

## Littoral energy mobilization dominates energy supply for top consumers in subarctic lakes

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### Abstract

We used stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopes to assess the energy sources supporting the top consumer (Arctic char, *Salvelinus alpinus*) in nine subarctic lakes in northern Sweden. The  $\delta^{13}\text{C}$  of littoral (epipellic algae) and pelagic (bacterioplankton and phytoplankton) energy sources were clearly separated in the lakes, as reflected in habitat-specific consumers (zoobenthos, zooplankton). Char were enriched in  $^{13}\text{C}$  compared with pelagic energy sources and prey and isotopically more similar to littoral energy sources and prey. The contribution of littoral energy sources to char body carbon was estimated to range between 62% and 94% among the lakes. The reliance on littoral energy sources was independent of char size and did not change when char coexisted with a small-sized prey fish (nine-spined stickleback, *Pungitius pungitius*). The strong reliance of top consumers in subarctic lakes on littoral energy sources may be due to the higher energy mobilization and larger sizes of primary consumers in littoral than in pelagic habitats.

The energy flow through the ecosystem, i.e., from the energy mobilizers at the base of the food web to top energy consumers, is of fundamental importance for the function of lake ecosystems. Mobilization and transfer of energy within the food web sets the limit for production at higher trophic levels, and the presence of several diverse energy-flow pathways may affect ecosystem properties such as food-web dynamics and nutrient cycling (Polis et al. 1997). Still, energy flow between benthic and pelagic compartments has received little attention, reflecting both methodological constraints and a scarcity of whole-lake studies (Vadeboncoeur et al. 2002).

Research into lake energy flow has largely focused on pelagic food webs. Pelagic energy mobilization derives from photosynthesis and from bacterioplankton growing on allochthonous organic carbon (Tranvik 1989; Jones 1992; Karlsson et al. 2002). The energy mobilization at the base of the food web is consumed, redistributed in the food web, and subsequently transferred to top consumers such as fish. However, recent studies have shown that benthic resources are of great importance for lake food webs, since fish communities may make considerable use of zoobenthos (Schindler and Scheuerell 2002). In the profundal zone, exploitation of benthic resources can be regarded as mainly comprising the re-

cycling of energy mobilized in the pelagic zone. However, photosynthesis by benthic algae may constitute a large part of lake energy mobilization in small unproductive lakes (Björk-Ramberg and Ånell 1985; Vadeboncoeur et al. 2002). Owing to distinct separation in isotopic signatures of mobilized organic carbon, it is possible to determine the fraction of littoral and pelagic energy sources supporting food webs, and littoral energy mobilization has been suggested to be of considerable importance for top consumers in unproductive lakes (Hecky and Hesslein 1995; Hobson and Welch 1995; Vander Zanden and Vadeboncoeur 2002).

Ecosystem energy flow also depends on the ability of consumers to exploit and grow on different resources. The presence of size structure in the top consumers, such as fish, in lake ecosystems evidently permits fish to use different resources over their ontogeny (Werner and Gilliam 1984; Persson 1988). As a consequence, energy sources and trophic position may vary between individuals of different size in fish populations. Despite their fundamental importance for the function of lake ecosystems, there exist very few estimates of the relative importance of littoral versus pelagic energy sources for ecosystem energy flow in unproductive lakes.

This study aims to determine the basic energy sources supporting top consumers in unproductive subarctic lakes. The study was performed by analyzing the stable isotopic composition of Arctic char (*Salvelinus alpinus*) and its potential food and energy sources in nine small subarctic lakes in northern Sweden. Char is the dominant fish species in subarctic lakes, commonly the sole fish species (allopatric lakes), but also found together with other species (sympatric lakes) such as nine-spined sticklebacks (*Pungitius pungitius*). Char is known to feed on both benthic and pelagic organisms, and large char may also feed on smaller conspecifics

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or other small prey fish (Klemetsen et al. 2003). In contrast to many fish top consumers where small individuals feed on zooplankton (Persson 1988; Post et al. 1999), a recent study has suggested that small char feed mainly on benthic near-shore prey (Byström et al. 2004). Sticklebacks are small sized and a more efficient forager on zooplankton than are char and have been shown to have strong effects on zooplankton resources (Hansson et al. 1990; Olofsson 2002; P. Byström unpubl. data).

Hence, we hypothesize that allopatric char populations in small unproductive lakes, irrespective of size structure and whether cannibalism is significant, should be supported mainly by littoral energy mobilization. On the other hand, in the presence of sympatric planktivorous prey fish such as sticklebacks, the main energy source for char may change over the course of char ontogeny as a result of the size dependency in consumption of sticklebacks by char.

