

Natural isotope indicators of fish migration at Prudhoe Bay, Alaska

Thomas C. Kline, Jr., William J. Wilson, and John J. Goering

Abstract: A dichotomy in the natural stable carbon isotope abundance measured in tissues of obligate freshwater and marine fishes from the Alaskan Arctic coastal plain suggested that the methodology can be used to differentiate recent freshwater from marine feeding in migratory fishes. Natural stable carbon isotope ratio of migratory fishes reflected differences of feeding habitat in relation to known life-history patterns. Use of the stable isotope methodology as a tool for proxy analysis of fish behavior in present and future Arctic environmental monitoring studies is suggested from analysis of age-specific isotopic ratio differences in broad whitefish (*Coregonus nasus*) and Arctic cisco (*Coregonus autumnalis*).

Résumé : Une dichotomie dans l'abondance des isotopes stables naturels de carbone mesurée dans les tissus de poissons strictement marins et dulcicoles de la plaine côtière de l'Arctique, en Alaska, laisse supposer que la méthode peut être utilisée pour distinguer, chez les espèces migratrices, l'alimentation récente en eau douce de l'alimentation en mer. La rapport des isotopes stables naturels de carbone chez les poissons migrateurs reflète des différences dans l'habitat d'alimentation qui sont en rapport avec des étapes connues du cycle vital. L'analyse des différences des rapports isotopiques selon l'âge chez le corégone tschir (*Coregonus nasus*) et le cisco arctique (*Coregonus autumnalis*) indique que la méthode des isotopes stables peut être utilisée comme outil pour l'analyse substitutive du comportement du poisson dans des études courantes et futures de surveillance de l'environnement arctique

[Traduit par la Rédaction]

Introduction

Isotope chemistry is a powerful tool for use in ecological studies because of naturally existing isotope gradients and the fidelity of consumer isotope ratios with their diet (Fry and Sherr 1984; Owens 1987; Wada et al. 1991). Large gradients occur in the natural abundance of the stable heavy isotope of carbon, ^{13}C , as well as the radioactive isotope of carbon, ^{14}C , between freshwater and marine habitats of the Alaskan Arctic coastal plain because of the existence of massive ^{14}C -depleted (because of radioactive decay) and ^{13}C -depleted (Barnett 1994) peat deposits. Peat provides an important carbon source (directly via peat-consuming invertebrates and indirectly via respiration of peat carbon) to coastal plain freshwater food chains (including anadromous and (or) amphidromous fishes) but not to coastal marine food chains (Schell 1983; Schell and Zieman 1989). Because stable isotope ratios are conserved during feeding processes, they make effective tracers of food sources used by anadromous and amphidromous fishes, enabling one to distinguish between peat versus marine carbon utilization by fishes (and other consumers).

The data obtained from stable isotope measurements are

unique in that they trace assimilated material. Nitrogen stable isotope ratios provide excellent definition of relative trophic level (Fry 1988; Wada et al. 1991; Hobson and Welch 1992; Kiriluk et al. 1995). The heavy isotope of nitrogen, ^{15}N , is enriched by about 0.34‰ (or 3.4‰ in conventional delta units, see Materials and methods) with each trophic level (Minagawa and Wada 1984) and can accurately indicate the trophic level of species within an ecosystem (Kling et al. 1992; Cabana and Rasmussen 1994). Carbon isotope signatures were used to trace multiple sources of carbon into food webs (Fry and Sherr 1984; Wada et al. 1991) by exploiting the ^{13}C gradient in Alaskan Arctic coastal plain food web carbon sources (Schell 1983; Schell and Zieman 1989) while using carbon to nitrogen (C/N) ratio and nitrogen stable isotope measurements to correct $^{13}\text{C}/^{12}\text{C}$ values for lipid storage and trophic level isotope effects (Kline 1997).

Fishes of the genus *Coregonus* and *Salvelinus* are abundant in the coastal and freshwaters of the Alaskan Arctic. In addition to being obligate freshwater spawners, they undergo summer feeding migrations into coastal waters during which they take on lipid reserves to maintain body condition through the subsequent winter season (Craig 1989; Fechhelm et al. 1995, 1996). Nearshore Beaufort Sea monitoring programs focusing on subsistence-harvested and commercially harvested Arctic cisco (*Coregonus autumnalis*), least cisco (*Coregonus sardinella*), and broad whitefish (*Coregonus nasus*) have been ongoing since the 1970s because of concerns over potential impacts on these species from oil development (Gallaway et al. 1991). Much of the focus of these monitoring studies has been assessing the impact of causeways because of their potential for altering the migratory behavior of these species (Gallaway et al. 1991).

These coregonine species are either amphidromous, because they seasonally migrate between the freshwater and marine environments and overwinter in freshwater, or anadromous,

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T.C. Kline, Jr.¹ Prince William Sound Science Center,
P.O. Box 705, Cordova, AK 99574, U.S.A.

W.J. Wilson. LGL Alaska Research Associates, Inc.,
4175 Tudor Centre Drive, Suite 202, Anchorage, AK 99508,
U.S.A.

J.J. Goering. Institute of Marine Science, School of Fisheries
and Ocean Sciences, University of Alaska-Fairbanks, Fairbanks,
AK 99775, U.S.A.

¹ Author to whom all correspondence should be addressed.
e-mail: tkline@grizzly.pwssc.gen.ak.us

because they undertake similar seasonal migrations but overwinter in brackish river delta environments (Craig 1984, 1989). Arctic cisco are anadromous, and they eventually spawn in freshwater tributaries of the Mackenzie River, at ages 6–9 (Gallaway et al. 1983). Least cisco, broad whitefish, and Dolly Varden (*Salvelinus malma*, Salmoninae) are amphidromous because they overwinter in freshwater. All of these species seasonally migrate out of river systems (deltas for Arctic cisco) into the nearshore Beaufort Sea to forage along the coast, returning in the fall to the rivers or river deltas to overwinter (Craig 1989). Maintenance of these populations depends on their continued ability to move back and forth between the freshwater and marine environments. In some portions of the Alaskan Arctic, the migratory pathways are complex because of the low topology and thermokarst features of the Arctic coastal plain and consequent intricate and tortuous pathways among lakes, streams, lagoons, and open water.

