Stable Isotope Analysis of Carbon Flow in a Tundra River System

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Stable isotope analysis was used to identify the major sources of carbon utilized by fish and aquatic invertebrates in the Koroc River, a tundra river system in northern Quebec. Juvenile arctic char (Salvelinus alpinus), together with adults and juveniles of other species of fish in freshwater, obtained their carbon from either allochthonous or autochthonous sources within the river system, via the invertebrate fauna. However, adult anadromous char caught in the river clearly derived their biomass carbon from feeding at sea. Despite the limited development of riparian vegetation throughout much of the lower river catchment, terrestrial organic matter was the most likely source of energy fueling the animal communities of small tributary streams and rapids of the mainstem Koroc. In contrast, epilithic algae made a significant contribution to food chains within Alik Lake, a deep basin along the main river channel. Aquatic mosses appeared to be of, at most, tertiary importance as a source of energy to the animal communities of the lake, despite their considerable biomass.

On s’est servi de la technique d’analyse des isotopes stables pour identifier les sources majeures de carbone utilisées par les poissons et les invertébrés aquatiques dans la rivière Koroc, système fluvial situé dans la toundra au Nouveau-Québec. Les jeunes omble chevaliers (Salvelinus alpinus), ainsi que les adultes et les jeunes d’autres espèces de poissons vivant en eaux douces, ont obtenu leur carbone de sources soit autochtones ou allochtones à l’intérieur du réseau hydrographique, via la faune des invertébrés. Cependant, les omble anadromes adultes capturés dans la rivière tiraient manifestement le carbone de leur biomasse de leur alimentation en mer. En dépit de la croissance limitée de la végétation riveraine dans la majeure partie du bassin inférieur de la rivière, c’est la matière organique d’origine terrestre qui constituait très probablement le source d’énergie qui alimentait les communautés animales des petits tributaires et des rapides du bras principal de la rivière Koroc. Par contre, les algues épilithiques contribuaient de façon significative aux chaînes alimentaires à l’intérieur du lac Alik, bassin profond qui longe le lit principal de la rivière. Les mousses aquatiques ont semblé venir, tout au plus, au troisième rang comme source d’énergie des communautés animales du lac, malgré leur biomasse considérable.

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A knowledge of the pattern of energy flow and material cycling is essential to our understanding of how ecosystems function. Early stream ecologists recognized the importance of allochthonous carbon as a major source of energy fueling forest stream ecosystems (see Hynes 1975). Subsequent research, particularly in the temperate forest systems of North America, has led to the development of a generalized model of stream structure and function, which emphasizes the sources of energy and nutrients and the way in which these materials move through stream ecosystems (Vannote et al. 1980; Newbold et al. 1982; Minshall et al. 1983, 1985). As a consequence, most of our knowledge of the structural and functional organization of lotic systems is derived from studies of streams in temperate regions.

Autochthonous sources of carbon, however, may make a significant contribution to the energy pathway of some lotic systems (Minshall 1978), such as desert streams and others that do not flow through dense forest (Busch and Fisher 1981; Naiman 1981; Rounick et al. 1982; Winterbourn et al. 1986). In contrast, tundra river systems appear to be similar in function to many temperate streams in that they are dependent on allochthonous sources of carbon, despite a conspicuous lack of riparian vegetation (Peterson et al. 1985a, 1986). Very little is known about the flow of energy in tundra streams but such information is essential to the successful management of arctic fisheries and the prediction of how such systems will respond to human disturbance.

Many river systems entering Ungava Bay, northern Quebec, support populations of the anadromous arctic char (Salvelinus alpinus L.), which may account for as much as half of the annual food supply in some traditional Inuit communities (Balikci 1980). In addition to this subsistence harvest, sport fishing for arctic char is an important source of income for many Inuit, and commercial fishing is coming to be regarded as a potentially significant source of revenue (Power and Barton 1987). While the general biology of arctic char is fairly well documented (Moore 1975a, b; Gillis et al. 1982; Johnson and Burns 1984; Dempson and Green 1985), little is known about the relationship between this species and other components of its riverine habitat, particularly with respect to energy flow.

