

Quantifying importance of marine prey in the diets of two partially anadromous fishes

Heidi K. Swanson, Karen A. Kidd, and James D. Reist

Abstract: The importance of marine prey sources for partially anadromous fishes has received little study and is complicated by considerable plasticity in life history. We determined proportional contributions of marine, freshwater benthic, and freshwater pelagic prey to anadromous and resident Arctic char (*Salvelinus alpinus*) and lake trout (*Salvelinus namaycush*) from several partially anadromous populations in the Canadian Arctic. Bayesian mixing models (MixSIR) applied to $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ ratios in lake-specific models indicated that marine prey accounted for 90%–91% of anadromous Arctic char diet and 60%–66% of anadromous lake trout diet. When these estimates were combined with proportion of anadromous individuals in partially anadromous populations, marine food sources accounted for 31%–44% of Arctic char population productivity and 16%–26% of lake trout population productivity. Although future research is needed to refine and quantify variability around these estimates, our results will allow better predictions of the effects of anthropogenic stressors on partially anadromous fishes.

Résumé : On a peu étudié l'importance des sources de proies marines pour les poissons partiellement anadromes et cette étude est compliquée par la très grande plasticité des cycles biologiques. Nous avons mesuré les contributions proportionnelles des proies marines, benthiques d'eau douce et pélagiques d'eau douce chez des ombles chevaliers (*Salvelinus alpinus*) et des touladis (*Salvelinus namaycush*) anadromes et sédentaires dans plusieurs populations partiellement anadromes dans l'Arctique canadien. Des modèles de mélange bayésiens (MixSIR) utilisés sur des rapports $\delta^{34}\text{S}$ et $\delta^{13}\text{C}$ dans des modèles spécifiques aux lacs indiquent que les proies marines représentent 90–91 % du régime alimentaire des ombles chevaliers anadromes et 60–65 % du régime alimentaire des touladis anadromes. Une fois ces estimations combinées à la proportion d'individus anadromes dans les populations partiellement anadromes, les sources alimentaires marines expliquent 31–44 % de la productivité de la population d'ombles chevaliers et 16–26 % de la productivité de la population de touladis. Bien qu'il faille des recherches supplémentaires pour préciser et mesurer la variabilité de ces estimations, nos résultats permettent de meilleures prédictions des effets des facteurs anthropiques de stress sur les poissons partiellement anadromes.

[Traduit par la Rédaction]

Introduction

Arctic char (*Salvelinus alpinus*) and lake trout (*Salvelinus namaycush*) are of economic, cultural, and subsistence importance in the Canadian Arctic, and their presence in Arctic lakes affects food web structure, contaminant bioaccumulation, and ecology of sympatric freshwater fishes (Van Oostdam et al. 2003; Swanson and Kidd 2010; Swanson et al. 2010a). Arctic char and lake trout have very plastic life histories, and in the Canadian Arctic, there are partially anadromous populations of both species (e.g., Johnson 1980; Swanson et al. 2010b). In these populations, some individuals remain freshwater residents, whereas others become anadromous after several years of rearing in freshwater. The importance of freshwater and marine food sources to partially

anadromous fish populations has received little study and is thus highly uncertain. This uncertainty complicates fisheries and habitat management and makes it difficult to predict how population viability and persistence will be affected by anthropogenic stressors.

Marine migrations are not obligate in partially anadromous fish populations, and individual fish may change their life history tactic (i.e., anadromous or freshwater resident) to maximize fitness if environmental conditions change (e.g., Nordeng 1983; Jonsson and Jonsson 1993). A preliminary study by Swanson and Kidd (2009) found that marine food sources accounted for ~95% of the diet of four anadromous Arctic char captured from one partially anadromous population, but further research is needed to refine this estimate and verify that it is applicable beyond the one studied popu-

Received 8 September 2010. Accepted 6 July 2011. Published at www.nrcresearchpress.com/cjfas on xx November 2011. J2011-0066

Paper handled by Associate Editor Marc Trudel.

H.K. Swanson.* Canadian Rivers Institute, Department of Biology, University of New Brunswick, 100 Tucker Park Road, Saint John, NB E2L 4L5, Canada; Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada.

K.A. Kidd. Canadian Rivers Institute, Department of Biology, University of New Brunswick, 100 Tucker Park Road, Saint John, NB E2L 4L5, Canada.

J.D. Reist. Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada.

Corresponding author: Heidi K. Swanson (e-mail: heidikswanson@yahoo.ca).

*Present address: Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada.

lation. There are currently no estimates of marine vs. freshwater prey use for partially semi-anadromous lake trout that were recently discovered in the Canadian Arctic (Swanson et al. 2010b). Lake trout are likely not capable of long-term survival in full-strength seawater (Hiroi and McCormick 2007), and evidence from otolith microchemistry suggests that they either make shorter marine migrations or use lower salinity habitats than Arctic char (Swanson et al. 2010b). This may mean that lake trout utilize marine prey sources to a lesser extent than Arctic char.

Stable isotope mixing models can be used to determine relative contributions of marine and freshwater prey (i.e., sources) to predator diets. Stable carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulfur ($\delta^{34}\text{S}$) isotope ratios can be used as tracers because all of these isotope ratios are elevated in marine food sources relative to freshwater food sources (Fry and Sherr 1984; Peterson and Fry 1987). $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ are often more useful than $\delta^{15}\text{N}$ in mixing models because they do not fractionate appreciably with trophic transfer (e.g., Connolly et al. 2004).

Once prey sources, predators of interest, and isotope tracers have been defined, there are a number of stable isotope mixing models that can be employed. One of the more recent models is MixSIR (Moore and Semmens 2008). This Bayesian model can incorporate prior information and account for uncertainty in isotope ratios and isotope fractionation.

The objective of this study was to determine the relative importance of marine and freshwater prey sources to several populations of partially anadromous Arctic char and lake trout in the Canadian Arctic. MixSIR models were used to determine proportional contributions of three prey sources (marine, freshwater benthic, freshwater pelagic) to diets of anadromous and resident fishes of both species. Using these results and previously published data on proportion of anadromous individuals in partially anadromous populations, marine contributions to population productivity were estimated.

