

# Effects of Partially Anadromous Arctic Charr (*Salvelinus alpinus*) Populations on Ecology of Coastal Arctic Lakes

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## ABSTRACT

Little research has been conducted on effects of iteroparous anadromous fishes on Arctic lakes. We investigated trophic ecology, fish growth, and food web structure in six lakes located in Nunavut, Canada; three lakes contained anadromous Arctic charr (*Salvelinus alpinus*) whereas three lakes did not contain Arctic charr. All lakes contained forage fishes and lake trout (*Salvelinus namaycush*; top predator). Isotope ratios ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) of fishes and invertebrates did not differ between lakes with and without anadromous Arctic charr; if anadromous Arctic charr deliver marine-derived nutrients and/or organic matter to freshwater lakes, these inputs could not be detected with  $\delta^{13}\text{C}$  and/or  $\delta^{15}\text{N}$ . Lake trout carbon (C):nitrogen (N) and condition were significantly higher in lakes with Arctic charr (C:N = 3.42,  $K = 1.1$ ) than in lakes without Arctic charr (C:N = 3.17,  $K = 0.99$ ), however, and nine-spine stickleback (*Pungitius pungitius*) condition was

significantly lower in lakes with Arctic charr ( $K = 0.58$ ) than in lakes without Arctic charr ( $K = 0.64$ ). Isotope data indicated that pre-smolt and resident Arctic charr may be prey for lake trout and compete with nine-spine stickleback. Linear distance metrics applied to isotope data showed that food webs were more compact and isotopically redundant in lakes where Arctic charr were present. Despite this, lake trout populations in lakes with Arctic charr occupied a larger isotope space and showed greater inter-individual isotope differences. Anadromous Arctic charr appear to affect ecology and feeding of sympatric freshwater species, but effects are more subtle than those seen for semelparous anadromous species.

**Key words:** anadromous Arctic charr; food webs; fish growth; stable isotopes; distance metrics; marine-derived nutrients.

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## INTRODUCTION

Semelparous anadromous fishes, such as Pacific salmon (*Oncorhynchus* spp.), deliver significant amounts of marine-derived nutrients (MDN) and organic matter to freshwater ecosystems through deposition of eggs and carcasses (for example, Naiman and others 2002). In freshwater nursery and migration habitats on the Pacific coast of North America, MDN appear to increase primary

productivity (for example, Naiman and others 2002), growth and biomass of stream invertebrates (for example, Minakawa and others 2002), and production and diversity of riparian plant communities (for example, Helfield and Naiman 2001).

Both semelparous and iteroparous anadromous fishes can move MDN into freshwater systems through egg deposition, excretion of metabolic products, and post-spawning or winter mortality (Durbin and others 1979; Jonsson and Jonsson 2003; Nislow 2004). Unlike semelparous fishes, however, iteroparous anadromous fishes do not die *en masse* after spawning. Effects of iteroparous anadromous fishes on freshwater systems may therefore be more subtle than those observed for semelparous anadromous fishes. Nevertheless, previous research has shown that iteroparous anadromous fishes can move marine-derived nitrogen and phosphorus to freshwater migration, spawning, and rearing habitats (Durbin and others 1979; Jonsson and Jonsson 2003). Also, freshwater benthic invertebrates can prey on eggs of iteroparous anadromous fishes (Jardine and others 2009).

Effects of iteroparous anadromous fishes on freshwater habitats may be more ecologically relevant and easier to detect in oligotrophic lakes, where it is more likely that MDN represent a significant portion of overall nutrient budgets (Nislow 2004). Little research has been conducted on the ecological role of iteroparous anadromous fishes in Arctic lakes, where food webs are relatively simple and lakes are often oligotrophic. Arctic charr (*Salvelinus alpinus*) is an iteroparous anadromous species that has a circumpolar distribution and may transport marine-derived nutrients and organic matter to Arctic lakes. In coastal regions of Arctic Canada, there are often sympatric subpopulations of anadromous and resident (wholly freshwater) Arctic charr. This life history strategy, where part of the population is anadromous and part is resident, is called partial anadromy, and is an example of partial migration (Jonsson and Jonsson 1993). Arctic charr rarely co-occur with lake trout (*Salvelinus namaycush*) in Arctic lakes unless part of the Arctic charr population is anadromous (that is, partially anadromous) (Johnson 1980). This is likely because Arctic lakes are relatively unproductive and cannot support two large-bodied predator species unless some of the fish are (at least partly) supported by the marine environment.

It is likely that partially anadromous Arctic charr populations affect freshwater food web structure in lakes where they are present. In the West Kitik-

meot region of Nunavut, Canada, anadromous Arctic charr rear in freshwater for 3–8 years before beginning annual marine migrations, and anadromous fish return to freshwater each fall to spawn and/or overwinter (Johnson 1980; Swanson and others 2010). Both pre-smolt and resident Arctic charr feed on freshwater prey items such as zooplankton, chironomids, detritus, and surface insects (Rikardsen and others 2003). This could lead to competition with species such as cisco (*Coregonus sardinella* and *Coregonus artedii*), lake whitefish (*Coregonus clupeaformis*), and ninespine stickleback (*Pungitius pungitius*) (Scott and Crossman 1973). Also, pre-smolt, resident, and small anadromous Arctic charr may be a prey source for lake trout populations. To date, there is little information on whether pre-smolt and resident Arctic charr affect growth and feeding in other forage fishes, or whether pre-smolt, resident, or small anadromous Arctic charr are preyed upon by lake trout. Results from a preliminary study conducted on four Arctic lakes (one lake with anadromous Arctic charr, three without) suggested that pre-smolt and resident Arctic charr function as an alternate prey source for lake trout and that lake trout have lower  $\delta^{15}\text{N}$  and higher carbon (C):nitrogen (N) (indicator of lipid, Post and others 2007) in lakes where Arctic charr are present (Swanson and Kidd 2009). These findings could not be tested statistically, however, because of limited replication.

Stable nitrogen (N;  $\delta^{15}\text{N}$ ) and carbon (C;  $\delta^{13}\text{C}$ ) isotope ratios are commonly used in freshwater food webs to determine trophic position and food source (for example, Peterson and Fry 1987), respectively. Because  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  are often elevated in marine food sources relative to freshwater food sources (Fry and Sherr 1984; Peterson and Fry 1987), these isotope ratios have also been used to detect MDN in freshwater from semelparous (for example, Kline and others 1990; Bilby and others 1996) and iteroparous (Jardine and others 2009) anadromous fishes. There can be long-term storage of MDN, such that elevated isotope ratios from MDN are detectable in freshwater biota throughout the year (that is, not only during or immediately after spawning; Walters and others 2009). Jardine and others (2009) found, however, that effects of iteroparous anadromous fishes on  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of freshwater invertebrates can be inconsistent among taxa, site, and element.

