Noddin cheerfully sifted through stomach contents of fish, while R. Wastle provided sage advice and assistance in the art & science of fish ageing.

The entire P-T lab was always a great source of advice and encouragement. Fellow Lake Trout aficionados, L. Chavarie and H. Swanson, deserve special thanks for putting up with my questions. I'll miss our many P-T events, whatever they were and wherever they occurred.

Lastly, but certainly not least, I’d like to thank my family for their love and wonderful support throughout this degree. They were by my side even though they were many miles away.

Table of Contents

List of Tables

List of Figures

List of Abbreviations

BIC: Between-individual Component

BURB: Burbot

CD: Mean Distance to Centroid

Chl-*a*: Chlorophyll-*a*

CISC: Cisco

CPUE: Catch-Per-Unit-Effort

CR: Range in $\delta^{13}C$

Fulton's *K*: Fulton's Condition Factor

HR: Horizontal Range

K: Brody Growth Coefficient

L_∞: Mean Asymptotic Length

LKCH: Lake Chub

LKTR: Lake Trout

LNSC: Longnose Sucker

NMS: Non-metric Multidimensional Scaling

NND: Mean Nearest Neighbour Distance

NNST: Ninespine Stickleback

NR: Range in $\delta^{15}N$

NVH: Niche Variation Hypothesis

RI: Relative Importance

RNWH: Round Whitefish

SCA: Stomach Contents Analysis

SD: Standard Deviation

SDNND: Standard Deviation of Nearest Neighbour Distance

SE: Standard Error

SIA: Stable Isotope Analysis

SLSC: Slimy Sculpin

TA: Total Area

TN: Total Nitrogen

TNW: Total Niche Width

TP: Total Phosphorus

V: Mean Individual Specialization

VR: Vertical Range

WIC: Within-individual Component

W_r: Relative Weight

1.0 Introduction

Understanding food web structure and trophic niches are principal aims of animal ecology. Traditionally, the trophic niche concept described the diet and trophic interactions of a population or species that linked it to all others organisms in a food web (Hutchinson 1957), and largely overlooked individual-level traits. However, recent literature has re-focused our attention to variation among foraging individuals and its effects on the population or species from which those individuals are drawn (e.g., Bolnick et al. 2003, Semmens et al. 2009, Araújo et al. 2011).

In his classic comparison of niche width (i.e., the range of resources a population exploits) and inter-individual variation between populations of birds, Van Valen (1965), like others (e.g., Wilson 1961), found that the constraining force of interspecific competition can keep populations' niches tightly packed together; correspondingly, decreased interspecific competition resulted in empty niche space and wider niches. In addition to increased population niche width, increased inter-individual variation was observed under reduced competition. Van Valen (1965) described this pattern in his 'niche variation hypothesis' (NVH), where an increase in a population's or species' niche width occurs via increased inter-individual variation in resource use. In contrast with the NVH, the 'parallel release hypothesis' (Bolnick et al. 2010) predicts that population niche breadth increases when all individuals in a population shift to use a greater number of the available resources without increasing inter-individual variation.

Van Valen's early empirical work was supported by Roughgarden (1972), whose mathematical model reinforced the relationship between inter-individual variation and population niche width. Roughgarden (1972) also proposed that a population's resource use is described by its total niche width (TNW), which is the sum of its two components: the within-individual component (WIC) and the between-individual component (BIC), where the WIC is the average variance of resources within individuals' diets, and the BIC is variation among individuals.

Subsequently, a number of empirical studies testing the NVH have emerged (see Bolnick et al. 2003, 2007, 2010), with empirical support for the NVH divided. Studies that have measured variance in consumer diet have found positive correlations between inter-individual variation and niche width over a wide-range of taxa (e.g., Costa et al. 2008, Araujo et al. 2009, Darimont et al. 2009). In contrast, studies relying on morphological measures as a dietary proxy have been less supportive (e.g., Malmquist 1985, Dennison and Baker 1991, Meiri et al 2005). Recent work on Threespine Stickleback (*Gasterosteus aculeatus*) has suggested this mixed support for the NVH may be due to moderate or weak correlation between morphology and diet (Bolnick and Paull 2009).

The NVH has been supported by studies conducted in freshwater ecosystems (e.g., Bolnick et al. 2007). Indeed, the ecological constraints thought to be precursors for population-specific increases in trophic niche width are well documented in both lentic and lotic ecosystems. Among fishes, ample literature has identified partitioning of prey resources to play a much stronger role in ecological partitioning than either habitat or time dimensions (see Ross 1986), with the trophic niche width of two or more competing species narrowing as a result of resource partitioning (Hodgson et al. 1997, de Mérona and Rankin-de-Mérona 2004, Amundsen et al. 2010). Because fish are often found to have ingested fewer and/or lower quality prey items in the presence of competitors (Hodgson et al. 1991, Dieterich et al. 2004), outcomes of interspecific competition for prey resources have commonly been documented as declines in condition (Tonn et al. 1986, Hodgson et al. 1991, Pardo et al. 2009) and growth (Fraser 1978, Hanson and Legget 1985, Marchetti 1999, McHugh and Budy 2006).

A variety of methods are available in ecological research to investigate the trophic niche. Stomach contents analysis (SCA) is a standard tool that can provide detailed information on prey composition in a consumer's diet. However, since the information obtained from SCA provides only a 'snapshot' of consumer diets, it is ideally associated with a longitudinal sampling program to identify any temporal variation in diet. But because of the expense and impracticality of repeatedly sampling the same individual over ecologically meaningful time-spans, a longitudinal approach is rarely employed (but see Bryan and Larkin 1972). Instead, methods that infer diet over longer temporal periods have been used to supplement the information provided by SCA (e.g., Beaudoin et al. 1999, Janjua and Gerdeaux 2011).

In the last 20 years, stable isotope analysis (SIA) has been increasingly employed in ecological research to understand diets and feeding relationships (Hobson and Wassenaar 1999, Thompson et al. 2005). SIA of tissues provides a dietary proxy that tracks the flow of elemental isotopes from resources to consumers. In particular, ratios of ^{13}C to ^{12}C and ^{15}N to ^{14}N (measured as $\delta^{13}C$ and $\delta^{15}N$, respectively; see below) are commonly analyzed. Because $\delta^{13}C$ is only slightly enriched between source and consumer (due to respiratory CO_2 being slightly isotopically lighter than assimilated carbon), it can provide an indication of the path of energy flow from producer to higher consumers (McCutchan et al. 2003). For instance, in freshwater ecosystems basal resources in the littoral zone can be differentiated from their pelagic counterparts on the basis of their $\delta^{13}C$ signatures; unlike algae in the pelagic zone, littoral algae is more enriched in ^{13}C because its boundary layer is CO_2 limited, making it difficult to preferentially take up the lighter isotope (^{12}C) (Hecky and Hesslein 1995). In contrast, $\delta^{15}N$ consistently undergoes a step-wise increase between successive trophic levels (McCutchan et al. 2003), because the lighter isotope (^{14}N) is preferentially excreted during protein transamination and deamination in consumers (Minagawa and Wada 1984). Thus, it can be useful as a trophic-level indicator, provided that it is standardized to the $\delta^{15}N$ signature of a taxon whose trophic level is known (Vander Zanden and Rasmussen 1999). Together, $\delta^{13}C$ and $\delta^{15}N$ reflect the prey materials assimilated by a consumer to indicate its long-term diet and position in a food web; in slow growing fish populations, isotopic turnover can take years (Hesslein et al. 1993). The primary drawback of SIA is that it provides an estimate of average diet, not a direct measure of feeding like SCA.

Traditionally, the results of SIA have been interpreted qualitatively using bi-plots, which present the $\delta^{13}C$ and $\delta^{15}N$ signatures of individuals (or population means) in isotopic space. Recent developments in quantitative measures for interpretation of SIA include dietary mixing models (e.g., Phillips and Gregg 2003, Moore and Semmens 2008) and linear distance metrics (Layman et al. 2007). Mixing models rely on an iterative statistical approach (e.g., IsoSource (Phillips and Gregg 2003)) or Bayesian probability (e.g., MixSIR (Moore and Semmens 2008)) to estimate relative proportions of organic carbon sources that support a consumer. Linear distance metrics, originally developed to assess community metrics, have been used successfully at the population level to explore niche width and inter-individual variation in two-dimensional isotopic space (e.g., Darimont et al. 2009, Quevedo et al. 2009, Swanson et al. 2010).

The additive nature of fish communities in low diversity regions like northern Canada, whereby a core of widely occurring species are supplemented in higher diversity lakes by a series of less common species, can provide a 'natural experiment' for studies comparing the effect of different communities on the trophic niche of a particular species of fish. Many of the small, shallow lakes that dot northern Canada share similar physical and chemical characteristics (Pienitz et al. 1997). In terms of their trophic status, these lakes can often be classified as oligotrophic. They contain depauperate assemblages of plankton, macroinvertebrates, and fish (Johnson 1976, Shortreed and Stockner 1986, Pienitz et al. 1997, Chu et al. 2003). For example, in the Lac de Gras watershed, NWT, fish community sampling of eleven lakes conducted between 2009 and 2011 revealed 0 - 7 species per lake (mean ± SE; 3.82 ± 0.64) (M. Hulsman, unpublished data). The larger-bodied fish in these lakes included varied combinations of Lake Trout (*Salvelinus namaycush*), Arctic Grayling (*Thymallus* *arcticus*), Round Whitefish (*Prosopium cylindraceum*), Longnose Sucker (*Catostomus catostomus*), Burbot (*Lota lota*), and Cisco (*Coregonus artedii*), with smaller fishes such as Slimy Sculpin (*Cottus cognatus*), Ninespine Stickleback (*Pungitius pungitius*), and Lake Chubb (*Couesius plumbeus*) also present. Within the NWT, adults of the larger-bodied fishes are known to consume similar food resources, including crustaceans, aquatic insects, molluscs, and mites; Lake Trout, Arctic Grayling, and Burbot also consume fishes (Scott and Crossman 1973, Birtwell et al. 2005, Stewart et al. 2007; M. Hulsman, unpublished data). In particular, Lake Trout is commonly regarded as an opportunistic generalist predator (Scott and Crossman 1973); the preferred diet of adults is generally pelagic forage fish, but in lakes lacking this prey type, littoral fishes, benthic invertebrates, and zooplankton make up the diet in variable proportions (Martin 1966, 1970; Pazzia et al. 2002). Within Lake Trout populations, inter-individual differences in trophic position have been documented (Vander Zanden et al. 2000). As large, versatile predators, Lake Trout and Burbot have the ability to interact as both direct predators on, and resource competitors with, the rest of the fish community (Scott and Crossman 1973, Cott et al. 2011).

The overall objective of my study was to use SIA and SCA to investigate if the presence or absence of other large-bodied fish species, as potential competitors and prey of Lake Trout, affect Lake Trout trophic ecology, condition, and growth rate in small, oligotrophic sub-arctic lakes. My specific objectives were to determine if:

1) Lake Trout diet shifts between lakes with and without other large-bodied fishes,

2) Lake Trout population trophic niche width and degree of inter-individual diet variation differ between lakes with and without other large-bodied fishes, and

3) Lake Trout condition and growth rate differ between lakes with and without other large-bodied fishes.

To address these objectives, I sampled six lakes within the Lac de Gras watershed, NWT, during the summers of 2009 - 2011. In three of these lakes, Lake Trout and Burbot are the only large-bodied fishes, while the remaining three lakes support, in addition to Lake Trout and Burbot, Round Whitefish, Longnose Sucker, and/or Cisco. All six lakes are pristine ecosystems, and have never been influenced by angling activity.

My study is directly relevant to natural resource management because industry-led fish colonization projects in the Northwest Territories have recently been initiated under Canada's *Fisheries Act*. These projects identify Arctic Grayling, Cisco, Lake Whitefish (*Coregonus clupeaformis*), Round Whitefish, and Longnose Sucker as target species for colonization (Golder 2001). As a result, there is high potential for these species to colonize small, oligotrophic lakes that currently support Lake Trout and Burbot as the only large-bodied fishes. My study should increase our ability to predict the effects of these policy driven ‘ecological experiments’ on northern Lake Trout populations during this era of increasing development across Canada’s sub-arctic.

2.0 Materials and methods

2.1 Study Area

The study was conducted within the Lac de Gras watershed, Northwest Territories, Canada, ca. 64°28’N, 110°14’W, in a region known as the Barrenlands (Figure 1 inset). The low topographical relief and glacial history of this area have resulted in an abundance of lakes and streams that cover ca. 21% of the landscape (Jones et al. 2003). The lakes are bordered by sedge tussock, low-tall shrub tundra (Bliss 1981), and boulders; their littoral zones support low densities of aquatic plants, including *Hippuris vulgaris*, *Potentilla palustris*, and *Sparganium augustifolium*, and are instead dominated by boulders and soft sediments, although small sections of both sand and gravel/cobble substrates can be found (M. Hulsman, personal observation). The presence of soft sediments could suggest that epipelic primary production is important in these ecosystems (Sierszen et al. 2003). The smaller lakes (ca. < 30 ha) are typically ice-free from mid-June to late-October. Sampling conducted on a subset of 10 lakes indicated that they undergo weak thermal stratification by mid-July (M. Hulsman, unpublished data).

Fieldwork was carried out in six study lakes that are located within a 7.5 km radius of each other (Figure 1). All of the lakes are small (mean ± 1 SE; 9.2 ± 2.5 ha) and have moderate maximum depths (9.7 ± 0.9 m); their littoral zones

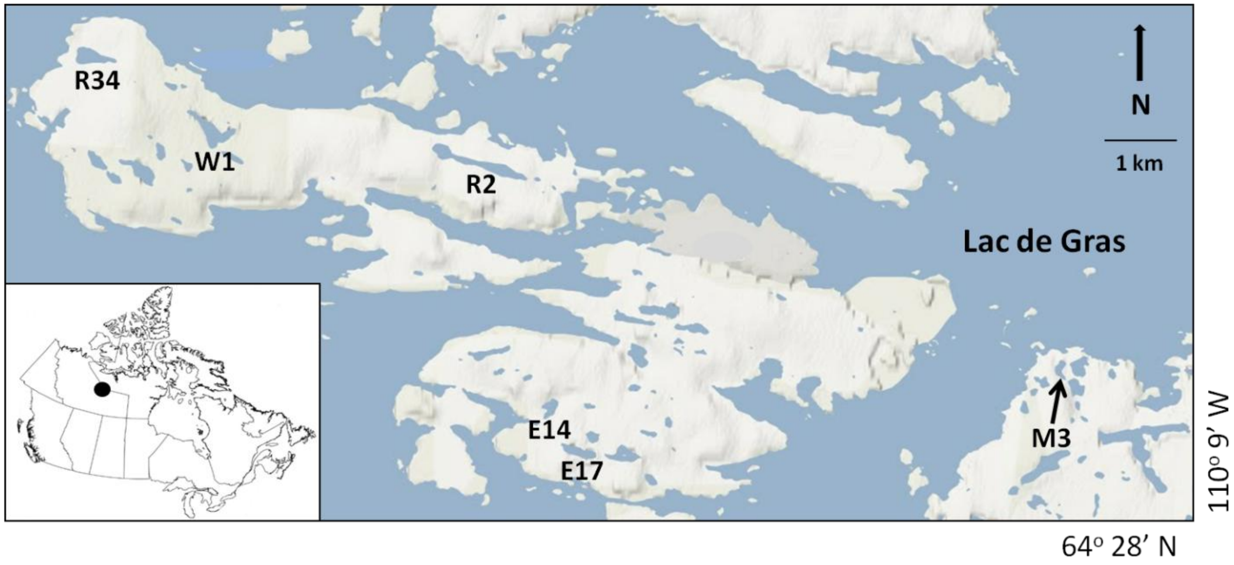


Figure 1 Map showing locations of the study lakes in the Lac de Gras watershed, Northwest Territories. ‘Class 1’ lakes (i.e., M3, E14, E17) support Lake Trout and only one other large-bodied fish (i.e., Burbot), whereas ‘Class 2’ lakes (W1, R34, R2) support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco). Inset: Location of the study area in Canada.

warm to a considerable temperature in the summer (mean ± 1 SE; 15.11 ± 0.14 ^{o}C) (Table 1). They are all oligotrophic and share similar pelagic chlorophyll-a levels and chemical characteristics, though two of the lakes (E14 and E17) have elevated levels of total nitrogen due to anthropogenic sources (Table 1). The lakes were designated as either 'Class 1' or 'Class 2', based on the composition of their fish community (Table 2). Class 1 lakes (M3, E14, and E17) supported Lake Trout and only one other large-bodied fish (Burbot), while Class 2 lakes (W1, R34, R2) supported Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco). At least one small-bodied species (i.e., Slimy Sculpin, Ninespine Stickleback, and Lake Chub) was also found in each lake (Table 2).

2.2 Field Procedures

2.2.1 Limnological Sampling

Water samples were collected offshore from 0.5 m below the surface of each lake. In 2009, one sample was collected in both July and August from lakes M3, W1, and R34. In 2010, one sample was collected in July from M3, W1, and R34, whereas one sample was collected in both July and August from lakes E14, E17, and R2. In 2011, one sample was collected in both July and August from all six lakes. Samples were collected following standard protocols (Biogeochemical Analytical Laboratory 2007) and kept cool until further processing.

Table 1 Limnological characteristics of the six study lakes, Northwest Territories, Canada. Temperature is mean littoral temperature measured over July and August 2010. Total nitrogen (TN), total phosphorous (TP), and Chl-a are displayed as mean lake values with their associated standard error (SE), calculated from measurements taken over three summers (2009-2011) for lakes M3, W1, and R34, and over two summers (2010-2011) for lakes E14, E17, and R2. TN, TP, and Chl-a were collected and analyzed following standard methods.

Lake	Area (ha)	Z_{max} (m)	Temperature ± SE (°C)	TN ± SE (µg/L)	TP ± SE (µg/L)	Chl-a ± SE (µg/L)
Class 1						
M3	3.0	7.5	15.3 ± 0.1	243.3 ± 10.8	8.7 ± 1.2	1.9 ± 0.4
E14	4.1	6.7	15.1 ± 0.1	1542.5 ± 75.5	8.3 ± 0.2	2.6 ± 0.5
E17	5.7	10.5	15.4 ± 0.1	607.0 ± 84.9	8.8 ± 0.6	2.5 ± 0.3
Mean	4.3 ± 0.8	8.2 ± 1.2	15.3 ± 0.1	797.6 ± 387.0	8.6 ± 0.2	2.3 ± 0.2
Class 2						
W1	13.7	11.5	15.2 ± 0.1	241.7 ± 9.4	10.6 ± 2.2	2.1 ± 0.1
R34	18.9	12.5	n/a	229.0 ± 17.7	9.0 ± 1.6	1.5 ± 0.1
R2	9.9	9.5	14.6 ± 0.1	246.0 ± 0	10.5 ± 0.4	2.2 ± 0.1
Mean	14.2 ± 2.6	11.2 ± 0.9	14.9 ± 0.2	238.9 ± 5.1	10.0 ± 0.5	1.9 ± 0.2

Table 2 Fish community composition of the six study lakes ("+" = present, "-" = absent). 'Class 1' lakes support Lake Trout (LKTR) and only one other large-bodied fish (Burbot; BURB), whereas 'Class 2' lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish (RNWH), Longnose Sucker (LNSC), and/or Cisco (CISC)). All lakes support at least one species of small-bodied fish, including Slimy Sculpin (SLSC), Ninespine Stickleback (NNST), and Lake Chub (LKCH).

	Piscivores		Large-bodied			Small-bodied		
Lake	LKTR	BURB	RNWH	LNSC	CISC	SLSC	NNST	LKCH
Class 1								
M3	+	+	-	-	-	+	-	-
E14	+	+	-	-	-	+	-	-
E17	+	+	-	-	-	+	-	-
Class 2								
W1	+	+	+	-	-	+	-	-
R34	+	+	+	+	-	+	+	+
R2	+	+	+	+	+	+	-	-

2.2.2 Fish Sampling

Fish were collected from July to early-September using a combination of Gee minnow traps, fyke nets, backpack electro-fishing, angling, and experimental (multi-mesh) gillnets. Total length (mm) was measured for Burbot, Slimy Sculpin, and Ninespine Stickleback, while fork length was measured for all other species; wet weight (g) was measured for every fish captured. In addition, hard structures (otoliths from dead small-bodied fish, pectoral fin rays from live large-bodied fish, and pectoral fin rays & otoliths from dead large-bodied fish) were collected from a subset of all individuals for age estimation.

Muscle tissue for SIA was collected from a sub-set of individuals of each fish species in each lake. Live fish were sedated with MS-222 (20 mg/L) prior to making a small incision slightly below and posterior to the dorsal fin; a biopsy needle was then used to collect a ca. 25 mg sample of white dorsal muscle from fish > 15 cm in length (McAndrew 1981). A scalpel was used to dissect white dorsal muscle from mortalities and small fish that were sacrificed because their length was less than the minimum-size recommended for biopsy. The biopsy needle and scalpel were sterilized with 95% ethanol between fish to prevent infection and disease transmission. All muscle tissue was frozen at -20 ^{o}C after collection.

I also collected stomach contents from a sub-set of the Lake Trout, Round Whitefish, Longnose Sucker, and Cisco captured in 2010 and 2011. Gastric lavage was performed on live fish (Foster 1977) and the stomach contents were preserved in a 90% ethanol solution. Subsequent dissection of a subset of Lake Trout stomachs (n = 6) revealed that gastric lavage had an average efficiency rate of 98% ± 0.5 (mean ± SE) (M. Hulsman, unpublished data), consistent with similar studies on other fish species (e.g., Foster 1977, Light et al. 1983, Hartleb and Moring 1995). The esophagus and stomach were removed intact from fish mortalities and frozen at -20 °C.