We hypothesized that stable isotope composition of fish tissues could be used to discern feeding strategies of the different life-history forms of Arctic fishes. Fish feed either on marine-derived or freshwater-derived production, depending on their life-history form or stage (freshwater resident, marine resident, or anadromous and (or) amphidromous). Each form tends to feed at a specific trophic level because of metabolic requirements, mouth structure, competition, and seasonal food availability. Hypothetically, the $^{13}\text{C}/^{12}\text{C}$ ratio in fish tissues can be used to indirectly determine migratory behavior by knowing where a fish sample was collected in relation to potential carbon sources. For example, a fish obtained from the marine habitat but containing a carbon signature consistent with freshwater feeding had to have recently migrated there. If a fish “switches” to alternative carbon sources because of environmental pressures (temperature–salinity changes, crowding, etc.), there will be a concomitant change in their isotopic composition.

This study examines $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ ratios in tissues of Alaskan North Slope freshwater, anadromous and (or) amphidromous, and marine fishes to explore the possible use of tissue isotope chemistry in Arctic ecological studies. Our objectives were to validate this methodology and to determine carbon signature differences in these different ecological life forms of Arctic fishes.

Materials and methods

Anadromous Arctic cisco and amphidromous least cisco, broad whitefish, and Dolly Varden were collected in fyke nets in coastal waters of the Prudhoe Bay region, Alaska (Fig. 1a), during the summers of 1994 and 1995 following the methods of Fechhelm et al. (1995, 1996). Two seasonal samples were collected each year, one in early season (24 June to 23 July 1994 and 23 June to 4 July 1995) and one in late season (11–22 August 1994 and 14–20 August 1995). Subsamples of fish were measured for length to the nearest millimetre. Sagittal otoliths were excised and then aged by counting annuli under a dissecting microscope at 10–70 \times magnification. Marine fourhorn sculpin (*Myoxocephalus quadricornis*) and Arctic flounder (*Pleuronectes glacialis*) were collected during the summer in the coastal fyke nets (above) and from gill nets set near the Chipp River delta (Fig. 1b), while the freshwater species Arctic grayling (*Thymallus arcticus*), lake trout (*Salvelinus namaycush*), longnose sucker (*Catostomus catostomus*), burbot (*Lota lota*), ninespine stickleback (*Pungitius pungitius*), and northern pike (*Esox lucius*) were collected

from gill and fyke nets placed in Teshekpuk Lake (1992) and in the Chipp River (1994 and 1995).

Whole fish carcasses (from Prudhoe Bay) or epaxial muscle tissue samples (from Teshekpuk Lake and Chipp River) were frozen and sent to our laboratories in either Fairbanks (1994) or Cordova (1995) for preparation for isotopic analysis. Preparation consisted of sampling epaxial muscle from Prudhoe Bay samples, followed by freeze-drying. Epaxial muscle samples sampled in the field (Teshekpuk Lake and Chipp River samples) were freeze-dried directly. Freeze-dried samples were ground to a fine powder with a dental amalgamator (Crescent Dental Wig-L-Bug). Ground freeze-dried samples stored in LSC vials were sent to the Stable Isotope Facility at the University of Alaska Fairbanks where replicate aliquots of ~1.5 mg were weighed to the nearest microgram and loaded into combustion boats for mass spectrometric analysis.

Isotopic determination

A Europa Scientific model 20/20 stable isotope analyzer equipped with a Europa Scientific Roboprep sample preparation and purification unit was used for the analysis. Analytical results include $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios in standard delta units, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, and percent carbon (%C) and percent nitrogen (%N) (grams carbon or nitrogen per gram dry weight).

The standard delta notation is used to express stable isotope ratios relative to international standards (air for nitrogen and Vienna Pee Dee belemnite (VPDB) for carbon) and is defined by the following expression:

$$(1) \quad \delta^{15}\text{N} \text{ or } \delta^{13}\text{C} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000\text{‰}$$

where $R = ^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$. The isotope standards have delta values of 0 by definition, i.e., $\delta^{15}\text{N} = 0$ for atmospheric N_2 . Naturally occurring $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values observed in biota range from ~0 to ~+20 and from ~0 to ~-50, respectively. Negative $\delta^{13}\text{C}$ values reflect the relative enrichment of ^{13}C in the limestone standard compared with biota.

Replicate isotopic analyses were performed on each sample using aliquots of ~1.5 mg dry weight. Samples were rerun when replication was poor (difference >0.6‰). Typically, replication yielded results that were within 0.2‰. The %C and %N data were used to calculate C/N atomic ratios. Means of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and C/N replicates were used for data modeling. Although $\delta^{15}\text{N}$ values of biota vary principally as a function of trophic level (Fry 1988), there can be significant nitrogen source isotope effects (Kline et al. 1997). Determination that nitrogen source isotope effects were not present was based on comparing $\delta^{15}\text{N}$ values of similar trophic level fishes across the study area. Following validation, $\delta^{15}\text{N}$ values were then used to normalize for the trophic enrichment of ^{13}C using the procedure described below. The lipid normalization procedure of McConnaughey and McRoy (1979) was used to remove lipid isotope effects (DeNiro and Epstein 1977). The combined normalizations for trophic level and lipid storage resulted in ^{13}C values dependent primarily on source, thus enabling the identification of the source of carbon in samples based on the natural ^{13}C gradient (Kline 1997).