## Materials and methods

Nine small lakes (Table 1), situated in the Scandinavian mountains on weathering-resistant bedrock (i.e., granite, gneiss, amphibolite) in subarctic northern Sweden (68°N, 18°E), were studied. Lakes 6 to 13 (following the nomenclature in Karlsson et al. 2002) have previously been studied regarding energy mobilization and transfer within the planktonic community (Karlsson et al. 2002, 2003), and lakes 8, 9, and 13 are currently under study regarding char population dynamics (Byström et al. 2004). The lakes are ice free for approximately 3 to 4 months per year and can be classified as discontinuous or continuous cold polymictic. The lakes all have a similar nutrient content during the ice-free season (Table 1, see Karlsson et al. 2002 for methods). All lakes contain Arctic char, and in three of the lakes (lake 6, Stuur Guossasjavri [G] and Stuur Soahkejavri [S]) char co-exist with nine-spined sticklebacks. In the littoral zone (i.e., the benthic communities down to the water depth where light permits photosynthesis) of lakes in the area, energy mobilization has been shown to be dominated by photosynthetic epipelagic algae (blue-green algae, diatoms) on soft sediments (Björk-Ramberg and Ånell 1985).

Sampling all variables except fish was performed monthly during the ice-free season, while fish sampling was performed in late summer and/or in winter under ice, 1 or 2 times per lake. Crustacean zooplankton were sampled 3 or 4 times per lake by vertically sampling the entire water column using a plankton net with a mesh size of 100  $\mu\text{m}$ ; the zooplankton were stored in filtered lake water for gut evacuation. Zooplankton were separated manually into cladocerans (*Daphnia longispina* and *Bosmina coregoni*, except in lakes 9, 11, and 12) and copepods (*Eudiaptomus graciloides*). Soft surface sediment was collected from shallow (1- to 2-m deep) parts of the lakes, one to three times per lake, using a sediment core sampler and gently scraping the surface organic layer of the sediment core into a container. Zoobenthos were collected at the same place as was the surface sediment in lake 6, G, and S by using a Ekman grab sampler (three times per lake). The dominant groups (Amphipoda—*Gammarus sp.*, Bivalvia—*Pisidium sp.*, Chiron-

Table 1. Limnological characteristics (summer mean  $\pm 1$  SD) of nine lakes in subarctic Sweden. Altitude (Alt) in meters above sea level (asl); lake surface area (Area); maximum lake depth ( $Z_{\text{max}}$ ); mean lake depth ( $Z_{\text{mean}}$ ); dissolved organic carbon (DOC); total nitrogen (TN); total phosphorus (TP);  $\delta^{13}\text{C}$  of cladoceran and copepod zooplankton (Zoo);  $\delta^{13}\text{C}$  of shallow surface sediment (Sed); size range,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of Arctic char; estimated littoral contribution to char body carbon ( $\text{LF}_{\text{char}}$ ); and the trophic position of char ( $\text{TP}_{\text{char}}$ ). Included are the total range obtained by assuming different values of  $\Delta_{\text{C}}$  and  $\Delta_{\text{N}}$  in the estimation of  $\text{LF}_{\text{char}}$  and  $\text{TP}_{\text{char}}$ . Sympatric lakes; 6, G, S; allopatric lakes; 7–9, 1–13.