Gillnetting surveys were also conducted to estimate the relative abundance (expressed as catch-per-unit effort (CPUE)) of each large-bodied fish species present in a given lake. The North American standard gillnet was used; it measures 24.8 m long (8 x 3.1 m panels) by 1.8 m deep, and has eight mesh sizes (38, 51, 64, 76, 89, 102, 114, and 127 mm stretched mesh) (Bonar et al. 2009). To standardize the surveys, I set eight nets in each lake perpendicular to shore for 24 hours (± 4 hr) following a depth stratified-random design. Specifically, in M3 and E14 (Z_{max}: 6.7 - 7.5 m), four nets each were allocated across the upper and lower halves. In E17, W1, R34, and R2 (Z_{max}: 9.5 - 12.5 m), three nets were allocated across each of the 0 - 3 m and 3 - 6 m strata, while two nets were allocated across the 6 - 12 m stratum. This depth stratification is generally consistent with that recommended by Sandstrom et al. (2008), so that the volume of water sampled in each stratum is approximately equal. To limit the intensity of effort, since over-exploitation of the fish community is a concern in small, sub-arctic lakes (Sierszen et al 2003), the eight net sets per lake were distributed over 2009 - 2011 for lakes M3, W1, and R34, and over 2010 - 2011 for lakes E14, E17, and R2.

2.2.3 Invertebrate Sampling

Samples of potential invertebrate prey were collected for SIA in both July and August 2010. Zooplankton were collected with an 80 µm Wisconsin net hauled vertically from 0.5 m above bottom. I collected benthic invertebrates from the soft sediments at various depths in each lake using a standard Ekman grab. Additional samples of benthic invertebrates were collected from hard substrates in the littoral zone with a kick net, and emerged aquatic insects were collected with a dip net from the water surface. Terrestrial invertebrates were collected with a dip net from shoreline vegetation.

2.3 Laboratory Procedures

2.3.1 Limnological Samples

All water samples were processed within 24 hours after collection. Samples collected for analysis of their total nitrogen (TN) and total phosphorus (TP) concentrations were frozen at -20 °C. Samples collected for analysis of their Chlorophyll-*a* levels were filtered onto ethanol pre-washed 0.7 µm glass fibre filters and frozen at -20 °C. All samples were shipped to the Biogeochemical Analytical Laboratory at the University of Alberta for analyses.

2.3.2 Samples for Stable Isotope Analysis

One to ten samples (mode = 5) were analyzed for each taxonomic group per lake. Samples were collected over the summer of 2010, with the exception of Lake Trout (2009: n = 2; 2011: n = 3) and Burbot (2011: n = 5) in M3 lake.

Because Lake Trout diet can be influenced by size-related factors (Martin and Oliver 1980), samples from 10 randomly selected individuals that fell within a lake-specific ca. 100 mm size class (Appendix 1) were submitted for SIA to minimize size variation. Size class for a given lake was dependent on the length-frequency distribution of its trout population; classes were selected to minimize, as much as possible, size differences among the six populations. The smallest individual analyzed (fork length = 347 mm) was still of sufficient size to exploit the full suite of available resources, including fish (Mittelbach and Persson 1998).

All aquatic invertebrates were held for 24 hours in Petri dishes containing de-ionized water to allow time for gut clearance; emerged aquatic insects and terrestrial invertebrates were held in empty Petri dishes. All organisms collected for SIA were identified to at least Order, with the exception of Ostracoda and Hirudinea, and frozen at -20^{o}C. Only soft tissues were used from snails and clams for SIA (Carabel et al. 2006). To determine if other invertebrates with calcareous structures contained relevant amounts of inorganic carbonates, I performed the ‘champagne test’ (Jaschinski et al. 2008) on a subsample of thawed coleopterans and zooplankton from each lake. I applied a small amount of 10% HCl to a sample; if carbonates are present in relevant amounts, the sample will effervesce. No effervescence was observed, indicating that no relevant amounts of inorganic carbonates were present. Still, two samples of Coleoptera were acidified with 10% HCl and submitted for SIA. Tissues from all other organisms were expected to have low amounts of inorganic carbonates, so were not treated with HCl (Pinnegar and Polunin 1999, Bunn et al. 2003, Carabel et al. 2006).

Each fish and invertebrate sample was rinsed in distilled water, oven dried for 48 hours at 65°C, and homogenized, before a 1 mg (± 0.2 mg) fraction was encapsulated in a 5 x 8 mm tin capsule for analysis of its stable carbon and nitrogen isotope ratios. Each sample was composed of tissue from a single individual, unless a composite sample was required to meet the mass requirement, as was often the case for invertebrate samples. In most cases, invertebrate sample categories were analyzed for both July and August to capture any seasonal variability in their isotopic signatures. Samples were analyzed with a Europa Scientific ANCA G/S/L elemental analyzer coupled to a Tracer/20 mass spectrometer at the University of Saskatchewan Stable Isotope Facility. A reference sample (egg albumen) was also run every 11 samples to measure instrument error, and duplicate sub-samples were run to assess the efficiency of the homogenization procedure. Results are reported as δ values and ‰ deviations from the international reference standards (i.e., PeeDee Belemnite for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$), calculated as:

$$\delta^{13}\mathrm{C} \text{ or } \delta^{15}\mathrm{N} = [(R_{\mathrm{SAMPLE}} / R_{\mathrm{STANDARD}}) - 1] \times 1000$$

where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$.

A sample's lipid content is accurately reflected by it carbon to nitrogen ratio (C:N) (Post et al. 2007). Because lipids are depleted in ${}^{13}C$, the $\delta^{13}C$ of samples with high lipid content (C:N > 3.5) can be inaccurate unless lipids are removed by chemical or mathematical procedures (Post et al. 2007). As most of my samples had C:N greater than 3.5, I adjusted the $\delta^{13}C$ values of all samples for differences in lipid concentration using the equation described in Post et al. (2007):

$$\delta^{13}\text{C adjusted} = \delta^{13}\text{C} - 3.32 + 0.99 \times \text{C:N}$$

2.3.3 Samples for Stomach Content Analysis

Invertebrates found in the stomach contents of Round Whitefish (n = 14-19 per lake), Longnose Sucker (n = 15 per lake), and Cisco (n = 15) were identified to order, family, or genus, depending on the taxon and degree of digestion. Identical procedures were conducted on stomach contents of Lake Trout (n = 8-19 per lake) that fell within the size classes on which SIA was performed. Individuals from each invertebrate taxon were counted, and lengths of the first 20 were measured under a dissecting microscope to the nearest 0.1 mm. The average dry mass (mg) of individual invertebrates was then estimated using taxon-specific, length-mass regression equations [zooplankton: (Bottrell et al. 1976, Persson and Ekbohm 1980, Rosen 1981); aquatic insects: (Leeper and Taylor 1998, Benke et al. 1999); adult aquatic and terrestrial insects: (Sabo et al. 2002); other Arthropoda: (Hódar 1996, Baumgartner and Rothhaupt 2003); Hirudinae: (Poepperl 1998); Mollusca (Benke et al. 1999, G. Mittelbach, unpublished data)].

Prey fishes found in the stomach contents of Lake Trout were identified to species unless the degree of digestion prevented this level of resolution, in which case they were documented as ‘fish remains’. The length of all intact fish was measured to the nearest 1 mm, and taxon-specific, length-mass regression equations were used to estimate the wet-mass of individual fish. In cases where a high-degree of digestion prevented identification and accurate measurement, the mean length and mean regression parameters for the prey fish species found in the stomach contents of Lake Trout from the same lake were used as an estimate. Following Hewett and Kraft (1993), prey fish wet-mass was converted to dry-mass by calculating the average of the body water content values ($\bar{x} = 0.758$) for *Esox lucius* (0.762; Diana and Mackay 1979), *Perca flavescens* (0.753; Hayes and Taylor 1994), and *Culaea inconstans* (0.759; Kelso 1973), and applying these to the wet-mass of each prey fish (i.e., [(1 - 0.758) × Wet Mass]).

I summarized diet composition at the population level using frequency of occurrence (% O_i), and percentage abundance of prey taxon (i) by number (% N_i) and by mass (% M_i) of all prey taxa. To provide a composite measure of % O, % N, and % M, I calculated the Relative Importance Index, RI (George and Hadley 1979), which scales the importance of each prey taxon so that the sum of the RIs for all prey taxa is 100. For a given fish population, the RI of prey taxon i is calculated as:

$$RI_i = 100 \times AI_i \,/\, \sum_{i=1}^{n} AI_i$$

where AI_i (= % O + % N + % M) is the absolute importance of prey taxon i, % O is the percentage of all non-empty stomachs in which prey taxon i occurred, % N is the percentage that items of prey taxon i contributed to the total number of prey items in all stomachs, % M is the percentage that the mass of prey taxon i

contributed to the total mass of prey items in all stomachs, and n is the number of prey taxa.

To explore inter-individual differences in foraging, diet patterns of individual Lake Trout were also summarized using a modified version of the Relative Importance Index. In this case, the calculation did not include % *O*, such that AI_i = % *N* + % *M*, where % *N* and % *M* were based on the number and mass, respectively of items that prey taxon *i* contributed to the total number and mass of all prey items in an individual's stomach.

2.3.4 Fish Age Estimation

After being cleaned of soft tissue, one otolith and the three leading rays from the left pectoral fin of each Lake Trout were embedded in Cold Cure epoxy. For each fin ray, an initial cut at the base of the fin removed the rough edge leftover from excision, and a 0.2 mm cross-section was then cut near the base using a low-speed saw (Buehler Isomet, Buehler Ltd., Lake Bluff, Illinois). Each embedded otolith was cut through its nucleus in a 0.5 mm thick transverse cross-section, and polished on the cut side that was nearest the nucleus using fine grit sandpaper. The second otolith from each fish was left whole and also polished.

Annuli of both sectioned and whole otoliths were read once under a microscope by two experienced readers at the Department of Fisheries & Oceans' Freshwater Institute. Internal Quality Assurance / Quality Control procedures run on the age estimates indicated that fish < 20 years old were most accurately aged using whole otoliths, whereas otolith cross sections were most accurate for estimating ages of fish ≥ 20 years (R. Wastle, DFO, pers. comm.). Consequently, when age estimates for a fish differed between the two methods (which occurred 41% of the time, with an average age difference of 1.56 years), the age from the whole otolith was used for fish < 20 years old, while the age from the sectioned otolioth was used for fish ≥ 20 years of age. The potential situation where age estimates from the whole otolith and cross section were on opposite sides of 20 years was never encountered.

Fin rays were read once by an experienced reader. A complementary otolith-fin ray comparison indicated that at all ages fin rays underestimated the age of Lake Trout compared to otoliths, and that the degree of error increased with age; however, the underestimation did not follow a consistent, mathematically correctable pattern (Appendix 2). As a result, I used otolith age in my growth analysis.

2.4 Data Analyses

2.4.1 Catch-Per-Unit-Effort

Catch-per-unit effort (CPUE) was calculated for each gillnet set by dividing the catch for each species by the soak time. CPUE for each species-lake combination was then calculated as the mean of the individual set CPUEs for each lake and expressed as number of fish caught per 100 hours soak time.

2.4.2 Diet Patterns and Overlap

The Bayesian mixing model, MixSIR (Moore and Semmens 2008), was used to estimate the contribution of three sources to the diet of each Lake Trout population. MixSIR incorporates uncertainty in fractionation and isotope signatures to produce source contribution estimates with associated probability distributions. Trichopteran larvae and copepods were included in the model as littoral and pelagic end-members, respectively. These sources were selected because qualitative examination of $\delta^{13}C_{adj}$ vs. $\delta^{15}N$ bi-plots revealed that across all of the study lakes, they had the greatest separation in $\delta^{13}C_{adj}$ and showed relatively low standard deviation; Slimy Sculpin, which was present in every lake, was also included in the model as a littoral prey fish member. In one lake (R34), the isotopic signature of Copepoda was estimated based on its mean isotopic distance from Cladocera (whose isotopic signature was known) in the other five study lakes. The three sources included in the model were identified as Lake Trout prey by SCA. Fractionation values per trophic level were assumed to be 0.4 ± 1.20‰ for $\delta^{13}C$ and 2.3 ± 1.61‰ for $\delta^{15}N$ (McCutchan et al. 2003). In Class 1 lakes, Lake Trout was assumed to be 1.0 trophic level above copepods and Slimy Sculpin, and 1.5 levels above Trichopteran larvae. Trophic level assumptions were similar for Class 2 lakes, but Lake Trout was assumed to be 1.5 levels above copepods, as Lake Trout were expected to feed occasionally on younger individuals of the large-bodied fish species in the lakes. For each run, priors were set as uninformative and 1,000,000 iterations were carried out.

Trophic relationships between Lake Trout and large-bodied fish species were qualitatively examined with $\delta^{13}C_{adj}$ vs. $\delta^{15}N$ bi-plots. Diet overlap was quantitatively compared based on RI values (% *O*, % *N*, and % *M*) of the 18 prey categories summed to include every individual in the population. Schoener's proportional similarity index (Schoener 1968) was calculated as:

$$\propto_{xy} = 1 - 0.5\ (\sum_{i=1}^{n} |p_{xi} - p_{yi}|)$$

where α_{xy} is the overlap between species *x* and species *y*, p_{xi} and p_{yi} are the proportions of prey category *i* in the diet of species *x* and species *y*, respectively, and n is the total number of prey categories. The index ranges from 0 (no diet overlap) to 1 (total diet overlap); an index value greater than 0.60 is indicative of biologically significant diet overlap (Wallace 1981).

2.4.3 Trophic Niche Width and Trophic Diversity

Ten Lake Trout from each population were plotted in $\delta^{13}C_{adj}$ vs. $\delta^{15}N$ bi-plot space, and six linear distance metrics were calculated for each population based on arrangement of the individuals. These quantitative metrics provide measures of population trophic structure, and include range in $\delta^{13}C_{adj}$ (CR), range in $\delta^{15}N$ (NR), total area (TA), mean distance to centroid (CD), mean nearest neighbour distance (NND), and standard deviation of nearest neighbor distance (SDNND) (Layman et al. 2007). CR describes differences in paths of energy flow to the population, and is calculated as the difference between the two individuals with the most divergent $\delta^{13}C_{adj}$ signatures. NR describes trophic-level differences in the population, and is calculated as the difference between the two individuals with the most divergent $\delta^{15}N$ signatures. TA is a measure of isotopic population niche width, and is calculated as the total area encompassed by the smallest convex hull containing all individuals in isotopic space. CD measures the average isotopic diversity in the population, and is calculated as the mean distance of each individual to its population's isotopic centroid (i.e., the mean $\delta^{13}C_{adj}$ and $\delta^{15}N$ for the population). NND is a measure of trophic redundancy, and is calculated as the mean of the linear distances to each individual's nearest neighbour in isotopic space, while SDNND reflects the evenness of the packing of individuals in isotopic space, which can indicate the presence of individual outliers (Layman et al. 2007). Linear distance metrics were calculated using the SIAR package (Stable Isotope Analysis in R; Parnell et al. 2008, 2010) in the open source statistical language R (R Development Core Team 2007).

These six metrics were also calculated for the Lake Trout prey community of each lake and used to interpret the metric values for the corresponding Lake Trout population, as isotopic range and distribution of prey resources affects inter-individual variation in consumer isotope ratios (Matthews and Mazumder 2004, Swanson et al. 2010). The prey community was defined on a lake-specific basis as those taxa present in the stomach contents of the ten Lake Trout used in the linear distance metrics. Because stable isotope signatures were unavailable for some members of the prey communities from certain lakes, these signatures were estimated based on the mean distance in $\delta^{13}C$ and $\delta^{15}N$ from a taxon (whose isotopic signature was known) in lakes where both groups were present. Taxa whose $\delta^{13}C$ and $\delta^{15}N$ signatures were estimated are identified in the bi-plots (Appendix 3).

To incorporate these same metrics into the analysis of stomach contents, I condensed Lake Trout prey items into 8 prey categories to reduce the complexity of the data set. Each prey item was assigned to one of the following ecological categories: zoobenthos, molluscs, pelagic zooplankton, littoral/benthic zooplankton, pelagic macroinvertebrates, free-swimming insects, terrestrial/emerged insects, or fish. An ordination was then performed on Arcsine square root transformed proportional prey RI values modified for individual diet (i.e., based on % *N* and % *M*). Non-metric multidimensional scaling (NMS) with a Sorenson distance measure (n = 250 iterations, 250 runs with real data, 249 runs with randomized data; stability level = 0.00001) was conducted in PC-ORD v.6 (McCune and Grace 2011), and individual trout from all six lakes were positioned in the same ordination space. The ordination scores for the Lake Trout in a given population were then used to calculate the linear distance metrics for that population via SIAR. Because linear distance metrics are influenced by sample size (in this case, the number of Lake Trout stomach content samples per lake) (Layman et al. 2011), all metrics were bootstrapped (n = 30) based on the minimum sample size in the data set (n = 8) to allow comparison of their mean values between classes of lake. The bootstrapping procedure was conducted by randomly selecting eight Lake Trout from each lake, upon which an ordination was performed. All ordinations used the same seed number. In all cases the mean value for each distance metric stabilized by the 30th bootstrap, so no further bootstrapping was necessary (Appendix 4).

In addition to the above metrics, I explored Lake Trout trophic niche width and trophic diversity using traditional measures for stomach contents data. Prey items were assigned to one of 18 taxonomic-/life history-based prey categories (Table 3), and RI values (% *N* and % *M*) modified for individual diet were calculated. The proportion of prey category *j* in the population's niche, q_j, was then expressed as:

$$q_j = \frac{\sum_i n_{ij}}{\sum_i \sum_j n_{ij}}$$

where n_{ij} represents the RI value for prey category *j* in individual *i*'s diet. The trophic niche width of each Lake Trout population was quantified with Levins' *D* (Levins 1968):

$$D = \frac{1}{\sum q_j^2}$$

where q_j is defined as above. The degree of individual specialization present in each population – which is an ecological equivalent of trophic diversity and similar to the CD metric – was calculated using the program IndSpec1 (Bolnick et al. 2002), which uses a modified version of Schoener's (1968) proportional similarity index to measure the overlap between the diet of individual *i* and the diet of the population from which it was drawn:

Table 3 Eighteen prey categories identified in the stomach contents of Lake Trout and used in select analyses of trophic ecology.

Prey category
Fish[a]
Chironomid larvae
Other Dipteran larvae[b]
Chironomid pupae
Other Dipteran pupae[b]
Dipteran adults
Trichopteran larvae
Trichopteran adults
Pelagic zooplankton - Cladocera[c]
Pelagic zooplankton - Copepoda[d]
Littoral / Benthic zooplankton[e]
Ostracoda
Terrestrial Coleoptera
Dystiscidae
Corixidae
Mollusca
Hirudinea
Hydrachnidia

[a] Slimy Sculpin, Ninespine Stickleback, Lake Chub, Cisco, Burbot, Longnose Sucker, and unidentified Remains

[b] Ceratopogonidae, Chaoboridae, Culicidae, Empididae, Simuliidae, and Tipulidae

[c] *Bosmina*, *Daphnia*, and *Holopedium*

[d] Calanoida and Cyclopoida

[e] Chydoridae and Macrothricidae

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j|$$

where p_{ij} is the proportion of prey category j in individual i's diet, and q_j is as described above. The extent of individual specialization (*IS*) in each population was then measured as the average of PS_i values (Bolnick et al. 2002); *IS* can range from near 0 (very high individual specialization) to 1 (no individual specialization). Following Araujo et al. (2009), I expressed this measure as the more intuitive $V = 1 – IS$, so that higher values indicate higher individual specialization.

2.4.4 Condition and Growth

Body condition of Lake Trout within the lake-specific 100 mm size classes was evaluated using relative weight (W_r; Wege and Anderson 1978) and Fulton's condition factor (*K*; Ricker 1975). Unlike Fulton's *K*, the relative weight equation does not assume isometric growth, as it compares observed weight (*W*) to that predicted from a standard weight-length regression (W_s):

$$W_r = \frac{W}{W_s} \times 100$$

where *W* is the weight (g) of each fish and W_s is the length-specific standard weight (g) as predicted from a species-specific weight-length relationship developed from surveys across a species geographic range. I used the W_s equation derived from 58 populations of Lake Trout from across North America by Piccolo et al. (1993):

$$\log_{10} W_s = -5.681 + 3.246 \times \log_{10}\mathrm{TL}$$

where TL is total length (mm). Since TL measurements were not available for all Lake Trout, I used fork length instead. Consequently, W_r values will be inflated, making the standard interpretation of good condition as $W_r \geq 100$ inaccurate. Still, W_r calculated from fork lengths is a useful metric for comparing Lake Trout condition within the set of study lakes. To provide a condition index that may be compared to Lake Trout populations outside of those in the current study, Fulton's K was also calculated:

$$K = W \times \frac{100}{L^3}$$

where W is wet weight (g) and L is fork length (cm).

The von Bertalanffy growth function (VBGF) was used to describe the growth of the Lake Trout populations, modeling it as:

$$L_t = L_\infty(1 - e^{(-K(t-t_0))})$$

where L_t is the estimated length-at-age t, L_∞ is the mean asymptotic length, K is the Brody growth coefficient, and t_0 is the hypothetical age at which length is zero (Ricker 1975). To fit the von Bertalanffy curve, I minimized the residual sum of squares by manipulating the growth parameters L_∞, K, and t_0 (Chen et al. 1992). As sample sizes for length-at-age data were low for each lake, data were pooled within each lake class to fit von Bertalanffy growth curves. Consequently, no statistical comparison was pursued to avoid pseudoreplication.