The aim of this study was to determine the principal source, or sources, of energy fueling the invertebrate and fish communities of a tundra river system, using stable carbon isotope

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tracing. This technique provides a powerful alternative approach to the traditional methods of assessing food resources used by consumers (see Fry and Sherr 1984; Rounick and Winterbourn 1986; Peterson and Fry 1987 for reviews). Stable isotope ratios of consumer tissue have been used to identify the major carbon pathways in many systems, including rivers and lakes (e.g. Rau 1980; Rounick et al. 1982), estuaries and salt marshes (e.g. Peterson et al. 1985b; Jackson et al. 1986), and the sea (e.g. McConnaughey and McRoy 1979; Fry et al. 1982). We used this technique to describe the major carbon pathways within the river system and, in particular, to assess the importance of riverine food chains to arctic char.

Study Area

Sampling sites were located within the lower catchment of the Koroc River, a fourth-order river which discharges into Ungava Bay approximately 30 km north of Kangiqsualujuaq, northern Quebec (Fig. 1). The Koroc originates in the Torngat Mountains on the Quebec/Labrador border and has a total drainage area of about 4050 km². The river bed consists of granitic boulders and bedrock ledges in tributary streams and mainstream rapids, while sand and fine gravel are the predominant substrata in the main channel from Hulik Lake to above Alipaqq Creek. Winter ice cover typically breaks up in mid-June and discharge increases erratically depending on weather through mid-July as snow melts in the Torngats, then generally declines until freeze-up in late October. River water is characterized by low conductivity (10–30 μS cm⁻¹) and is usually very clear with underwater visibility noted by divers at greater than 8 m, except during a brief period of maximum snowmelt when visibility was limited to 0.5–2 m (Stenzel 1987). During August 1987, three water samples, filtered through Whatman GF/C filters, contained 456 ± 11 μg L⁻¹ of suspended material (± SE).

Despite its relatively low latitude (58°46'N), the climate of the Koroc basin is subarctic and the northern tree-line parallels the coast of Ungava Bay coincident with the mouth of the river. Sparse to moderately dense stands of black spruce, willow, and birch occur in sheltered valleys along the Koroc but rarely more than 40 m above river level. The dominant type of vegetation throughout most of the basin is tundra, consisting of lichens, mosses, and dwarf shrubs. A list of common species found in the study area is given below.

Samples of fish, invertebrates, and plant material for stable isotope analysis were collected from nine sites within the lower part of the river system (Fig. 1). Sites 1 and 2 were located in the Koroc estuary, near the mouth of the river. The main river channel was sampled along the margin of the first set of rapids (Site 3) where the river empties into the estuary, and at a second set of rapids (Site 4) at the upper end of Alik Lake. Alik Lake, a deep basin of the main river channel (approximately 75 m²), was sampled along the shore at depths less than 1 m (Site 5) and at a depth of 10 m in the centre above the first rapids (Site 6). Dredging in deeper water (40 m) did not yield enough animals for isotopic analysis. Three small tributary streams were also sampled, all of which drain small lakes: Aapiq Creek enters the upper end of Alik Lake (Site 7), Onattalulq Creek enters the river above Hulik Lake (Site 8), and Alipaqq Creek (Site 9) enters the river about 30 km above the estuary (Fig. 1). Several other sites were also visited, but insufficient material was obtained for isotope analysis.

Materials and Methods

All collections were made between the 7th and 20th August 1987. A small seine net or hand net was used to catch juvenile fish at night with the aid of a gasoline lantern, along the shore of Alik Lake and from the mouths of Alipaqq and Aapiq Creeks. Sticklebacks (Gasterosteus aculeatus) and sculpins (Myoxocephalus sp.) were caught in Alik Lake and the estuary, respectively, using a simple dredge with a rectangular opening 30 × 50 cm and a tapered collecting net of 1-mm mesh. Adult arctic char, brook trout (Salvelinus fontinalis), and lake trout (Salvelinus namaycush) were caught in the mainstem Koroc and Alik Lake by angling. Muscle tissue from five additional arctic char was provided by T. Boivin: all were sexually immature, ranging from 43.5 to 52.5 cm fork length, weighing 875 to 1700 g, and were caught in gill-nets from Hulik Lake during November 1985.