Materials and methods

Field sampling

During the open-water seasons of 2006–2008, anadromous and freshwater-resident (i.e., resident) Arctic char and lake trout were captured in four lakes and outflows located near Hope Bay, Nunavut, Canada (68.1°N, 106.6°W; Fig. 1). Anadromous and resident lake trout were captured in Glenn, Roberts, and Nauyuk lakes, whereas anadromous and resident Arctic char were captured in Hovaktok, Nauyuk, and Roberts lakes. Sampling for anadromous fishes took place in late summer and early fall when fishes were moving upstream, whereas sampling for resident fishes occurred throughout the summer. The target sample size was 20 fish/species/lake (anadromous and resident individuals could not be externally identified in most cases). Fishes were captured using a backpack electrofisher (Type 12, Smith-Root Inc., Vancouver, Washington), sinking gill nets (mesh sizes 1.9 to 8.9 cm stretched mesh), and angling. Because we found that $\delta^{34}\text{S}$ ratios differed significantly among lakes (see Results), fish caught in estuaries had to be excluded from further analysis unless their freshwater origin could be independently de-

termined from a tag (for information on tagging studies, see Miramar Hope Bay Ltd. 2005).

Anadromous and resident fishes were differentiated in a previous study using analyses of otolith microchemistry (Swanson et al. 2010b). Because isotopic turnover is likely at least one year in these fishes (e.g., Hesslein et al. 1993; MacAvoy et al. 2001) and may be much longer, anadromous fishes that had not completed at least two continuous marine migrations before capture were excluded from further analysis. Captured fishes were measured (to the nearest millimetre) and weighed (to the nearest gram) in the field and dissected for dorsal muscle tissue. Descriptive statistics on fish length, age, and stomach contents are presented in the online supplementary data (Supplemental Tables S1 and S2).¹

Freshwater food sources (i.e., endmembers in the stable isotope mixing models) were represented by invertebrates. Isopods (*Saduria entomon*) represented a freshwater benthic food source (endmember), whereas zooplankton represented a freshwater pelagic food source (endmember). Isopods and zooplankton were collected from all lakes and from two sites in the marine environment of Melville Sound (Fig. 1). Isopods were collected with kick nets and an Ekman grab in at least two open-water seasons between 2006 and 2008. Between two and 12 replicates were collected from each sampling site. Bulk zooplankton samples were collected in 2008 using horizontal tows with a 153 μm net (0.25 m diameter opening). Three replicates were collected from each lake and from each site in Melville Sound.

Marine food sources were represented by the marine forage fishes capelin (*Mallotus villosus*) and Pacific herring (*Clupea pallasii*). These fishes were noted in several stomachs of anadromous fishes (H. Swanson, unpublished data) and were collected with fyke nets in 2008 from two sites in Melville Sound (Fig. 1). Fishes were measured, weighed, and dissected for dorsal muscle tissue. All samples were frozen within 12 h of collection and processing.

Laboratory analyses

Fish tissue, whole isopods, 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 to form a composite sample. From each lake, two to 12 isopod and zooplankton samples and a minimum of five fish per species – life history type were analyzed for stable C and S isotope ratios. Eight marine forage fishes (four each of Pacific herring and capelin) from Melville Sound were analyzed for stable C and S isotope ratios.

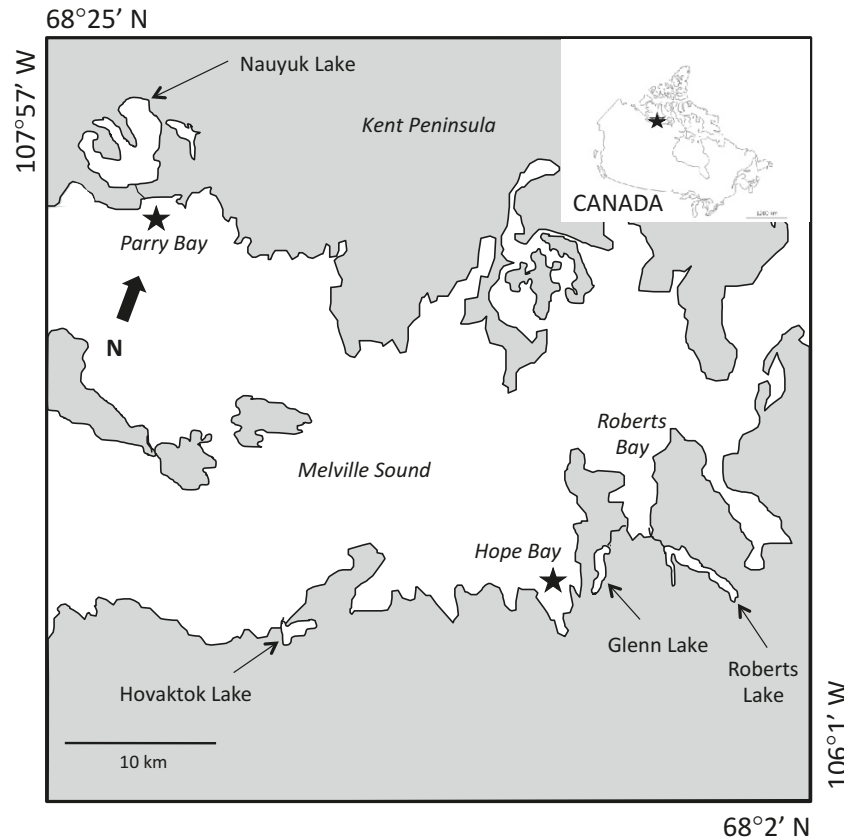
Stable C and S isotope ratios were determined at the University of New Brunswick and Northern Arizona University, respectively, using methods described in Swanson et al. (2010b). Isotope ratios are expressed as parts per mil (‰) delta values ($\delta^{13}\text{C}$, $\delta^{34}\text{S}$) from international standards.

Data analysis

Statistical analyses were performed in SAS (version 9.1.3, SAS Institute Inc. 2002). Alpha (α) was set at 0.05. Before mixing models were run, $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ ratios were compared among endmembers and lakes with analyses of variance

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/f2011-111>.

Fig. 1. Map of the study area in the West Kitikmeot region of Nunavut, Canada. Lake trout (*Salvelinus namaycush*) were collected from Glenn, Roberts, and Nauyuk lakes, and Arctic char (*Salvelinus alpinus*) were collected from Roberts, Hovaktok, and Nauyuk lakes. Stars represent sampling locations in Melville Sound.