Layman and others (2007) recently proposed six linear distance metrics that can be applied to stable isotope data and used to quantify food web structure. Metrics are applied in two dimensions ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ), and include total area (TA),  $\delta^{15}\text{N}$  range

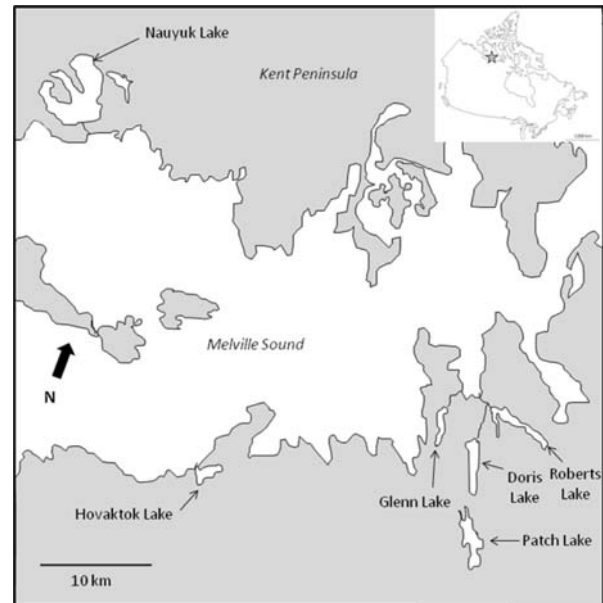
(NR),  $\delta^{13}\text{C}$  range (CR), mean distance to centroid (CD), mean nearest neighbor distance (NND), and standard deviation of nearest neighbor distance (STDNND; Layman and others 2007). Together, these metrics provide information on range and diversity of isotope ratios in food webs, as well as how closely (NND; that is, isotopic redundancy) and evenly (STDNND) species/taxa are packed in isotope space. Layman and others (2007) suggested that these metrics could also be used at the population level to explore intraspecific variation in isotope niche; this was recently demonstrated by Darimont and others (2009).

This study compared three lakes with partially anadromous Arctic charr populations to three lakes with no Arctic charr. Our objectives were to: (1) investigate whether Arctic charr are a likely prey source for lake trout, and examine whether the presence of Arctic charr affects  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ , C:N, growth, and condition of sympatric lake trout; (2) determine which forage fish species may compete with pre-smolt and resident Arctic charr, and test whether  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ , C:N, and condition in these species differ between lakes with and without Arctic charr; (3) determine if there is long-term storage of MDN in lakes with anadromous Arctic charr; and (4) use linear distance metrics (Layman and others 2007) to compare whole food web structure and inter-individual differences in lake trout diet between lakes with and without anadromous Arctic charr.

## MATERIALS AND METHODS

### Sample Collection

Fish, zooplankton, and benthic invertebrates were collected from six lakes in the West Kitikmeot region of Nunavut, Canada, during summers 2006–2008 (Figure 1). Lake area, maximum depth, and volume are shown in Appendix I in supplementary material. Fish and benthic invertebrate samples were collected from Doris, Glenn, Patch, and Roberts lakes in 2006, 2007, and 2008, and from Hovaktok and Nauyuk lakes in 2007 and 2008 (logistic constraints precluded 2006 sampling). Three lakes contained anadromous, pre-smolt, and resident Arctic charr (Roberts, Hovaktok, and Nauyuk) whereas three lakes contained no Arctic charr (Doris, Patch, and Glenn). All lakes contained lake trout, and all lakes but Hovaktok contained lake whitefish, ninespine stickleback, and cisco. The only forage fish species present in Hovaktok Lake was fourhorn sculpin (*Myxocephalus quadricornis*); this species was also found in Glenn Lake.



**Figure 1.** Map of the study lakes (West Kitikmeot region, Nunavut, Canada). Roberts, Hovaktok, and Nauyuk lakes have partially anadromous populations of Arctic charr. Anadromous charr migrate to Melville Sound (marine) each summer. There are no Arctic charr in Doris, Glenn, or Patch lakes. Anadromous lake trout were found in Glenn, Hovaktok, Nauyuk, and Roberts lakes.

Approximately 10–20 individuals/fish species/lake were captured in each lake with a backpack electrofisher, gill nets (1.9–8.9 cm stretched mesh), minnow traps, fyke nets, seine nets, and angling during the course of the study. All fish were measured (nearest mm) and weighed (nearest g) in the field and all fish except ninespine stickleback and fourhorn sculpin were dissected for dorsal muscle tissue and saggittal otoliths. Sex was determined for all fish except ninespine stickleback. Preliminary analyses conducted on muscle tissue and whole bodies of ninespine stickleback and fourhorn sculpin revealed that isotope ratios did not differ between these tissue types (mixed models,  $F < 2.32$ ,  $P > 0.13$ ,  $df > 1,11$ ). Whole bodies were thus used for the majority of analyses, and whole body and muscle data were pooled for these two species. Tissue samples were frozen immediately after processing and otoliths were cleaned and dried.

Mysids (*Mysis relicta*), chironomids (Chironomidae), amphipods (*Gammarus lacustris* and *Hyaella azteca*), and isopods (*Saduria entomon*) were collected from the study lakes in 2006–2008 with kick nets and an Ekman grab. Between two and five replicates/taxa were collected from each lake.

Invertebrates were sorted to major taxon and frozen whole. Bulk zooplankton samples were collected in 2008 using horizontal tows with a 153  $\mu\text{m}$  net (0.25 m diameter opening), and were frozen within 12 h of collection.

## Laboratory Analyses

Fish tissue, whole benthic invertebrates, and bulk zooplankton samples were freeze-dried and ground to a fine powder with a mortar and pestle. When single benthic invertebrates did not provide enough mass for stable isotope analysis, multiple individuals were pooled (within sampling dates) to form a composite sample. A minimum of three samples (composite or individual) per invertebrate taxon was analyzed for each lake.

Stable C and N isotope analysis for fish and invertebrates were performed using standard protocols at the Stable Isotope in Nature Laboratory at the University of New Brunswick, Fredericton, NB. Carbon and nitrogen content were converted to molar ratios (C:N), and stable C and N isotope ratios are expressed as parts per mil (‰) delta values ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) relative to international standards [Pee-Dee Belemnite (C) and  $\text{N}_2$  gas (N)]. Replicate analyses of internal laboratory standards (for example, NIST 1577b, bovine liver) typically yielded standard deviations of  $\pm 0.15\text{‰}$  for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ . Mean difference  $\pm$ SD between 59 duplicate sub-samples was  $0.12 \pm 0.14\text{‰}$  for  $\delta^{15}\text{N}$  and  $0.12 \pm 0.23\text{‰}$  for  $\delta^{13}\text{C}$ .

When two otoliths were available, lake trout age was determined using the “break and burn” technique (Chilton and Beamish 1982). Under reflected light, one year was defined as an opaque zone (summer) followed by a translucent hyaline zone (winter). When only one otolith was available, ages were determined from sectioned and polished otoliths used for microchemical analyses (see Swanson and others 2010). Ages were read from a subsample of otoliths using both methods. Mean difference ( $\pm$ SE) between aging methods was  $1.1 \pm 1.3$  years ( $n = 86$ ) (R. Wastle, Fisheries and Oceans Canada, Winnipeg, MB, unpubl. data).

## Data Analysis

During data analysis, we discovered that some of the captured lake trout in Glenn (26%), Nauyuk (40%), Hovaktok (14%), and Roberts (42%) lakes were anadromous (Swanson and others 2010). Anadromous lake trout were excluded from statistical analyses; all results presented for lake trout represent resident, wholly freshwater fish.

Interpretations of some analyses (for example, testing for marine subsidy) were altered, however, to include assessment of potential effects of anadromous lake trout. Life history types of Arctic charr and lake trout were differentiated using otolith microchemistry and stable isotope analysis (Swanson and others 2010). A subset of lake whitefish, cisco, and fourhorn sculpin were also analyzed for otolith microchemistry; all forage fishes analyzed were freshwater residents (H. Swanson, unpubl. data).