2.4.5 Statistical Analyses

The Kolmogorov-Smirnov test was used to examine data for normality and Levene's median test was used to test for homogeneity of variances. Independent samples t-tests conducted in SPSS v.19 (SPSS, Inc., Chicago, Illinois) were used to assess differences between Class 1 and Class 2 Lake Trout populations for the six linear distance metrics, Levins' D, V, W_r, and K. Lake was considered the level of replication for all tests. I assessed significance using an α-level of 0.10 to minimize type-II error, and to detect ecologically meaningful patterns in data-sets with modest sample sizes.

3.0 Results

3.1 Stable Isotope Analysis

Acidifying samples to remove carbonates was deemed unnecessary, as mean difference ± SD in $\delta^{13}C$ between treated and untreated sub-samples was only 0.28 ± 0.08‰ (n = 2). Precision and replicability of SIA was good; standard deviation of reference egg albumen samples (n = 82) was ± 0.069‰ for $\delta^{13}C$ and ± 0.051‰ for $\delta^{15}N$. Mean difference ± SD between duplicate sub-samples of fish and invertebrates was 0.40 ± 0.59‰ for $\delta^{13}C$ (n = 10) and 0.16 ± 0.11‰ for $\delta^{15}N$ (n = 10).

3.2 Catch-Per-Unit-Effort

Lake Trout CPUE varied among lakes, and there was no systematic difference between lake classes (Table 4). The other large-bodied fishes had greater CPUE than Lake Trout in two of three Class 2 lakes.

3.3 Diet Patterns and Overlap

Qualitative examination of $\delta^{13}C_{adj}$ vs. $\delta^{15}N$ bi-plots for each lake revealed that the $\delta^{13}C_{adj}$ signatures of Lake Trout populations in Class 1 lakes aligned more closely with pelagic than littoral sources (Appendix 3). Conversely, in Class 2 lakes, the relatively less negative $\delta^{13}C_{adj}$ signatures of Lake Trout populations suggested diets that were based more on littoral than pelagic sources (Appendix 3). Furthermore, relative to their respective prey communities, Lake Trout populations in Class 1 lakes appeared to have lower $\delta^{15}N$ signatures than populations in Class 2 lakes.

Results from the mixing model analyses indicated that Lake Trout populations used resources differently between the lake classes (Appendix 5). Mean proportional contribution of zooplankton was 0.64 in Class 1 lakes and 0.25 in Class 2 lakes, whereas the contribution of littoral forage fish was 0.25 and 0.69 in Class 1 and 2 lakes, respectively (Figure 2). Mean proportional contribution of littoral invertebrates was low in both lake classes (Figure 2).

Results from the mixing model were generally consistent with patterns identified in the RI values of the 18 categories of prey. Fish were identified as a

Table 4 Mean catch-per-unit-effort ± SE (fish net^{-1} 100 hr^{-1}) for the large-bodied fish species (excluding Burbot) present in the six study lakes. 'Class 1' lakes support Lake Trout and only one other large-bodied fish (i.e., Burbot), whereas 'Class 2' lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco). Absence from a lake is indicated by dashed lines.

	Class 1			Class 2		
Species	M3	E14	E17	W1	R34	R2
Lake Trout	7.4 ± 3.1	10.1 ± 5.0	12.5 ± 3.0	15.0 ± 3.7	3.7 ± 1.5	12.9 ± 1.4
Round Whitefish	---	---	---	7.7 ± 2.6	10.1 ± 2.9	18.4 ± 6.9
Longnose Sucker	---	---	---	---	22.9 ± 6.7	23.8 ± 5.7
Cisco	---	---	---	---	---	19.6 ± 16.6

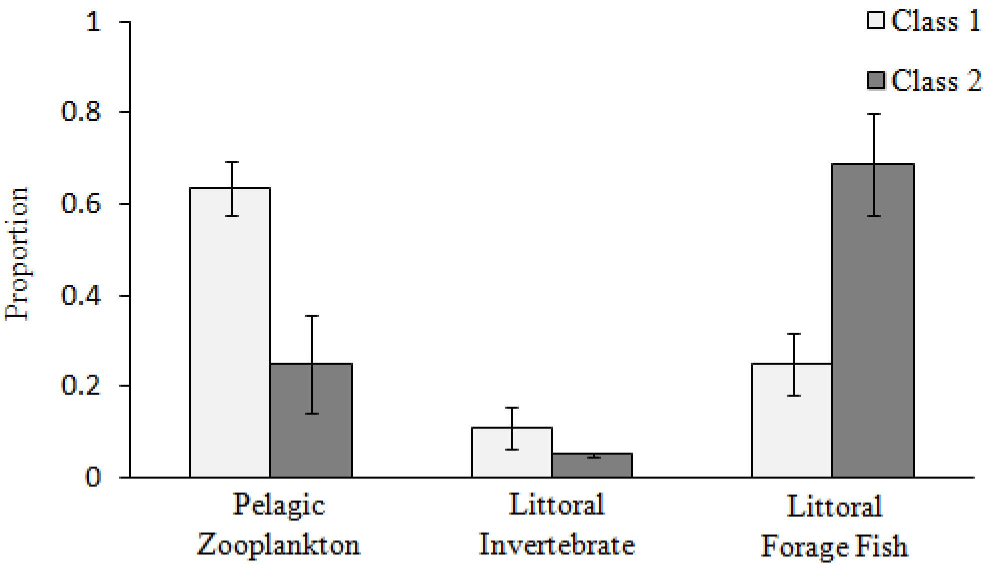


Figure 2 Mean (± SE) median contributions of three food sources to Lake Trout in Class 1 and Class 2 lakes estimated using the MixSIR model. 'Class 1' lakes support Lake Trout and only one other large-bodied fish (i.e., Burbot), whereas 'Class 2' lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco). N = 3 populations for both lake classes.

much more important diet category in Class 2 than in Class 1 lakes, with mean RI values of 20.4% and 5.2%, respectively (Figure 3). The majority of fish were classified as remains, but when identification was possible, Slimy Sculpin and Ninespine Stickleback (both littoral species) were the most common fishes in Lake Trout diet; other fishes included Lake Chub, Cisco, and juveniles of Burbot and Longnose Sucker (Table 5). Littoral invertebrate prey categories – in particular, Corixidae, Trichopteran larvae, Dytiscidae, and Mollusca – had higher mean RI values for the Class 1 Lake Trout populations (Figure 3), which is also consistent with results from the mixing model. Overall, pelagic zooplankton (summed mean RIs of Cladocera and Copepoda) were of similar importance to Lake Trout populations in Class 1 (29.4%) and Class 2 lakes (27.4%). The mean RI values of all other prey categories were minimally different between Lake Trout populations in the two lake classes.

Qualitative examination of $\delta^{13}C_{adj}$ vs. $\delta^{15}N$ bi-plots for Class 2 lakes suggested that Lake Trout used some of the same resources as the other large-bodied fishes (Appendix 3). Round Whitefish and Cisco were deficient in ^{13}C relative to Lake Trout, indicating that diet overlap between these species and trout would likely have been strongest for pelagic resources. Conversely, Longnose Sucker displayed $\delta^{13}C_{adj}$ signatures that were similar to those of Lake Trout; any overlap between the diets of these species is expected to have primarily resulted from consumption of littoral prey. Burbot, the other large-bodied fish present in all lakes, displayed a trophic position similar to Lake Trout in lakes where large individuals of this species were sampled. Stomach content samples of Burbot (n

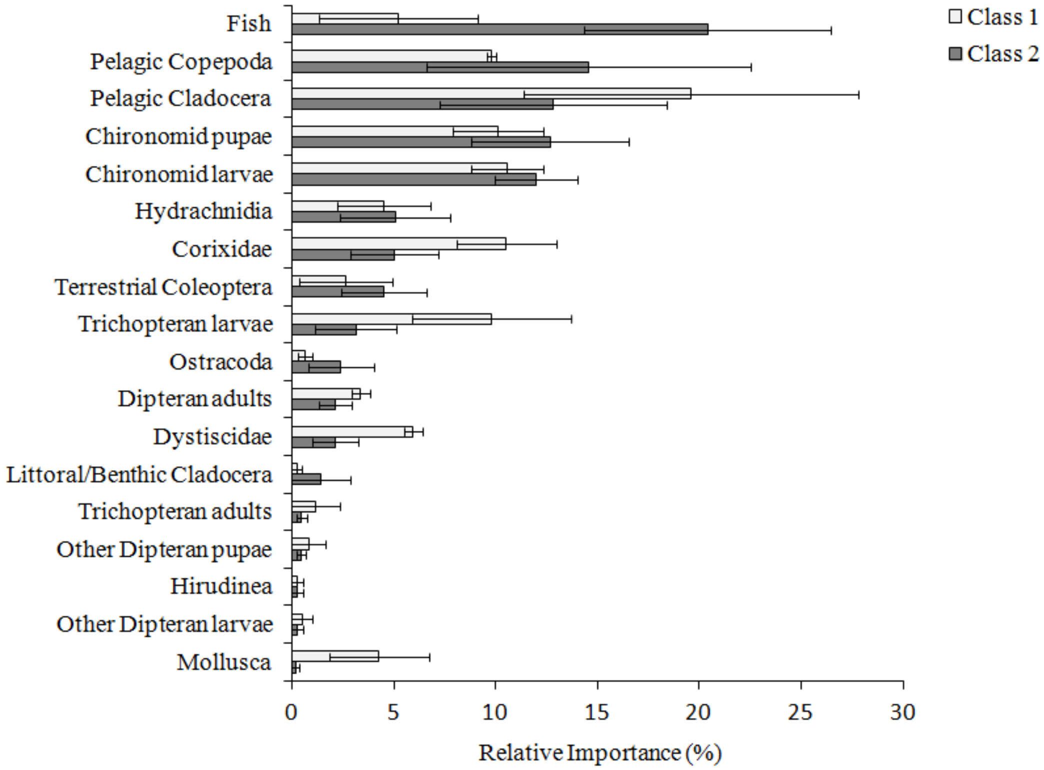


Figure 3 Mean (± SE) Relative Importance (%) of 18 prey categories to the diet of Lake Trout in Class 1 and Class 2 lakes. Relative Importance is the average of three diet measures calculated for a prey category, including % frequency of occurrence, % total numbers, and % total mass. 'Class 1' lakes support Lake Trout and only one other large-bodied fish (i.e., Burbot), whereas 'Class 2' lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco). N = 3 populations for both lake classes.

Table 5 Identity and number of prey fish consumed by Lake Trout in the study lakes. Prey fish included Slimy Sculpin (SLSC), Ninespine Stickleback (NNST), Lake Chub (LKCH), and Cisco (CISC). Absence from a lake is indicated by dashed lines.

	SLSC	NNST	LKCH	CISC	BURB (S)[a]	LNSC (S)[b]	Remains[c]	**Total**
Class 1								
M3	2	---	---	---	0	---	2	4
E14	0	---	---	---	0	---	2	2
E17	0	---	---	---	0	---	1	1
Class 2								
W1	1	---	---	---	0	---	6	7
R34	6	4	1	---	0	0	11	22
R2	2	6	---	2	1	2	14	27
Total	11	10	1	2	1	2	36	63

[a] Small Burbot (< 75 mm)

[b] Small (< 75 mm) Longnose Sucker

[c] Unidentified Fish

= 3) contained few prey items: corixid adults, zooplankton, and chironomid larvae were the only groups identified.

Comparison of stomach contents indicated moderate diet overlap between Lake Trout and the other large-bodied species in Class 2 lakes, as measured by Schoener's proportional similarity index (Table 6). Typically, Lake Trout had RI values similar to the other large-bodied fishes for many of the invertebrate prey, but there were enough differences to limit overlap in diet. For instance, Lake Trout consumed a greater diversity of prey than any other large-bodied species in a given lake (Figure 3; Appendix 6).

3.4 Trophic Niche Width and Trophic Diversity

Linear distance metrics calculated using stable isotope data indicated that Lake Trout populations had more divergent energy flow pathways and increased isotopic diversity in the presence of other large-bodied fishes (Appendix 1). That is, populations in Class 2 lakes had significantly greater mean CR ($t_4 = 2.743$, $P = 0.052$) and mean CD ($t_4 = 3.944$, $P = 0.017$) than Class 1 lakes; mean values for NR and TA were also greater in Class 2 lakes, but not significantly so (t-tests: $P \geq 0.10$ for both metrics) (Figure 4). In contrast, trophic redundancy (NND) and evenness of the packing of individual niches (SDNND) were similar between lake classes (t-tests: $P \geq 0.10$) (Figure 4). None of the linear distance metrics of prey communities differed significantly between Class 1 and Class 2 lakes (t-tests: $P \geq 0.10$; Figure 5).

Table 6 Dietary overlap (0 = no overlap, 0.60 = biologically significant overlap, 1.0 = complete overlap) between Lake Trout and other large-bodied fishes in Class 2 lakes (excluding Burbot). ‘Class 2’ lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco). Overlap was based on the relative importance (%) of 18 prey categories to the diet of each species, and calculated with Schoener’s proportional similarity index. Dashes indicate the absence of a species-pair combination.

	Round Whitefish	Longnose Sucker	Cisco
W1 Lake Trout	0.57	---	---
R34 Lake Trout	0.39	0.39	---
R2 Lake Trout	0.53	0.51	0.34

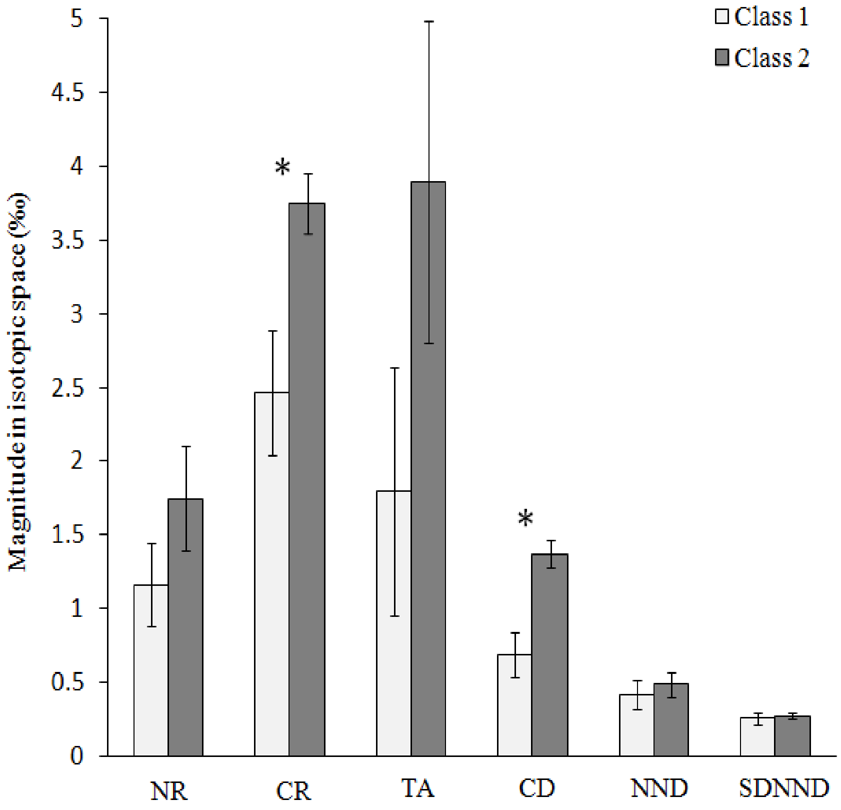


Figure 4 Mean (± SE) linear distance metrics (NR: range in $\delta^{15}N$; CR: range in $\delta^{13}C_{adj}$; TA: total area; CD: mean distance to centroid; NND: mean nearest neighbour distance; SDNND: standard deviation of nearest neighbour distance) based on stable isotope data for Class 1 and Class 2 Lake Trout populations. 'Class 1' lakes support Lake Trout and only one other large-bodied fish (i.e., Burbot), whereas 'Class 2' lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco). T-tests were used to test for differences between lake classes (*: $P < 0.1$). N = 3 populations for both lake classes.

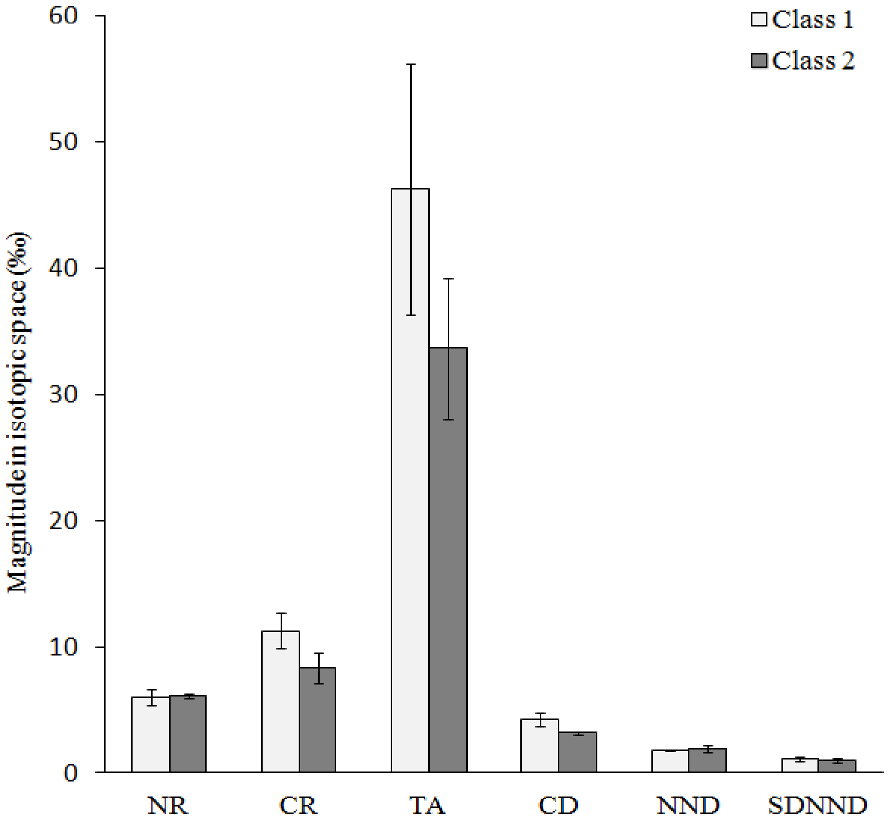


Figure 5 Mean (± SE) linear distance metrics (NR: range in $\delta^{15}N$; CR: range in $\delta^{13}C_{adj}$; TA: total area; CD: mean distance to centroid; NND: mean nearest neighbour distance; SDNND: standard deviation of nearest neighbour distance) based on stable isotope data for Class 1 and Class 2 Lake Trout prey communities. ‘Class 1’ lakes support Lake Trout and only one other large-bodied fish (i.e., Burbot), whereas ‘Class 2’ lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco). Prey community is defined on a lake-specific basis as the items found in the stomach contents of Lake Trout. None of the metrics differed between lake classes (t-tests; $P \geq 0.1$). N = 3 populations for both lake classes.

Linear distance metrics from stomach content ordinations did not follow the pattern of their isotopic counterparts. Instead, individual Lake Trout were significantly more evenly packed in ordination space (i.e., had lower SDNND) in Class 2 than in Class 1 lakes ($t_4 = 3.420$, $P = 0.027$; Figure 6), whereas none of the other metrics differed significantly between lake classes (t-tests: $P \geq 0.10$; Figure 6). The NMS ordinations had a mean minimum stress of 11.68 and mean cumulative r^2 of 92% for the 30 bootstraps conducted to standardize sample sizes across lakes. Traditional measures of population niche width (Levins' *D*) and mean individual specialization (*V*) for interpreting stomach contents data also revealed no differences in Lake Trout trophic ecology between Class 1 and Class 2 lakes (t-tests: $P \geq 0.10$; Figure 7).

3.5 Condition and Growth

The mean relative weight and condition of Lake Trout populations were both significantly higher in Class 1 than Class 2 lakes (Appendix 7; (W_r): $t_4 = 2.273$, $P = 0.085$, Figure 8a; (Fulton's *K*): $t_4 = 3.385$, $P = 0.028$, Figure 8b). However, the von Bertalanffy growth functions applied to the pooled length-at-age data of Lake Trout revealed similar growth patterns in Class 1 and Class 2 lakes (Figure 9). Mean asymptotic length (L_∞) of Lake Trout was slightly higher in Class 1 (501 mm) than Class 2 lakes (476 mm); the Brody growth coefficient (*K*) (i.e., the rate at which populations approach L_∞) was similar between Class 1 (0.139) and Class 2 lakes (0.220). Due to low sample sizes and the resultant pooling of data, growth could not be statistically compared between lake classes.