(ANOVAs) and t tests. Within anadromous fishes, $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ ratios were compared between species with a mixed model. Fork length and age were tested as covariates, and lake was a random effect. $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ ratios were then compared between anadromous and resident fishes for each lake and species with analyses of covariance (ANCOVA); fork length was the covariate. Relationships between isotope ratios and fish fork length are presented for each species – life history type in the supplementary data.¹

MixSIR models (Moore and Semmens 2008) were run for anadromous and resident Arctic char and lake trout in each lake, except for Arctic char in Nauyuk Lake (see $\delta^{34}\text{S}$ comparisons in Results). Models were run using three endmembers (marine, freshwater benthic, freshwater pelagic) and two isotope tracers ($\delta^{34}\text{S}$ and $\delta^{13}\text{C}$). Marine food sources were represented by pooled isotope data for capelin and Pacific herring, freshwater benthic food sources were represented by isopods, and freshwater pelagic food sources were represented by zooplankton. Fractionation for both $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ was assumed to be $+0.4\text{‰}$ per trophic level (McCutchan et al. 2003). Neither stomach contents nor stable isotope ratios indicated that any of the captured Arctic char were cannibalistic. Arctic char and lake trout were assumed to be 1.5 trophic levels above isopods, two trophic levels above zooplankton, and one trophic level above marine forage fishes. Standard deviation for $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ fractionation was calculated to be 1.87‰ and 1.26‰ per trophic level, respectively (calculated from McCutchan et al. 2003). Priors

were set to be uninformative and 1 000 000 iterations were used for each run. Model diagnostics for MixSIR were acceptable for all runs; more than 1000 posterior draws were used, there were no duplicate draws, the number of unique parameter vectors in the resample was always equal to the number of iterations, and the maximum importance ratio was always less than 0.001 (Semmens and Moore 2008).

Proportional contributions of marine prey were qualitatively compared between fish species and life history types. To estimate marine contributions to population productivity, 95% confidence intervals for proportional contributions of marine prey to anadromous fish diet were multiplied by species-specific proportions of anadromous fishes in each partially anadromous population (calculated from Swanson et al. 2010b).

Results

$\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ ratios

As expected, $\delta^{34}\text{S}$ ratios effectively separated freshwater and marine endmembers, whereas $\delta^{13}\text{C}$ ratios effectively separated freshwater benthic and pelagic endmembers. There was a minimum separation of 14‰ between marine and freshwater endmember $\delta^{34}\text{S}$, and a minimum separation of 7‰ between freshwater benthic and pelagic $\delta^{13}\text{C}$ (Table 1). Both of these differences were significant (ANOVA, $F_{[\geq 2,50]} \geq 9.93$, $P \leq 0.0002$). We observed unexpectedly high among-lake variation in freshwater endmember $\delta^{34}\text{S}$;

Table 1. Mean \pm standard deviation and sample size (N) for $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ ratios determined for marine and freshwater endmembers.

	$\delta^{34}\text{S}$ (‰)			$\delta^{13}\text{C}$ (‰)		
	Freshwater benthic	Freshwater pelagic	Marine	Freshwater benthic	Freshwater pelagic	Marine
Glenn	-8.69 ± 0.72 (6)	-7.62 ± 0.14 (3)	18.02 ± 0.58 (8)	-24.30 ± 2.25 (6)	-32.05 ± 0.04 (3)	-23.62 ± 1.14 (8)
Hovaktok	4.17 ± 0.81 (2)	3.26 ± 0.07 (3)	18.02 ± 0.58 (8)	-24.32 ± 1.63 (5)	-32.03 ± 0.03 (3)	-23.62 ± 1.14 (8)
Nauyuk	-11.11 ± 1.13 (2)	-8.88 ± 0.12 (3)	18.02 ± 0.58 (8)	-22.07 ± 1.35 (6)	-30.10 ± 0.04 (3)	-23.62 ± 1.14 (8)
Roberts	3.21 ± 0.78 (12)	1.85 ± 0.13 (3)	18.02 ± 0.58 (8)	-24.00 ± 1.81 (9)	-32.51 ± 0.12 (3)	-23.62 ± 1.14 (8)

the range was approximately 15‰ (Table 1), and although $\delta^{34}\text{S}$ did not differ between freshwater benthic and pelagic endmembers (t test, $t_{[32]} = 0.73$, $P = 0.47$), among-lake differences were significant (ANOVA, $F_{[3,26]} = 897$, $P < 0.0001$). $\delta^{13}\text{C}$ ratios in freshwater endmembers did not differ among lakes (ANOVA, $F_{[3,34]} = 2.71$, $P = 0.06$).

Qualitative comparisons of $\delta^{34}\text{S}$ between fishes and endmembers revealed that mixing models would likely be successful for all lake–species combinations, with the exception of Arctic char from Nauyuk Lake. In general, $\delta^{34}\text{S}$ ratios for anadromous Arctic char were very close to those of marine endmembers, whereas $\delta^{34}\text{S}$ ratios for resident Arctic char were very close to those of freshwater endmembers (Fig. 2a). In Nauyuk Lake, however, resident Arctic char had $\delta^{34}\text{S}$ ratios that were inconsistent with freshwater feeding (Fig. 2a). Arctic char from Nauyuk Lake were thus not included in mixing models, and possible reasons for high $\delta^{34}\text{S}$ ratios in these resident char are discussed below. Qualitative comparisons also indicated that anadromous lake trout utilized marine prey sources to a lesser extent than anadromous Arctic char (Fig. 2b). Results of a mixed model indicated that anadromous Arctic char had significantly higher $\delta^{34}\text{S}$ ratios than anadromous lake trout ($F_{[1,46]} = 92.3$, $P < 0.0001$). Neither fork length nor age were significant in this model ($F_{[\geq 1,41]} \leq 0.93$, $P \geq 0.28$). In each lake and for both species, $\delta^{34}\text{S}$ ratios were significantly higher in anadromous fishes than in resident fishes (ANCOVAs, $F_{[\geq 1,8]} \geq 52.03$, $P \leq 0.0001$).