Statistical analyses were performed with SAS<sup>®</sup> version 9.1.3 (SAS Institute 2002). Data from all years were pooled to enable statistical analysis, but isotope ratios of the baseline organism were compared among years (see below). Because  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ , and C:N of fish are often related to body size, fork length was included as a covariate in analyses of these variables. Whenever size-adjusted least-squared means were calculated, we used 650 mm fork length as the covariate level of comparison for lake trout, 400 mm for lake whitefish, 300 mm for resident and pre-smolt Arctic charr, 270 mm for cisco, 100 mm for fourhorn sculpin, and 50 mm for ninespine stickleback. These sizes were within the captured range of sizes in each lake. Homogeneity of variance was assessed by examination of residual plots. Testing of residuals was achieved with Kolmogorov–Smirnov and Shapiro–Wilk statistics. Alpha was set at 0.05.

When  $\delta^{15}\text{N}$  is compared among lakes, it is necessary to correct for differences at the base of the food web (for example, Post 2002). Isopods, chironomids, mysids, and zooplankton were the only invertebrate taxa captured in all lakes. We did not use zooplankton for baseline calculations because samples were not available for all years that fish were collected. Of the remaining candidates for baseline adjustment, mysids were the most common food item for fishes (H. Swanson, unpubl. data). Also, mysid  $\delta^{13}\text{C}$  ratios were reasonably similar to those of most fish species, mysid  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  ratios did not differ significantly among years (ANOVAs,  $F < 2.39$ ,  $P > 0.11$ ,  $df = 2,22$ ), and mysid  $\delta^{15}\text{N}$  was significantly different among lakes (ANOVA,  $F = 9.03$ ,  $P = 0.0001$ ,  $df = 5,21$ ). Fish  $\delta^{15}\text{N}$  was adjusted for baseline using the following formula:

$$\text{adjusted } \delta^{15}\text{N} (\delta^{15}\text{N}_{\text{adj}}) = \delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{mysid}} \quad (1)$$

where  $\delta^{15}\text{N}_{\text{mysid}}$  was the arithmetic mean mysid  $\delta^{15}\text{N}$  for each lake (all years pooled). This was only done when  $\delta^{15}\text{N}$  was compared among lakes. Within lakes, unadjusted  $\delta^{15}\text{N}$  values were used.



Variation in lipid content among fishes has the potential to confound analyses of  $\delta^{13}\text{C}$  because lipids are relatively depleted in the heavier isotope (Post and others 2007). We found a significant negative relationship between fish  $\delta^{13}\text{C}$  and C:N (linear regression,  $t = -7.69$ ,  $P < 0.0001$ ,  $df = 1,469$ ). Muscle  $\delta^{13}\text{C}$  values were therefore adjusted for lipid content using the following formula (Post and others 2007):

$$\text{adjusted } \delta^{13}\text{C} (\delta^{13}\text{C}_{\text{adj}}) = \delta^{13}\text{C} - 3.32 + 0.99 \times \text{C:N} \quad (2)$$

After adjustment, there was no relationship between  $\delta^{13}\text{C}$  and C:N (linear regression,  $t = -1.04$ ,  $P = 0.30$ ,  $df = 1,469$ ).

Fish condition was estimated using Fulton's condition factor ( $K$ ) (Ricker 1975), and was calculated for each fish as:

$$K = W \times 100/L^3 \quad (3)$$

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

Biplots of  $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$  were qualitatively examined to determine if lake trout likely feed on resident and pre-smolt Arctic charr or anadromous Arctic charr, and whether pre-smolt and resident Arctic charr show overlap in resource use with other forage species (indicated by overlap in isotope ratios), such as cisco, lake whitefish, and/or nine-spine stickleback. Isotope ratios were compared among forage fishes in each lake using an analysis of variance (ANOVA; no size covariate because species did not often overlap in size). Pairwise differences were evaluated with a post-hoc Dunnett's test; resident and pre-smolt Arctic charr were set as the control. The largest fish recorded in a lake trout stomach was 502 mm (H. Swanson, unpubl. data). Thus, resident Arctic charr larger than 500 mm were excluded from this analysis.

For lake trout and forage fish species that showed overlap in isotope ratios with resident and pre-smolt Arctic charr,  $\delta^{15}\text{N}_{\text{adj}}$ ,  $\delta^{13}\text{C}_{\text{adj}}$ , and C:N ratios were compared among lakes with analyses of covariance (ANCOVA; fork length covariate), and condition was compared among lakes with an ANOVA. Pairwise differences were assessed with a post-hoc Tukey's test and interpreted in the context of presence or absence of partially anadromous Arctic charr populations. Although not a direct test of our research questions, this approach was used as an initial exploratory analysis because of low replication within each lake treatment ( $n = 3$  for each of Arctic charr and no Arctic charr); pairwise differences had the potential to yield more infor-

mation than  $t$ -tests. If pairwise differences indicated a charr-induced effect, least-squares means (LSmeans) were calculated at a standardized size for each lake and compared between lake types (with and without Arctic charr) with a  $t$ -test. Pairwise differences were also interpreted in the context of whether any anadromous fishes were present [that is, comparing Glenn (anadromous lake trout present but no anadromous Arctic charr), Hovaktok, Nauyuk, and Roberts lakes to Doris and Patch lakes].

To determine if isotope ratios were enriched (via marine subsidy) in lakes with anadromous Arctic charr, species-specific fish  $\delta^{15}\text{N}_{\text{adj}}$  and  $\delta^{13}\text{C}_{\text{adj}}$  ratios were compared among lakes with an ANCOVA (except lake trout and ninespine stickleback; tested above), and taxa-specific invertebrate  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  ratios were compared among lakes with an ANOVA. Pairwise differences were interpreted in the context of presence/absence of anadromous Arctic charr and presence/absence of anadromous fishes in general (that is, including Glenn Lake as a lake with anadromous fishes).

Absolute growth rates for lake trout were calculated by dividing both fork length and mass by age. Absolute growth rates for length and mass were then compared among lakes with an ANOVA. If pairwise differences indicated a charr-induced effect, means for each lake were compared between lake types (with and without Arctic charr) with a  $t$ -test. Pairwise differences were also interpreted in the context of whether any anadromous fishes were present.

Linear distance metrics were applied to stable isotope data to assess whole food web structure (Layman and others 2007). Because number and type of species present may affect the calculated metrics, this analysis was restricted to Nauyuk, Roberts, Doris, and Patch lakes (two lakes with anadromous Arctic charr and two lakes without). All lakes contained resident lake trout, lake whitefish, cisco, ninespine stickleback, mysids, isopods, chironomids, and zooplankton. Roberts and Nauyuk lakes also contained anadromous Arctic charr and anadromous lake trout, but only pre-smolt and resident Arctic charr and resident lake trout were used in metric calculations. Hovaktok Lake was excluded because the only forage fish species present was fourhorn sculpin. Glenn Lake was excluded because it contained fourhorn sculpin in addition to the other forage species and was the only lake that contained anadromous lake trout but no anadromous Arctic charr (Swanson and others 2010). Because Glenn Lake was excluded from this analysis, we could not determine

an independent effect of the presence of anadromous Arctic charr; results were interpreted as effects of both anadromous Arctic charr and anadromous lake trout on food web structure.