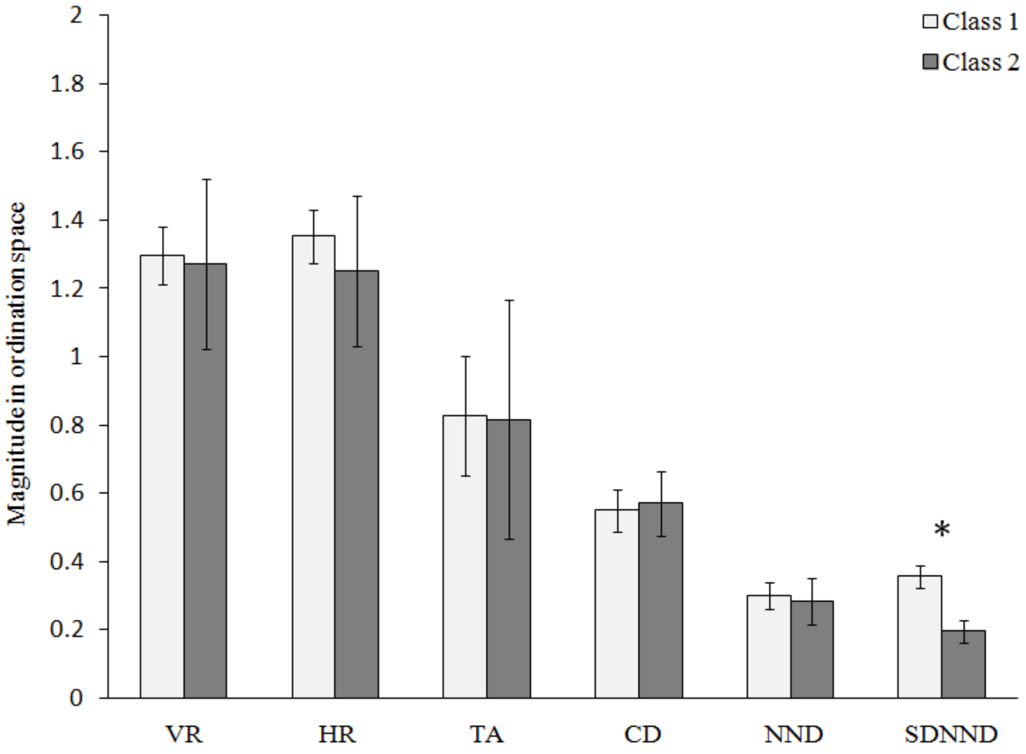


Figure 6 Mean (± SE) linear distance metrics (VR: vertical range; HR: horizontal range; TA: total area; CD: mean distance to centroid; NND: mean nearest neighbour distance; SDNND: standard deviation of nearest neighbour distance) based on ordination scores for stomach contents data for Class 1 and Class 2 Lake Trout populations. ‘Class 1’ lakes support Lake Trout and only one other large-bodied fish (i.e., Burbot), whereas ‘Class 2’ lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco). T-tests were used to test for differences between lake classes (*: $P < 0.1$). N = 3 populations for both lake classes.

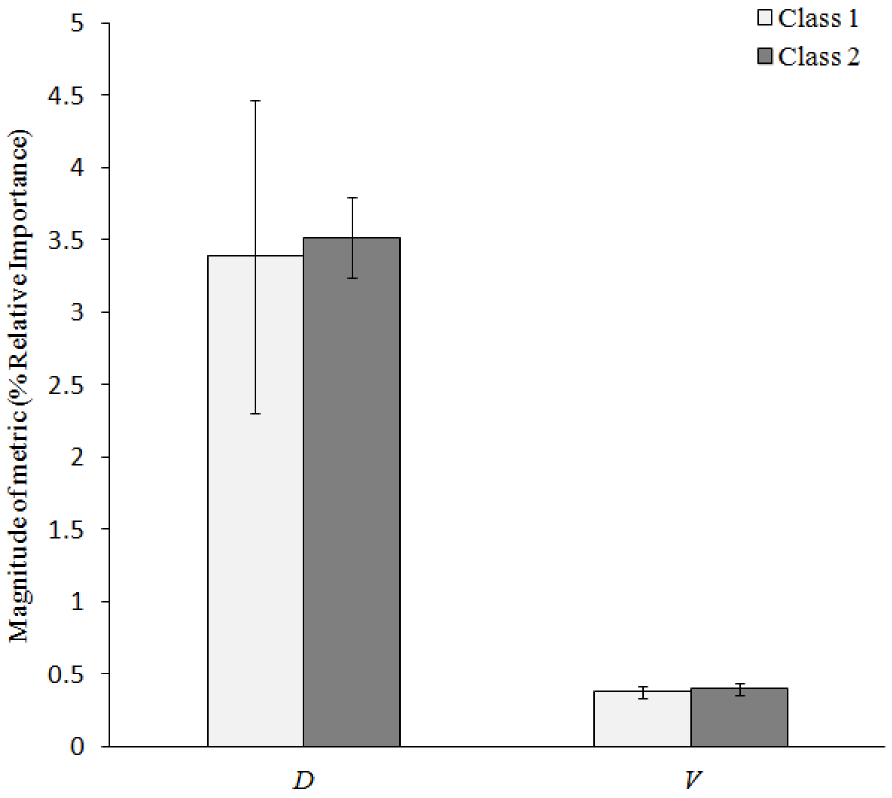


Figure 7 Mean (± SE) measures of Levin's niche width (*D*) and individual specialization (*V*) for Class 1 and Class 2 Lake Trout populations based on stomach contents data. 'Class 1' lakes support Lake Trout and only one other large-bodied fish (i.e., Burbot), whereas 'Class 2' lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco). Neither metric differed between lake classes (t-tests; $P \geq 0.1$). N = 3 populations for both lake classes.

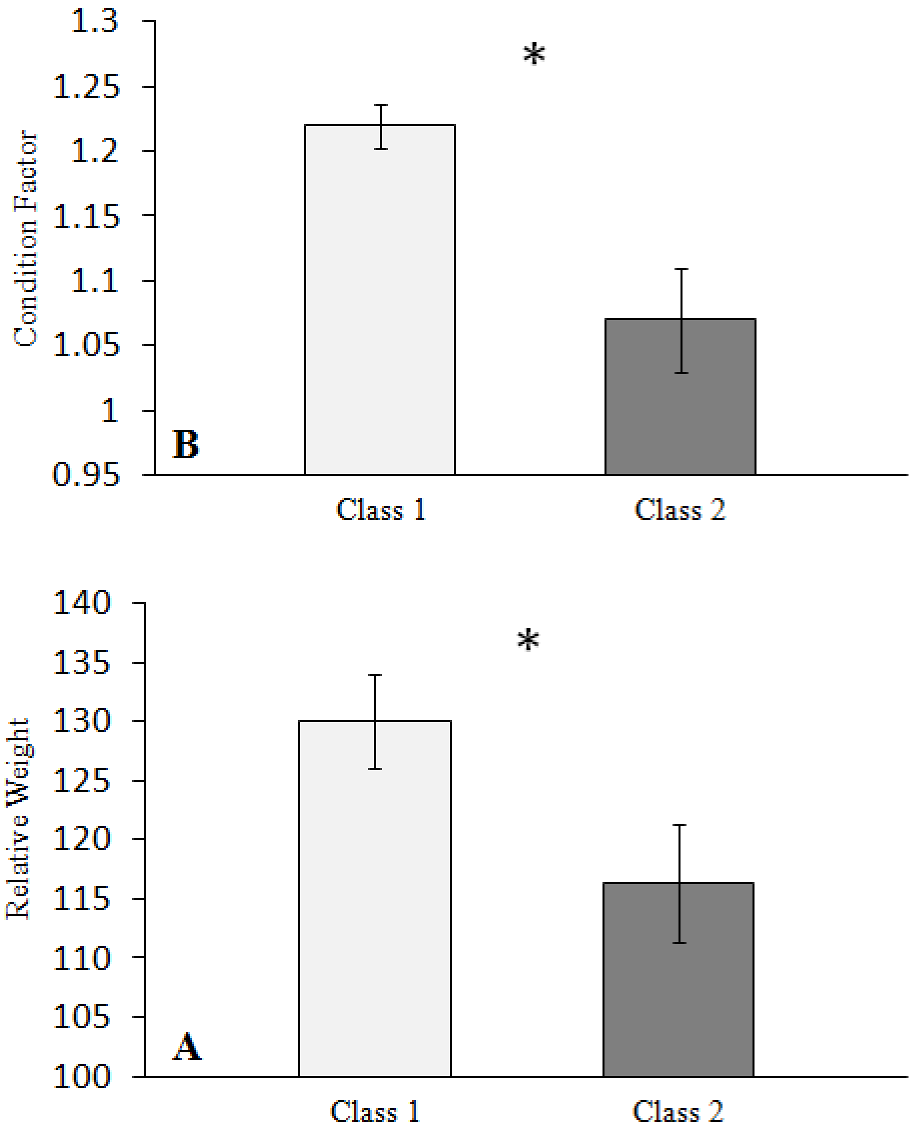


Figure 8 Mean (± SE) relative weight (**A**) and condition factor (**B**) of Lake Trout populations in Class 1 and Class 2 lakes. ‘Class 1’ lakes support Lake Trout and only one other large-bodied fish (i.e., Burbot), whereas ‘Class 2’ lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco). A t-test was used to test for a difference between lake classes (*: $P < 0.1$). N = 3 populations for both lake classes.

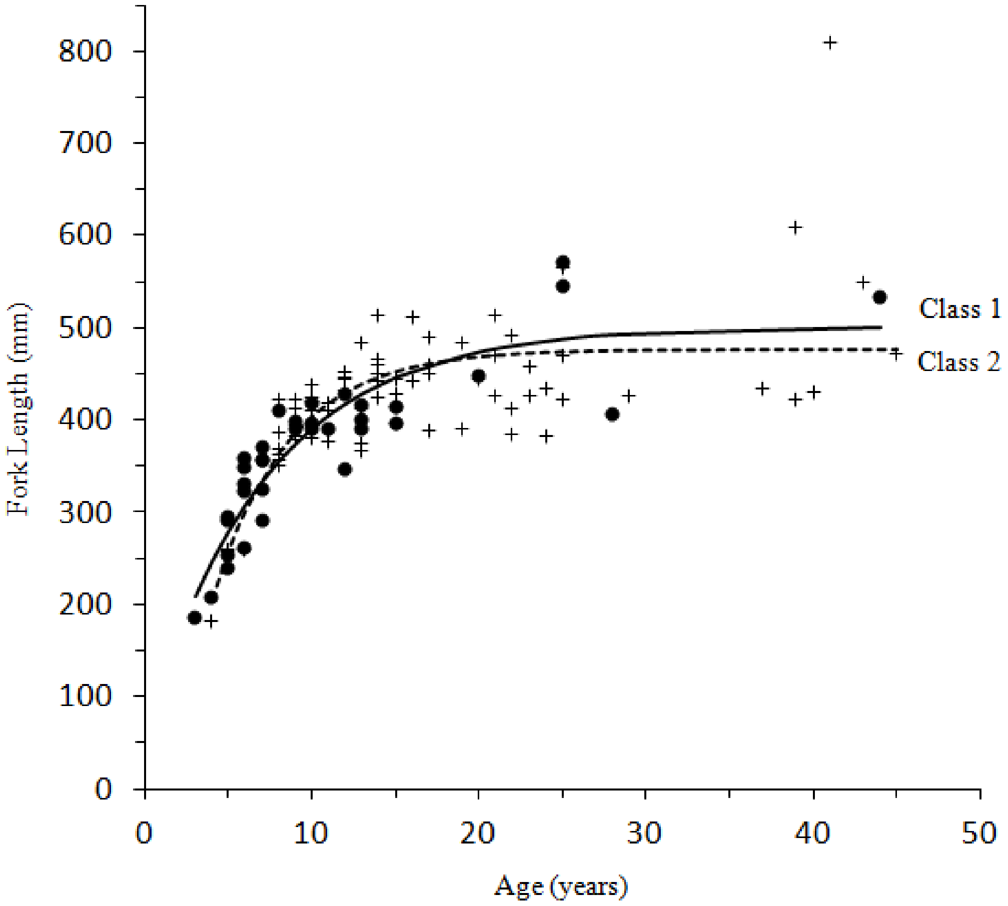


Figure 9 von Bertalanffy growth functions fitted to length-at-age data of individual Lake Trout pooled by Class 1 (*circles, solid lines*) and Class 2 (*crosses, dashed line*) lakes. 'Class 1' lakes support Lake Trout and only one other large-bodied fish (i.e., Burbot), whereas 'Class 2' lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco). von Bertalanffy growth parameters are provided in the text.

4.0 Discussion

4.1 Diet Overlap and Niche Shifts

Lake Trout can interact as both competitor and predator with other fishes. Both SCA and SIA revealed Lake Trout had moderate diet overlap with Round Whitefish, Longnose Sucker, and Cisco in Class 2 lakes, indicating that inter-specific competition for resources was possible. Perhaps with the exception of Cisco in R2, both SCA and SIA suggested that Lake Trout did not consume substantial amounts of other large-bodied fish species. Indeed, most of the Round Whitefish and Longnose Sucker captured in experimental gillnets were larger than what Lake Trout are capable of consuming (up to half of their body size (Behnke 2002); M. Hulsman, unpublished data), and condition and growth of Lake Trout should have been higher in Class 2 than Class 1 lakes if they had consumed pelagic fish from the former lakes in any great proportion (Martin 1966, Pazzia et al. 2002). Although Lake Trout may consume YOY and small juveniles of these species, it seems likely that adult Round Whitefish and Longnose Sucker function more as resource competitors of Lake Trout than as prey.

Mixing model results and relative importance values indicate that Lake Trout consumed more zooplankton and fewer littoral forage fish in the absence of other large-bodied fishes. In other northern lakes, fish predation has been found to significantly lower zooplankton biomass (e.g., Johnson et al. 2010). Although zooplankton density was not measured in my study lakes, it is reasonable to assume that competition for zooplankton would be greater in Class 2 than Class 1 lakes due to the presence of Round Whitefish and Cisco, especially since these species had high relative abundances. It is well established that the ciscoes are zooplanktivorous (Scott and Crossman 1973) and, although Round Whitefish is more commonly considered a benthivore (Scott and Crossman 1973, O'Brien 1979, Merrick 1992), some populations prey heavily on zooplankton (Rawson 1951, Martin 2001, Steinhart et al. 2007). Indeed, the high relative importance values for copepods and cladocerans, and the position of Round Whitefish in isotopic space, indicate that it is likely a significant predator of zooplankton in Class 2 lakes. Accordingly, the apparent shift in Lake Trout diet from littoral fishes in Class 2 lakes to zooplankton in Class 1 lakes is consistent with a release from competition with Round Whitefish and Cisco and, to a lesser extent, Longnose Sucker for zooplankton. Inter-specific competition for littoral resources would likely be lower than competition for zooplankton, since there was no evidence that Round Whitefish, Longnose Sucker, and Cisco consumed fish in my study. In addition, although the other large-bodied fishes did forage on some of the same littoral invertebrates as Lake Trout, the diversity of invertebrate prey present in this zone could facilitate greater partitioning and thus reduce competition; for instance, RI values for Corixidae and Dystiscidae indicated they were relatively important to Lake Trout, but were either not consumed or of low importance in the diets of the other large-bodied fishes. Although I suggest that Lake Trout diet is influenced by competitors, the possibility that shifts in Lake Trout diet were driven by different availabilities and abundances of ambient resources cannot be disregarded since resource distributions are unknown for either lake class.

In a similar study that investigated the effect of fish competitors on Lake Trout trophic patterns in temperate lakes that lacked pelagic forage fish, Vander Zanden et al. (1999) found that Lake Trout shifted its diet from littoral forage fishes to pelagic zooplankton in the presence of competitors. This shift to pelagic prey was due to the foraging nature of the competitors, namely Smallmouth Bass (*Micropterus dolomieu*) and Rock Bass (*Ambloplites rupestris*), which are known to consume large quantities of littoral prey. In contrast, the competitors in my study were either primarily littoral (Longnose Sucker) or primarily pelagic (Round Whitefish and Cisco) foragers. I suggest that competition was stronger for pelagic than littoral resources because of the lower diversity of prey in the former, which is why Lake Trout in Class 2 lakes primarily consumed littoral resources.

Lake Trout's reliance on littoral carbon resources in Class 2 lakes is consistent with the findings of Chételat et al. (2010), who found that arctic fish typically relied on energy flow driven by littoral-benthic algae. Similarly, the carbon composition of Lake Trout in two small lakes of the Toolik Lake region of Alaska was predominately benthic, derived from a diet that likely contained large proportions of Slimy Sculpin and snails (Sierszen et al. 2003). Yet, in three more southern arctic lakes, phytoplankton was a more important energy source for Lake Whitefish, Arctic Char, and Lake Trout (Hecky and Hesslein 1995, Kidd et al. 1998, Power et al. 2002), which is consistent with the carbon sources supporting Lake Trout in the Class 1 lakes from my study. Interestingly, the average pelagic Chl-*a* concentration of lakes in my study (2.13 µg/l) was more than 4-fold higher than those reported in Sierszen et al. (2003), which could explain the higher reliance of Class 1 Lake Trout on pelagic zooplankton in the absence of increased competition.

4.2 Trophic Niche Width and Trophic Diversity

Stomach contents analysis alone did not provide strong evidence for differences between fish communities in Lake Trout trophic characteristics, including population niche width (Levins' *D*) and trophic diversity (degree of individual specialization). However, linear distance metrics performed on stomach contents data did show that individual Lake Trout were significantly less evenly packed in ordination space in Class 1 than in Class 2 lakes. This could indicate that Class 1 populations contained more individual trout outliers in ordination space (outlier analysis identified one individual – it was not removed from the dataset), which may have inflated the values of the other metrics calculated for this lake class (Newsome et al. 2012). The general lack of difference between lake classes, combined with outliers in Class 1 populations, would suggest generally (non-outlier driven) greater niche width and diet variation in Class 2 populations. Removal of outliers, however, would have further constrained sample size for the analysis.

Indeed, linear distance metrics calculated using stable isotope data indicated that Lake Trout populations in Class 2 lakes had significantly broader range in $\delta^{13}C_{adj}$ signatures and significantly greater isotopic diversity than populations in Class 1 lakes. The former was due to greater inter-individual divergence in resource use, via individual trout consuming different resources or different proportions of the same resources. The greater isotopic diversity was due to a greater proportion of individual trout positioned near the periphery of their respective convex hulls in Class 2 as compared to Class 1 lakes, and perhaps because populations in Class 2 lakes had (non-significantly) larger isotopic population niche widths. Populations in Class 2 lakes also had non-significantly broader ranges in $\delta^{15}N$ than Class 1 populations. Thus, differences in isotopic diversity were due more to expansion along the $\delta^{13}C_{adj}$ niche dimension than the $\delta^{15}N$ dimension in Class 2 Lake Trout populations, indicating that the difference in isotopic diversity was mainly driven by Class 2 populations consuming prey that relied on basal resources with more varied $\delta^{13}C$ values. In contrast, trout in both lake classes had similar degrees of trophic redundancy. These seemingly contrasting results (i.e., different isotopic diversity but similar levels of isotopic redundancy) were perhaps due to different groups of individuals within Class 2 populations having different feeding patterns (i.e., minor clumping of individuals in isotopic space); however, distinct resource polymorphisms were not observed (M. Hulsman, personal observation) and would be unlikely in lakes of these small sizes (Eshenroder 2008). Class 1 and 2 populations also displayed little difference in how evenly their constituent individuals were packed in isotopic space. This suggests that the significant differences in isotopic niche measures were driven by true diet variation, and not by outliers.

Evidence for dietary differences between Lake Trout populations in Class 1 and Class 2 lakes was also strengthened by the fact that their prey communities shared similar isotopic structure; if anything, Class 1 lakes tended to support more isotopically diverse prey communities. Higher values of isotopic niche metrics in Class 2 lakes were therefore not attributable to isotopically more diverse prey communities.

The observed patterns in population niche width and diet variation are inconsistent with the niche variation hypothesis (NVH; Van Valen 1965). Because Class 1 Lake Trout populations should have experienced reduced inter-specific competition, the NVH would predict these populations to exhibit a wider niche width and greater inter-individual variation in resource use than Class 2 populations. Instead, Class 1 populations had significantly less inter-individual variation and smaller trophic niche widths in isotopic space than Class 2 populations.

Alternatives to the NVH regarding effects of competitive ecological release on population niche width include the ‘parallel release hypothesis’ (Bolnick et al. 2010), which predicts that population niche width increases when all individuals in a population shift to use a greater number of the available resources without increasing inter-individual variation. Bolnick et al. (2010) found that the form of ecological release experienced by Threespine Stickleback was competitor dependent and could involve either niche expansion, consistent with the NVH, or a qualitative trend towards decreased total niche width, as increased individual niche width was offset by decreased inter-individual variation. This ‘individual release hypothesis’ (Bolnick et al. 2010) could describe the diet patterns observed in the Lake Trout populations of Class 1 lakes.

However, the integrative nature of stable isotopes makes it impossible to determine definitively if Lake Trout in Class 1 lakes tended to specialize on similar subsets of resources, or to generalize on many resources in similar proportions (as predicted by the individual release hypothesis). Interpreting the stable isotope-based linear distance metrics in relation to the mixing model results, however, reveals additional information about Lake Trout trophic ecology in the different lake classes.

The lower inter-individual variation observed in Class 1 populations is likely because these trout derived a greater proportion of their carbon from pelagic than littoral sources. For example, cladocerans and copepods – which were the main resources available in the pelagic zone, and important components in the diets of Class 1 populations – displayed a very narrow range in their $\delta^{13}C_{adj}$ signatures relative to the range of the more diverse littoral resources. In contrast, populations that consume a higher proportion of littoral resources, such as those in Class 2 lakes, would likely show a wider range in $\delta^{13}C_{adj}$ and increased degree of inter-individual variation. I suggest that the differences between Lake Trout populations are because individuals in Class 1 lakes forage on a similar subset of resources (primarily zooplankton) rather than on a larger range of the available resources in similar proportions.

4.3 Condition and Growth

Lake Trout populations in Class 1 lakes were in significantly better condition (W_r and Fulton's K) than Class 2 populations, although their von

Bertalanffy growth parameters were similar. The combined evidence of SCA and SIA indicated that populations in Class 2 lakes consumed more forage fish than their Class 1 counterparts, so it was initially surprising that the latter were in better condition, and had a similar growth trajectory. Energy expenditures associated with foraging should be higher for fish that forage on smaller prey, because of the increased energy demands associated with locating and consuming more prey (Kerr 1971a,b; Sherwood et al. 2002a,b). Empirical comparisons have found that such energy costs result in growth differences, with non-piscivorous populations growing at slower rates and reaching smaller sizes than piscivorous ones (Martin 1966, Pazzia et al. 2002).