Benthic invertebrates were collected from Sites 3–5 and 7–9 using a D-frame net (240-μm mesh). Large rocks were turned and scrubbed to remove attached plants and animals, and areas of gravel or sand were vigorously disturbed by kicking with the net held downstream. Aquatic mosses and accumulations of coarse detritus were also collected and sorted for invertebrates. Plankton was collected from Alik Lake (Site 6) and the estuary (Sites 1 and 2) by horizontal tows of a 0.5-m diameter conical net (156-μm mesh) at depths of 1–3 m. The epibenthos at these deeper sites in Alik Lake and the estuary was sampled with the dredge.

Samples of aquatic plants and coarse detritus were removed from fish and invertebrate collections, supplemented with material gathered by hand, and rinsed thoroughly to remove animals and fine detritus. Small areas (5 cm²) of the surfaces of rocks in the littoral margins of Alik Lake were scraped to provide an estimate of the standing crop of epilithic periphyton and material for isotope analysis. Samples of the major terrestrial plants were collected around Alik Lake and Alipaaq Creek. The tundra groundcover in parts of the valley had been reduced to a thick mat of loose peat through trampling by caribou. Samples of this material also were collected as it was considered to be a likely source of organic matter entering the river during periods of heavy rainfall or snowmelt.

Invertebrates were sorted live from the bulk samples and vouchers of each taxon preserved in 70% ethanol. Vouchers of terrestrial plants were pressed and dried. A small piece of muscle tissue was removed from each of the larger fish, while small sculpins, sticklebacks and large invertebrates were eviscerated. Smaller invertebrates were kept alive in fine mesh cages until their guts had emptied. All samples of animal and plant tissue were oven dried at 50–100°C, wrapped in aluminum foil and sealed in plastic bags with dessicant.

Stable Isotope Analysis

Subsamples of approximately 10 mg dry weight of fish, invertebrate and plant matter were pulverized into a fine powder. Crustaceans and molluscs were first acidified with 1 N HCl, washed with distilled water and redried to prevent contamination of the organic carbon from the carbonate fraction in shell or exoskeleton (Haines and Montague 1979). Several individuals of some of the smaller taxa were pooled to obtain an adequate sample. All of the organic carbon present in these samples was then oxidized in a Leco furnace (Drummie 1976) and the resulting CO₂ purified and analysed in a Micromass
FIG. 1. Location of the Koroc River system and the nine sites sampled in this study.

903 triple collector ratio mass spectrometer (Vacuum Gage Co.). Ratios of $^{13}$C to $^{12}$C were expressed as $\delta^{13}$C (‰), where

$$\delta^{13}C = \frac{^{13}C/^{12}C \text{ sample} - ^{13}C/^{12}C \text{ PDB standard}}{^{13}C/^{12}C \text{ PDB standard}} \times 1000.$$  

The PDB standard refers to the international carbonate standard prepared from the fossil skeleton of a belemnite from the PeeDee formation, South Carolina (Craig 1957). The analytical precision, based on six measurements of a graphite standard over a 9-wk period, was 0.5% ($x = 25.99, 1 \text{ SE} = 0.12\%$). In addition, eight pairs of replicate samples of fish tissue were found to have a mean difference ($\overline{z}_{BSE}$) of 0.27 ± 0.08‰.

Results

Terrestrial and Aquatic Vegetation

The most common riparian species in the lower catchment of the Koroc River were willow (Salix planifolia), alder (Alnus crispa), and birch (Betula glandulosa). These grew to heights of up to 2.5 m along some stream margins but quickly decreased in size with increasing altitude on wet hillsides. Tamarack (Larix laricina) and black spruce (Picea mariana) were also common on the valley slopes, though few individuals were more than 4 m in height. The mean $\delta^{13}$C value of leaves from these five species was $-27.8\%$, the same as that found for decomposing leaves collected from the shallows of Alik Lake and small tributary streams (Fig. 2). On an areal basis, the ground cover consisted primarily of lichens (Cladina stellaris, Arctoparmelia centrifuga, Haematomma laponicum), mosses, and other low-growing plants such as Empetrum nigrum, Ledum decumbens, and in wetter areas, Carex saxatilis. These species, together with the samples of loose detritus, were slightly more $^{13}$C enriched with a mean $\delta^{13}$C of $-26.4\%$ (Fig. 2).