As mentioned above, $\delta^{13}\text{C}$ ratios did not separate marine and freshwater endmembers as well as $\delta^{34}\text{S}$ ratios. Marine endmembers, freshwater benthic endmembers, anadromous Arctic char, and anadromous lake trout had similar and relatively enriched $\delta^{13}\text{C}$ (Figs. 2c, 2d). The freshwater pelagic endmember (zooplankton) had more negative $\delta^{13}\text{C}$ ratios, and $\delta^{13}\text{C}$ ratios for resident fishes indicated use of both freshwater benthic and pelagic food sources (Figs. 2c, 2d). Anadromous Arctic char had significantly less negative $\delta^{13}\text{C}$ ratios than resident Arctic char in Nauyuk and Roberts lakes (ANCOVAs, $F_{[\geq 1,16]} \geq 4.66$, $P < 0.05$). There was no significant difference in $\delta^{13}\text{C}$ between anadromous and resident Arctic char in Hovaktok Lake (ANCOVA, $F_{[1,18]} = 0.06$, $P = 0.81$). In all lakes, anadromous lake trout had significantly less negative $\delta^{13}\text{C}$ ratios than resident lake trout (ANCOVAs, $F_{[\geq 1,21]} \geq 9.34$, $P < 0.006$) (Fig. 2d). A mixed model indicated that anadromous lake trout had significantly more enriched $\delta^{13}\text{C}$ than anadromous Arctic char ($F_{[1,55]} = 41.99$, $P < 0.0001$). Similar to the $\delta^{34}\text{S}$ analysis, neither fork length nor age were significant covariates in this model ($F_{[\geq 1,47]} \leq 1.67$, $P \geq 0.2$).

Mixing models

Results from MixSIR models indicated that marine food sources accounted for 90%–91% (median) of anadromous

Arctic char diet and 60%–66% of anadromous lake trout diet (Table 2; Fig. 3). The remainder of anadromous lake trout diet was primarily accounted for by freshwater benthic sources; only 1% of anadromous lake trout diet was estimated to originate from freshwater pelagic sources (Table 2; Fig. 3). Of the small proportion of freshwater food sources contributing to anadromous Arctic char diet, benthic sources were more important than pelagic sources (5%–8% vs. 2%–3%, respectively) (Table 2). In three of four lakes, freshwater benthic prey accounted for a larger proportion (66%–73%) of resident fish diet than freshwater pelagic prey (17%–34%), but in Roberts Lake, freshwater pelagic prey were more important (Table 2; Fig. 3).

At the population level, anadromous Arctic char used more marine food sources than anadromous lake trout. We estimated that marine food sources accounted for 31%–44% of the productivity of sampled Arctic char populations and 16%–26% of the productivity of sampled lake trout populations (Table 3).

Discussion

Isotope ratios in endmember taxa

Consistent with the review of Connolly et al. (2004), marine and freshwater food sources were better separated by $\delta^{34}\text{S}$ than by $\delta^{13}\text{C}$. Using $\delta^{34}\text{S}$ as an isotope tracer was more complex than expected, however, because of high among-lake variability in $\delta^{34}\text{S}$ ratios. This meant that mixing models had to be run separately for each lake.

$\delta^{34}\text{S}$ ratios in freshwater endmembers ranged more than 15‰ among the study lakes, and this was not likely a result of differences in endmember feeding ecology or habitat use. Sulfur does not fractionate appreciably with trophic transfer (e.g., Peterson and Fry 1987), so it is unlikely that observed among-lake variation in $\delta^{34}\text{S}$ resulted from differences in endmember trophic level. It is also unlikely that these differences reflected variation in habitat use. Zooplankton (freshwater pelagic endmember) and isopods (freshwater benthic endmember) did not have significantly different $\delta^{34}\text{S}$. If $\delta^{34}\text{S}$ did not differ significantly between two taxa known to occupy different habitats, it is unlikely that habitat use would differ enough within taxa to explain among-lake variability in $\delta^{34}\text{S}$ ratios. High among-lake variation in freshwater endmember $\delta^{34}\text{S}$ ratios likely reflects variation in sulfate source.

Sources of sulfate to lakes include the surrounding catchment, atmospheric deposition, and anthropogenic inputs (Wetzel 2001). Atmospheric deposition of sulfate is likely similar among lakes (due to the relatively small spatial scale), and none of the lakes has any significant anthropogenic inputs of sulfate. Underlying geology does differ among lakes, but although Hovaktok and Nauyuk lakes have the most similar underlying geology, they also show the greatest differen-

Fig. 2. (a, b) $\delta^{34}\text{S}$ and (c, d) $\delta^{13}\text{C}$ ratios in endmembers and (a, c) anadromous and resident Arctic char (*Salvelinus alpinus*) and (b, d) lake trout (*Salvelinus namaycush*). Plots include ratios for freshwater benthic prey (isopods; shaded squares), freshwater pelagic prey (zooplankton; shaded triangles), marine prey (forage fish; open diamonds), and anadromous (solid circles) and resident fishes (open circles). Points for marine prey and anadromous Arctic char are coincident in (a), and points for freshwater endmembers and resident lake trout are coincident in (b). Marine and freshwater prey items were better separated by $\delta^{34}\text{S}$ than by $\delta^{13}\text{C}$.