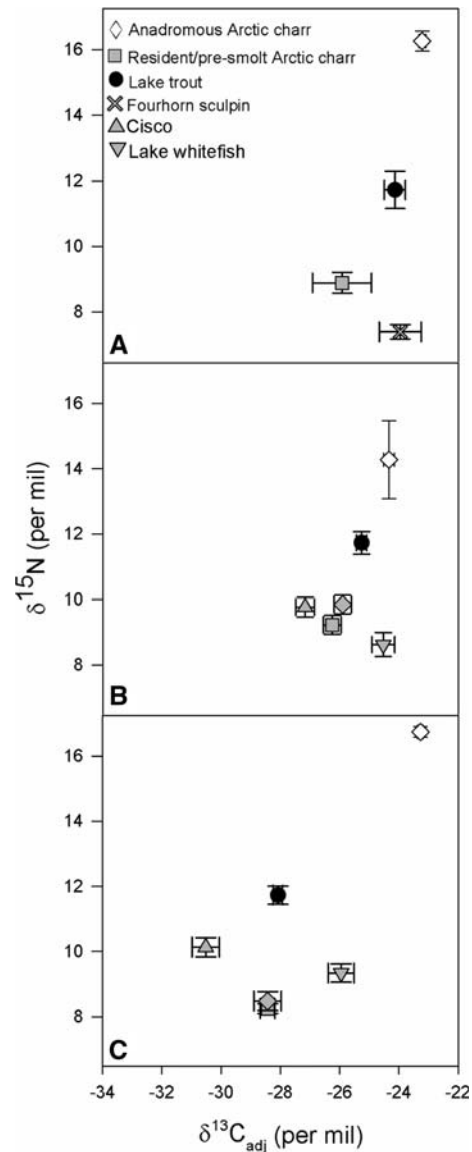
Total area (convex hull encompassing most divergent points in  $\delta^{15}\text{N}$ – $\delta^{13}\text{C}$  space), CR, NR, CD, NND, and STDNND were calculated for each of the four food webs according to Layman and others (2007). For fish, LSmean  $\delta^{13}\text{C}_{\text{adj}}$  and LSmean  $\delta^{15}\text{N}$  at species-specific standardized sizes were used in metric calculations. Delta $^{15}\text{N}$  was not adjusted for baseline because invertebrates, including mysids, were included in metric calculations. For invertebrates, lake-specific mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were used in metric calculations. Qualitative comparisons among lakes were made in the context of presence/absence of anadromous Arctic charr and anadromous lake trout.

Distance metrics were applied to lake trout populations in Doris, Patch, Nauyuk, and Roberts lakes (same lakes used for whole food web analysis) to compare isotope niche and inter-individual differences in isotope ratios. Metrics were calculated using residual values of  $\delta^{13}\text{C}_{\text{adj}}$  and  $\delta^{15}\text{N}$ , after variation due to sex (except for ninespine stickleback; sex was not determined in this species), age, and fork length was removed using general linear models; these variables can affect inter-individual variation in isotope ratios (for example, Matthews and Mazumder 2004). Metrics calculated for each lake trout population were compared to metrics calculated for each prey community, defined as forage fishes and invertebrates, because range and distribution of prey resources also affect inter-individual variation in predator isotope ratios (for example, Matthews and Mazumder 2004). Qualitative comparisons among lakes were made in the context of presence/absence of anadromous Arctic charr and lake trout.

## RESULTS

### Stable Isotope Ratios, C:N, Growth, and Fish Condition

Qualitative evaluation of  $\delta^{15}\text{N}$ – $\delta^{13}\text{C}_{\text{adj}}$  biplots for lake trout and forage fish species in Hovaktok, Nauyuk, and Roberts lakes (with Arctic charr) indicate that lake trout do not appear to use the same food resources as resident and pre-smolt Arctic charr, and that lake trout likely feed on a variety of forage fishes, including resident and pre-smolt Arctic charr (Figure 2A, B, C). Anadromous Arctic charr were not within the mixing space of lake trout (Figure 2A, B, C); thus, it does not ap-



**Figure 2.** Mean  $\pm$  SE  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}_{\text{adj}}$  for anadromous Arctic charr (*white diamond*), resident lake trout (*black circle*), cisco (*gray triangle*), lake whitefish (*gray inverted triangle*), ninespine stickleback (*gray diamond*), fourhorn sculpin (*gray X*), and resident and pre-smolt Arctic charr (*gray square*) in Hovaktok (**A**), Nauyuk (**B**), and Roberts (**C**) lakes. Resident and pre-smolt Arctic charr and ninespine stickleback are coincident points in Roberts Lake (**C**). Pairwise differences (Dunnett's test) in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}_{\text{adj}}$  between resident and pre-smolt Arctic charr and other forage species are summarized in Appendix II in supplementary material.

pear that lake trout feed on anadromous Arctic charr. Values of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}_{\text{adj}}$  shown for anadromous Arctic charr in Figure 2A, B, C do not represent fish less than 500 mm (an appropriate forage size), however, because very few captured anadromous Arctic charr were in this size range.

Isotope ratios of resident and pre-smolt Arctic charr were neither consistently nor significantly different from those of other forage fish species (see summary of post-hoc Dunnett's tests in Appendix II in supplementary material) (Figure 2A, B, C). In Hovaktok Lake, resident and pre-smolt Arctic charr had significantly higher  $\delta^{15}\text{N}$  than fourhorn sculpin (only other forage species) ( $t$ -test,  $t = 14.70$ ,  $P = 0.0021$ ,  $df = 1,13$ ), but there was no significant difference in  $\delta^{13}\text{C}_{\text{adj}}$  ( $t$ -test,  $t = 2.61$ ,  $P = 0.1304$ ,  $df = 1,13$ ) (Figure 2A, Appendix II in supplementary material). There were significant differences in  $\delta^{15}\text{N}$  (ANOVAs,  $F > 2.92$ ,  $P < 0.045$ ,  $df > 1,13$ ) and  $\delta^{13}\text{C}_{\text{adj}}$  (ANOVAs,  $F > 9.55$ ,  $P < 0.0001$ ,  $df > 3,43$ ) among forage fish species in Nauyuk and Roberts lakes (Appendix II in supplementary material). Resident and pre-smolt Arctic charr had significantly more enriched  $\delta^{13}\text{C}_{\text{adj}}$  than cisco and significantly less enriched  $\delta^{13}\text{C}_{\text{adj}}$  than lake whitefish, but differences in  $\delta^{15}\text{N}$  between resident and pre-smolt Arctic charr and other forage species were not consistent between the two lakes (Appendix II in supplementary material, Figure 2B, C). Resident and pre-smolt Arctic charr appear to use very similar food resources to ninespine stickleback in lakes where both species are present (that is, Nauyuk and Roberts lakes); these species had very similar isotope ratios (Figure 2B, C).

Lake trout  $\delta^{15}\text{N}_{\text{adj}}$  and  $\delta^{13}\text{C}_{\text{adj}}$  differed significantly among lakes (ANCOVAs,  $F > 6.29$ ,  $P < 0.0001$ ,  $df = 5,114$ ), but there was no pattern with respect to the presence or absence of Arctic charr (Figure 3). There was also no pattern in lake trout  $\delta^{15}\text{N}_{\text{adj}}$  and  $\delta^{13}\text{C}_{\text{adj}}$  with respect to presence/absence of anadromous fishes in general (that is, comparing Glenn, Hovaktok, Nauyuk, and Roberts lakes to Doris and Patch lakes) (Figure 3).