Aquatic plants showed considerable variation in $\delta^{13}$C values and were more $^{13}$C enriched than most terrestrial plants. Aquatic mosses in the tributary streams and mainstem rapids were found growing only in small clumps on stones, but formed a thick carpet over much of the bottom of the lake at depths of 3–10 m. Samples from the tributary streams and Alik Lake had similar mean $\delta^{13}$C values ($-25.1\%$), however, small clumps from the rapids were more $^{13}$C depleted (Fig. 2). The only other aquatic macrophyte recorded, Hippuris vulgaris, was found in small patches growing up through the moss in Alik Lake at depths of 3–5 m. This species was far more $^{13}$C enriched than the mosses, with a mean $\delta^{13}$C value of $-21.5\%$ (Fig. 2).

Despite the lack of shading by terrestrial vegetation, stones forming the beds of tributary streams and at depths of less than 1 m in the mainstem rapids appeared to be free of epilithic algae. As a consequence, we were unable to collect sufficient material for stable isotope analysis. Rock scrapes from a depth of about 35 cm along the margin of Alik Lake, however, yielded a mean (+1 SE) dry weight of 1.2 ± 0.1 mg cm⁻². This epilithon was the most ¹³C enriched of the samples from freshwater with a mean δ¹³C value of −17.8% (Fig. 2). The only other epilithon sampled was a thick, brown mat on stones at the outlet of the headwater lake above Aapic Creek. This consisted mainly of fungus, decomposing moss fragments and diatoms, and had a mean δ¹³C value of −22.4‰.

The dominant marine macroalgae were Fucus, found in the lower intertidal and shallow subtidal zones of the estuary, and Laminaria, which was abundant at depths of about 4–5 m below low tide. The ¹³C values of samples of kelp were similar to that of epilithic algae from Alik Lake but Fucus was slightly more ¹³C enriched (Fig. 2).

Aquatic Invertebrates

The mean δ¹³C values of the more common aquatic invertebrates from the small tributary streams and rapids of the main river channel were similar to that of leaves of the terrestrial vegetation (Fig. 3). Notable exceptions were larvae of Simulium spp. and nymphs of Siphlonurus quebecensis, collected at the outfall of the headwater lake on Aapic Creek. Both of these taxa were ¹³C depleted with respect to other lotic invertebrates and had mean δ¹³C values of only −31.0 and −30.5‰, respectively. Blackfly larvae and Rhynchophila from the mainstem rapids were also ¹³C depleted with respect to the rest of the lotic fauna, but to a lesser extent. Larvae of Tipula were found in the finer sediments of the tributary streams and mainstem rapids, and generally were more ¹³C enriched than other taxa (Fig. 3). These larvae showed considerable variation in δ¹³C values between the tributary streams, ranging from −27.0‰ in Alipaaq Creek to −23.7‰ in Onatualuq Creek.

In general, invertebrates from Alik Lake were more ¹³C enriched than those in the tributary streams and rapids of the main river channel (Fig. 3). Of the taxa found in both lotic and lentic habitats, Siphlonurus quebecensis and Tanytisididae showed a marked difference in δ¹³C values. Samples of the former species from Alik Lake were ¹³C enriched by 10‰ more than those from Aapic Creek. In contrast, δ¹³C values of Lepidostoma promineins showed little habitat difference, indicating a similar ultimate dietary source. Likewise, δ¹³C values of lentic samples of Tipula were similar to those for Onatualuq Creek and the mainstem rapids. The contents of guts from S. quebecensis and Tipula from Alik Lake and the tributary streams were examined microscopically. No differences were apparent and all guts contained about 95% detritus and 5% diatoms, filamentous algae and fungal hyphae. The fingernail clam, Pisidium ventricosum was the most ¹³C depleted of the benthic invertebrate fauna of Alik Lake and had a mean δ¹³C value similar to those of taxa collected from lotic habitats (−27.8‰).

Horizontal plankton tows at depths of 1–3 m and oblique tows from 10 m to the surface, failed to collect any invertebrates from Alik Lake during daylight. At night (23:30), however, the net clogged within 5 min when towed horizontally at low speed (3–5 km h⁻¹). In decreasing order of abundance, the catches consisted of Holopodium gibberrum, Leptodiaptomus minutus, Heteronoe pupurialis, Bosmina spp., and an unidentified cyclopoid copepod, as well as small numbers of chironomid larvae and pupae. Samples of this plankton were also ¹³C depleted compared with most of the benthic fauna of the lake (Fig. 3).