Normalization protocols

Normalization for lipid content is needed because lipid synthesis and storage can alter ^{13}C content (DeNiro and Epstein 1977). The normalization technique used was developed by McConnaughey and McRoy (1979) and validated by Kline (1997). The C/N atomic ratio derived from mass spectrometry provided an inexpensive proxy for lipid content that was used to calculate lipid-normalized $\delta^{13}\text{C}$ (expressed as $\delta^{13}\text{C}'$).

The consistent enrichment of ^{15}N in animal tissues compared with that in their diet was used to compute a relative trophic level (TL) by comparing $\delta^{15}\text{N}$ values with a reference TL value (e.g., Cabana and Rasmussen 1994). The $\delta^{15}\text{N}$ values of higher TLs were calculated by

Fig. 1. (a) Fish and hydrographic monitoring stations (diamonds) in the Prudhoe Bay region (1994 and 1995) and (b) freshwater (circles) and marine (square) fish sampling stations in the Ikpikpuk River region including Teshekpuk Lake (1992) and Chipp River (1994 and 1995).

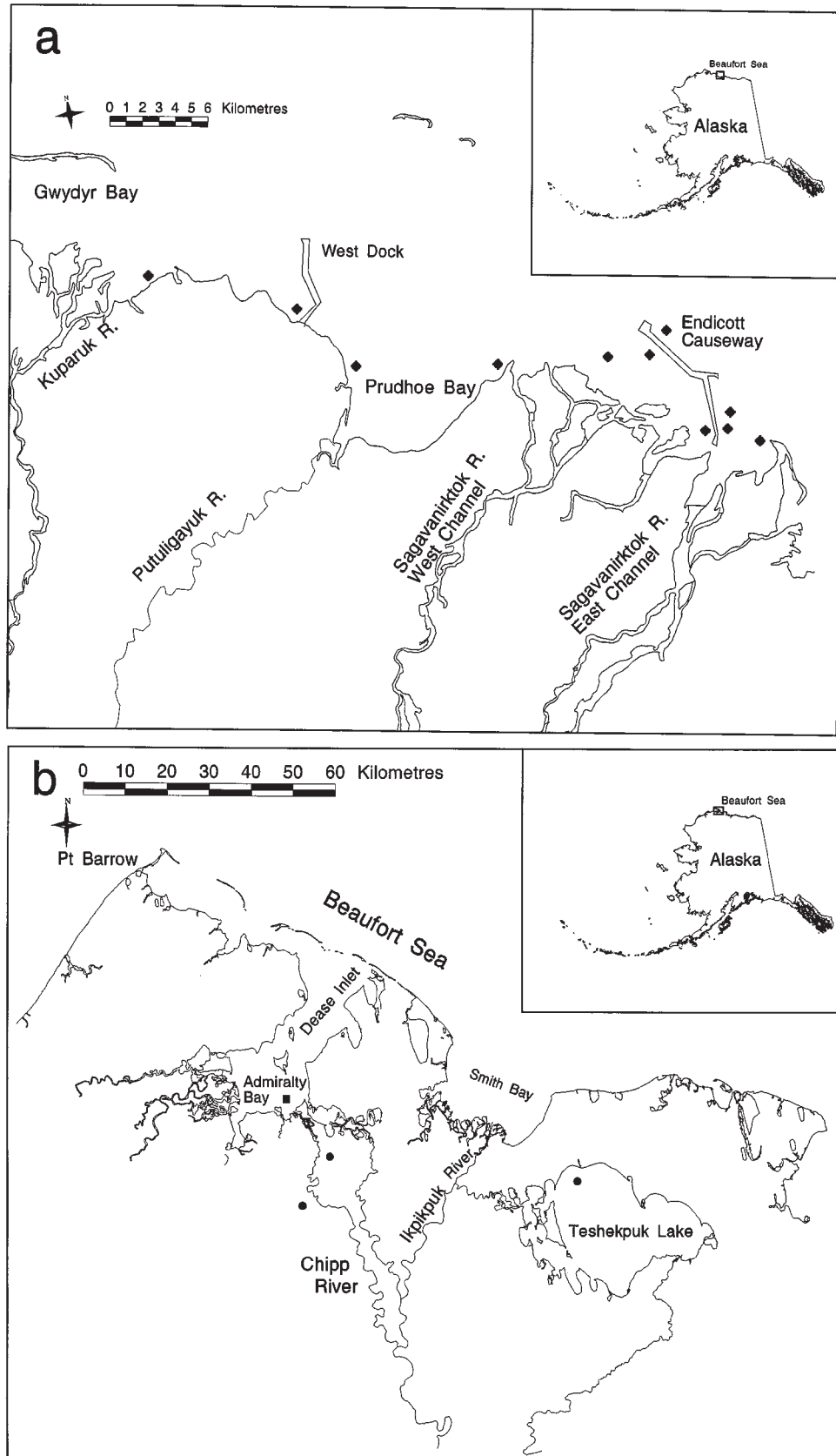
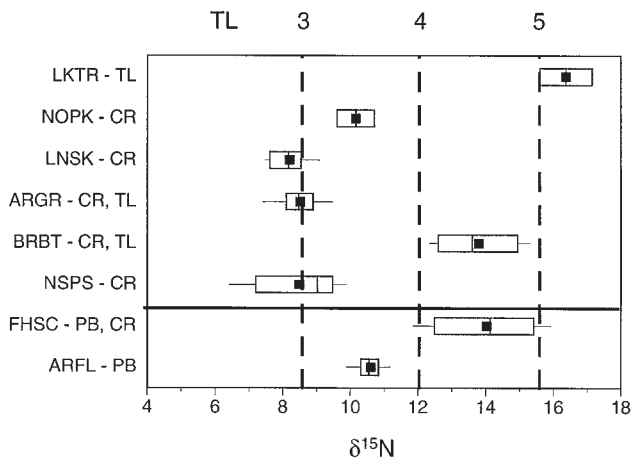