For Lake Trout in Class 1 lakes to be in better condition than those in Class 2 lakes, prey must be plentiful and foraging costs must be lower for a diet that contains few fish and many invertebrates than for a diet of many fish and few invertebrates. With the exception of Cisco, all of the fish species identified in the stomach contents of Lake Trout frequently inhabit the littoral zone in northern lakes (Scott and Crossman 1973, Hanson et al. 1992). Even in the sub-arctic, littoral zones can warm considerably in the summer. Five of my study lakes (temperature data are unavailable for the sixth) warmed to an average temperature of 15.1 ± 0.1 °C over July and August in 2010; this temperature is above the 8 °C to 12 °C range generally considered physiologically optimum for Lake Trout growth (Christie and Regier 1988). As a result, forays into the littoral zone to search for prey fish would be energetically costly (Morbey et al. 2006).

To offset these higher energetic costs, littoral foraging Lake Trout would have to increase their energy intake. Individual trout in Class 1 (primarily zooplankton foraging) populations had 2.4-fold more prey items and similar prey biomass in their stomachs to their Class 2 (primarily littoral foraging) counterparts (M. Hulsman, unpublished data). Similarly, Pazzia et al. (2002) found that consumption rates of non-piscivorous Lake Trout (diet of 11% littoral fishes) were 1.9 - 3.3-fold higher than in piscivorous populations (diet of nearly 100% fish, mostly Cisco), although after consumption rates were corrected for prey caloric content, energy intake was approximately equal. In the study lakes, it is possible that foraging on the large energy resource available in lower trophic levels could offset or even exceed the advantage of exploiting fish that are usually small, rare (McDonald et al. 1982), and seek refuge in the littoral zone (Hanson et al. 1992), because search time may be lower for the former. Perhaps not coincidentally, the Lake Trout population (R2) that consumed the most fish (based on MixSIR estimates) was also lowest in condition.

A related explanation for the lower condition of Lake Trout in Class 2 lakes is based on the relationship between productive capacity and fish density. Previous studies have indicated that salmonid production, growth, and condition are constrained by availability of food resources (e.g., Bowlby and Roff 1986, Gibson and Haedrich 1988, Deegan et al. 1997). In my study, although both lake classes had similar levels of pelagic Chl-*a*, Class 2 lakes had higher relative abundances of large-bodied fishes (based on CPUE). While Class 2 lakes are larger, the difference in size is proportionally less than the difference in relative abundance, indicating that Class 2 lakes contain more large-bodied fish on a per area basis. As a result, per-capita prey availability could be lower in Class 2 than Class 1 lakes due to higher total densities of fish. Lower per-capita prey availability could increase the amount of energy individual trout spend searching to obtain an equivalent number of prey items, which would increase the cost of foraging in these lakes.

5.0 Conclusion

My study presents comparative evidence that Lake Trout populations in different competitive but otherwise similar small, sub-arctic lake environments use resources differently. By shifting from littoral to pelagic prey, trout populations displayed narrower isotopic niche widths and reduced inter-individual variation in diet when released from competition with other-large-bodied fishes, a pattern inconsistent with the NVH. Because these changes in trophic niche traits appear to result from reduced reliance on littoral resources and increased consumption of pelagic zooplankton, I suggest that individual trout in Class 1 lakes forage on more similar subsets of resources. In the context of Roughgarden's (1972) framework for total niche width, this pattern of foraging would suggest low within-individual and low between-individual components, resulting in low total niche width. Given the available information, it is impossible to know why Lake Trout populations deviated from other animal taxa in their response to ecological release, but perhaps the answer lies in features of the northern environment. For instance, in unproductive lakes, the small population size of a top predator like Lake Trout may be inadequate to drive strong intraspecific competition for resources, such as zooplankton; as a result, the diversifying effect of intraspecific competition could be diminished.

Interestingly, although the diet of trout in Class 1 lakes contained a greater proportion of zooplankton, these fish appeared to grow at similar rates and were in better condition than their Class 2 counterparts, which consumed a greater proportion of littoral resources, including prey fish. While it is unknown if the better condition of Class 1 Lake Trout results in increased reproductive output and survival, others have shown that body mass is positively related to gamete production (Hayward and Gillooly 2011) and is of critical importance for overwinter survival, especially in arctic populations that may be near their physiological limits (McDonald et al. 1996).

These findings are directly relevant to natural resource management as fish colonization projects have recently been initiated in the Northwest Territories under Canada's *Fisheries Act*. The objective of these projects is to increase the productive capacity of small, depauperate lakes by enhancing their connectivity to a large waterbody, which is the source of potential colonists (Golder 2001). The richness and relatively high abundances of other large-bodied species in Class 2 lakes suggest that this objective is achievable. However, the results of my study suggest that colonization by large-bodied species may result in competition with native Lake Trout for the available resources in these oligotrophic lakes. In particular, if the colonists are species that consume large proportions of zooplankton (e.g., Arctic Grayling, Round Whitefish, and Lake Whitefish are target species), then Lake Trout populations that currently rely on this resource may shift to more littoral prey, which could have negative consequences for their body condition, although their growth may be unaffected. Overall, before ‘ecological experiments’ such as these are conducted, careful thought should be given to the potential that there could be consequences to the native populations.

Literature Cited

Amundsen, P., R. Knudsen and H.T. Bryhni. 2010. Niche use and resource partitioning of Arctic charr, European whitefish and grayling in a subarctic lake. Hydrobiologia 650: 3-14.

Araújo, M.S., D.I. Bolnick, L.A. Martinelli, A.A. Giaretta and S.F. dos Reis. 2009. Individual-level diet variation in four species of Brazilian frogs. Journal of Animal Ecology 78: 848-856.

Araújo, M.S., D.I. Bolnick and C.A. Layman. 2011. The ecological causes of individual specialisation. Ecology Letters 14: 948-958.

Baumgartner D. and K.O. Rothhaupt. 2003. Predictive length–mass regressions for freshwater invertebrates in a pre-alpine lake littoral. International Review of Hydrobiology 88: 453-463.

Beaudoin, C.P., W.M. Tonn, E.E. Prepas and L.I. Wassenaar. 1999. Individual specialization and trophic adaptability of northern pike (*Esox luscious*): an isotope and dietary analysis. Oecologia 120: 386-396.

Benke, A.C., A.D. Huryn, L.A. Smock and J.R. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18: 308-343.

Bertolo, A. and P. Magnan. 2005. The relationship between piscivory and growth of white sucker (*Catostomus commersoni*) and yellow perch (*Perca flavescens*) in headwater lakes of the Canadian Shield. Canadian Journal of Fisheries and Aquatic Sciences 62: 2706-2715.

Biogeochemical Analytical Laboratory, Department of Biological Sciences, University of Alberta. 2007. P-006: Subsampling Water Samples in the Field, Revision 1.0.

Birtwell, I.K., S.C. Hamis and N.Y. Kahn. 2005. Commentary on the management of fish habitat in northern Canada: information requirements and policy considerations regarding diamond, oil sands and placer mining. Canadian Technical Report of Fisheries and Aquatic Sciences 2606.

Bliss, L.C. 1981. North American and Scandinavian tundras and polar deserts. In: Bliss, L.C., Heal, O.W. and Moore, J.J., editors. Tundra ecosystems: A comparative analysis. Cambridge University Press, Cambridge, MA. pp. 8-46.

Bolnick, D.I., T. Ingram, W.E. Stutz, L.K. Snowberg, O.L. Lau and J.S. Paull. 2010. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. Proceedings of the Royal Society B 277: 1789-1797.

Bolnick, D.I. and J. Paull. 2009. Morphological and dietary differences between individuals are weakly but positively correlated within a population of threespine stickleback. Evolutionary Ecology Research 11: 1217-1233.

Bolnick, D.I., R. Svanback, M.S. Araújo and L. Persson. 2007. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. Proceedings of the National Academy of Sciences 104: 10075-10079.

Bolnick, D.I., R. Svanback, J.A. Fordyce, L.H. Yang, J.M. Davis, C.D. Hulsey and M.L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. American Naturalist 161: 1-28.

Bolnick, D.I., L.H. Yang, J.A. Fordyce, J.M. Davis and R. Svänback. 2002. Measuring individual-level resource specialization. Ecology 83: 2936-2941.

Bonar, S. A., W. A. Hubert and D. W. Willis, editors. 2009. Standard methods for sampling North American freshwater fishes. American Fisheries Society, Bethesda, MD. 335 p.

Bottrell, H.H., A. Duncan, Z.M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurosawa, P. Larsson and T. Weglenska. 1976. A review of some problems in zooplankton production studies. Norwegian Journal of Zoology 24: 419-456.

Bowen, S.H. 1996. Quantitative description of the diet. In: Murphy, B.R. and D.W. Willis, editors. Fisheries Techniques, 2nd edn. American Fisheries Society, Bethesda, MD. 513-532.

Bowlby, J.N. and J.C. Roff. 1986. Trout biomass and habitat relationships in southern Ontario streams. Transactions of the American Fisheries Society 115: 503-514.

Bryan, J.E. and P.A. Larkin. 1972. Food specialization by individual trout. Journal of the Fisheries Research Board of Canada 29: 1615-1624.

Bunn, S.E., P.M. Davies and M. Winning. 2003. Sources of organic supporting the food web of an arid zone floodplain river. Freshwater Biology 48: 619-635.

Byron, E.R., P.T. Whitman and C.R. Goldman. 1983. Observations of copepod swarms in Lake Tahoe. Limnology and Oceanography 28: 378-382.

Carabel, S., E. Godinez-Dominguez, P. Verisimo, L. Fernandez and J. Freire. 2006. An assessment of sample processing methods for stable isotope analyses of marine food webs. Journal of Experimental Marine Biology and Ecology 336: 254-261.

Chen, Y., D.A. Jackson and H.H. Harvey. 1992. A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. Canadian Journal of Fisheries and Aquatic Sciences 49: 1228-1235.

Chételat, J., L. Cloutier and M. Amyot. 2010. Carbon sources for lake food webs in the Canadian High Arctic and other regions of Arctic North America. Polar Biology 33: 1111-1123.

Christie, G.C. and H.A. Regier. 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. Canadian Journal of Fisheries and Aquatic Sciences 45: 301-314.

Chu, C., C.K. Minns and N.E. Mandrak. 2003. Comparative regional assessment of factors impacting freshwater fish biodiversity in Canada. Canadian Journal of Fisheries and Aquatic Sciences 60: 624-634.

Costa, G.C., D.O. Mesquita, G.R. Colli and L.J. Vitt. 2008. Niche expansion and the niche variation hypothesis: does the degree of individual variation increase in depauperate assemblages? The American Naturalist 172: 868-877.

Cott, P.A., T.A. Johnston and J.M. Gunn. 2011. Food web position of burbot relative to lake trout, northern pike, and lake whitefish in four sub-Arctic boreal lakes. Journal of Applied Ichthyology 27: 49-56.

Darimont, C.T., P.C. Paquet and T.E. Reimchen. 2009. Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. Journal of Animal Ecology 78: 126-133.

de Mérona, B. and J. Rankin-de-Mérona. 2004. Food resource partitioning in a fish community of the central Amazon floodplain. Neotropical Icthyology 2: 75-84.

Diana, J.S. and W.C. Mackay. 1979. Timing and magnitude of energy deposition and loss on the body, liver, and gonads of northern pike (*Esox lucius*). Journal of the Fisheries Research Board of Canada 36: 481-487.

Dieterich, A., D. Baumgartner and R. Eckmann. 2004. Competition for food between Eurasian perch (*Perca fluviatilis* L.) and ruffe (*Gymnocephalus cernuus* [L.]) over different substrate types. Ecology of Freshwater Fish 13: 236-244.

Deegan, L.A., B.J. Peterson, H. Golden, C.C. McIvor and M.C. Miller. 1997. Effects of fish density and river fertilization on algal standing stocks, invertebrate communities, and fish production in an arctic river. Canadian Journal of Fisheries and Aquatic Sciences 54: 269-283.

Dennison, M. D. and A. J. Baker. 1991. Morphometric variability in continental and Atlantic island populations of chaffinches (*Fringilla coelebs*). Evolution 45: 29-39.

Dupuch, A., P. Magnan, A. Bertolo, L.M. Dill and M. Proulx. 2009. Does predation risk influence habitat use by northern redbelly dace (*Phoxinus eos*) at different spatial scales? Journal of Fish Biology 74: 1371-1382.

Eshenroder, R.L. 2008. Differentiation of deep-water lake charr *Salvelinus namaycush* in North American lakes. Environmental Biology of Fishes 83: 77–90.

Foster, J.R. 1977. Pulsed gastric lavage: an efficient method of removing the stomach contents of live fish. Progressive Fish-Culturist 39: 166-169.

Fraser, J.M. 1978. The effect of competition with Yellow perch on the survival and growth of planted Brook trout, Splake, and Rainbow trout in a small Ontario lake. Transactions of the American Fisheries Society 107: 505-517.

Garcia-Berthou, E. and R. Moreno-Amich. 2000. Food of introduced pumpkinseed sunfish: ontogenetic diet shift and seasonal variation. Journal of Fish Biology 57: 29-40.

George, E.L. and W.F. Hadley. 1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieui*) young of the year. Transactions of the American Fisheries Society 108: 253-261.

Gibson, R.J. and R.L. Haedrich, R.L. 1988. The exceptional growth of juvenile Atlantic salmon (*Salmo salar*) in the city waters of St. Johns, Newfoundland, Canada. Polskie Archiwum Hydrobiologii 35: 385-407.

Golder Associates Ltd. 2001. Conceptual design and compensation workplan for the fish habitat compensation program, Diavik Diamond Mines Inc, Lac de Gras. 24 p.

Hanson, K.L., A.E. Hershey and M.E. McDonald. 1992. A comparison of slimy sculpin (*Cottus cognatus*) populations in arctic lakes with and without piscivorous predators. Hydrobiologia 240: 189-201.

Hanson, J.M. and W.C. Leggett. 1985. Experimental and field evidence for inter- and intraspecific competition in two freshwater fishes. Canadian Journal of Fisheries and Aquatic Sciences 42: 2864-286.

Hartleb, C.F. and J.R. Moring. 1995. An improved gastric lavage device for removing stomach contents from live fish. Fisheries Research 24: 261-265.

Hayes, D.B. and W.W. Taylor. 1994. Changes in the composition of somatic and gonadal tissues of Yellow Perch following White Sucker removal. Transactions of the American Fisheries Society 123: 204-216.

Hayward, A. and J.F. Gillooly. 2011. The cost of sex: quantifying energetic investment in gamete production by males and females. PLoS One 6: e16557.

Hecky, R.E. and R.H. Hesslein. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. Journal of the North American Benthological Society 14: 631-653.

Hesslein, R.H., K.A. Hallard and P. Ramlal. 1993. Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (Corregonus nasus) in response to a change in diet traced by ^{34}S, ^{13}C, and ^{15}N. Canadian Journal of Fisheries and Aquatic Sciences 50: 2071-2076.

Hewett, S.W. and C.E. Kraft. 1993. The relationship between growth and consumption in fishes. Transactions of the American Fisheries Society 122: 814-821.

Hobson K. A. and L. I. Wassenaar. 1999. Stable isotope ecology: an introduction. Oecologia 120: 312-313.

Hódar, J.A. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. Acta Oecologica 17: 421-433.

Hodgson, J.R., X. He, D.E. Schindler and J.F. Kitchell. 1997. Diet overlap in a piscivore community. Ecology of Freshwater Fish 6: 144-149.

Hodgson, J.R., C.J. Hodgson and S.M. Brooks. 1991. Trophic interaction and competition between largemouth bass (*Micropterus salmoides*) and rainbow trout (*Onchorhyncus mykiss*) in a manipulated lake. Canadian Journal of Fisheries and Aquatic Sciences 48: 1704-1712.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 415-427.

Janjua, M.Y. and D. Gerdeaux. 2011. Evaluation of food web and fish dietary niches in oligotrophic Lake Annecy by gut content and stable isotope analysis. Lake and Reservoir Management 27: 115-127.

Jaschinski, S., T. Hansen and U. Sommer. 2008. Effects of acidification in multiple stable isotope analyses. Limnology and Oceanography: Methods 6: 12-15.

Johnson, L. 1976. Ecology of Arctic populations of Lake Trout, *Salvelinus namaycush*, Lake Whitefish, *Coregonus clupeaformis*, Arctic Char, *S. Alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories. Journal of the Fisheries Research Board of Canada 33: 2459-2488.

Johnson, C.R., C. Luecke, S.C. Whalen and M.E. Evans. 2010. Direct and indirect effects of fish on pelagic nitrogen and phosphorus availability in oligotrophic Arctic Alaskan lakes. Canadian Journal of Fisheries and Aquatic Sciences 67: 1635-1648.

Jones, N.E., W.M. Tonn, G.J. Scrimgeour and C. Katopodis. 2003. Ecological characteristics of streams in the Barrenlands near Lac de Gras, N.W.T., Canada. Arctic 56: 249-261.

Kelso, J.R.M. 1973. Seasonal energy changes in walleye and their diet in West Blue Lake, Manitoba. Transactions of the American Fisheries Society 102: 363-368.

Kerr, S.R. 1971a. Prediction of fish growth efficiency in nature. Journal of the Fisheries Research Board of Canada 28: 809-814.

Kerr, S.R. 1971b. A simulation model of lake trout growth. Journal of the Fisheries Research Board of Canada 28: 815-819.

Kidd, K.A., R.H. Hesslein, B.J. Ross, K. Koczanski, G.R. Stephens and D.C.G. Muir. 1998. Bioaccumulation of organochlorines through a remote freshwater food web in the Canadian Arctic. Environmental Pollution 102: 91-103.

Layman, C.A., D.A. Arrington, C.G. Montana and D.M. Post. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure. Ecology 88: 42-48.

Leeper, D.A. and B.E. Taylor. 1998. Abundance, biomass and production of aquatic invertebrates in Rainbow Bay, a temporary wetland in South Carolina, USA. Archiv für Hydrobiologie 143: 335-362.

Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton, NJ. 132 p.

Light, R.W., P.H. Adler and D.E. Arnold. 1983. Evaluation of gastric lavage for stomach analyses. North American Journal of Fisheries Management 3: 81-85.

Magnan, P. and G.J. FitzGerald. 1982. Resource partitioning between brook trout (*Salvelinus fontinalis* Mitchill) and creek chub (*Semotilus atromaculatus* Mitchill) in selected oligotrophic lakes of southern Quebec. Canadian Journal of Zoology 60: 1612-1617.

Malmquist, M.G. 1985. Character displacement and biogeography of the pygmy shrew in northern Europe. Ecology 66: 372-377.

Marchetti, M.P. 1999. An experimental study of competition between the native Sacramento perch (*Archoplites interruptus*) and introduced bluegill (*Lepomis macrochirus*). Biological Invasions 1: 55-65.

Martin, K.A. 2001. A limnological study of selected lakes in the Lac de Gras area, Northwest Territories with special reference to fish contaminants. Canadian Technical Manuscript Report of Fisheries and Aquatic Sciences 2385. 78 p.

Martin, N.V. 1966. The significance of food habitats in the biology, exploitation, and management of Algonquin Park, Ontario, lake trout. Transactions of the American Fisheries Society 115: 515-521.

Martin, N.V. 1970. Long-term effects of diet on the biology of the lake trout and the fishery in Lake Opeongo, Ontario. Journal of the Fisheries Research Board of Canada 27: 125-146.

Martin, N.V. and C.H. Oliver. 1980. The lake charr, *Salvelinus namaycush*. In: Balon, E.K., Editor. Charrs, salmonid fishes of the genus *Salvelinus*. Dr. W. Junk Publishers, The Hague. pp. 205-277.

Matthews, B. and A. Mazumder. 2004. A critical evaluation of intra-population variation of δ^{13}C and isotopic evidence of individual specialization. Oecologia 140: 361-371.

McAndrew, B.J., 1981. Muscle biopsy technique for fish stock management. Veterinary Record 108: 516.

McCune, B. and M.J. Mefford. 2011. PC-ORD. Multivariate analysis of ecological data. Version 6. MjM Software, Gleneden Beach, Oregon, USA.

McCutchan, J.H., W.M. Lewis, C. Kendall and C.C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102: 378-390.

McDonald, M.E., B.E. Cuker and S.C. Mozley. 1982. Distribution, production, and age structure of slimy sculpin in an Arctic lake. Environmental Biology of Fishes 7: 171-176.

McDonald, M.E., A.E. Hershey, and M.C. Miller. 1996. Global warming impacts on lake trout in arctic lakes. Limnology and Oceanography 41: 1102-1108.

McHugh, P. and P. Budy. 2006. Experimental effects of non-native brown trout (*Salmo trutta*) on the individual- and population-level performance of native Bonneville cutthroat trout (*Oncorhynchus clarkia utah*). Transactions of the American Fisheries Society 135: 1441-1455.

Meiri, S., T. Dayan and D. Simberloff. 2005. Variability and sexual size dimorphism in carnivores: testing the niche variation hypothesis. Ecology 86: 1432-1440.

Merrick, G.W., A.E. Hershey and M.E. McDonald. 1992. Salmonid diet and the size, distribution, and density of benthic invertebrates in an arctic lake. Hydrobiologia 240: 225-233.

Minagawa, M. And E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. Geochimica et Cosmochimica Acta 48: 1135-1140.