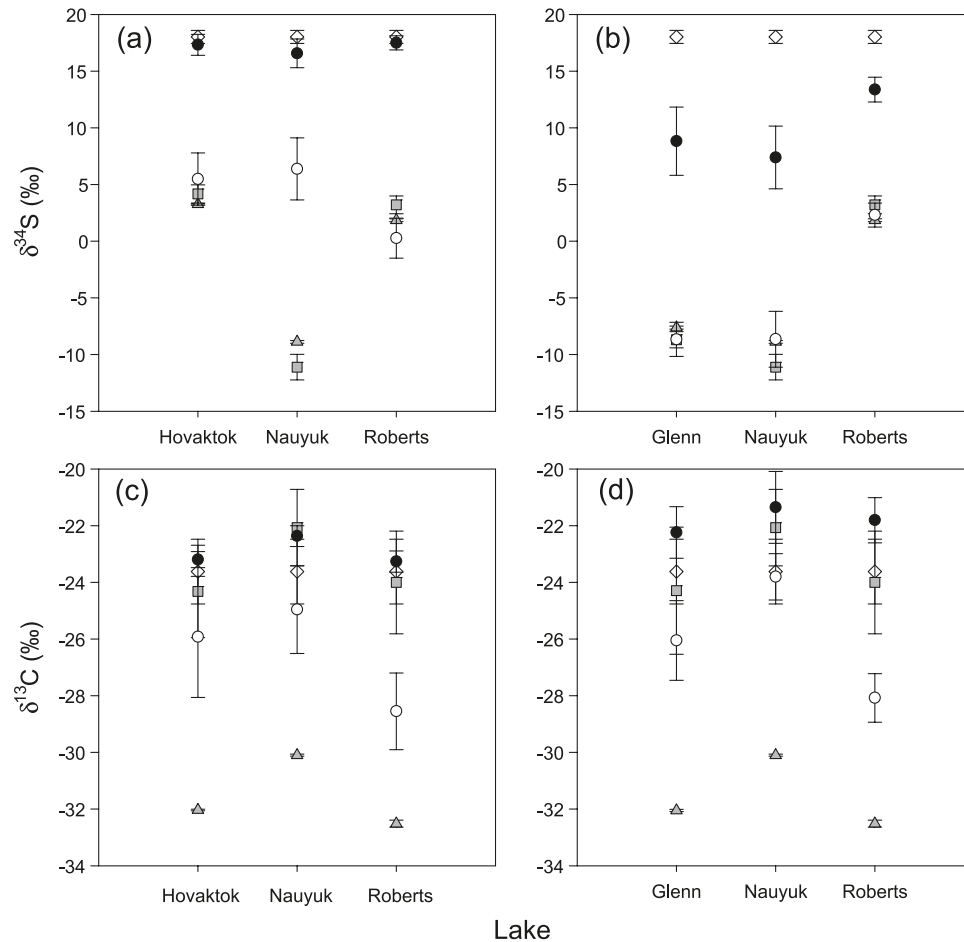


Table 2. Estimates of proportional contributions of food sources to anadromous and resident Arctic char (*Salvelinus alpinus*) and lake trout (*Salvelinus namaycush*).

		N	Marine			Freshwater benthic			Freshwater pelagic		
			Lower 95% CI	Median	Upper 95% CI	Lower 95% CI	Median	Upper 95% CI	Lower 95% CI	Median	Upper 95% CI
Hovaktok	Anadromous Arctic char	15	0.85	0.90	0.95	0.02	0.08	0.13	0	0.02	0.07
	Resident Arctic char	3	0.03	0.1	0.16	0.63	0.73	0.85	0.09	0.17	0.25
Roberts	Anadromous Arctic char	9	0.85	0.91	0.96	0	0.05	0.12	0	0.03	0.09
	Resident Arctic char	24	0	0.01	0.02	0.28	0.36	0.43	0.56	0.63	0.71
Glenn	Anadromous lake trout	9	0.60	0.64	0.67	0.31	0.35	0.39	0	0.01	0.04
	Resident lake trout	34	0	0.004	0.02	0.59	0.66	0.73	0.27	0.34	0.41
Nauyuk	Anadromous lake trout	8	0.57	0.60	0.64	0.33	0.38	0.42	0.01	0.01	0.06
	Resident lake trout	15	0.01	0.05	0.08	0.59	0.67	0.76	0.20	0.29	0.37
Roberts	Anadromous lake trout	6	0.58	0.66	0.73	0.24	0.33	0.41	0	0.01	0.05
	Resident lake trout	23	0	0.02	0.05	0.36	0.43	0.50	0.49	0.55	0.62

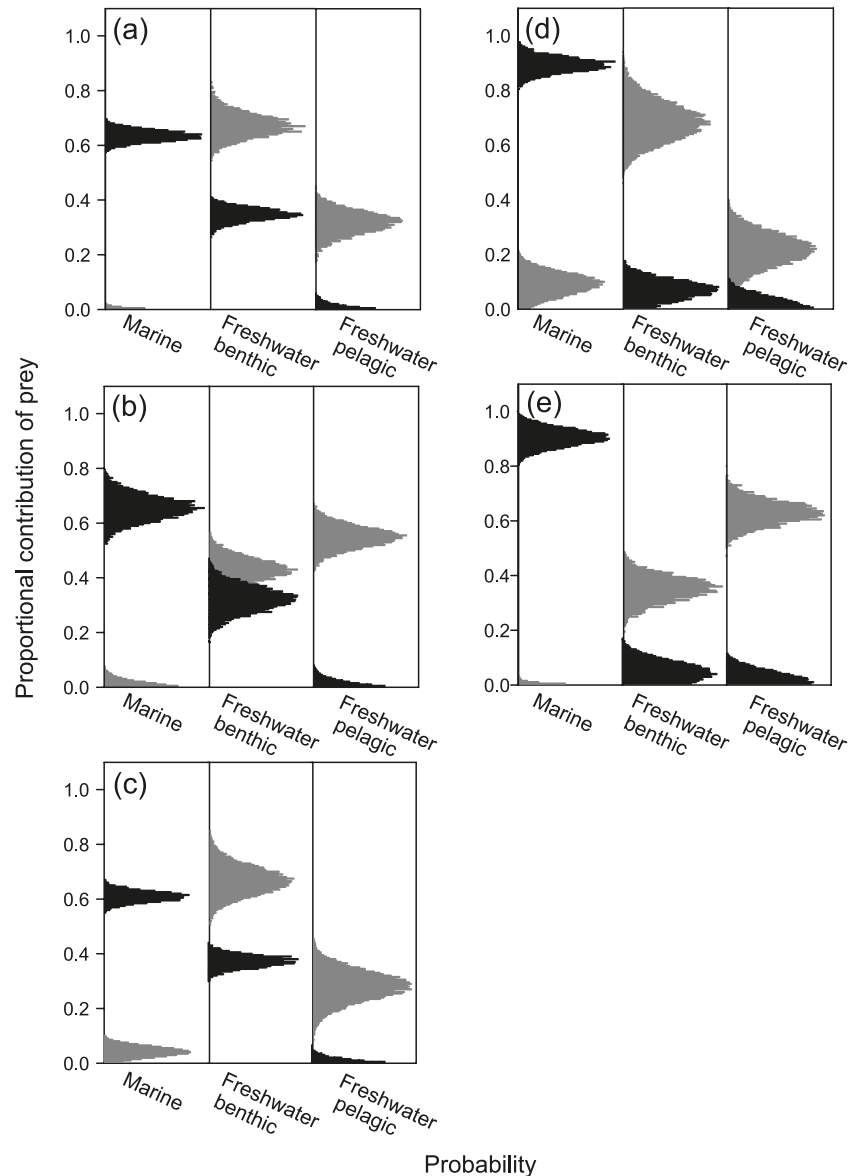
Note: Arctic char, *Salvelinus alpinus*; lake trout, *Salvelinus namaycush*. CI, confidence interval.

ces in endmember $\delta^{34}\text{S}$ ratios (Fraser 1964; Kerr and Knight 1998).