Mysids, eucarid shrimps (Natantia), and gammarid amphipods (mainly Gammarus oceanicus) dominated the catches in both the plankton and benthic dredge hauls from the Koroc estuary. These three taxa had mean δ¹³C values of −19.9, −19.6, and −18.5‰, respectively (Fig. 3). Bivalve and gastropod (mostly Littorina sp.) molluscs were abundant on the blades of Fucus and Laminaria. The carbon isotope ratios of the bivalves were similar to those of the most ¹³C enriched freshwater invertebrates, however, δ¹³C values of the gastropods were considerably higher (Fig. 3).

Fish

The only species of fish observed in tributary streams were juvenile (3–10 cm total length (TL)) and adult (>30 cm TL) brook trout, and juvenile (3–12 cm TL) arctic char. Samples of all of these fish had δ¹³C values similar to those of most of the invertebrates found within these habitats, though juvenile char were slightly more ¹³C enriched than the brook trout (Fig. 4). Stable carbon isotope ratios of juvenile arctic char, and adult brook trout, lake trout, and sticklebacks from Alik Lake were very similar, and all were more ¹³C enriched than fish from the
Discussion

The utility of stable isotope tracing of energy flow in ecosystems depends on the existence of differences in isotope ratios among potential sources of energy available to consumers (Peterson and Fry 1987) but such variation is not always present. For example, Peterson et al. (1986) had little success with this technique in an Alaskan tundra stream because of the relative similarity of isotope ratios among different sources of organic matter. In the Koroc River system, however, terrestrial plants were isotopically distinct from aquatic macrophytes and both marine and freshwater algae. With the exception of samples collected from stones in the mainstem rapids, aquatic mosses were also more $^{13}$C enriched than terrestrial vegetation, although only by about 2%.

There was little evidence of epilithic algae in the small tributaries and mainstem rapids. Tundra streams have been shown to be nutrient limited and have a low primary productivity, despite ample insolation during summer (Peterson et al. 1985a; 1986). Although primary productivity was not measured in the Koroc system, the invertebrates from these habitats were generally too $^{13}$C depleted to have derived a significant amount of energy from this source. Similarly, moss was too $^{13}$C enriched to be the likely source of assimilated carbon because consumers generally have higher $^{13}$C values than their food (DeNiro and Epstein 1978; Peterson and Fry 1987). Terrestrial organic matter, particularly in the form of leaves shed from riparian trees and shrubs, seems to be the most likely source of energy fueling the invertebrate communities of lotic habitats in the Koroc.

The most notable exceptions among the invertebrates from lotic habitats were the simulids and S. quebecensis collected from the headwaters of Aapic Creek. None of the samples of potential food materials collected in this study were sufficiently $^{13}$C depleted to be a likely source of energy for these taxa. However, phytoplankton in the lake drained by this stream may well be sufficiently $^{13}$C depleted (e.g. Rau 1978) to account for the low isotope ratios of the simulids. Unfortunately, our samples of phytoplankton were insufficient for the analysis of stable carbon isotope ratios. Nymphs of Siphlonurus are known to be omnivorous (Edmunds 1960), so S. quebecensis may feed on blackfly larvae as well as on other materials exported from the lake.

In marked contrast to the small streams and rapids of the main river, the benthic fauna of Alik Lake did not appear to be as dependent on terrestrial sources of carbon. Moreover, despite its considerable biomass, the thick carpet of moss did not appear to contribute significantly to the energy pool. The preferential loss of $^{12}$C during respiration usually results in the enrichment of consumer tissue relative to its food but only by about 1% (DeNiro and Epstein 1978). Most benthic taxa in the lake were about 3% more enriched in $^{13}$C than the moss and, as a result, it is unlikely that this potential source of energy was being exploited to any great extent. The tissues of mosses seem to be especially refractory and are consumed by only a few species of freshwater invertebrates (Hynes 1970), even after they begin to decompose (Davies 1975; Welch 1976). The stable carbon isotope ratio of the small macrophyte, Hippuris vulgaris, was identical to that of several invertebrate taxa in the lake but is unlikely to be a major source of carbon because of its sparse distribution and abundance.