Mittelbach, G.G. and L. Persson. 1998. The ontogeny of piscivory and its ecological consequences. Canadian Journal of Fisheries and Aquatic Sciences 55: 1454-1465.

Moore, J.W. and B.X. Semmens. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecology Letters 11: 470-480.

Morbey, Y.E., P. Addison, B.J. Shuter and K. Vascotto. 2006. Within-population heterogeneity of habitat use by lake trout *Salvelinus namaycush*. Journal of Fish Biology 69: 1675-1696.

Newsome, S.D., J.D. Yeakel, P.V. Wheatley and M.T. Tinker. 2012. Tools for quantifying isotopic niche space and dietary variation at the individual and population level. Journal of Mammalogy 93: 329-341.

O’Brien, W.J., C. Buchanan and J.F. Haney. 1979. Arctic zooplankton community structure: exceptions to some general rules. Arctic 32: 237-247.

Pardo, R., I. Vila and J.J. Capella. 2009. Competitive interaction between introduced rainbow trout and native silverside in a Chilean Stream. Environmental Biology of Fishes 86: 353-359.

Parnell, A., R. Inger, S. Bearhop and A.L. Jackson. 2008. SIAR: Stable isotope analysis in R.

Parnell, A.C., R. Inger, S. Bearhop and A.L. Jackson. 2010. Source partitioning using stable isotopes: coping with too much variation. PLoS ONE 5 e9672.

Pazzia, I., M. Trudel, M. Ridgway and J.B. Rasmussen. 2002. Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 59: 1593-1605.

Persson, G., and Ekbohm, G. 1980. Estimation of dry weight in zooplankton populations: methods applied to crustacean populations from lakes in the Kuokkel Area, Northern Sweden. Archiv für Hydrobiologie 89: 225-246.

Phillips, D.L. and J.W. Gregg. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136: 261-269.

Piccolo, J.J., W.A. Hubert and R.A. Whaley. 1993. Standard weight equation for Lake Trout. North American Journal of Fisheries Management 13: 401-404.

Pienitz, R., J.P. Smol and D.R.S. Lean. 1997. Physical and chemical limnology of 59 lakes located between the southern Yukon and the Tuktoyaktuk Peninsula, Northwest Territories (Canada). Canadian Journal of Fisheries and Aquatic Sciences 54: 330-346.

Pinnegar, J.K. and N.V.C. Polunin. 1999. Differential fractionation of $\delta^{13}C$ and $\delta^{15}N$ among fish tissues: implications for the study of trophic interactions. Functional Ecology 13: 225-231.

Poepperl, R. 1998. Biomass determination of aquatic invertebrates in the Northern German lowland using the relationship between body length and dry mass. Faunistisch-Ökologische Mitteilungen 7**:** 379-386.

Post, D.M., C.A. Layman, D.A. Arrington, G. Takimoto, J. Quattrochi and C.G. Montana. 2007. Getting to the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152: 179-189.

Power, M., G.M. Klein, K.R.R.A. Guiger and M.K.H. Kwan. 2002. Mercury accumulation in the fish community of a sub-Arctic lake in relation to trophic position and carbon sources. Journal of Applied Ecology 39: 819-830.

Quevedo, M., R. Svanbäck and P. Eklöv. 2009. Intrapopulation niche partitioning in a generalist predator limits food web connectivity. Ecology 90: 2263-2274.

R Development Core Team. 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rawson, D.S. 1951. Studies of the fish of Great Slave Lake. Journal of the Fisheries Research Board of Canada 8: 207-240.

Riber, H.H. and R.G. Wetzel. 1987. Boundary-layer and internal diffusion effects on phosphorus fluxes in lake periphyton. Limnology and Oceanography 32: 1181-1194.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191. Fisheries Research Board of Canada, Ottawa, ON. 382 p.

Rosen, R.A. 1981. Length-dry weight relationships of some freshwater zooplankton. Journal of Freshwater Ecology 1: 225-229.

Ross, S.T. 1986. Resource partitioning in fish assemblages: a review on field studies. Copeia 1986: 352-388.

Roughgarden, J. 1972. Evolution of niche width. The American Naturalist 106: 683-718.

Sabo, J.L., J.L. Bastow and M.E. Power. 2002. Lenth-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. Journal of the North American Benthological Society 21: 336-343.

Sandstrom, S., M. Rawson and N. Lester. 2008. Manual for broad-scale fish community monitoring using large mesh gillnets and small mesh gillnets. Ontario Ministry of Natural Resources, Peterborough, ON. 22 p.

Schoener, T.W. 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49: 704-726.

Scott, W.B. and E.J. Crossman. 1973. Freshwater Fishes of Canada. Fisheries Research Board of Canada, Ottawa, ON. 966 p.

Sellers, T.J., B.R. Parker, D.W. Schindler and W.M. Tonn. 1998. Pelagic distribution of lake trout (*Salvelinus namaycush*) in small Canadian shield lakes with respect to temperature, dissolved oxygen, and light. Canadian Journal of Fisheries and Aquatic Sciences 55: 170-179.

Semmens, B.X., E.J. Ward, J.W. Moore, C.T. Darimont. 2009. Quantifying inter- and intra-population niche variability using hierarchical Bayesian stable isotope mixing models. PLoS ONE 4(7): e6187. doi:10.1371/journal.pone.0006187.

Sherwood, G.D., J. Kovecses, A. Hontela and J.B. Rasmussen. 2002a. Simplified food webs lead to energetic bottlenecks in polluted lakes. Canadian Journal of Fisheries and Aquatic Sciences 59: 1-5.

Sherwood, G.D., I. Pazzia, A. Moeser, A. Hontela and J.B. Rasmussen. 2002b. Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild fish. Canadian Journal of Fisheries and Aquatic Sciences 59: 229-241.

Shortreed, K.S. and J.G. Stockner. 1986. Trophic status of 19 subarctic lakes in the Yukon Territory. Canadian Journal of Fisheries and Aquatic Sciences 43: 797-805.

Sierszen, M.E., M.E. McDonald and D.A. Jensen. 2003. Benthos as the basis for arctic lake food webs. Aquatic Ecology 37: 437-445.

Snucins, E.J. and J.M. Gunn. 1995. Coping with a warm environment: behavioural thermoregulation by lake trout. Transactions of the American Fisheries Society 124: 118-123.

Steinhart, G.B., M. Mineau and C.E. Kraft. 2007. Status and recovery of round whitefish (*Prosopium cylindraceum*) in New York, USA. Final Report to State Wildlife Grant T-3-1, NYSDEC, Bureau of Wildlife, Albany, NY. 59 p.

Stewart, D.B., N.J. Mochnacz, J.D. Reist, T.J. Carmichael and C.D. Sawatzky. 2007. Fish diets and food webs in the Northwest Territories: Arctic grayling (*Thymallus arcticus*). Canadian Manuscript Report of Fisheries and Aquatic Sciences 2796.

Swanson, H.K., K.A. Kidd and J.D. Reist. 2010. Effects of partially anadromous Arctic charr (*Salvelinus alpinus*) populations on ecology of coastal Arctic lakes. Ecosystems 11: 261-274.

Thompson D. R., S. J. Bury, K. A. Hobson, L. I. Wassenaar and J. P. Shannon. 2005. Stable isotopes in ecological studies. Oecologia 144: 517-519.

Tinker, M.T., G. Bentall and J.A. Estes. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proceedings of the National Academy of Sciences 105: 560-565.

Tonn, W.M., C.A. Paszkowski and T.C. Moermond. 1986. Competition in *Umbra-Perca* assemblages: experimental and field evidence. Oecologia 69: 126-133.

Vadeboncoeur, Y., E. Jeppesen, M.J. Vander Zanden, H.H. Schierup, K. Christoffersen and D.M. Lodge. 2003. From Greenland to green lakes: cultural eutrophication and the loss of benthic pathways in lakes. Limnology and Oceanography 48: 1408-1418.

Van Valen, L. 1965. Morphological variation and width of ecological niche. The American Naturalist 99: 377-390.

Vander Zanden, M.J., J.M. Casselman and J.B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401: 464-467.

Vander Zanden, M.J. and J.B. Rasmussen. 1999. Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecology 80: 1395-1404.

Vander Zanden, M.J., B.J. Shuter, N.P. Lester and J.B. Rasmussen. 2000. Within- and among-population variation in the trophic position of a pelagic predator, lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 57: 725-731.

Vijverberg, J., M. Boersma, W.L.T. van Dusen, W. Hoogenboezem, E.H.R.R. Lammens, W.M. Mooij. Seasonal variation in the interactions between piscivorous fish, planktivorous fish and zooplankton in a shallow eutrophic lake. Hydrobiologia 207: 279-286.

Wallace, R.K. 1981. An assessment of diet-overlap indexes. Transactions of the American Fisheries Society 110: 72-76.

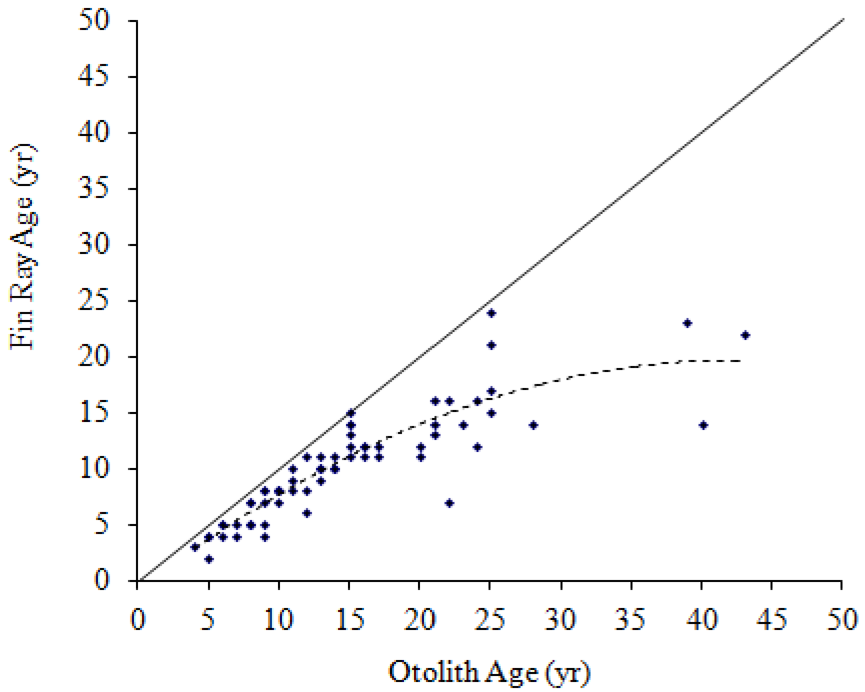
Wege, G.J. and R.O. Anderson. 1978. Relative weight (W_r): a new index of condition for largemouth bass. In: G.D. Novinger and J.G. Dillard, editors. New approaches to the management of small impoundments. American Fisheries Society, North Central Division, Bethesda, MD. pp. 79-91.

Wilson, E.O. 1961. The nature of the taxon cycle in the Melanesion ant fauna. The American Naturalist 95: 169-193.

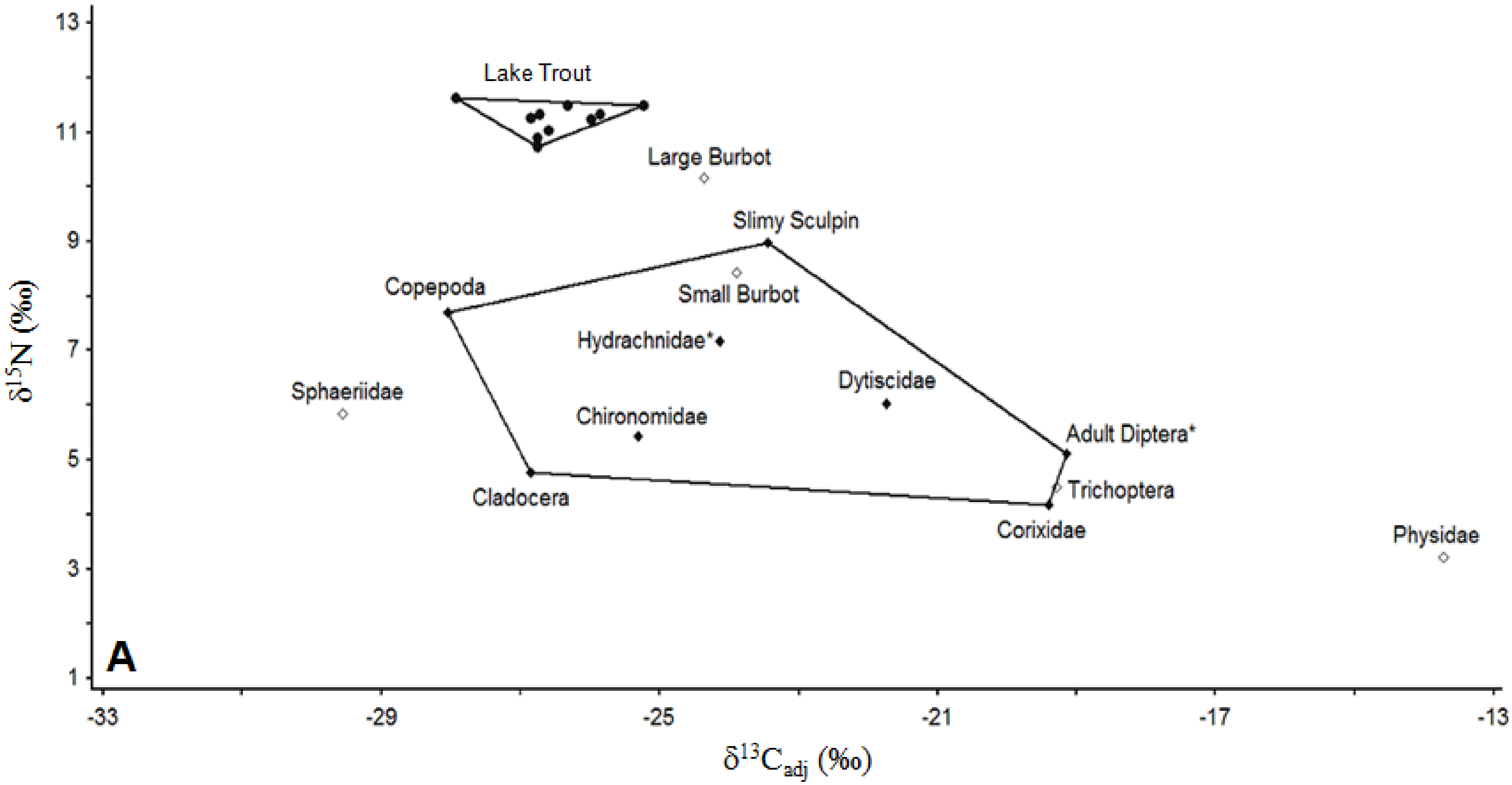
Appendix 1 Size range and linear distance metric (NR: range in δ^{15}N; CR: range in $\delta^{13}C_{adj}$; TA: total area; CD: mean distance to centroid; NND: mean nearest neighbour distance; SDNND: standard deviation of nearest neighbour distance) results based on stable isotope data for Lake Trout populations in the six study lakes. 'Class 1' lakes support Lake Trout and only one other large-bodied fish (i.e., Burbot), whereas 'Class 2' lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco). Metric values are in ‰ notation.

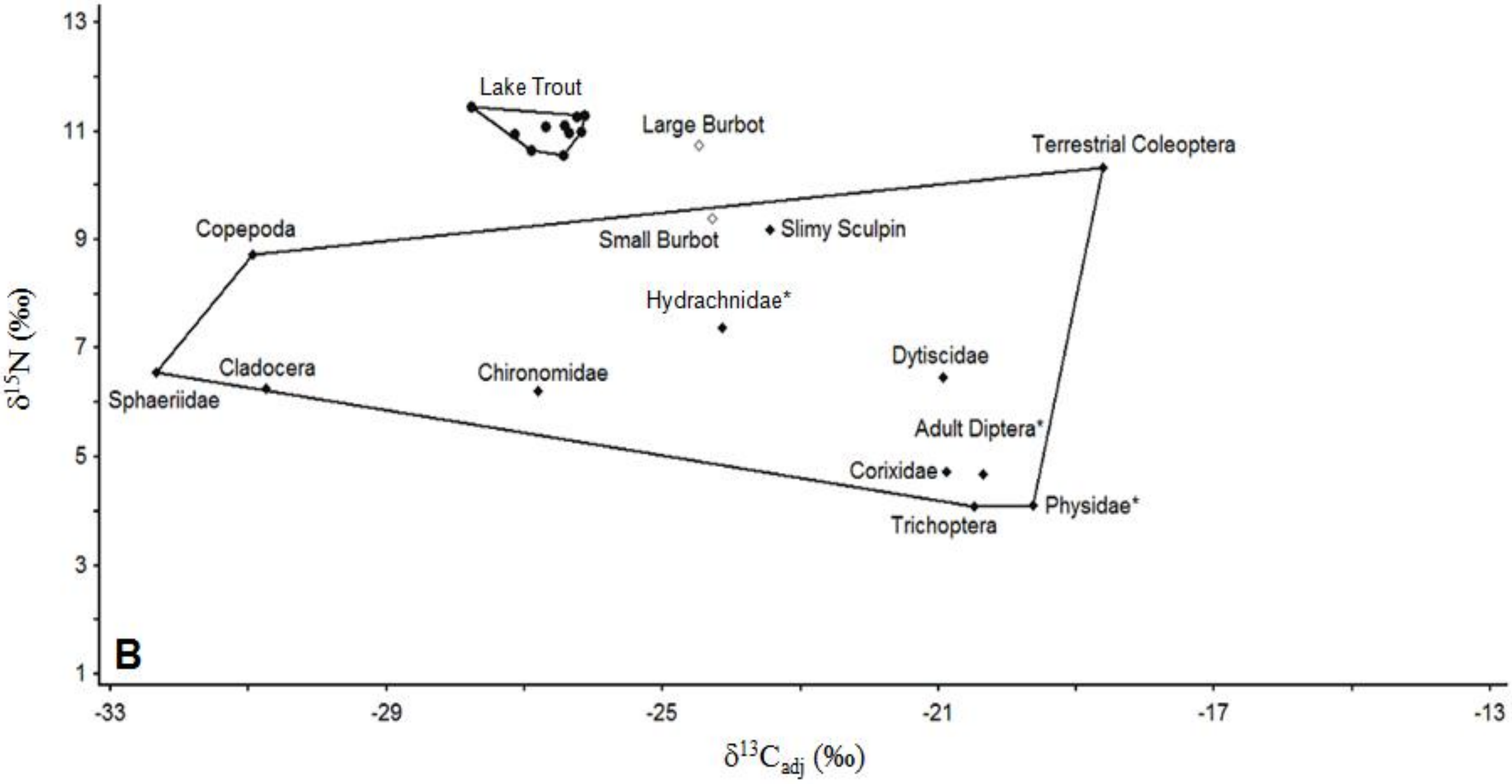
Lake	Metric						
	FL (mm)[a]	NR	CR	TA	CD	NND	SDNND
Class 1							
M3	516 - 572	0.88	2.70	1.11	0.61	0.33	0.33
E14	385 - 439	0.88	1.64	0.81	0.48	0.30	0.21
E17	347 - 429	1.72	3.05	3.47	0.97	0.62	0.22
Class 2							
W1	367 - 438	1.36	3.70	2.26	1.37	0.32	0.32
R34	412 - 493	1.42	3.43	3.46	1.21	0.51	0.25
R2	396 - 473	2.46	4.13	5.97	1.53	0.62	0.25

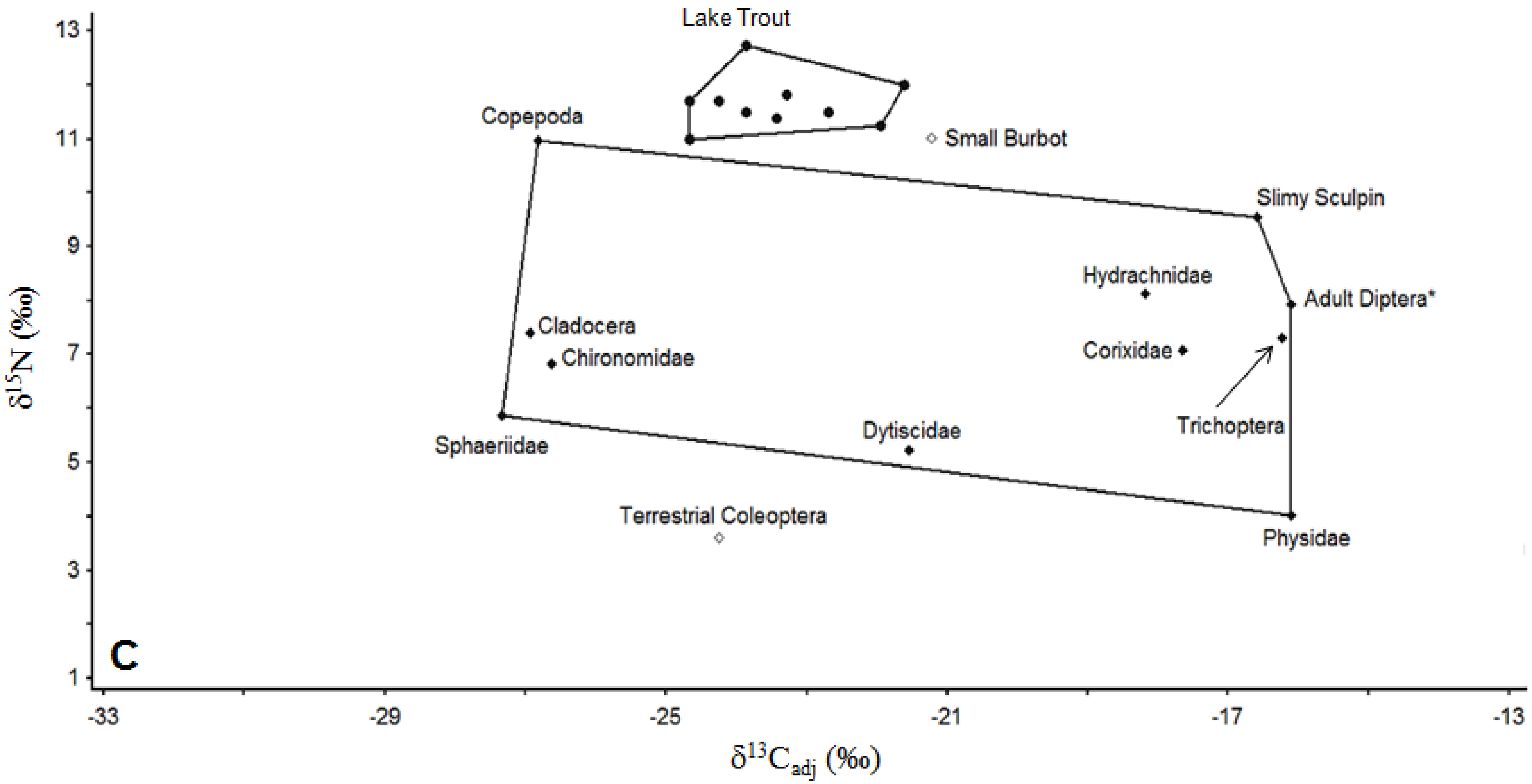
[a] Range in fork length (FL) of Lake Trout used in the analysis