Variation in $\delta^{34}\text{S}$ ratios among lakes may reflect variations in Holocene geomorphology. Approximately 9000 years B.P., the study area was deglaciated and inundated by a marine in-

cursor (Kerr 1994; Kerr and Knight 1998). Water and sediments of the study lakes were of marine origin at the time of isolation and by inference had marine $\delta^{34}\text{S}$ ratios. Variation in $\delta^{34}\text{S}$ ratios among lakes may reflect differences in timing of isolation from marine incursion, relative rates of flushing

Fig. 3. Proportional contributions of marine, freshwater benthic, and freshwater pelagic prey to (a, b, c) anadromous lake trout (*Salvelinus namaycush*) and (d, e) Arctic char (*Salvelinus alpinus*) in (a) Glenn, (b, e) Roberts, (c) Nauyuk, and (d) Hovaktok lakes. Anadromous fishes are represented by solid distributions, whereas resident fishes are represented by shaded distributions. Proportional contributions of marine prey were larger for anadromous Arctic char than for anadromous lake trout. (b, e) Resident fishes in Roberts Lake fed more on freshwater pelagic prey than on freshwater benthic prey. (a, c, d) In other lakes, resident fishes fed more on freshwater benthic prey.



with meteoric waters, differences in depth of marine-origin lake sediments, and differences in concentrations of marine-origin sulfur compounds. Further research is necessary to confirm this. This analysis highlights the importance of determining variation in $\delta^{34}\text{S}$ ratios among freshwater systems before applying mixing models. We also suggest that, similar to $\delta^{15}\text{N}$, $\delta^{34}\text{S}$ ratios may sometimes require baseline correction before statistical analysis.

Differences in isotope ratios between anadromous and resident fishes

Similar to previous studies (Doucett et al.1999; Swanson et al. 2010b) and with the exception of Arctic char in Hovaktok Lake, anadromous Arctic char and lake trout had enriched $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ ratios compared with resident Arctic

char and lake trout. An interspecies comparison revealed that anadromous Arctic char had significantly higher $\delta^{34}\text{S}$ ratios than anadromous lake trout. This is consistent with previous, preliminary results presented for Roberts Lake (Swanson et al. 2010b).

$\delta^{34}\text{S}$ ratios in Arctic char from Nauyuk Lake were unexpectedly high and indicated that resident individuals of this species used a freshwater habitat that was not sampled (i.e., a prey source is missing). Because resident lake trout had similar $\delta^{34}\text{S}$ to freshwater endmembers in Nauyuk Lake, the results for resident Arctic char were not due to sampling or laboratory error. They likely reflect a unique migration strategy used by Arctic char in Nauyuk Lake.

Upstream and downstream migrations of anadromous Arctic char were monitored at Nauyuk Lake during the 1970s

Table 3. Estimates of marine source contributions to population productivity.

		Lower 95% CI	Upper 95% CI	Proportion of anadromous individuals ^a	Marine contributions to population productivity (5%–95%)
Hovaktok	Anadromous Arctic char	0.85	0.95	0.46	0.39–0.44
Roberts	Anadromous Arctic char	0.85	0.96	0.36	0.31–0.35
Glenn	Anadromous lake trout	0.60	0.67	0.26	0.16–0.17
Nauyuk	Anadromous lake trout	0.57	0.64	0.40	0.23–0.26
Roberts	Anadromous lake trout	0.58	0.73	0.30	0.17–0.22

Note: Arctic char, *Salvelinus alpinus*; lake trout, *Salvelinus namaycush*. CI, confidence interval of marine food source contribution.

^aProportion of individuals that are anadromous in partially anadromous populations of Arctic char and lake trout. These estimates were calculated from data presented in Swanson et al. (2010b).

and 1980s by Fisheries and Oceans Canada (Johnson 1989). During the course of this research, no spawning areas for Arctic char were discovered in Nauyuk Lake, and extensive tagging studies revealed that anadromous Arctic char in Nauyuk Lake employ a two-year migration strategy that utilizes Willow Lake, a small, shallow system upstream of Nauyuk Lake, for spawning and rearing. Anadromous Arctic char return from the sea each fall to overwinter in Nauyuk Lake. During the following spring, prespawning adults move upstream to Willow Lake, and spawning occurs that fall. Juveniles hatch and rear in Willow Lake. As smolts, they move through Nauyuk Lake before beginning annual marine migrations (Johnson 1989). High $\delta^{34}\text{S}$ ratios observed in resident Arctic char were therefore likely a reflection of prey $\delta^{34}\text{S}$ ratios in Willow Lake rather than Nauyuk Lake.

Mixing-model results

It appears that resident Arctic char and lake trout use both benthic and pelagic food sources in the study lakes and that there is among-lake variation in habitat and (or) prey use. Previous research has shown that food webs in unproductive Arctic lakes are often supported more by benthic–littoral production than by pelagic production (e.g., Hecky and Hesslein 1995; Karlsson and Byström 2005). As such, we expected freshwater benthic food sources to contribute more to resident fish diet than freshwater pelagic food sources. This was true for Glenn, Hovaktok, and Nauyuk lakes but not for Roberts Lake. In Roberts Lake, pelagic food sources accounted for approximately 60% of resident Arctic char and lake trout diet. Determining and predicting dominant sources of production in Arctic lakes should be a future research priority in the face of increasing fish habitat alteration and northern industrial development.

Although anadromous Arctic char and lake trout may only use marine habitats for 3–6 weeks each year in the Canadian Arctic (e.g., Johnson 1980), the majority of prey consumed by these fishes is of marine origin. Marine food sources accounted for a larger portion of anadromous Arctic char diet than anadromous lake trout diet. Lake trout have less osmoregulatory capacity than many other salmonids, and until very recently, lake trout were thought to be an obligately freshwater species (see Swanson et al. 2010b). It is thus likely that lake trout have lower salinity tolerance than Arctic char and either make shorter marine migrations than Arctic char or migrate to lower salinity habitats than Arctic char. This is consistent with inferences made from otolith microchemistry analyses (Swanson et al. 2010b).