Lake	Alt (m asl)	Area (km <sup>2</sup> )	$Z_{\text{max}}$ (m)	$Z_{\text{mean}}$ (m)	DOC (mg L <sup>-1</sup> )	TN ( $\mu\text{g L}^{-1}$ )	TP ( $\mu\text{g L}^{-1}$ )	Zoo ( $\delta^{13}\text{C}$ )	Sed ( $\delta^{13}\text{C}$ )	Length (mm)	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Arctic char	
														$\text{LF}_{\text{char}}$ (%)	$\text{TP}_{\text{char}}$
6	445	0.05	4.4	1.7	4.7 $\pm$ 0.8	230 $\pm$ 0	5.8 $\pm$ 1.6	-32.4 $\pm$ 0.2	-22.3 $\pm$ 0.3	105–460	7	-23.3 $\pm$ 1.0	7.5 $\pm$ 1.0	78 (66–85)	3.8 (3.7–3.9)
G	570	0.30	6.5	2.2	4.9 $\pm$ 0.9	233 $\pm$ 15	7.6 $\pm$ 1.6	-31.2 $\pm$ 1.6	-21.5 $\pm$ 1.8	91–535	25	-24.2 $\pm$ 1.3	8.9 $\pm$ 0.5	62 (51–68)	3.6 (3.5–3.7)
S	487	0.35	2.3	10.1	3.8 $\pm$ 0.3	127 $\pm$ 29	4.4 $\pm$ 1.2	-34.4 $\pm$ 2.0	-20.8 $\pm$ 0.4	294–575	5	-24.5 $\pm$ 3.0	8.6 $\pm$ 0.7	64 (54–69)	4.1 (3.9–4.3)
7	510	0.04	4.2	1.9	5.0 $\pm$ 0.7	244 $\pm$ 179	4.8 $\pm$ 1.9	-34.7 $\pm$ 0.6	-23.4 $\pm$ 0.4	235–411	7	-25.8 $\pm$ 0.7	7.6 $\pm$ 0.5	69 (59–75)	3.7 (3.6–3.9)
8	710	0.04	8.2	2.8	3.2 $\pm$ 0.5	113 $\pm$ 35	7.9 $\pm$ 1.1	-32.6 $\pm$ 0.5	-24.6 $\pm$ 0.2	59–400	26	-25.0 $\pm$ 0.8	8.1 $\pm$ 0.5	80 (66–89)	3.8 (3.7–3.9)
9	712	0.04	8.5	2.8	3.6 $\pm$ 0.6	207 $\pm$ 136	7.9 $\pm$ 4.3	-31.3 $\pm$ 0.9	-23.6 $\pm$ 0.3	94–239	22	-23.9 $\pm$ 1.2	7.4 $\pm$ 0.6	83 (69–91)	3.3 (3.2–3.5)
11	850	0.02	8.2	2.2	3.3 $\pm$ 0.5	248 $\pm$ 103	5.9 $\pm$ 0.8	-32.4 $\pm$ 0.4	-24.3	147–345	5	-25.1 $\pm$ 1.0	7.1 $\pm$ 0.4	67 (58–72)	3.2 (3.1–3.3)
12	865	0.11	10.7	4.5	3.5 $\pm$ 0.5	187 $\pm$ 17	6.8 $\pm$ 2.4	-33.9 $\pm$ 0.2	-24.2 $\pm$ 0.5	88–220	9	-26.6 $\pm$ 0.7	8.6 $\pm$ 0.3	66 (57–72)	3.3 (3.3–3.5)
13	993	0.17	15.8	4.7	2.7 $\pm$ 0.4	142 $\pm$ 34	5.5 $\pm$ 1.0	-31.0 $\pm$ 0.7	-22.5 $\pm$ 0.4	80–488	15	-21.9 $\pm$ 0.5	7.9 $\pm$ 0.6	94 (81–100)	3.4 (3.3–3.5)

omidae, Ephemeroptera, Isopoda, and noncarnivorous Trichoptera) were separated and washed with distilled water. For bivalves, only the soft body tissue was used for analysis. In lake G, surface sediment and zoobenthos were collected at three depths (1, 3, and 6 m). Char and sticklebacks were sampled using Ella traps (mesh size, 6 mm, www.ellafishing.com) and gillnets (Nordic 12) distributed in the pelagic, littoral, and profundal habitats of the lakes. Part of the fish dorsal muscle was used for analysis. Material for isotopic analysis was dried at 65°C, homogenized when necessary, and stored frozen until analysis. Analysis of stable isotopes was carried out using a Carlo Erba EA 1108 elemental analyzer connected to a Fison Optima isotope ratio mass spectrometer at continuous flow. Results are expressed by the  $\delta$  notation in per mil (‰) as  $\delta = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$  where  $R = {}^{13}\text{C}/{}^{12}\text{C}$  or  ${}^{15}\text{N}/{}^{14}\text{N}$ . The analytical precision was 0.2‰.