Fig. 2. Determination of TL (upper axis label) from $\delta^{15}\text{N}$ with variability indicated by computer-fitted (Deltagraph Pro 3.0, Deltapoint Inc.) box and whisker plots. Freshwater-resident fishes (LKTR, lake trout ($N = 2$); NOPK, northern pike ($N = 2$); LNSK, longnose sucker ($N = 16$); ARGR, Arctic grayling ($N = 22$); BRBT, burbot ($N = 12$); NSPS, ninespine stickleback ($N = 25$)) were collected from the Alaskan Arctic coastal plain in 1992 and 1994, while marine fishes (FHSC, fourhorn sculpin ($N = 22$); ARFL, Arctic flounder ($N = 19$)) were collected from the Alaskan Arctic coastal plain in 1994. TL, CR, and PB after species codes refer to the sampling locations Teshekpuk Lake, Chipp River, and Prudhoe Bay, respectively. The whiskers indicate the 10th and 90th percentiles. The 25th, 50th, and 75th percentiles are indicated by the boxes whereas the mean value is shown as a symbol.



adding the trophic enrichment factor, ϵ_N (see eq. 2 below), to a reference TL value. Although obligate herbivores, i.e., TL = 2, thus well defined by TL, are suitable for the reference TL, a substantial sample size (e.g., ~1000) may be required (Kline 1997). Instead, TLs of fishes in this study were determined in relation to low-TL fishes which were assumed to be TL = 3.

Normalization for TL enabled comparison of $\delta^{13}\text{C}'_{\text{TL}}$ values among species or individuals within a species with multiple TL, since residual $^{13}\text{C}/^{12}\text{C}$ delta values reflected carbon source. The normalization procedure used the trophic enrichment factors, ϵ_C and ϵ_N (Fry and Sherr 1984; Minagawa and Wada 1984), and the $\delta^{15}\text{N}$ value of the reference TL. Normalized values were computed using the following relationship:

$$(2) \quad \delta^{13}\text{C}'_{\text{TL}} = \delta^{13}\text{C}' - \epsilon_C/\epsilon_N(\delta^{15}\text{N}_{\text{sample}} - \delta^{15}\text{N}_{\text{reference}})$$

where $\delta^{13}\text{C}'_{\text{TL}}$ is the ^{15}N -based TL-normalized derivative of $\delta^{13}\text{C}'$, $\epsilon_C = 1$, and $\epsilon_N = 3.4$.

Validation of trophic level determination and normalization procedures

In general, $\delta^{15}\text{N}$ of aquatic organisms reflect their TL (Owens 1987; Fry 1988; Wada et al. 1991; Cabana and Rasmussen 1994). Although $\delta^{15}\text{N}$ values of terrestrial, freshwater, and estuarine organisms are similar (Owens 1987), processes that introduce nitrogen with anomalous $\delta^{15}\text{N}$ values (thus affecting TL assessment) to the system may occur (e.g., Kline et al. 1997), particularly at the freshwater-marine ecotone (France 1995). Validation consisted of demonstrating no nitrogen source isotope effect in nonmigratory fish species from the North Slope. Their $\delta^{15}\text{N}$ variability was qualitatively assessed in relation to known feeding habits (Craig and McCart 1976; Craig et al. 1984; Craig 1989). The lack of significant nitrogen source isotope effect would be confirmed if the variability in $\delta^{15}\text{N}$ accounted for by TL was greater than differences in $\delta^{15}\text{N}$ among species of similar TL.

Mixing model

The following isotopic mixing model based on Kline et al. (1997) was used to assess the percentage of a source of a given element in a consumer, given the existence of two sources with a significant stable isotope disparity:

$$(3) \quad \%A = \frac{\delta_B - \delta_{\text{sample}}}{\delta_B - \delta_A} \times 100\%$$

where δ_A and δ_B are the delta values of the two sources and δ_{sample} is the delta value of the sample.

Results

Freshwater and marine fishes

Nonmigratory fishes, consisting of freshwater species from the Chipp River and Teshekpuk Lake and marine species from the Prudhoe Bay region and the mouth of the Chipp River, had $\delta^{15}\text{N}$ ranging from ~7 to ~17 (Fig. 2). The most positive $\delta^{15}\text{N}$ values, ~17, were found in Teshekpuk Lake lake trout. Longnose sucker, Arctic grayling, and ninespine stickleback had $\delta^{15}\text{N}$ ~8.5, which was assumed to correspond to TL = 3. Higher TLs were estimated in relation to TL = 3 (Fig. 2). Northern pike, Arctic flounder, burbot, and fourhorn sculpin had $\delta^{15}\text{N}$ values >8.5, corresponding to TL >3, but less than the $\delta^{15}\text{N}$, and therefore TL, of lake trout.

Nonmigratory fishes were dichotomous in $\delta^{13}\text{C}'_{\text{TL}}$ with marine species' values greater than freshwater species' values by at least 2‰ (Fig. 3a). Within the freshwater group, lake trout and burbot had $\delta^{13}\text{C}'$ elevated by ~1‰ compared with the others. Normalization of $\delta^{13}\text{C}'$ values for trophic level (i.e., $\delta^{13}\text{C}'_{\text{TL}}$) removed this difference, making lake trout and burbot more similar to other freshwater fishes (Fig. 3b). Only ninespine stickleback had a very broad $\delta^{13}\text{C}'$ range. In summary, fishes feeding in freshwater had $\delta^{13}\text{C}'_{\text{TL}}$ ~-30 to ~-27 whereas fishes feeding in the marine environment had $\delta^{13}\text{C}'_{\text{TL}}$ ~-22.