Lake trout C:N and condition varied significantly among lakes (ANCOVA (C:N),  $F = 2.93$ ,  $P = 0.016$ ,  $df = 5, 111$ , Figure 4; ANOVA (condition),  $F = 9.54$ ,  $P < 0.0001$ ,  $df = 5,125$ , Figure 5), and pairwise differences indicated that both were higher in lakes with anadromous Arctic charr than in lakes without anadromous Arctic charr (Tukey's test,  $P < 0.05$ ).  $T$ -tests (on LSmeans) showed that lake trout C:N and condition were significantly higher in lakes with anadromous Arctic charr ( $t \geq 3.14$ ,  $P \leq 0.035$ ,  $df = 4$ ). Absolute linear growth rates for lake trout did not differ significantly among lakes (ANOVA,  $F = 1.21$ ,  $P = 0.31$ ,  $df = 5,123$ ) (Table 1). Absolute mass growth rates for lake trout differed significantly among lakes (ANOVA,  $F = 13.4$ ,  $P < 0.0001$ ,  $df = 5,122$ ), but pairwise differences did not indicate a pattern with respect

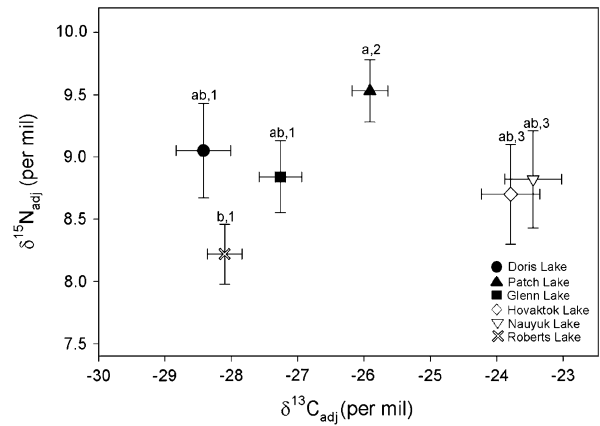
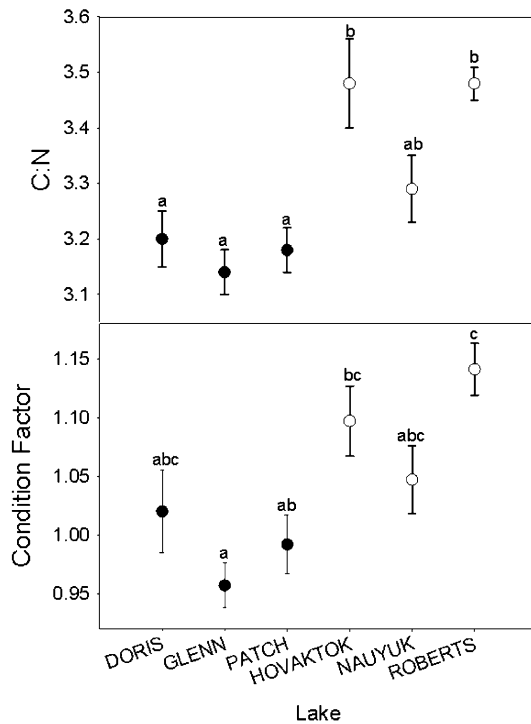


Figure 3. LS Mean  $\delta^{15}\text{N}_{\text{adj}}$  and  $\delta^{13}\text{C}_{\text{adj}} \pm \text{SE}$  (at 650 mm) for resident lake trout in Doris lake trout in Doris (black circle), Glenn (black square), Patch (black triangle), Hovaktok (white diamond), Nauyuk (white inverted triangle), and Roberts (white X) lakes. Black symbols indicate lakes without Arctic charr and white symbols indicate lakes with Arctic charr. Pairwise differences (Tukey's tests) are indicated by letters ( $\delta^{15}\text{N}_{\text{adj}}$ ) and numbers ( $\delta^{13}\text{C}_{\text{adj}}$ ).

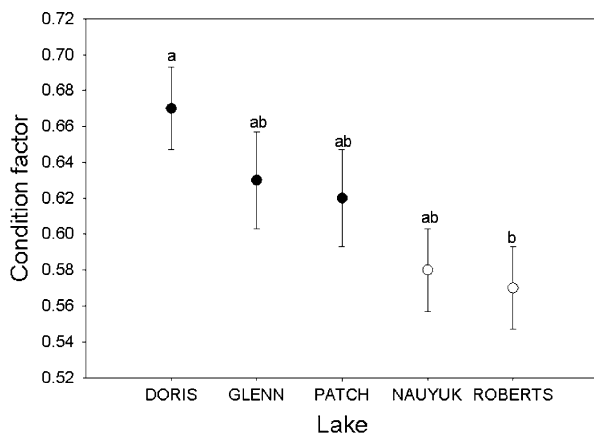
to presence/absence of anadromous Arctic and/or anadromous lake trout (Table 1; Tukey's test,  $P < 0.05$ ).

As mentioned above, qualitative assessment of isotope overlap between forage fish species revealed that ninespine stickleback may use similar food resources to resident and pre-smolt Arctic charr (Figure 2). Ninespine stickleback  $\delta^{15}\text{N}_{\text{adj}}$ ,  $\delta^{13}\text{C}_{\text{adj}}$ , C:N, and condition differed significantly among lakes [ANCOVAs (all except condition),  $F > 15.78$ ,  $P \leq 0.0001$ ,  $df = 4, \geq 50$ ; ANOVA (condition),  $F = 2.95$ ,  $P = 0.027$ ,  $df = 4,61$ ]. Pairwise differences for  $\delta^{15}\text{N}_{\text{adj}}$ ,  $\delta^{13}\text{C}_{\text{adj}}$ , and C:N did not indicate differences between lakes with and without anadromous Arctic charr and/or anadromous lake trout (see Appendix III in supplementary material for  $\delta^{15}\text{N}_{\text{adj}}$  and  $\delta^{13}\text{C}_{\text{adj}}$  LSmeans), but pairwise differences (Tukey's test,  $P < 0.05$ ; Figure 5) and a Satterthwaite (unequal variance)  $t$ -test indicated that ninespine stickleback had significantly lower condition in lakes where Arctic charr were present ( $t = 3.93$ ,  $P = 0.03$ ,  $df = 2.93$ ).

Cisco and lake whitefish  $\delta^{15}\text{N}_{\text{adj}}$  and  $\delta^{13}\text{C}_{\text{adj}}$  differed significantly among lakes (ANCOVAs,  $F \geq 2.88$ ,  $P \leq 0.03$ ,  $df \geq 4,42$ ), but pairwise differences did not indicate differences between lakes with and without anadromous Arctic charr and/or anadromous lake trout (see Appendix III in supplementary material for LSmeans and pairwise comparisons). For the four invertebrate taxa caught in all lakes (mysids, isopods, chironomids, and



**Figure 4.** LSmean C:N (at 650 mm) (A) and LSmean condition factor (B) ±SE for resident lake trout in each of the study lakes. Black symbols indicate lakes without Arctic charr and white symbols indicate lakes with Arctic charr. Pairwise differences (Tukey’s test) are indicated with letters.