Although it is likely that anadromous lake trout utilize ma-

rine prey sources to a lesser extent than Arctic char, it is also possible that slower turnover rates in anadromous lake trout resulted in lower $\delta^{34}\text{S}$ ratios and lower estimates of marine food source contributions. When organisms switch food sources, the rate of change in isotope ratios depends on tissue turnover rates. Isotopic turnover occurs through both growth and metabolic replacement (e.g., MacAvoy et al. 2001), and tissue turnover rates are faster in fast-growing organisms with high metabolic rates. Anadromous lake trout grow more slowly than anadromous Arctic char (Swanson et al. 2010b). Also, anadromous lake trout have more freshwater-derived tissue to replace than Arctic char because they are larger when they begin marine migrations (Swanson et al. 2010b).

Stomach content analyses may help to confirm whether anadromous lake trout utilize more freshwater food sources than anadromous Arctic char after onset of marine migrations. Unlike anadromous Arctic char (Rikardsen et al. 2003), sexually mature anadromous lake trout appear to feed in freshwater after returning from marine migrations in fall (H. Swanson, unpublished data). If confirmed in the future, this may be explained by the fact that anadromous lake trout have significantly lower lipid stores than anadromous Arctic char (Swanson et al. 2010b). Feeding in freshwater overwinter may thus be an energetic necessity for anadromous lake trout.

Marine prey sources supported between 31% and 44% of partially anadromous Arctic char populations and between 16% and 26% of partially anadromous lake trout populations. These estimates are a starting point and require substantial further investigation. It is likely that importance of marine prey sources varies with lake productivity, marine productivity, ease of marine access for anadromous fishes, and structure of the freshwater fish community. If it had been possible to run mixing models for Arctic char in Nauyuk Lake, marine food sources would likely have accounted for as much as 85% of population productivity. This is because 90% of individuals captured in Nauyuk Lake were anadromous (compared with 46% and 36% in Hovaktok and Roberts lakes, respectively) (Swanson et al. 2010b). Uncertainty and among-lake variation in proportion of anadromous fishes is likely high and is virtually unstudied. Estimating these proportions may be further complicated by the fact that fidelity to natal lakes can be low for anadromous Arctic char (this is unstudied in lake trout) (Gyselman 1994). Also, although the presence of true residents has been confirmed in all of the study lakes (see Swanson et al. 2010b), it is impossible to distinguish presmolts from residents when fishes are young and small. This likely leads to underestimations of the pro-

portion of anadromous individuals in partially anadromous populations. Although it is not currently possible to determine which juvenile Arctic char and lake trout will become anadromous, it might be possible to determine the proportion of juvenile Arctic char and lake trout that had anadromous mothers; a recent study has shown that $\delta^{34}\text{S}$ ratios in otolith cores of *Oncorhynchus nerka* reflect maternal diet and can be used to determine whether fish were born to anadromous sockeye mothers or freshwater kokanee mothers (Godbout et al. 2010).

Arctic char and lake trout are an important subsistence, commercial, and cultural resource in the Canadian Arctic (Van Oostdam et al. 2003), and predicting effects of industrial development and habitat disturbance on these species is of considerable concern to regulators, industry, and northern communities. Partially anadromous fishes such as Arctic char and lake trout show considerable plasticity in life history. This plasticity complicates efforts to quantify use of marine and freshwater habitats and makes it difficult to predict effects of anthropogenic stressors on fish population productivity and persistence. Acquiring better estimates of the proportion (and uncertainty) of anadromous individuals in partially anadromous fish populations should be a priority for future research, along with expanding the spatial scale of the research. Intensive sampling of migrations using two-way fish fences and stable isotope analysis of fish tissues with variable turnover rates could lend insight into timing and duration of marine migrations. Lastly, bioenergetics modeling could complement further mixing-model analysis by providing an alternative method for determining importance of marine food sources to individual fitness and population productivity.

Acknowledgements

Funding was provided by Miramar Mining Corporation, Golder Associates Ltd., the Northern Scientific Training Program, Canadian International Polar Year funding to the project "Climate Change and Variability Effects on Charrs in the Arctic" (J.D. Reist, P.I.), and Natural Sciences and Engineering Research Council of Canada grants to K.A. Kidd (Collaborative Research and Development, Canada Research Chair, and Discovery) and H.K. Swanson (Canada Graduate Scholarship). The Garfield Weston Foundation, the Canadian Northern Studies Trust, and the Arctic Institute of North America provided additional funding for H.K. Swanson. This project was made possible by assistance from S. Noel (Heli Explore), K. Martell, M. Kullman, G. Ash, S. Earle, P. Emery, A. Holzapfel, T. Antill, K. Kristensen, C. Classen, J. Yetman, and A. Mercer. R. Sherlock contributed substantially to the understanding and discussion of local geology and $\delta^{34}\text{S}$ ratios.