The littoral contribution to char body carbon ( $\text{LF}_{\text{char}}$ ) and the trophic position of char ( $\text{TP}_{\text{char}}$ ) were estimated using a two-source mixing model including both the isotopic signatures of littoral and pelagic base energy sources and the trophic isotopic fractionation (Vander Zanden and Rasmussen 2001) of C ( $\Delta_{\text{C}} = 0.47\text{‰}$ ) and N ( $\Delta_{\text{N}} = 3.46\text{‰}$ ) between consumer and diet in the food web. The isotopic signal of the pelagic baseline ( $\delta^{13}\text{C}_{\text{pel}}$ ,  $\delta^{15}\text{N}_{\text{pel}}$ ) was estimated from the isotopic signal of zooplankton, assuming that zooplankton body carbon (mean of cladocerans and copepods,  $\delta^{13}\text{C}$ ) are derived from pelagic energy mobilization by phytoplankton and bacterioplankton (Karlsson et al. 2003) and that cladocerans and copepods act as primary and secondary consumers, respectively (Matthews and Mazumder 2003; Karlsson et al. 2004; J. Karlsson unpubl. data). The  $\delta^{13}\text{C}$  of the littoral baseline ( $\delta^{13}\text{C}_{\text{lit}}$ ) was approximated by the isotopic signal of the shallow surface sediment (Fig. 1). The  $\delta^{15}\text{N}$  of the littoral baseline ( $\delta^{15}\text{N}_{\text{lit}}$ ) used in the model was estimated by assuming a  $\Delta_{\text{N}}$  of 3.46‰ between epipelagic algae and zoobenthos. This  $\Delta_{\text{N}}$  between epipelagic algae and zoobenthos is higher than the  $\Delta_{\text{N}}$  observed in the lakes (2.0‰, see results) but is used for the sake of simplicity to enable the use of a constant  $\Delta_{\text{N}}$  in the estimation of  $\text{LF}_{\text{char}}$  and  $\text{TP}_{\text{char}}$ . Thus  $\text{LF}_{\text{char}}$  can be calculated as

$$\text{LF}_{\text{char}} = [\delta^{13}\text{C}_{\text{char}} - \delta^{13}\text{C}_{\text{pel}} - (\delta^{15}\text{N}_{\text{char}} - \delta^{15}\text{N}_{\text{pel}}) \times \text{TS}] \div (1 - \text{TS} \times \text{BS}) / (\delta^{13}\text{C}_{\text{lit}} - \delta^{13}\text{C}_{\text{pel}}) \quad (1)$$

where TS is the slope of the trophic fractionation of C and N in the food web ( $\Delta_{\text{C}}/\Delta_{\text{N}}$ , 0.47/3.46‰) and BS is the slope of the linear relationship between the pelagic and littoral baselines in each lake according to Meili et al. (1996).  $\text{TP}_{\text{char}}$  can then be calculated as

$$\text{TP}_{\text{char}} = 1 + [(\delta^{15}\text{N}_{\text{char}} - \delta^{15}\text{N}_{\text{pel}} - (\delta^{13}\text{C}_{\text{lit}} - \delta^{13}\text{C}_{\text{pel}}) \times \text{BS} \times \text{LF}_{\text{char}}) / \Delta_{\text{N}}] \quad (2)$$

The various assumptions made contained uncertainties, and the influence of these on the estimation of  $\text{LF}_{\text{char}}$  and  $\text{TP}_{\text{char}}$  was tested by including minimum and maximum values of  $\Delta_{\text{C}}$  (0.2 to 1‰, del Giorgio and France 1996) and  $\Delta_{\text{N}}$  (3.46  $\pm$  0.23‰, Vander Zanden and Rasmussen 2001). Estimating  $\text{LF}_{\text{char}}$  and  $\text{TP}_{\text{char}}$  using the isotopic composition of clams (profundal) and snails (only found in lake G) as the isotopic

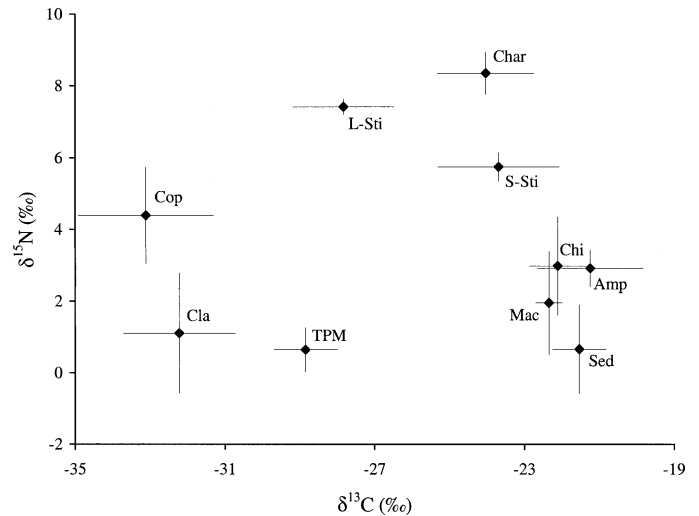


Fig. 1. Stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopic composition (mean  $\pm$  1 SD) of shallow surface sediment (Sed) and of consumers in pelagic and shallow littoral habitats in lakes 6, G, and S in northern Sweden. Sticklebacks are from lake 6 and represents the mean value ( $\pm$ 1 SD) of small (S-Sti) and large (L-Sti) sized fishes. Included is also typical isotopic composition of pelagic total particulate matter (TPM) (lakes 6 to 13, from Karlsson et al. 2004). Abbreviations: Amphipoda (Amp); Chironomidae (Chi); Macroinvertebrates (Mac = Ephemeroptera and Trichoptera); Copepoda (Cop); and Cladocera (Cla).