**Figure 5.** LSmean condition factor ±SE for ninespine stickleback in Doris, Glenn, Patch, Nauyuk, and Roberts lakes. Black symbols indicate lakes without Arctic charr and white symbols indicate lakes with Arctic charr. Pairwise differences (Tukey’s test) are indicated with letters.

zooplankton), there were significant among-lake differences in  $\delta^{15}\text{N}$  for zooplankton, chironomids, and mysids (ANOVAs,  $F \geq 4.68$ ,  $P \leq 0.0046$ ,

$df \geq 5,12$ ). There were significant among-lake differences in  $\delta^{13}\text{C}$  for all taxa (ANOVAs,  $F \geq 6.01$ ,  $P \leq 0.0008$ ,  $df \geq 5,10$ ). Pairwise differences did not indicate differences between lakes with and without anadromous Arctic charr and/or anadromous lake trout, however (see means in Appendix III in supplementary material). Together with earlier among-lake comparisons of  $\delta^{15}\text{N}_{\text{adj}}$  and  $\delta^{13}\text{C}_{\text{adj}}$  for lake trout and ninespine stickleback, these analyses suggest that if anadromous Arctic charr or anadromous lake trout impart a marine subsidy to freshwater lakes, it may not be detectable with stable isotope analysis.

### Linear Distance Metrics Using Stable Isotope Data

Qualitative comparisons of metrics applied to whole food webs revealed that food webs occupied less area and were more isotopically redundant in lakes with anadromous Arctic charr and lake trout. TA, CD, NND, and NR were lower in lakes with anadromous Arctic charr and lake trout (Table 2, Figure 6). Standard deviation of NND and CR showed no pattern with respect to presence/absence of anadromous fishes (Table 2).

Linear distance metrics indicated that lake trout populations occupied more isotope space and had greater inter-individual variation in lakes with anadromous fishes; TA, NND, STDNND, and NR were larger (Table 2, Figure 7). This occurred despite the fact that TA, NND, and CD for prey communities (forage fish and invertebrates) were smaller in lakes with anadromous fishes (Table 2, Figure 7). Due to the low number of lake replicates ( $n = 2$  for each treatment), linear distance metric results could not be tested statistically.

## DISCUSSION

### Comparison of Isotope Ratios Between Lakes With and Without Anadromous Fishes

We found no isotopic evidence that lake trout, forage fishes, or any invertebrate taxa were feeding on marine-derived organic matter or that marine-derived nutrients had been re-mineralized and incorporated into freshwater food webs. Although stable isotope ratios differed significantly among lakes for most species and taxa analyzed, pairwise differences did not indicate that anadromous Arctic charr or anadromous lake trout were imparting a marine subsidy to lakes where they were present. This is in contrast to previous research conducted



**Table 1.** Absolute Growth Rates for Resident Lake Trout in Each of the Study Lakes

Lake	Absolute growth rate (mm y <sup>-1</sup> )	Standard error	Absolute growth rate (g y <sup>-1</sup> )	Standard error	Pairwise differences
Doris	28	1.11	104	1.21	a
Glenn	25	1.06	29	1.11	c
Patch	28	1.08	83	1.15	ab
<i>Hovaktok</i>	23	1.09	45	1.17	bc
<i>Nauyuk</i>	22	1.09	45	1.17	bc
<i>Roberts</i>	27	1.07	75	1.13	ab

**Table 2.** Metrics Calculated for Whole Food Webs, Prey Communities, and Lake Trout Populations

	Lake	Metric						
		N <sup>a</sup>	TA	NND	STDNND	NR	CR	CD
Food webs	Doris	8	40.9	2.39	1.26	9.33	6.38	3.39
	Patch	8	46.4	2.62	1.70	9.63	8.42	3.53
	<i>Nauyuk</i>	9 <sup>b</sup>	34.6	1.83	1.60	8.95	8.11	3.19
	<i>Roberts</i>	9 <sup>b</sup>	25.6	1.92	1.20	8.26	6.56	2.45
Lake trout	Doris	10	0.25	0.21	0.18	0.35	1.66	0.29
	Patch	19	3.55	0.27	0.17	1.83	3.69	1.05
	<i>Nauyuk</i>	16	4.51	0.43	0.30	3.05	2.57	0.84
	<i>Roberts</i>	25	5.92	0.35	0.38	2.47	4.75	0.82
Prey items	Doris	7	28.4	2.44	1.06	5.46	6.38	3.06
	Patch	7	32.2	2.63	1.80	5.93	8.42	3.28
	<i>Nauyuk</i>	8 <sup>b</sup>	23.5	1.67	1.55	5.56	8.11	2.93
	<i>Roberts</i>	8 <sup>b</sup>	19.4	1.82	1.19	5.55	6.56	2.20

Lakes in italics contain anadromous Arctic charr.

<sup>a</sup> N represents numbers of individual lake trout and numbers of prey species.

<sup>b</sup> The additional prey species is resident and pre-smolt Arctic charr.

on habitats that support semelparous anadromous fishes (for example, Kline and others 1990; Bilby and others 1996), or other iteroparous anadromous fishes, such as Atlantic salmon (*Salmo salar*) and alewife (*Alosa pseudoharengus*) (Jardine and others 2009; Walters and others 2009). It is possible that we did not detect MDN with stable isotope analysis because samples were collected approximately 10 months after the last salmonid spawning event and approximately 2 months after fry emergence, and isotopic turnover may have diluted the marine signal. For the coregonine forage fishes and resident lake trout in this study, however, turnover is likely at least one year (for example, Hesslein and others 1993; MacAvoy and others 2001), and may be much longer, because growth is very slow at northern latitudes.

It is possible that isotopic turnover in sampled fishes was too slow to detect a marine signal. MacAvoy and others (2001) found that although blue catfish (*Ictalurus furcatus*) feed on anadromous *Alosa* species during annual *Alosa* spawning runs,

isotopic enrichment is not observed in catfish due to slow isotopic turnover and high inter-individual variability in catfish isotope signatures. These authors suggest that importance of ephemeral prey items (such as marine-derived eggs and fry) in diet may be underestimated when isotopic turnover of predators is slow. Isotopic turnover of sampled invertebrate species and ninespine stickleback was likely faster than that for resident lake trout, lake whitefish, and cisco. If slow turnover in these latter fishes was masking isotopic evidence for MDN, we would expect to see evidence of MDN in isotope ratios from invertebrates and ninespine stickleback. We did not find this, however.