References

- Connolly, R.M., Guest, M.A., Melville, A.J., and Oakes, J.M. 2004. Sulfur stable isotopes separate producers in marine food-web analysis. *Oecologia* (Berl.), **138**(2): 161–167. doi:10.1007/s00442-003-1415-0. PMID:14593525.
- Doucett, R.R., Hooper, W., and Power, G. 1999. Identification of anadromous and nonanadromous adult brook trout and their progeny in the Tabusintac River, New Brunswick, by means of multiple-stable-isotope analysis. *Trans. Am. Fish. Soc.* **128**(2): 278–288. doi:10.1577/1548-8659(1999)128<0278:IOAANA>2.0.CO;2.
- Fraser, J.A. 1964. Geological notes on the northeastern District of Mackenzie, Northwest Territories. Geological Survey of Canada Paper 63–40.
- Fry, B., and Sherr, E.B. 1984. $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contrib. Mar. Sci.* **27**: 13–47.
- Godbout, L., Trudel, M., Irvine, J.R., Wood, C.C., Grove, M.J., Schmitt, A.K., and McKeegan, K.D. 2010. Sulfur isotopes in otoliths allow discrimination of anadromous and non-anadromous ecotypes of sockeye salmon (*Oncorhynchus nerka*). *Environ. Biol. Fishes.* **89**(3–4): 521–532. doi:10.1007/s10641-010-9689-7.
- Gyselman, E.C. 1994. Fidelity of anadromous Arctic char (*Salvelinus alpinus*) to Nauyuk Lake, N.W.T., Canada. *Can. J. Fish. Aquat. Sci.* **51**(9): 1927–1934. doi:10.1139/f94-194.
- Hecky, R.E., and Hesslein, R.H. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *J. N. Am. Benthol. Soc.* **14**(4): 631–653. doi:10.2307/1467546.
- Hesslein, R., Hallard, K., and Ramlal, P. 1993. Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}\text{S}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$. *Can. J. Fish. Aquat. Sci.* **50**(10): 2071–2076. doi:10.1139/f93-230.
- Hiroi, J., and McCormick, S.D. 2007. Variation in salinity tolerance, gill Na^+/K^+ -ATPase, $\text{Na}^+/\text{K}^+/\text{2Cl}^-$ cotransporter and mitochondria-rich cell distribution in three salmonids *Salvelinus namaycush*, *Salvelinus fontinalis* and *Salmo salar*. *J. Exp. Biol.* **210**(6): 1015–1024. doi:10.1242/jeb.002030. PMID:17337714.
- Johnson, L. 1980. The Arctic char, *Salvelinus alpinus*. In Charrs, salmonid fishes of the genus *Salvelinus*. Edited by E.K. Balon. Dr. W. Junk Publishers, The Hague, Netherlands. pp. 15–98.
- Johnson, L. 1989. The anadromous Arctic char (*Salvelinus alpinus*) of Nauyuk Lake, N.W.T., Canada. *Physiol. Ecol. Jpn.* **1**(Special Volume): 201–227.
- Jonsson, B., and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. *Rev. Fish Biol. Fish.* **3**(4): 348–365. doi:10.1007/BF00043384.
- Karlsson, J., and Byström, P. 2005. Littoral energy mobilization dominates energy supply for top consumers in subarctic lakes. *Limnol. Oceanogr.* **50**(2): 538–543. doi:10.4319/lo.2005.50.2.0538.
- Kerr, D.E. 1994. Late Quaternary stratigraphy and depositional history of the Parry Peninsula–Perry River area, District of Mackenzie, Northwest Territories. Geological Survey of Canada Bulletin No. 465.
- Kerr, D.E., and Knight, R.D. 1998. Surficial geology and implications for drift prospecting, Hope Bay volcanic belt area, Northwest Territories. Geological Survey of Canada, Ottawa, Ontario, Current Research 1998-A. pp. 21–28.
- MacAvoy, S.E., Macko, S.A., and Garman, G. 2001. Isotopic turnover in aquatic predators: quantifying the exploitation of migratory prey. *Can. J. Fish. Aquat. Sci.* **58**(5): 923–932. doi:10.1139/f01-045.
- McCutchan, J.H., Jr., Lewis, W.M., Kendall, C., and McGrath, C.C. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*, **102**(2): 378–390. doi:10.1034/j.1600-0706.2003.12098.x.
- Miramar Hope Bay Ltd. 2005. Final environmental impact statement, Doris North Project Nunavut, Canada. Submitted to Nunavut Impact Review Board. Available at <http://www.nirb.ca/Reviews.html> [filed under Completed reviews, Doris North Gold Project 2006].
- Moore, J.W., and Semmens, B.X. 2008. Incorporating uncertainty

- and prior information into stable isotope mixing models. *Ecol. Lett.* **11**(5): 470–480. doi:10.1111/j.1461-0248.2008.01163.x. PMID:18294213.
- Nordeng, H. 1983. Solution to the “char problem” based on Arctic char (*Salvelinus alpinus*) in Norway. *Can. J. Fish. Aquat. Sci.* **40**(9): 1372–1387. doi:10.1139/f83-159.
- Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* **18**(1): 293–320. doi:10.1146/annurev.es.18.110187.001453.
- Rikardsen, A.H., Amundsen, P., and Bodin, P.J. 2003. Growth and diet of anadromous Arctic char after their return to freshwater. *Ecol. Freshwat. Fish.* **12**(1): 74–80. doi:10.1034/j.1600-0633.2003.00001.x.
- SAS Institute Inc. 2002. SAS/STAT user’s guide, version 9.1. SAS Institute Inc., Cary, North Carolina.
- Semmens, B.X., and Moore, J.W. 2008. MixSIR: a Bayesian stable isotope mixing model, version 1.0. Available at <http://conserver.iugo-cafe.org/> [accessed 1 March 2010].
- Swanson, H.K., and Kidd, K.A. 2009. A preliminary investigation of the effects of anadromous Arctic char on food web structure and nutrient transport in coastal Arctic lakes. *In Challenges for diadromous fishes in a dynamic global environment. Edited by A.J. Haro, K.L. Smith, R.A. Rulifson, C.M. Moffit, R.J. Klauda, M.J. Dadswell, R.A. Cunjak, J.E. Cooper, K.L. Beal, and T.S. Avery.* American Fisheries Society Symposium 69, Bethesda, Maryland. pp. 465–483.
- Swanson, H.K., and Kidd, K.A. 2010. Mercury concentrations in Arctic food fishes reflect the presence of anadromous Arctic charr (*Salvelinus alpinus*), species, and life history. *Environ. Sci. Technol.* **44**: 3286–3292. doi:10.1021/es100439t. PMID:20384334.
- Swanson, H.K., Kidd, K.A., and Reist, J.D. 2010a. Effects of partially anadromous Arctic char (*Salvelinus alpinus*) on ecology of coastal Arctic lakes. *Ecosystems (N.Y.)*, **13**(2): 261–274. doi:10.1007/s10021-010-9316-7.
- Swanson, H.K., Kidd, K.A., Babaluk, J.A., Wastle, R.J., Yang, P.P., Halden, N.M., and Reist, J.D. 2010b. Anadromy in Arctic populations of lake trout (*Salvelinus namaycush*): otolith microchemistry, stable isotopes, and comparisons with Arctic char (*Salvelinus alpinus*). *Can. J. Fish. Aquat. Sci.* **67**(5): 842–853. doi:10.1139/F10-022.
- Van Oostdam, J., Donaldson, S., Feeley, M., and Tremblay, N. (Editors). 2003. Canadian Arctic Contaminants Assessment Report II: toxic substances in the Arctic and associated effects — human health. Indian and Northern Affairs Canada, Ottawa, Ont.
- Wetzel, R.G. 2001. Limnology lake and river ecosystems. 3rd ed. Academic Press, San Diego, California.