baselines of primary consumers (e.g., Post 2002) revealed only small differences between results obtained by the two methods (mean difference:  $\text{LF}_{\text{char}} = 4\text{‰}$ ,  $\text{TP}_{\text{char}} = 0.1$ ). Assumptions in isotopic baseline estimates produce the greatest uncertainties for cross-system comparisons of  $\text{LF}_{\text{char}}$  and  $\text{TP}_{\text{char}}$  (Post 2002). Thus, the extent of the influence of fish size on  $\text{LF}_{\text{char}}$  and  $\text{TP}_{\text{char}}$  was assessed by comparatively analyzing data comprising (1) values obtained from all lakes and (2) values obtained within individual lakes characterized by a large range in char size (<100 to >400 mm).

## Results

We found great differences in  $\delta^{13}\text{C}$  value between different consumers in the lakes, reflecting their use of base energy sources of clearly different isotopic compositions. Zooplankton had low  $\delta^{13}\text{C}$  values ( $-34.7$  to  $-31.0\text{‰}$ ) compared both with other consumers and with the shallow surface sediment in the lakes ( $-24.6$  to  $-20.8\text{‰}$ ; see Fig. 1, Table 1). The relatively low  $\delta^{13}\text{C}$  values for zooplankton in the lakes has been shown to be a result of their reliance on energy mobilized by phytoplankton and bacterioplankton, which produce organic carbon of relatively low  $\delta^{13}\text{C}$  (Karlsson et al. 2003). The  $\delta^{13}\text{C}$  values for bivalves in lake G also reflect a predominant reliance on pelagic energy mobilization, but subsidized by benthic carbon sources as indicated by the increasing  $\delta^{13}\text{C}$  of bivalves with decreasing depth (Fig. 2). In contrast, the  $\delta^{13}\text{C}$  values for most zoobenthos were similar to that of the surface sediment, particularly at shallow depths (Fig. 1, Fig. 2). The higher  $\delta^{13}\text{C}$  values of shallow surface sediment compared with those of pelagic organic matter

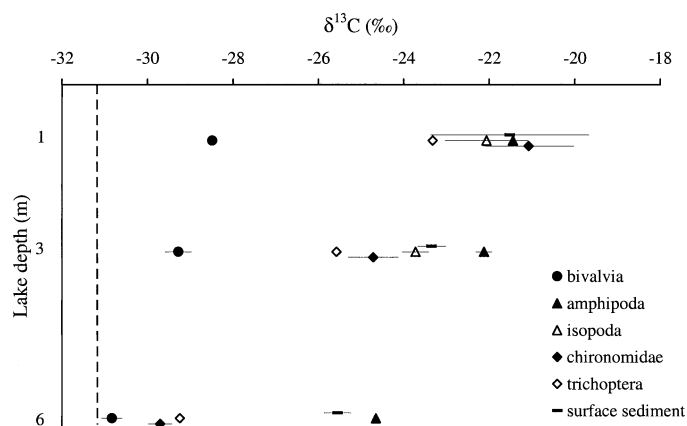


Fig. 2. Stable carbon isotopic composition ( $\delta^{13}\text{C}$ ) of surface sediment and benthic organisms (summer mean  $\pm$  1 SD) at 1-, 3-, and 6-m depths in lake G in northern Sweden. The zooplankton  $\delta^{13}\text{C}$  signal is indicated by the dashed vertical line.

(Fig. 1, Table 1) and deep-water sediments (Fig. 2) in the lakes are in line with the values found in other lakes of the area (Karlsson et al. 2003). This reflects the high contribution of organic carbon by epipelagic algae in the shallow sediments. Photosynthesis by epipelagic algae is mainly controlled by light availability, which results in decreasing production with increasing depth in subarctic lakes (Björk-Ramberg 1983; Hansson 1992). Values of  $\delta^{13}\text{C}$  are often relatively high in benthic algae, where  $\text{CO}_2$  uptake is diffusion limited because of the thick boundary layers, resulting in low discrimination against  $^{13}\text{C}$  (Hecky and Hesslein 1995). High rates of photosynthesis in benthic,  $^{13}\text{C}$ -enriched algae and the lower settling rate of pelagic,  $^{13}\text{C}$ -depleted organic matter in shallow than in deep sediments (Björk-Ramberg 1983) result in a predominance of  $^{13}\text{C}$ -enriched organic carbon from benthic photosynthesis in the shallow sediments. Thus, the data indicate that different base energy sources support zoobenthos at different depths and that the  $\delta^{13}\text{C}$  values for shallow surface sediments will adequately represent the  $\delta^{13}\text{C}$  values for energy mobilized by benthic algae.