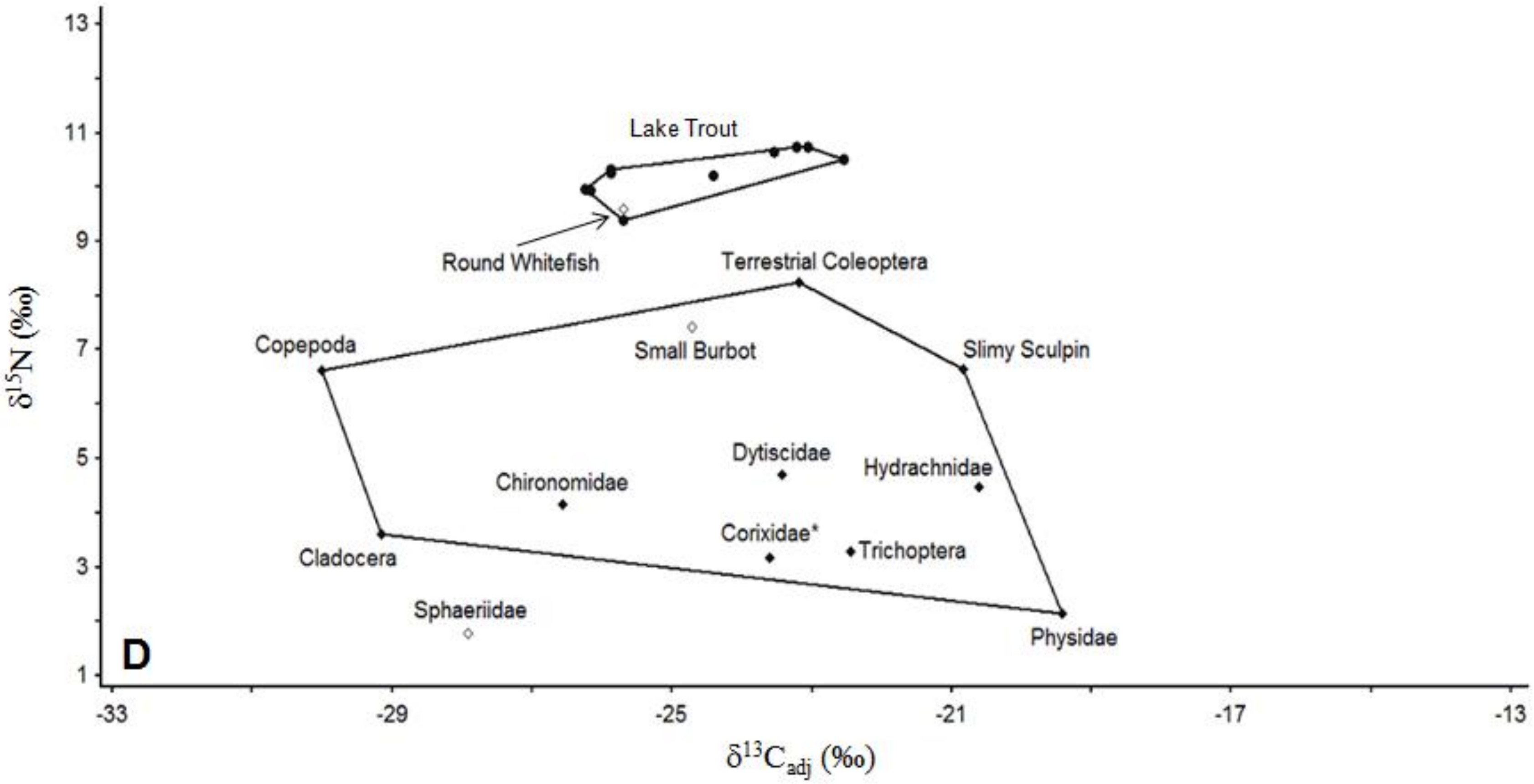


Appendix 2 Comparison of assigned ages for paired otoliths and fin rays from Lake Trout. Ageing structures are pooled samples from eight small lakes in the Lac de Gras watershed, Northwest Territories. The 1:1 line (solid) and trendline (dashed) are depicted.

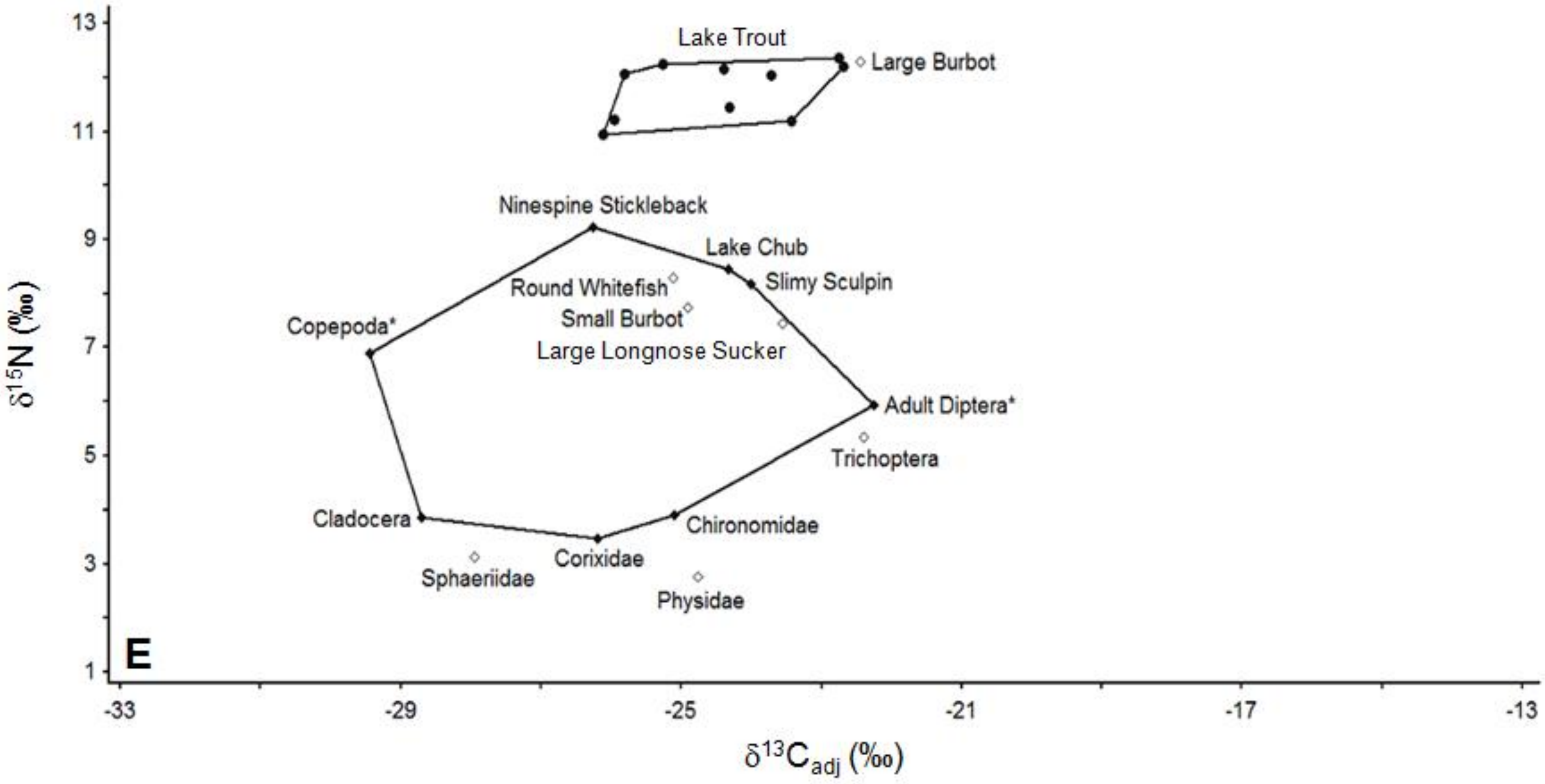

Lake Trout
Large Burbot
Slimy Sculpin
Small Burbot
Copepoda
Hydrachnidae*
Dytiscidae
Sphaeriidae
Chironomidae
Adult Diptera*
Trichoptera
Cladocera
Corixidae
Physidae
A
13
11
9
7
5
3
1
-33
-29
-25
-21
-17
-13
$\delta^{15}N$ (‰)
$\delta^{13}C_{adj}$ (‰)


B
Lake Trout
Large Burbot
Terrestrial Coleoptera
Copepoda
Small Burbot
Slimy Sculpin
Hydrachnidae*
Cladocera
Chironomidae
Dytiscidae
Sphaeriidae
Adult Diptera*
Corixidae
Physidae*
Trichoptera
δ15N (‰)
δ13Cadj (‰)
13
11
9
7
5
3
1
-33
-29
-25
-21
-17
-13

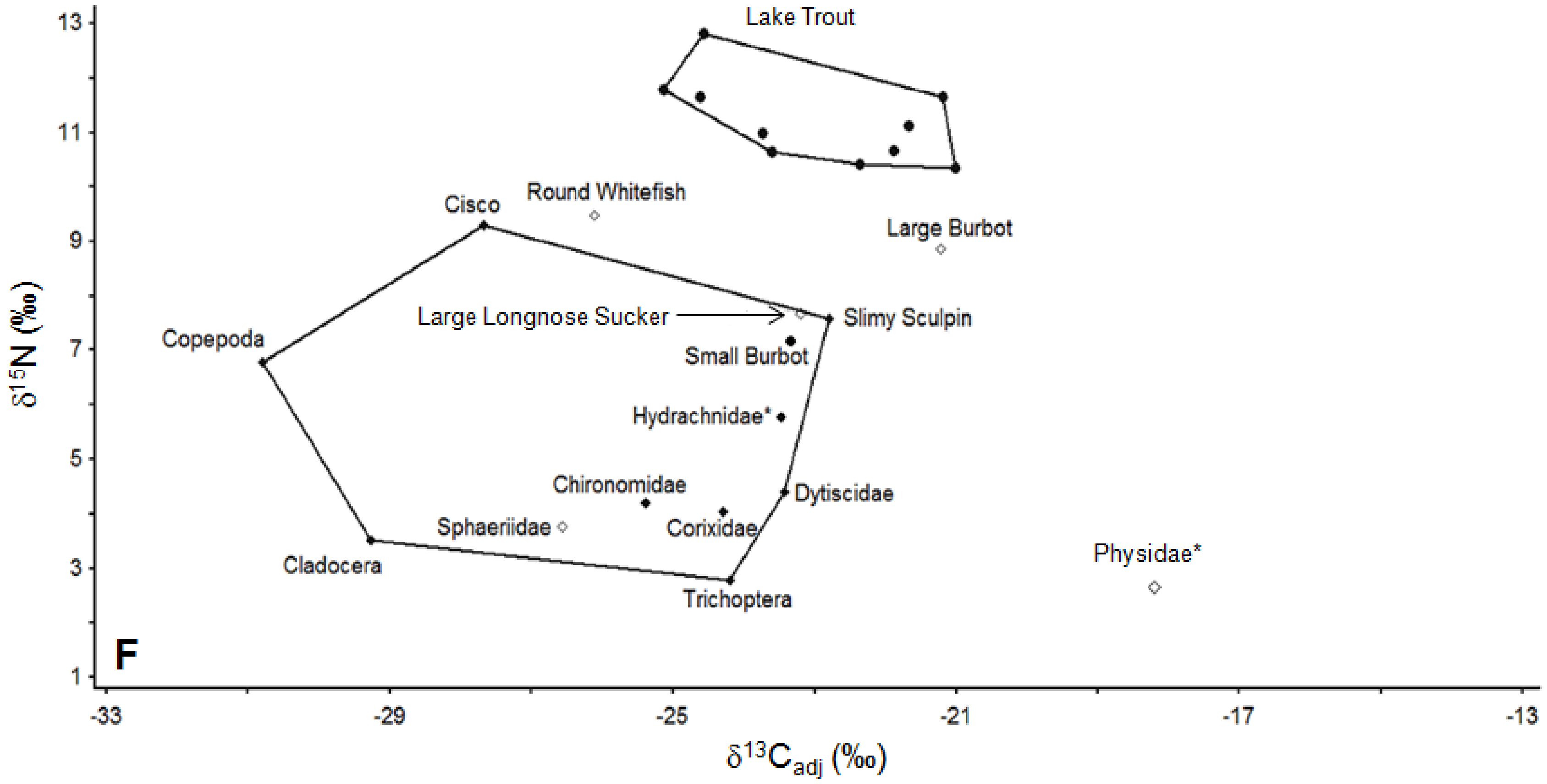

Lake Trout
Copepoda
Small Burbot
Slimy Sculpin
Hydrachnidae
Adult Diptera*
Cladocera
Chironomidae
Corixidae
Trichoptera
Dytiscidae
Sphaeriidae
Terrestrial Coleoptera
Physidae
C
13
11
9
7
5
3
1
-33
-29
-25
-21
-17
-13
$\delta^{15}N$ (‰)
$\delta^{13}C_{adj}$ (‰)



Lake Trout
Round Whitefish
Terrestrial Coleoptera
Small Burbot
Copepoda
Slimy Sculpin
Dytiscidae
Hydrachnidae
Chironomidae
Corixidae*
Trichoptera
Cladocera
Sphaeriidae
Physidae
D
13
11
9
7
5
3
1
-33
-29
-25
-21
-17
-13
$\delta^{15}N$ (‰)
$\delta^{13}C_{adj}$ (‰)

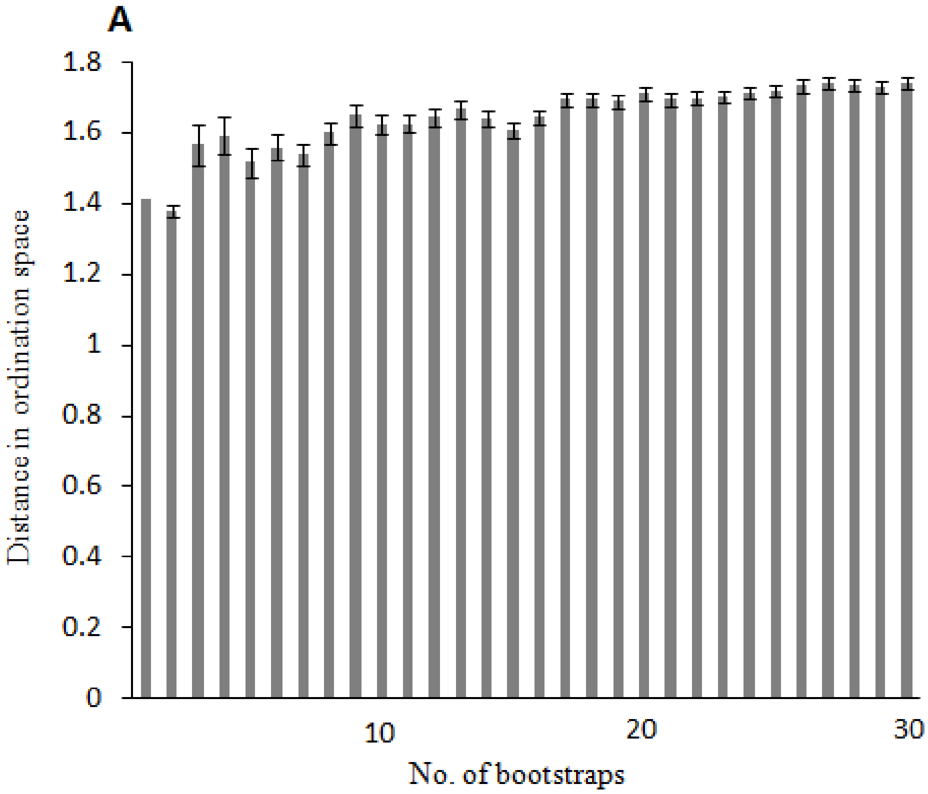


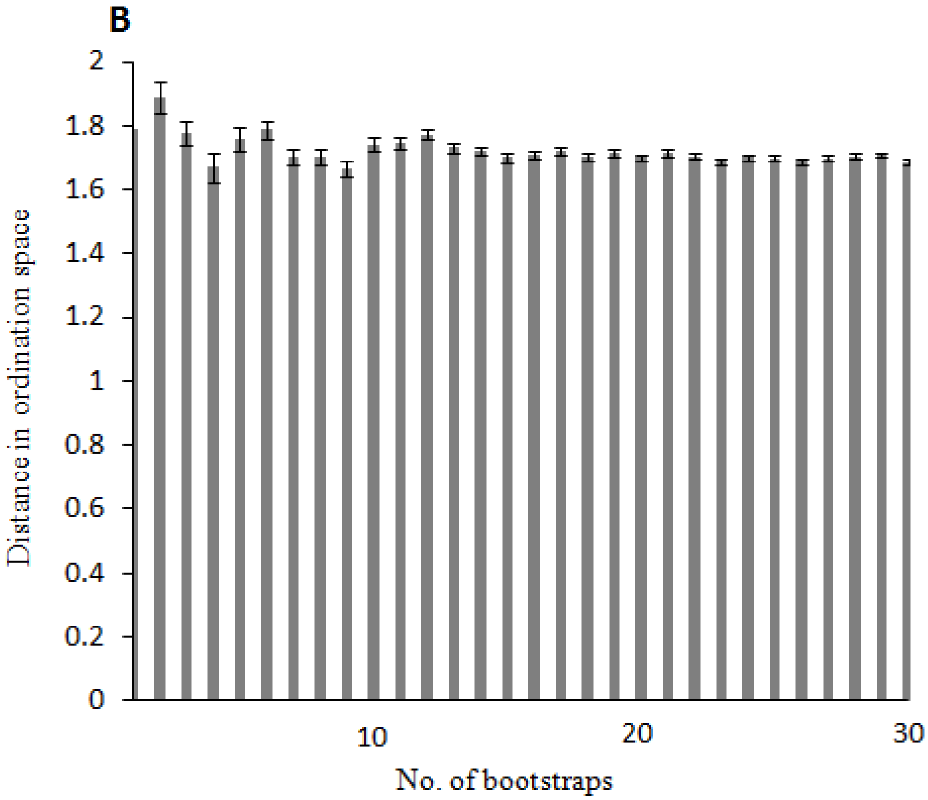
13
11
9
7
5
3
1
δ¹⁵N (‰)
-33
-29
-25
-21
-17
-13
δ¹³Cadj (‰)
Lake Trout
Large Burbot
Ninespine Stickleback
Lake Chub
Slimy Sculpin
Round Whitefish
Small Burbot
Large Longnose Sucker
Copepoda*
Adult Diptera*
Trichoptera
Cladocera
Chironomidae
Corixidae
Sphaeriidae
Physidae
E