Anadromous and (or) amphidromous species

Fishes that migrate between freshwater and marine habitats had $\delta^{13}\text{C}'_{\text{TL}}$ ranging from -30 to -21, and thus encompassed the range of $\delta^{13}\text{C}'_{\text{TL}}$ values found for marine and freshwater nonmigratory species (Fig. 4, compare with Fig. 3b). Migratory species had distinctive curves when $\delta^{13}\text{C}'_{\text{TL}}$ and $\delta^{15}\text{N}$ were plotted as a function of body size (Figs. 4 and 5). The data suggest shifts in food source (Fig. 4) and TL (Fig. 5) as a function of length (and thus age) as well as differences among the species.

Cohort feeding histories

Shifts in $\delta^{13}\text{C}'_{\text{TL}}$ and $\delta^{15}\text{N}$ values of Arctic cisco and broad whitefish by cohort or year-class (Fig. 6) suggest age-specific differences in food source or TL during 1994-1995. Noteworthy is the shift to more positive $\delta^{13}\text{C}'_{\text{TL}}$ values in the older age-classes. Interannual variation in $\delta^{13}\text{C}'_{\text{TL}}$ was apparent even in older fish (ages 4-6, i.e., 1990 and 1991 year-classes).

The relative importance of marine carbon in the feeding history of the broad whitefish and Arctic cisco cohorts shown in Table 1 was determined using as end members δ_A and δ_B (eq. 3), the $\delta^{13}\text{C}'_{\text{TL}}$ values of obligate marine and freshwater fishes which were $\sim -22 \pm 0.5$ and $\sim -28 \pm 1.0$, respectively (Fig. 3b). The data suggest 100% dependence on marine carbon by age 3 for both species.

Discussion

Trophic level

Alaska Arctic coastal plain fish $\delta^{15}\text{N}$ values and interpreted TLs were similar to those reported in the literature and generally consistent with no $\delta^{15}\text{N}$ source effects (France 1995), supporting $\delta^{15}\text{N}$ value based TL estimation and normalization of $\delta^{13}\text{C}'$ for the study area. The highest $\delta^{15}\text{N}$ value of +17, and therefore highest relative TL of 5 determined for lake trout in our study, was similar to the mean $\delta^{15}\text{N}$ value and interpreted TL of Lake Ontario lake trout (Kiriluk et al. 1995), although greater than that reported at two sites in the lower Mackenzie River basin, Canada (Hesslein et al. 1991). Conversely, the $\delta^{15}\text{N}$ of northern pike found in the Chipp River was less than those from the Kukjuktuk Creek system and a few of those from Travaillant Lake, both in the Mackenzie River system (Hesslein et al. 1991), while ninespine stickleback from all Mackenzie River system and this study's sites were comparable. Longnose sucker from the Chipp River had $\delta^{15}\text{N}$ values that were similar to those of white sucker from Travaillant Lake (Hesslein et al. 1991). The $\delta^{15}\text{N}$ values of fourhorn sculpin from Prudhoe Bay and the Chipp River were similar to the $\delta^{15}\text{N}$ reported for Arctic sculpin (*Myoxocephalus scorpiodes*) from the Canadian high Arctic (Hobson and Welch 1992). Broad whitefish were consistently lower in $\delta^{15}\text{N}$ than Arctic cisco, least cisco, or Dolly Varden, implying a lower TL (Fig. 5) which is also anatomically suggested by their small gape and mollusc and aquatic insect feeding habit (McPhail and Lindsey 1970).