The  $\delta^{15}\text{N}$  values for consumers were fairly similar in both littoral and pelagic habitats (Fig. 1). Still, the zoobenthos (mean length in mm  $\pm$  1 SD) among lakes: Amphipoda =  $10.7 \pm 0.4$ , Chironomidae =  $9.5 \pm 0.5$ , Macroinvertebrate =  $14.0 \pm 5.4$ ) were approximately 1 order of magnitude larger than the zooplankton (Copepoda =  $1.0 \pm 0.1$ , Cladocera =  $0.6 \pm 0.1$ ), implying a great difference in size structure between primary consumers in benthic and pelagic habitats. There were relatively small differences between the  $\delta^{15}\text{N}$  values for shallow surface sediment and for zoobenthos (see Fig. 1; mean difference among lakes:  $2.0 \pm 0.36\text{‰}$ ), indicating a  $\Delta_N$  in the lower range of reported values (Vander Zanden and Rasmussen 2001).

Mean char  $\delta^{13}\text{C}$  values ranged between  $-26.6$  and  $-21.9\text{‰}$  among the lakes and were found to be enriched in  $^{13}\text{C}$  compared with pelagic energy sources and to be more isotopically similar to littoral energy sources (Table 1, Fig. 1). The clear separation in  $\delta^{13}\text{C}_{\text{lit}}$  and  $\delta^{13}\text{C}_{\text{pel}}$  enables differentiation between the uses of these energy sources by char in the lakes.  $\text{LF}_{\text{char}}$  was estimated at between 62% and 94%

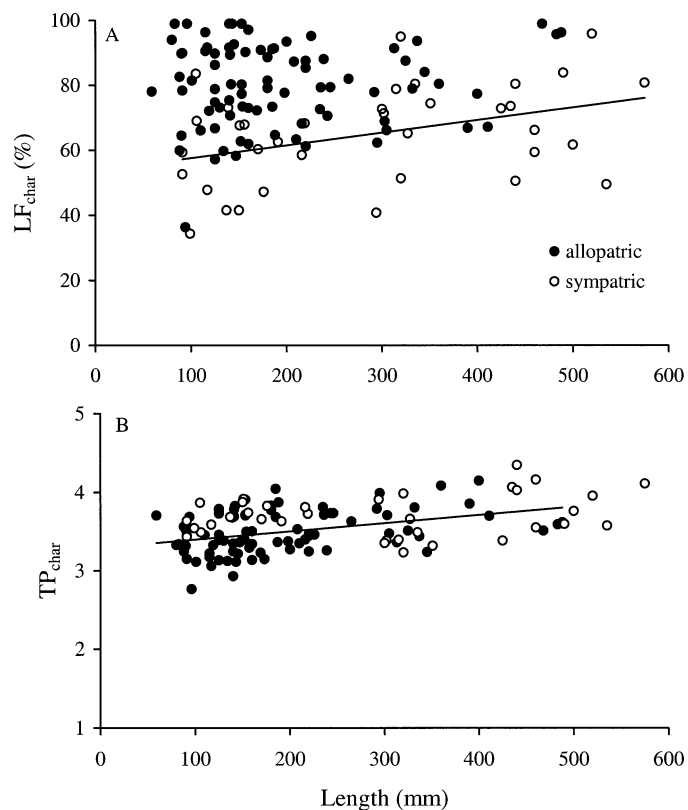


Fig. 3. (A) Littoral contribution to char body carbon ( $\text{LF}_{\text{char}}$ ) in allopatric ( $r^2 = 0.000$ ,  $p = 0.970$ ) and sympatric ( $\text{LF}_{\text{char}} = 53.64 + 0.039 \text{ length}$ ,  $r^2 = 0.15$ ,  $p = 0.020$ ,  $n = 36$ ) lakes in northern Sweden. (B) Char trophic position ( $\text{TP}_{\text{char}}$ ) in allopatric ( $\text{TP}_{\text{char}} = 2.34 + 0.52 \log \text{ length}$ ,  $r^2 = 0.144$ ,  $p < 0.001$ ,  $n = 83$ ) and sympatric ( $r^2 = 0.100$ ,  $p = 0.060$ ) lakes in northern Sweden.