It is possible that MDN are only detectable in areas adjacent to or directly in spawning grounds used by anadromous Arctic charr or anadromous lake trout. We studied relatively large lakes, and samples were collected opportunistically throughout the lakes. Also, it is possible that MDN are more likely to be detected in years when returns of anadromous fish are large and spawning aggrega-

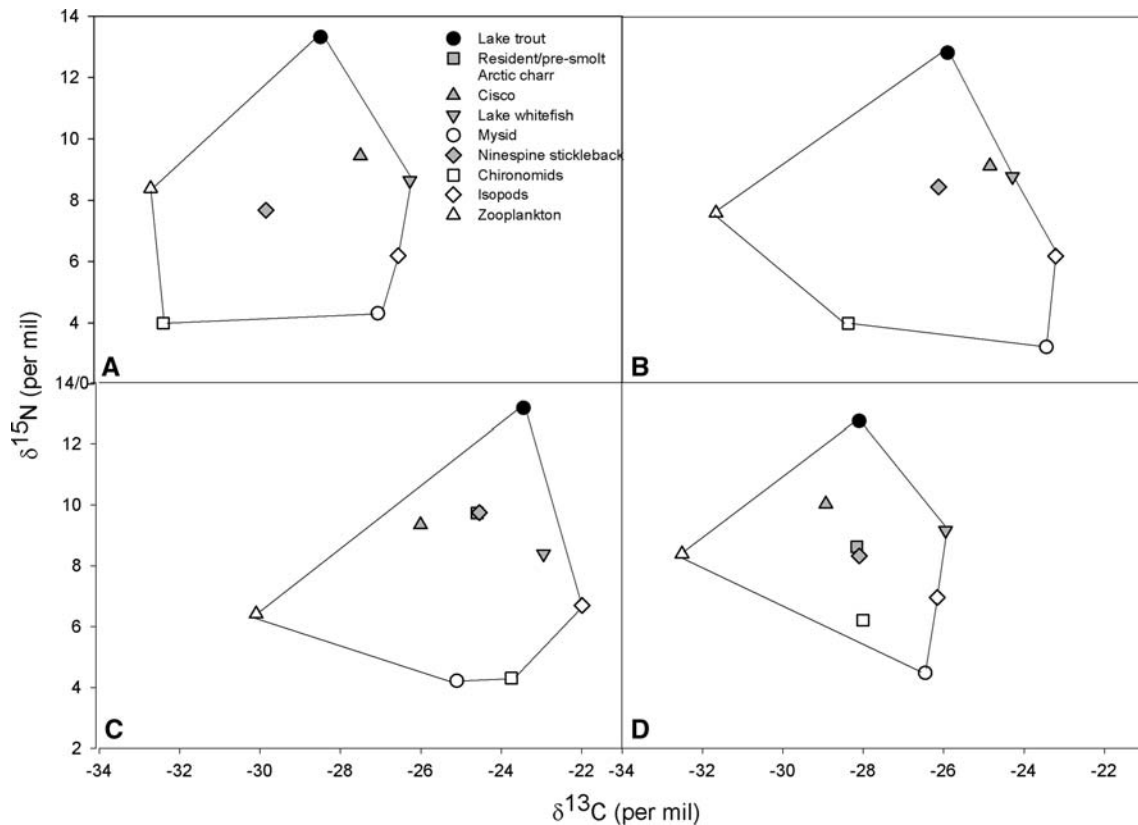


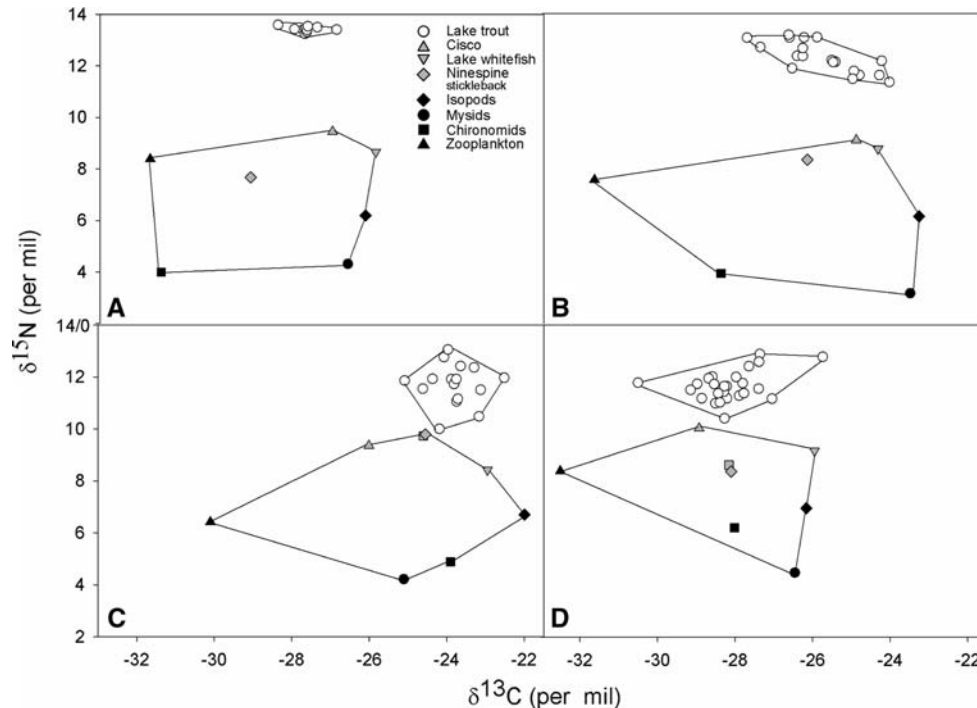
Figure 6. Illustration of food webs in  $\delta^{15}\text{N}$ – $\delta^{13}\text{C}$  space in Doris (A; no anadromous fish), Patch (B; no anadromous fish), Nauyuk (C; anadromous fish), and Roberts (D; anadromous fish) lakes. Each symbol represents LSmean (fish) or mean (invertebrate) values for resident lake trout (*black circle*), lake whitefish (*gray inverted triangle*), cisco (*gray triangle*), ninespine stickleback (*gray diamond*), resident and pre-smolt Arctic charr (*gray square*), isopods (*white diamond*), mysids (*white circle*), chironomids (*white square*), and zooplankton (*white triangle*). Polygons illustrate convex hulls used in TA calculations.

tions correspondingly dense (Jardine and others 2009). In a previous study, Swanson and Kidd (2009) found that the absolute amount of MDN delivered by anadromous Arctic charr can vary widely between years and that, in some years, migrations of anadromous Arctic charr actually result in net export of nutrients from lakes. In addition, Johnson (1989) found that the number of returning anadromous Arctic charr to Nauyuk Lake varied between approximately 1000 and 11,000 individuals (per year) during eight years of monitoring. Further research on potential effects of MDN delivered by anadromous Arctic charr and/or lake trout should take place over several years, at several times during the year, and include sampling sites near spawning areas. To better predict effects of anadromous fish presence on isotope ratios of freshwater biota, relative abundance and density of all fish species should also be determined. We found that anadromous Arctic charr represented 36–88% of all Arctic charr captured in Hovaktok, Nauyuk, and Roberts lakes, whereas anadromous

lake trout represented 14–42% of all lake trout captured in Glenn, Hovaktok, Nauyuk, and Roberts lakes (Swanson and others 2010). Relative abundance of Arctic charr, lake trout, and forage fishes could not be calculated in this study, however, because sampling time, sampling gear, and sampled habitats were not standardized among lakes.

### Effects of Partially Anadromous Arctic Charr on Fish C:N, Growth, and Condition

It did not appear that any of the life history types of Arctic charr used similar food resources to resident lake trout. Resident and pre-smolt Arctic charr were within the isotope mixing space of resident lake trout and were a likely prey item for resident lake trout, but this could not be confirmed because resident and pre-smolt Arctic charr did not have consistently different stable isotope ratios from other forage fishes. Anadromous Arctic charr were not within the mixing space of resident lake trout



**Figure 7.** Illustration of resident lake trout populations and prey communities in  $\delta^{15}\text{N}$ – $\delta^{13}\text{C}$  space for Doris (**A**; no anadromous fish), Patch (**B**; no anadromous fish), Nauyuk (**C**; anadromous fish), and Roberts (**D**; anadromous fish) lakes. Values for individual lake trout (*white circles*) are residual  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}_{\text{adj}}$  (see methods), values for forage fishes (*gray symbols*) are lake-specific LSmean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}_{\text{adj}}$ , and values for invertebrates (*black symbols*) are lake-specific mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ . Polygons represent TA calculations for resident lake trout populations (*white circles*) and prey communities (*gray and black symbols*). Prey communities included cisco (*gray triangle*), lake whitefish (*gray inverted triangle*), ninespine stickleback (*gray diamond*), resident and pre-smolt Arctic charr (*gray square*, **C** and **D**), isopods (*black diamond*), chironomids (*black square*), mysids (*black circle*), and zooplankton (*black triangle*).

and did not appear to be an important prey source, but further isotope analyses on small, forage-sized anadromous Arctic charr are necessary to confirm this finding.