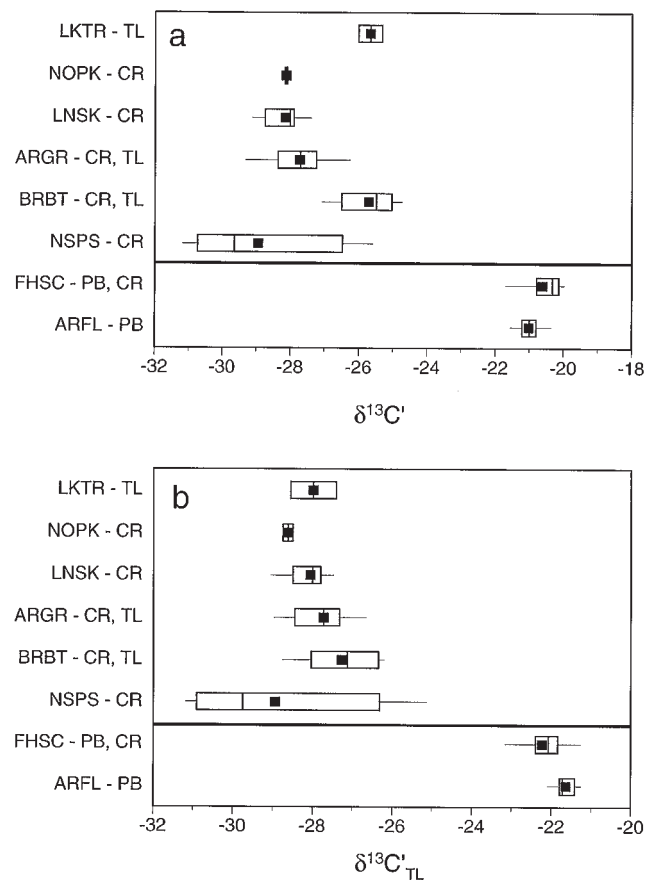
$^{13}\text{C}/^{12}\text{C}$ gradient

The difference in $\delta^{13}\text{C}'_{\text{TL}}$ values of obligate freshwater and coastal marine fishes (Fig. 3b) confirms the existence of a $^{13}\text{C}/^{12}\text{C}$ gradient in Alaskan Arctic coastal plain biota reported by Schell (1983) and Schell and Ziemann (1989). Furthermore, trends in isotopic composition in relation to the size of migratory fishes (Fig. 4) suggest feeding habit shifts dependent on migratory behavior that are consistent with known life-history patterns (Craig 1989). For example, Craig (1989) described two types of life-history patterns of coastal plain anadromous fishes. The char life-history pattern of delayed migration from freshwater involves fry remaining year-round in streams until age 3 or 4 when they begin annual migrations to sea to feed. This life-history pattern is reflected in the Dolly Varden $\delta^{13}\text{C}'_{\text{TL}}$, since the switch to the more positive $\delta^{13}\text{C}'_{\text{TL}}$ of marine carbon occurred at a larger size of nearly 300 mm in length (age ~4, Craig 1989). These results contrast with broad whitefish and Arctic cisco which follow the cisco life-history pattern (Craig 1989) where fish annually migrate to the marine environment to feed at all ages. Accordingly, the broad whitefish and Arctic cisco data show the marine $\delta^{13}\text{C}'_{\text{TL}}$ signature by 100 mm (Fig. 4b). The consistency of $\delta^{13}\text{C}'_{\text{TL}}$ with known life-history patterns of Alaskan Arctic coastal plain fishes suggests that $\delta^{13}\text{C}'_{\text{TL}}$ can be used as a migratory indicator in this region. This is unlike the Mackenzie River delta area, which does not have a $^{13}\text{C}/^{12}\text{C}$ gradient (Hesslein et al. 1991).

Age-dependent isotopic variability and shifts

Because of the predictable relationship between natural stable isotope abundance of consumers and their diet (reviewed by

Fig. 3. Dichotomy in (a) $\delta^{13}\text{C}'$ and (b) $\delta^{13}\text{C}'_{\text{TL}}$, shown as box and whisker plots, between two marine and five freshwater fishes as in Fig. 2. Variation in $\delta^{13}\text{C}'$ among freshwater species due to differences in TL shown in Fig. 3a are removed in Fig. 3b.



Wada et al. 1991), it is being used here to characterize the recent feeding history of Prudhoe Bay area fishes as either freshwater or marine. Juvenile fishes rapidly change their isotopic composition in proportion to addition of new tissue, while differences in isotopic signatures between individuals in groups of older, slow-growing fish reflect different food "choices" because temporal variations are averaged out (Hesslein et al. 1993). The potential diet choice in this study consisted of the spatial and apparent isotopic dichotomy between freshwater and marine carbon (Fig. 3). Arctic fishes are generally long-lived and have slow growth, especially upon reaching sexual maturity (Craig 1989). Based on the results of Hesslein et al. (1993), mature fishes were not expected to vary significantly with time, since temporal variation in feeding would be averaged out. However, the variability in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}'_{\text{TL}}$ of coregonines in our study did not appear to decrease with increased fish size as expected (Figs. 4 and 5). In contrast, Dolly Varden decreased in isotopic range as a function of size. Larger (>300 mm) Dolly Varden range by about 2‰ in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}'_{\text{TL}}$, similar to coregonines. However, smaller Dolly Varden exhibited far greater ranges compared with the coregonines, suggesting a greater diversity of feeding niches by individual fish. For example, fish between 250 and 300 mm in length ranged from 100% freshwater feeding to 100% marine feeding and had a two-TL range (Figs. 4 and 5).

Fig. 4. $\delta^{13}C'_{TL}$ shifts as a function of length of four North Slope salmonid fishes that are anadromous or amphidromous (Dolly Varden char ($N = 46$) from 1994 (triangles, dotted line), least cisco ($N = 57$) from 1994 (squares, dashed-dotted line), Arctic cisco ($N = 148$) from 1994 and 1995 (crosses, dashed line), and broad whitefish ($N = 181$) from 1994 and 1995 (circles, solid line)) sampled in the Sagavanirktok River delta suggest species-dependent change in carbon source (M, marine; T, transitional; F, freshwater) during life history. Second-order polynomial regressions were computer-fitted (Deltagraph Pro 3.0, Deltapoint Inc.) to the data. The delayed shift in Dolly Varden char is consistent with this species' life-history pattern (Craig 1989).

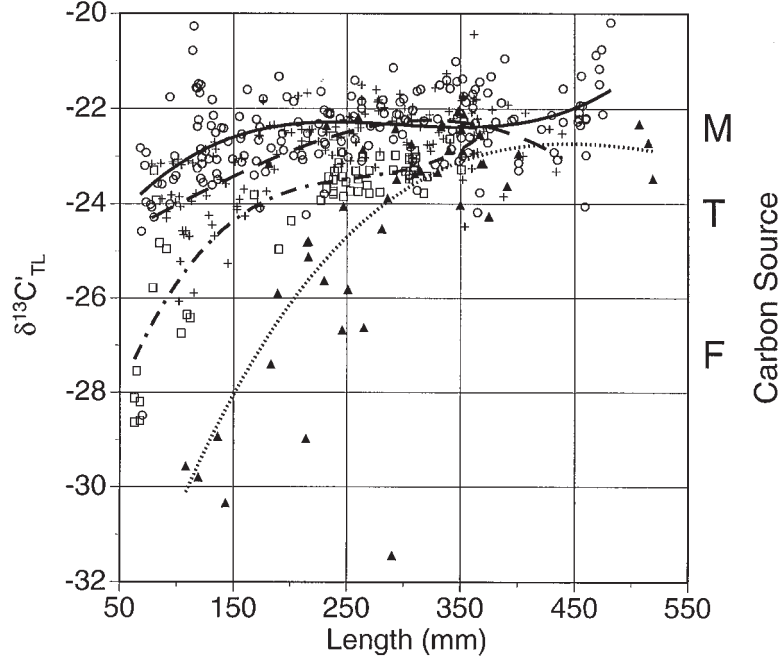


Fig. 5. Shifts in $\delta^{15}N$ as a function of length four North Slope salmonid fishes that are anadromous or amphidromous (Dolly Varden char ($N = 46$) (triangles, solid line), least cisco ($N = 57$) (crosses, dashed line), Arctic cisco ($N = 148$) (circles, dotted line), and broad whitefish ($N = 181$) (squares, dashed-dotted line)) sampled in the Sagavanirktok River delta suggest species-dependent differences in relative TL as well as increases during life history. Regression lines are second-order computer-fitted to the data as in Fig. 4.