in the lakes (mean: 74%), with no clear difference between allopatric and sympatric lakes ( $t$ -test,  $p = 0.275$ ). Including uncertainties relating to  $\Delta_C$  and  $\Delta_N$  resulted in a minimum estimated mean  $\text{LF}_{\text{char}}$  of 62% and a maximum of 80%. No significant correlation was found between  $\text{LF}_{\text{char}}$  and char size in the allopatric lakes, either when comparing char between all lakes (Pearson correlation coefficients, 0.055) or within individual lakes (Lake 8,  $-0.178$ , Lake 13,  $0.160$ ). There were significant correlations between  $\text{LF}_{\text{char}}$  and char size in the sympatric lakes, both when comparing char from all lakes (Fig. 3) and from within lake G ( $\text{LF}_{\text{char}} = 4.45 + 24.70 \log \text{ length}$ ,  $r^2 = 0.24$ ,  $p = 0.014$ ,  $n = 25$ ). The slopes of the relationships imply relatively small changes in  $\text{LF}_{\text{char}}$  with char size (e.g.,  $\text{LF}_{\text{char}} = 54\%$  and  $68\%$  of 100- to 400-mm char in lake G). In contrast to char, stickleback  $\delta^{13}\text{C}$  values varied considerably with size (Fig. 1) with higher values ( $t$ -test,  $p = 0.05$ ) in small (range: 16 to 31 mm, mean  $\delta^{13}\text{C} \pm 1 \text{ SD} = -23.7 \pm 1.6\text{‰}$ ,  $n = 11$ ) than in large (range: 48 to 57 mm,  $\delta^{13}\text{C} = -27.8 \pm 1.3\text{‰}$ ,  $n = 13$ ) sticklebacks.

Mean char  $\delta^{15}\text{N}$  values ranged between 7.1 and 8.9‰ among the lakes and were clearly  $^{15}\text{N}$  enriched compared with both littoral and pelagic resources. Char  $\delta^{15}\text{N}$  values varied only slightly within lakes (Table 1) despite considerable differences in char size. Mean  $\text{TP}_{\text{char}}$  values were estimated at between 3.2 and 4.1 in the lakes (mean, 3.6), with



a tendency toward a higher  $TP_{\text{char}}$  in sympatric lakes ( $t$ -test,  $p = 0.065$ ).  $TP_{\text{char}}$  values increased with increasing char size in allopatric lakes, both when comparing char from all the lakes (Fig. 3) and within lakes 8 ( $\log TP_{\text{char}} = 0.45 + 0.058 \log \text{length}$ ,  $r^2 = 0.43$ ,  $p < 0.001$ ,  $n = 25$ ) and 13 ( $TP_{\text{char}} = 3.14 + 0.00094 \text{length}$ ,  $r^2 = 0.65$ ,  $p < 0.001$ ,  $n = 15$ ). The slopes of the relationships imply that  $TP_{\text{char}}$  increases approximately 0.3 trophic position units over a 300-mm change in char size (e.g., 100 to 400 mm). In the sympatric lakes there was no relationship between char length and  $TP_{\text{char}}$  (Fig. 3).

## Discussion

As predicted by our hypothesis, the results suggest that top consumers in the studied lakes rely heavily on littoral energy mobilization.  $LF_{\text{char}}$  values were estimated at between 62% and 94% in the lakes (Table 1), despite great variation in both the size structures of the char populations and in lake morphometry. This high  $LF_{\text{char}}$  remained consistent even when accounting for uncertainties in  $\Delta_C$  and  $\Delta_N$ . In accordance with our expectations for char in allopatric lakes, large-sized individuals also mainly relied on littoral energy mobilization. However, the data show only a small increase in  $TP_{\text{char}}$  with char size in the lakes (Fig. 3), implying that zoobenthos was the main resource component for char of all sizes in the lakes. This is consistent with the results of gut content analysis of char from three of the lakes (Byström et al. 2004; P. Byström and J. Andersson unpubl. data). However, even if the large char were mainly cannibals, their energy support would still be of littoral origin since their potential victims were supported by littoral energy mobilization (cf. Hobson and Welch 1995).