Epilithic algae were the most abundant $^{13}$C enriched food source available to consumers in Alik Lake and may have contributed to the elevated $^{13}$C values of the benthic fauna. Algae could enter the food chain through grazing on stone surfaces in the euphotic zone of the lake as well as through sedimentation of epilithic algae that has been eroded from rocks upstream. As it settles, such material would be entrained by the thick bed of moss where dense populations of Siphlonurus, chironomids, and enchytraeid worms were recorded, the most $^{13}$C enriched invertebrates in the lake.

There is also a possibility that marine sources of carbon are responsible for the $^{13}$C enrichment of the fauna of Alik Lake. The rapids separating the lake from the level of spring high tides have a vertical drop of about 15 m, so direct tidal influx of seawater into the lake is unlikely. In addition, even though the deeper portions of the lake are below mean sea level, the benthic fauna consists of strictly freshwater taxa, including Tubificidae (Rhyacodrilus sp.), P. ventricosum, and Hydracarina. However, marine carbon may be introduced and incorporated into the food chains of the lake via the movements of arctic char. Both Alik and Hulik Lakes are major overwintering sites for arctic char in the Koroc River system (Boivin 1987). Adult char do not feed while in freshwater (Dutil 1986) from roughly September through mid-June, but do metabolize a large fraction of their lipid reserves accumulated while feeding at sea (Boivin 1987). Marine carbon may enter the freshwater food chain through respiration, as well as by the decomposition of fish that die during winter. Pacific salmon (Onchorhyncus spp.), which die shortly after spawning in freshwater streams, have been shown to make a significant contribution to the energy flow of rivers (e.g. Richey et al. 1975; Johnson and Ringer 1979). In contrast, arctic char are multiple spawners and postreproductive mortality may not be very great (Johnson 1980).

Clearly the benthic invertebrates of Alik Lake obtain their dietary carbon from at least two sources; most likely epilithic algae and terrestrial organic matter. However, we are unable to rule out possible contributions from aquatic moss, which has a considerable biomass in the lake, and marine sources. This problem of assessing the relative importance of several primary food resources may be resolved by the use of other stable isotopes, such as $^{15}$N and $^{32}$S, which can provide far greater resolution than the single carbon isotope tracer (Peterson et al. 1986).
1985b; Peterson and Fry 1987). Stable sulfur and nitrogen isotopes would be particularly useful in determining the contribution of marine sources of energy to food chains in the Koroc system. Unfortunately, our samples were insufficient to allow such determinations.

Fish in the small streams appeared to derive most of their energy from terrestrial sources via the benthic invertebrate fauna. It was apparent, however, that fish in Alik Lake did not derive all of their energy from feeding on the benthos, because their bodies were $^{13}$C depleted compared with most invertebrates in the lake. They also must derive part of their energy from either plankton or drifting organisms from up-river, both of which had lower $^{13}$C values than the benthic fauna of the lake. The unusually low $^{13}$C values of juvenile brook trout from Alik Lake suggests that these fish have fed predominantly on plankton or perhaps simulids or other $^{13}$C depleted invertebrates from the tributary streams or rapids. Furthermore, the differences in $^{13}$C values between juvenile arctic char and juvenile brook trout in Alik Lake and the tributary streams also suggest partitioning of food resources in both habitats. Stenzel (1987) found that juvenile arctic char remain within restricted areas at least over short periods of time. Differences in $^{13}$C values of juvenile arctic char and juvenile and adult brook trout between Alik Lake and the tributary streams indicates that there is little movement of these fish within the Koroc system over the longer term.

Despite the potential export of dissolved and particulate organic matter from the river system (Peterson et al. 1986), terrestrial carbon does not appear to make a significant contribution to the estuarine food web. This may be a general feature of the nearshore communities of arctic embayments (Schell 1983). Of the estuarine invertebrates we sampled, only bivalves had $^{13}$C values indicative of a diet which may include detrital carbon carried by the river. However, these did not account for a large proportion of the estuarine invertebrate fauna and are rarely, if ever, eaten by arctic char. Mysis, shrimps, and amphipods, which are the most important invertebrate components of the diet of arctic char in the Koroc estuary (Adams 1987), had $^{13}$C values indicative of a dependence on marine sources of energy (Rounick and Winterbourn 1986). The high $^{13}$C values of adult char caught in the Koroc River confirm that these fish obtain most of their biomass carbon from feeding at sea.

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