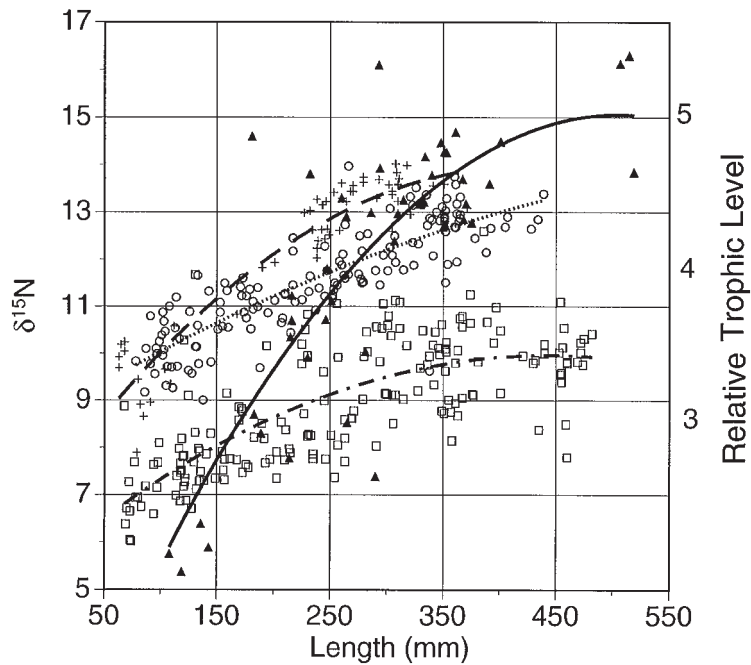
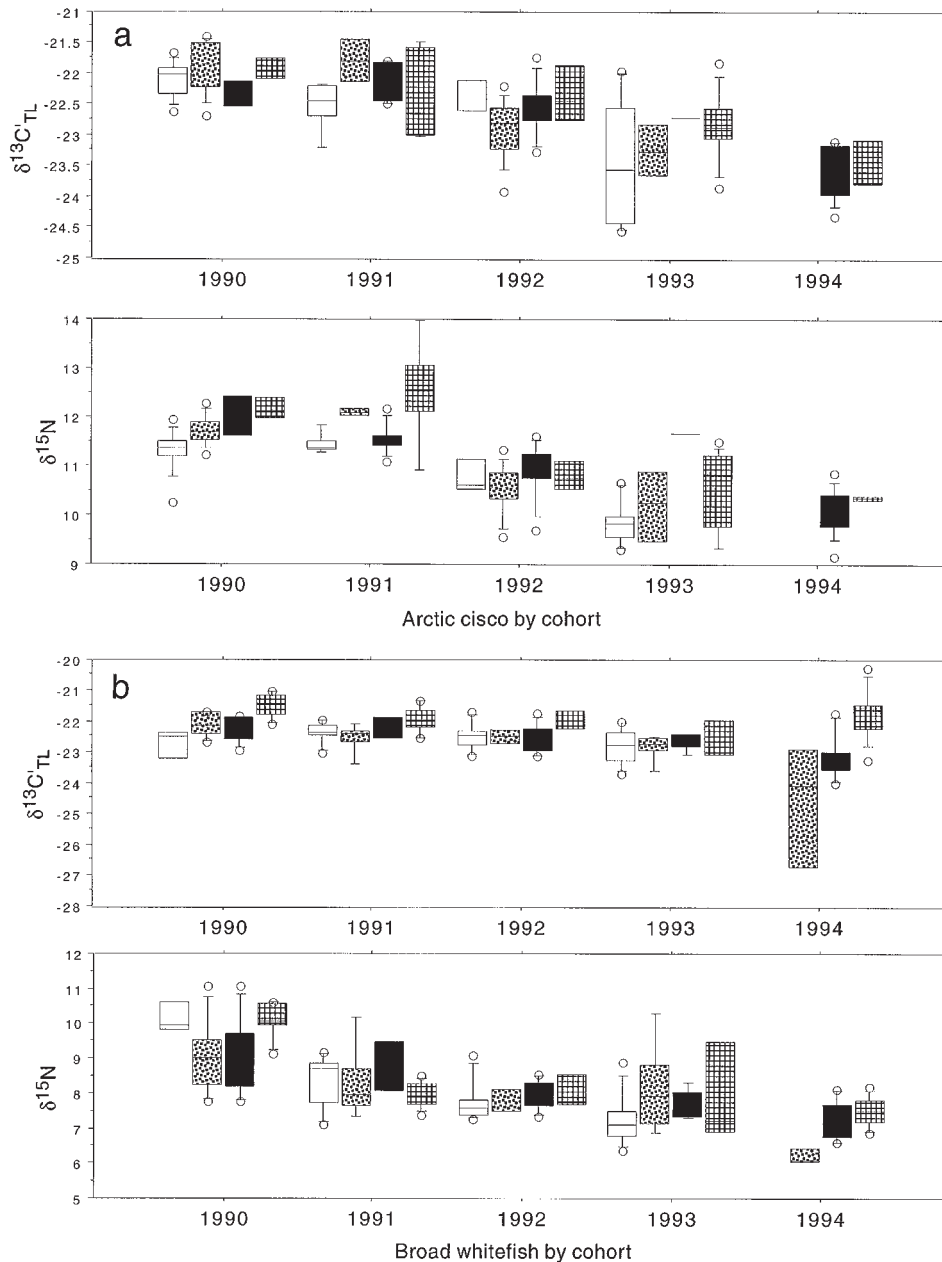