In the sympatric lakes, char also consumed nine-spined sticklebacks (Olofsson 2002; P. Byström and F. Olofsson unpubl. data). In contrast to char, stickleback carbon sources varied with fish size: large sticklebacks seemed to rely largely on pelagic energy sources, while small sticklebacks relied mainly on littoral energy sources (Fig. 1). However, since char mainly consumed small-sized sticklebacks (stickleback mean size  $\pm 1$  SD in char stomachs; lake G,  $29 \pm 10$  mm; lake 5,  $28 \pm 4$  mm, P. Byström and F. Olofsson unpubl. data), this diet did not change the main energy source supporting char, since small sticklebacks mainly relied on littoral energy mobilization. Neither did it result in any significant change in  $TP_{\text{char}}$  with char size since small sticklebacks have relatively low  $\delta^{15}\text{N}$  values ( $5.7 \pm 0.4\text{‰}$ ) compared with those of small char (Table 1). Thus even in sympatric lakes containing planktivorous prey fish, the main energy source for the top consumer was of littoral origin, even if the top consumer fed on prey fish. With the available data we can only speculate as to the mechanisms underlying this result. Stomach contents of large char suggested that small-sized sticklebacks are the main prey of large char, and thus that small sticklebacks may restrict their habitat use to the littoral zone since it offers refuge from predation (cf. Byström et al. 2004, and references therein). On the other hand, large sticklebacks may be relatively invulnerable to char predation and can thus to a larger extent feed on the

relatively unexploited pelagic resource. Still, in lakes with sticklebacks, pelagic energy mobilization may be indirectly linked to char, since the great reliance of adult sticklebacks on pelagic energy mobilization contributes to the production of new stickleback recruits on which char feed.

Some of the observed patterns in energy-flow and trophic relationships may be attributed to the specific ontogeny of the studied top consumer (Arctic char). However, there is reason to believe that the findings of this study may apply to unproductive lakes in general, because of the greater energy mobilization and hence resource production in the littoral than in the pelagic habitats of such lakes. The energy mobilization by phytoplankton and bacterioplankton is very low in these lakes, presumably because of low nutrient content that is largely allocated to bacterioplankton production (Karlsson et al. 2002; Jansson et al. 2003). Moreover, earlier studies in the region have shown that benthic primary production is very significant for total primary production, especially in shallow lakes where the light climate permits photosynthesis over a large portion of the lakes' bottom areas. Björk-Ramberg and Ånell (1985) estimated that benthic algae constituted 70%, 78%, and 83% of whole-lake primary production over three different years in a shallow lake ( $Z_{\text{max}} = 4.5$  m,  $Z_{\text{mean}} = 1.2$  m). In a deeper lake ( $Z_{\text{max}} = 13.7$  m,  $Z_{\text{mean}} = 6.0$  m), the production by epipelagic algae and phytoplankton was similar (Björk-Ramberg 1983). In contrast, Bodin and Nauwerck (1968) found that epipelagic algae constituted only 15% of whole-lake primary production in a large, deep lake ( $Z_{\text{max}} = 43.5$  m,  $Z_{\text{mean}} = 16.5$  m). Thus, based on the chemistry and morphometry of the studied lakes (Table 1), it can be expected that photosynthesis by benthic algae is the main source of total lake energy mobilization in a majority of the studied lakes and, as shown in our study, also the major energy source for top consumers.

Littoral energy sources dominated the energy support of char, even in the deep lakes studied (Table 1) where, based on production data from the area, pelagic processes could be expected to be of greater importance for lake energy mobilization, and hence for the energy support for top consumers (Vadeboncoeur et al. 2002). However, energy support for top consumers also depends on the resource availability in the food web. Data presented in Fig. 1 suggest a small difference in trophic position between the zooplankton and zoobenthos in the lakes, even though zoobenthos are approximately one order of magnitude larger than zooplankton (*see results*). This is probably a result of the size differences at the base of the food web, i.e., benthic algae are concentrated as a biofilm while bacterioplankton and phytoplankton are diluted and of small size (Lodge et al. 1988; Hecky and Hesslein 1995). It can be expected that the differences in food-web size structure should affect the energy support of char, since the efficiency of feeding on small-sized prey, such as zooplankton, decreases dramatically with the increasing size of the char, compared with the foraging efficiency on macroinvertebrates (Jansen et al. 2003; P. Byström and J. Andersson unpubl. data). Therefore, owing to differences in food-web size structure and hence resource availability, a higher proportion of the energy mobilization is expected to be transferred to char in littoral- than in pelagic-based food webs, explaining the strong reliance of char on littoral energy mo-

bilization even in the relatively deep lakes examined in this study.

In conclusion, the data from the study indicate that top consumers greatly rely on littoral energy sources in subarctic lakes. We suggest that this is an effect of the higher mobilization and transfer of energy in littoral than in pelagic food webs, causing relatively high littoral energy flow to top consumers. Furthermore, the data suggest that the dominance of littoral energy-flow pathways influences food-web configuration, i.e., high resource production in littoral habitats results in a low degree of ontogenetic variation in the base energy sources used by the top consumer. Since a majority of world lakes are small and shallow (Wetzel 1990), and many are also naturally unproductive, recognizing the importance of littoral energy-flow pathways is central to understanding lake ecosystem function.

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