Isotope biplots revealed that resident and pre-smolt Arctic charr and ninespine stickleback likely rely on similar food resources. Consistent with this, ninespine stickleback condition was significantly lower in lakes with Arctic charr. Studies of diet overlap (using stomach content analyses) and habitat use are needed to determine how resident and pre-smolt Arctic charr may affect feeding and foraging of sympatric ninespine stickleback, and if interspecific competition between these two species results in lower ninespine stickleback condition. It is possible that resident and pre-smolt Arctic charr force ninespine stickleback into sub-optimal habitats and/or affect size and availability of prey for ninespine stickleback.

Although  $\delta^{13}\text{C}_{\text{adj}}$ ,  $\delta^{15}\text{N}_{\text{adj}}$ , and absolute growth rates in lake trout were not affected by the presence of Arctic charr, other aspects of the species' ecology were affected. Lake trout had significantly higher

C:N (that is, lipid stores) and condition in lakes where Arctic charr were present. Although this is consistent with previous, preliminary results (Swanson and Kidd 2009), resident fishes usually grow faster in lakes with anadromous Pacific salmon (for example, Moore and others 2008). Resident, pre-smolt, and/or anadromous Arctic charr may affect lake trout C:N and condition by functioning as an alternate prey source. It is also possible that lakes with Arctic charr have higher productivity and/or overall prey biomass; this warrants further investigation. Regardless of the cause, higher lake trout C:N and condition may affect fecundity and/or frequency of spawning. Lake trout fecundity increases with fish size (and therefore condition at a specified length). Also, spawning is often intermittent (that is, not every year) in lakes north of  $60^{\circ}\text{N}$ , presumably because energy stores are limited (Martin and Olver 1980). Lake trout in lakes with Arctic charr may spawn more frequently and be relatively more fecund because they are in better condition and have greater lipid stores.

The presence of partially anadromous lake trout in four of the six lakes (confirmed midway through the study) confounded the study design. Because Glenn Lake contained anadromous lake trout but no anadromous Arctic charr, however, we are able to say with some confidence that there is an independent effect of partially anadromous Arctic charr populations on condition of ninespine stickleback, and condition and C:N of resident lake trout; condition in ninespine stickleback was higher in Glenn Lake than in Nauyuk or Roberts Lake, and condition and C:N of resident lake trout was lower in Glenn Lake than in any other lake.

### Effects of Anadromous Fishes on Food Web Structure and Resident Lake Trout Diet Variation

Unlike the analyses presented above, there was no way to separate effects of anadromous Arctic charr from those of anadromous lake trout in comparisons of whole food web structure and inter-individual differences in resident lake trout isotope ratios. Food webs occupied less isotope space and were more isotopically redundant in lakes with anadromous fishes. Increased trophic redundancy (smaller NND) in lakes with anadromous fishes occurred because isotope ratios of ninespine stickleback and resident and pre-smolt Arctic charr were almost identical; this decreased NND for the whole food web. Smaller food web area in lakes with anadromous fishes reflected the fact that fewer species points lay on the exterior of convex hulls (this also led to decreased CD). Also,  $\delta^{15}\text{N}$  range was smaller in lakes with anadromous fishes. This was interesting, because all food webs were defined by the same species (except for non-anadromous Arctic charr) at the same size, and because the comparison of food web structure between lake types was confounded by ecosystem size. Lakes with anadromous fishes were larger, and therefore might be expected to have longer food chains (for example, Post and others 2000). The smaller  $\delta^{15}\text{N}$  range in lakes with anadromous fishes may reflect decreased cannibalism in resident lake trout. This might occur if prey availability is greater in lakes with anadromous fishes, and the prevalence of cannibalism correspondingly lower. Cannibalistic lake trout tended to be the largest, oldest individuals, and they preyed on conspecifics that were up to  $\frac{1}{2}$  of their own length (H. Swanson, unpubl. data). Forage fishes likely had lower  $\delta^{15}\text{N}$  than intermediate-sized lake trout. A decrease in cannibalism could lower mean lake trout  $\delta^{15}\text{N}$ , and thus  $\delta^{15}\text{N}$  range for the whole food web. Relative

abundance of each fish species and stomach content data are needed to test this. Sample size was obviously low for comparisons of whole food web structure ( $n = 2$  for each lake treatment), and further research with increased replication is necessary.

Qualitative comparisons of linear distance metrics among resident lake trout populations showed that lake trout used more isotope space (larger TA), displayed less isotopic redundancy (longer NND), were less evenly packed (higher STDNND), and had a larger range in  $\delta^{15}\text{N}$  in lakes where anadromous fishes were present. In short, resident lake trout showed more inter-individual differences in diet in lakes with anadromous fishes. Sample sizes of lake trout were not equal among lakes, but there were no systematic differences in sample size between lakes with and without anadromous fishes.

Greater inter-individual differences in resident lake trout diet did not result from access to more isotopically diverse prey in lakes with anadromous fishes. Prey communities in these lakes occupied less isotope space (smaller TA), and were more isotopically redundant (shorter NND). As discussed above, isotope ratios of resident and pre-smolt Arctic charr were very similar to those of other forage fishes. Increased niche width and greater inter-individual differences in resident lake trout diet were therefore not due to the presence of an additional, isotopically distinct prey source.

The fact that both niche space (TA) and inter-individual differences (NND) in resident lake trout were higher in lakes with anadromous fishes is consistent with the niche variation hypothesis, which states that there is a positive relationship between population niche size and individual specialization (Van Valen 1965). Previous research on Eurasian perch (*Perca fluviatilis*) and threespine stickleback (*Gasterosteus aculeatus*) has shown that niche width and inter-individual variation in diet both increased with intensity of intraspecific competition (Bolnick and others 2007). It is possible that increased intraspecific competition in lakes with anadromous fishes is causing lake trout to show more inter-individual differences in diet. This could be because lakes with anadromous fishes support more lake trout. When anadromous lake trout return from the sea in early fall, intraspecific competition likely increases. Preliminary data show that about 25% of anadromous lake trout flesh is freshwater-derived (H. Swanson, unpubl. data), indicating that there is limited feeding in freshwater after onset of annual marine migrations.

Results of this study have implications for fisheries management in the Arctic; production of



subsistence and commercial fisheries is related to fish condition, and we found that lake trout condition was significantly higher in lakes with anadromous Arctic charr. From an ecological perspective, our results show that anadromous Arctic charr may affect the ecology of sympatric freshwater species in coastal Arctic lakes, but that in contrast to semelparous Pacific salmon species, these effects are mediated through interactions of Arctic charr in the freshwater food web, rather than by transport of MDN.

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