Fig. 6. Carbon and nitrogen isotopic shifts of cohorts (year of birth on *x*-axes) of (a) Arctic cisco and (b) broad whitefish during four samplings (24 June to 23 July 1994 (open), 11–22 August 1994 (stippled), 23 June to 4 July 1995 (solid), and 14–20 August 1995 (cross-hatched)) shown as box and whisker plots (the five horizontal lines display the 10th, 25th, 50th, 75th, and 90th percentiles), while outliers are shown as symbols. Outliers and percentiles were omitted by computer programming (Statview 4.5, Abacus Concepts, Inc.) for box and whiskers with small *N* as appropriate.



Age 1 and 2 Arctic cisco and broad whitefish (Fig. 6; Table 1) have notable $\delta^{13}\text{C}'_{\text{TL}}$ and corresponding percent marine carbon estimation differences between the species. Arctic cisco were more negative by $\sim 1\%$, suggesting a 5–20% greater affinity for freshwater-derived carbon than broad whitefish (Table 1).

The change in $\delta^{13}\text{C}'_{\text{TL}}$ between late summer 1994 and early summer 1995 (Fig. 6) suggested a turnover of much of the carbon, probably later in 1994 before entering the rivers. Our observation is consistent with that of Schell (1983) who found $\delta^{13}\text{C}$ values in coregonines sampled in October and November that were consistent with continued feeding on marine carbon

into the fall. In 1994, the salinity in the Prudhoe Bay area decreased anomalously to low values in late summer when it more typically increases. This may have lengthened the time that these fish spent in the estuary, since the variable that drives them back into the rivers, salinity, became more benign. They could have stayed longer and fed more in late 1994 than is typical. This may have allowed them to change their isotopic composition; otherwise, the late 1994 and early 1995 values of younger cohorts would have been more similar than determined here (compare adjacent stippled and black boxes and whiskers in Fig. 6).

Table 1. Percent estuarine carbon computed from mean $\delta^{13}C'_{TL}$ values in Fig. 6 using eq. 3 with -28 ± 1.0 and -22 ± 0.5 as the end members.

Year-class	Age (years)	Arctic cisco				Broad whitefish			
		1994 sampling		1995 sampling		1994 sampling		1995 sampling	
		Early season	Late season	Early season	Late season	Early season	Late season	Early season	Late season
1990	4–5	98	102	95	101	88	98	95	109
1991	3–4	92	103	97	96	94	91	97	101
1992	2–3	95	80	91	95	92	92	91	101
1993	1–2		85	88	86	87	86	90	91
1994	0–1			73	76		55	80	106

Note: The accuracy of the estimate based on the $\delta^{13}C'_{TL}$ range of marine fishes of $\pm 8.3\%$ accounts for values $>100\%$.

Our study suggests that, because of the lower trophic position suggested by their $\delta^{15}N$ (Fig. 5), broad whitefish may be able to store energy in a “poor feeding condition,” while other species could not. Potentially, measurements of natural stable isotope abundance of fishes in an extreme condition year such as experienced in the Prudhoe Bay region in 1991 could provide evidence of an alternative hypothesis: that broad whitefish shifted feeding to alternative food sources which would in turn cause a shift to different isotopic values because of the change in source of carbon and nitrogen. For example, Fechhelm et al. (1995, 1996) tracked the early- and late-summer condition of individual cohorts of broad whitefish and Arctic cisco over time. Through this analysis, they were able to detect inconsistencies between species and among years in summer energy accumulation. For example, they noted that in the summer of 1991, 75% of Arctic cisco cohorts lost lipid reserves (Fechhelm et al. 1996), while all the broad whitefish cohorts gained lipid reserves (Fechhelm et al. 1995). Fechhelm et al. (1996) noted that 1991 was a very “fresh” year in the Sagavanirktok delta and that Dolly Varden, Arctic flounder, and fourhorn sculpin also exhibited poor condition. They postulated that poor feeding conditions existed throughout the area.

We have shown that anadromous and (or) amphidromous fish have a certain isotopic signature whereas marine and freshwater fishes have another, confirming the freshwater-marine isotopic dichotomy and utilization of ^{13}C -depleted carbon reported by Schell (1983). Within the anadromous and (or) amphidromous group, we can show shifts in trophic level with increase in size, presumably because as fish grow, they are more capable of searching further and accepting different (larger) prey. Natural stable isotope abundance is a technique that could assess changes in the migrational patterns of these fishes, such as changing time of seaward migration to later in life as seen in Dolly Varden. We have also shown that fish at a given size in one year might show a different signature in another year, possibly due to environmental gradients that differed in the two years that enabled those fish to feed in different areas or on different prey. This is especially relevant in the Alaskan Arctic where fishes display widely varying life-history strategies for seasonal feeding and migration to cope with a dynamic and harsh Arctic environment.

Although considerable, environmental impact studies on North Slope fishes have shown little detrimental effect and have contributed considerably to advances in understanding fish life histories in the central Alaskan Beaufort Sea (Gallaway et al. 1997; Wilson and Gallaway 1997). Stable isotope

analysis may be an important tool in further advancing this knowledge. Natural stable isotope abundance data provide additional understanding of the feeding ecology of important subsistence and commercial fish and provide a useful tool for analyzing effects of nearshore development in Arctic fishes.

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