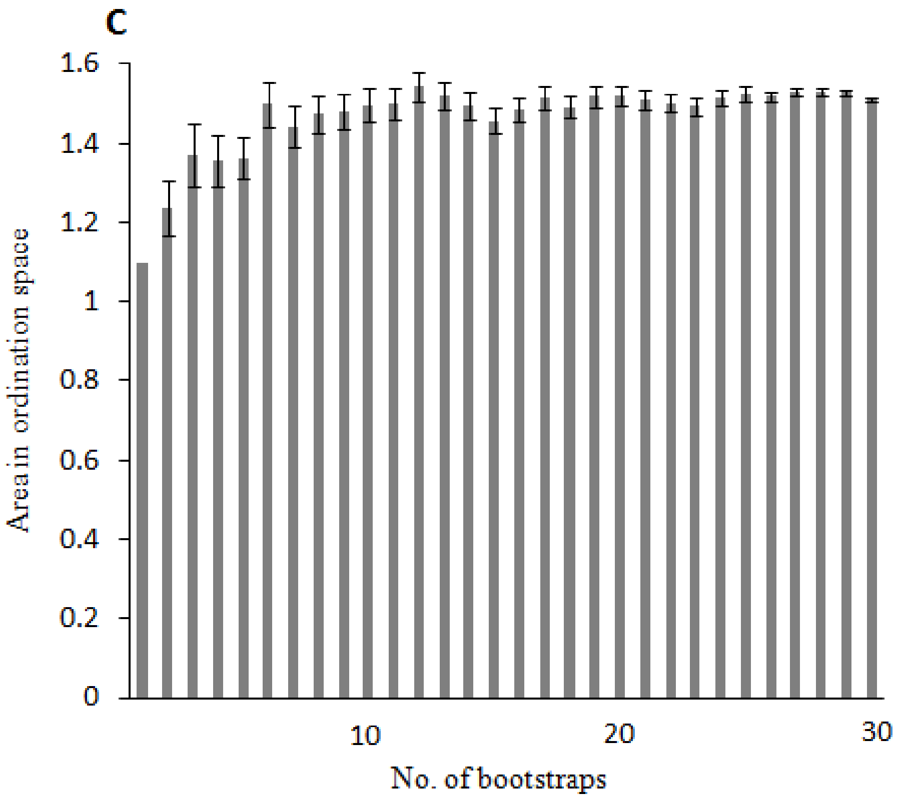


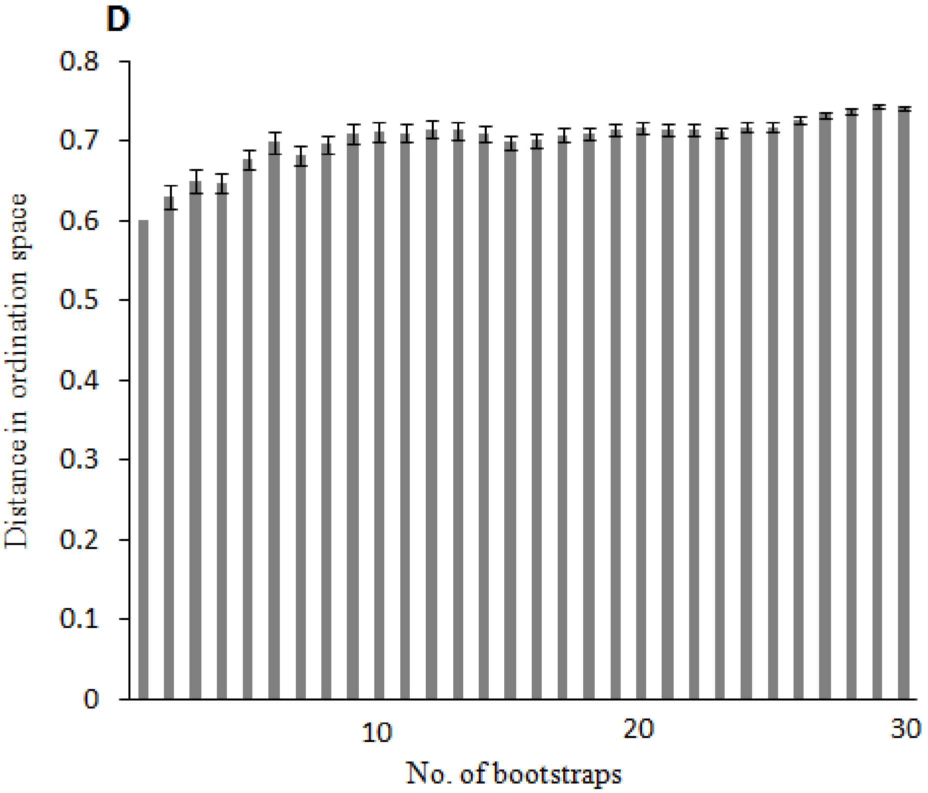
Lake Trout
Round Whitefish
Cisco
Large Burbot
Large Longnose Sucker
Slimy Sculpin
Copepoda
Small Burbot
Hydrachnidae*
Chironomidae
Dytiscidae
Sphaeriidae
Corixidae
Cladocera
Trichoptera
Physidae*
F
13
11
9
7
5
3
1
-33
-29
-25
-21
-17
-13
$\delta^{15}N$ (‰)
$\delta^{13}C_{adj}$ (‰)

Appendix 3 Lake Trout populations (*black circles*) and their prey communities (*black diamonds*) in $\delta^{13}C_{adj}$ vs. $\delta^{15}N$ space in M3 (**A**; Class 1), E14 (**B**; Class 1), E17 (**C**; Class 1), W1 (**D**; Class 2), R34 (**E**; Class 2), and R2 (**F**; Class 2) lakes. Values for Lake Trout are individual $\delta^{13}C_{adj}$ and $\delta^{15}N$ signatures, whereas values for all other organisms are mean population $\delta^{13}C_{adj}$ and $\delta^{15}N$ signatures. Convex hulls represent total area calculations for Lake Trout populations and prey communities; prey community is defined on a lake-specific basis as the items found in the stomach contents of Lake Trout. Organisms not present in Lake Trout diet but collected during sampling are also included (*open diamonds*). An asterisk (*) indicates that isotopic signature was estimated; see Methods section for details.

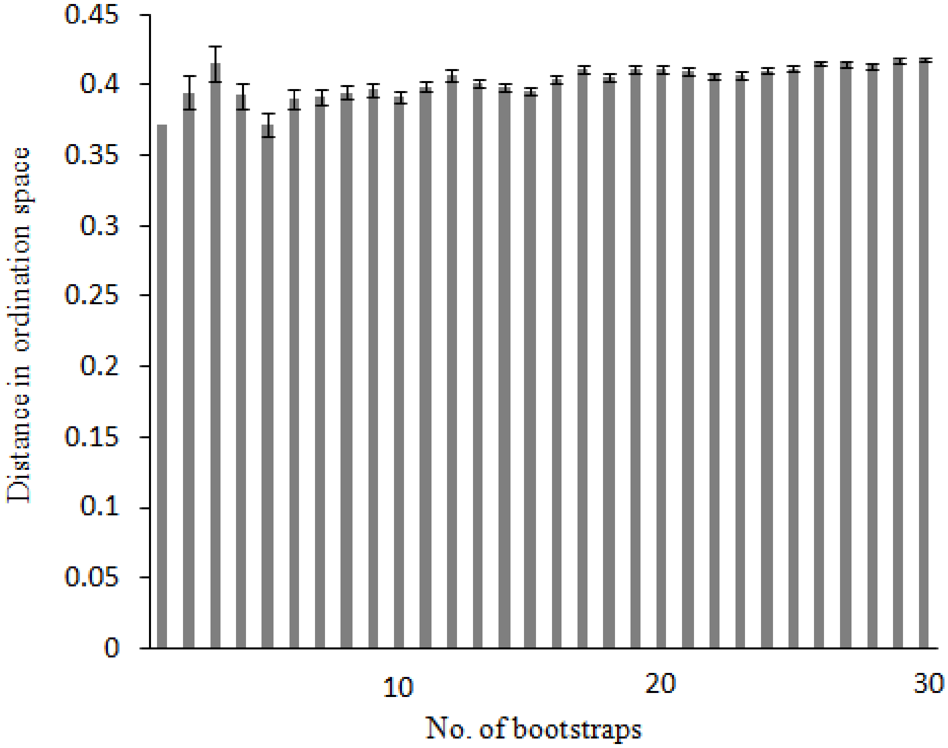

A
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Distance in ordination space
10
20
30
No. of bootstraps


B
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Distance in ordination space
10
20
30
No. of bootstraps


C
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
10
20
30
Area in ordination space
No. of bootstraps

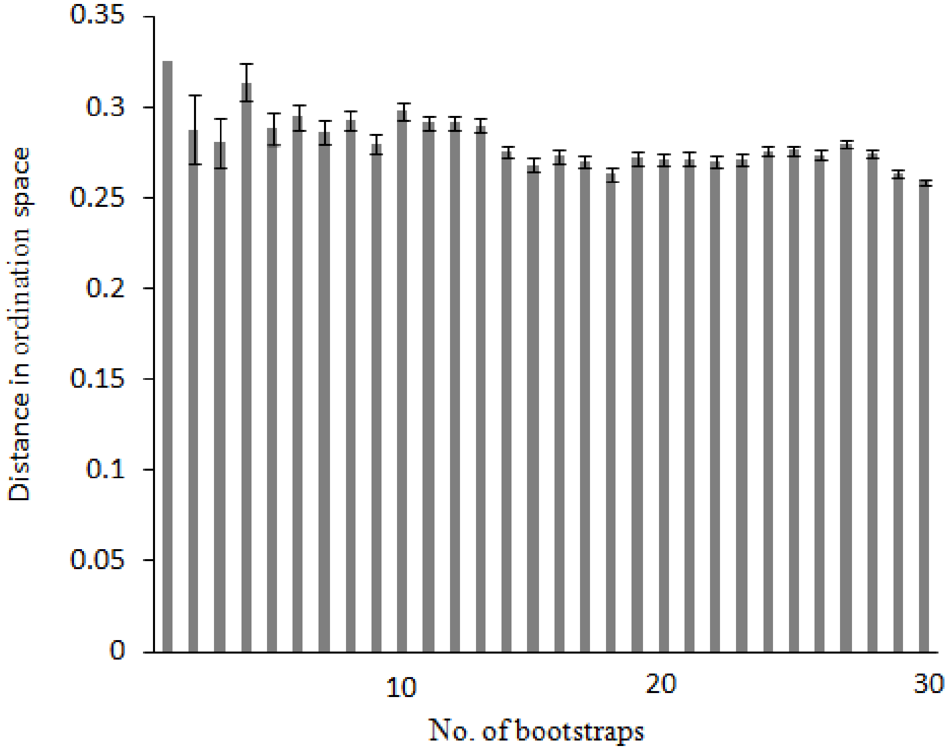

D
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
10
20
30
Distance in ordination space
No. of bootstraps

E



0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Distance in ordination space
10
20
30
No. of bootstraps

F

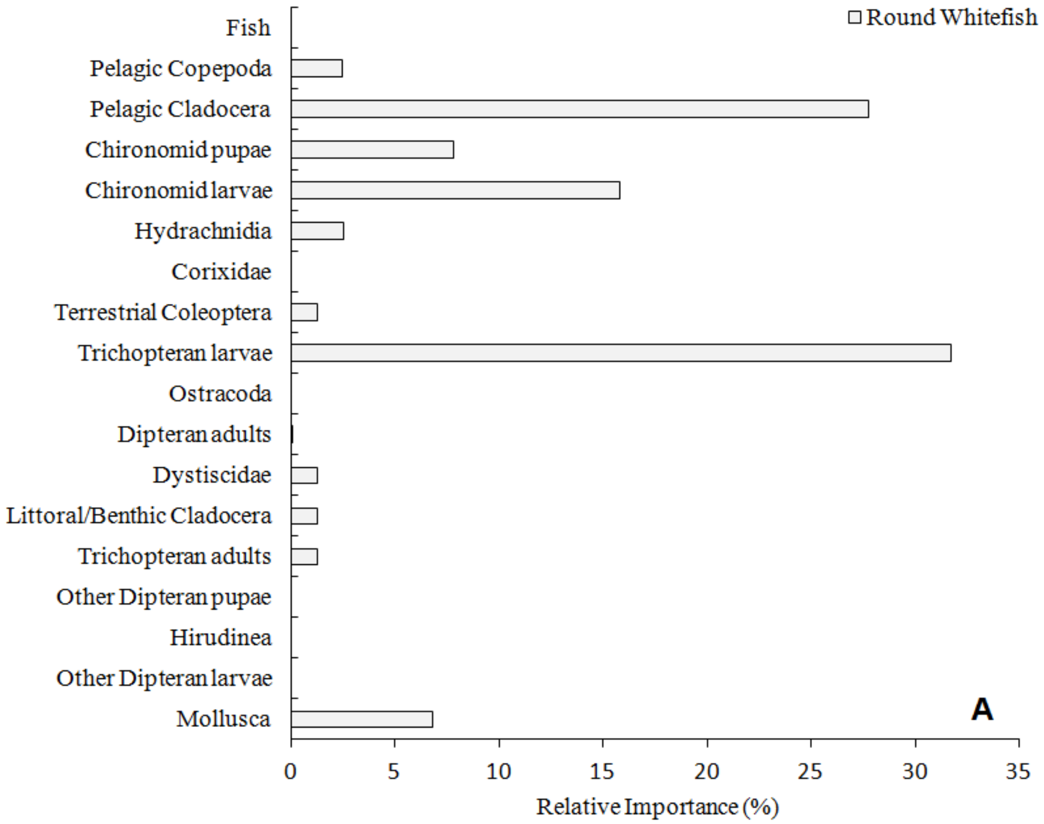


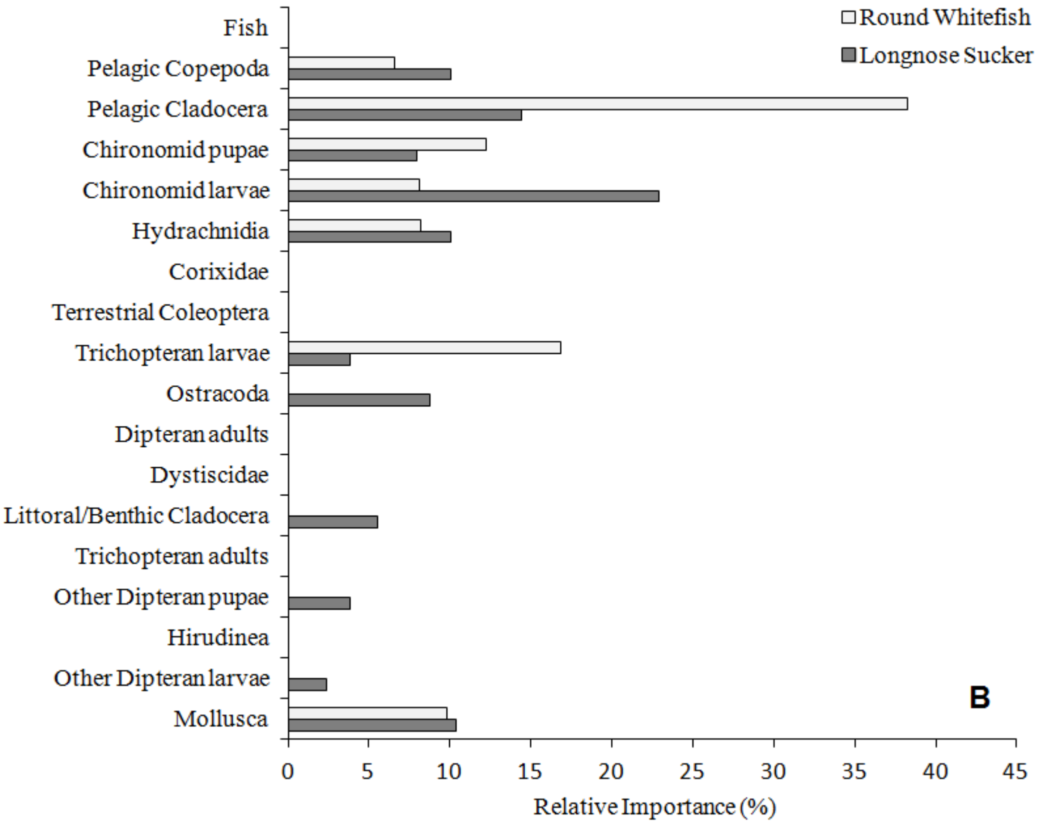
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Distance in ordination space
10
20
30
No. of bootstraps

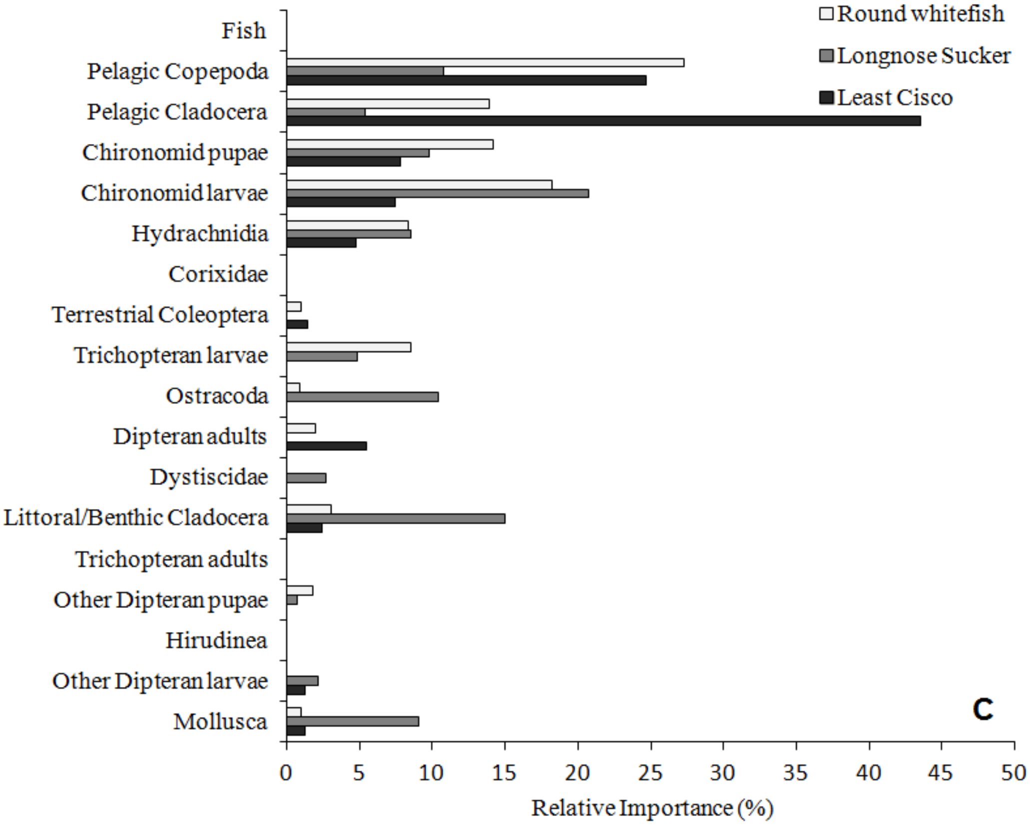
Appendix 4 Mean (± SE) linear distance metric (Vertical Range (**A**), Horizontal Range (**B**), Total Area (**C**), Mean Distance to Centroid (**D**), Mean Nearest Neighbour Distance (**E**), Standard Deviation of Nearest Neighbour Distance (**F**)) values for bootstraps based on ordination scores for stomach contents data of Lake Trout in W1 lake. Mean metric values for all other lakes were examined and also stabilized by the 30th bootstrap. See text for bootstrapping methods.

Appendix 5 Median (and 5th to 95th percentile) proportional contributions of three food sources to Lake Trout in the six study lakes estimated using the MixSIR model. Also shown are mean values for the median source contributions by lake class. ‘Class 1’ lakes support Lake Trout and only one other large-bodied fish (i.e., Burbot), whereas ‘Class 2’ lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco).

Lake	Source		
	Pelagic Zooplankton	Littoral Invertebrate	Forage Fish
Class 1			
M3	0.716 (0.586 - 0.836)	0.029 (0.002 - 0.099)	0.251 (0.093 - 0.395)
E14	0.522 (0.453 - 0.592)	0.11 (0.025 - 0.208)	0.368 (0.225 - 0.496)
E17	0.669 (0.595 - 0.748)	0.191 (0.038 - 0.324)	0.133 (0.016 - 0.302)
Mean	**0.636**	**0.11**	**0.251**
Class 2			
W1	0.464 (0.383 - 0.542)	0.06 (0.005 - 0.197)	0.466 (0.333 - 0.571)
R34	0.173 (0.050 - 0.302)	0.048 (0.004 - 0.194)	0.771 (0.564 - 0.912)
R2	0.116 (0.020 - 0.225)	0.047 (0.004 - 0.148)	0.824 (0.712 - 0.934)
Mean	**0.251**	**0.052**	**0.687**


☐ Round Whitefish
Fish
Pelagic Copepoda
Pelagic Cladocera
Chironomid pupae
Chironomid larvae
Hydrachnidia
Corixidae
Terrestrial Coleoptera
Trichopteran larvae
Ostracoda
Dipteran adults
Dystiscidae
Littoral/Benthic Cladocera
Trichopteran adults
Other Dipteran pupae
Hirudinea
Other Dipteran larvae
Mollusca
A
0
5
10
15
20
25
30
35
Relative Importance (%)


Round Whitefish
Longnose Sucker
Fish
Pelagic Copepoda
Pelagic Cladocera
Chironomid pupae
Chironomid larvae
Hydrachnidia
Corixidae
Terrestrial Coleoptera
Trichopteran larvae
Ostracoda
Dipteran adults
Dystiscidae
Littoral/Benthic Cladocera
Trichopteran adults
Other Dipteran pupae
Hirudinea
Other Dipteran larvae
Mollusca
B
0
5
10
15
20
25
30
35
40
45
Relative Importance (%)



Appendix 6 Relative Importance (%) of 18 prey categories to diets of the non-piscivorous, large-bodied fishes present in the Class 2 lakes W1 (**A**; Round Whitefish), R34 (**B**; Round Whitefish, Longnose Sucker), and R2 (**C**; Round Whitefish, Longnose Sucker, Cisco). ‘Class 2’ lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco).

Appendix 7 Relative Weight (W_r) and Fulton's Condition Factor (K) of Lake Trout populations in the six study lakes. 'Class 1' lakes support Lake Trout and only one other large-bodied fish (i.e., Burbot), whereas 'Class 2' lakes support Lake Trout and at least two other large-bodied species (i.e., Burbot, plus Round Whitefish, Longnose Sucker, and/or Cisco).

	Class 1			Class 2		
Condition Index	M3	E14	E17	W1	R34	R2
W_r	122	137	132	121	120	107
K	1.20	1.25	1.20	1.11	1.11	0.99