Limnol. Oceanogr., 48(1), 2003, 269–276

Control of zooplankton dependence on allochthonous organic carbon in humic and clear-water lakes in northern Sweden

Jan Karlsson and Anders Jonsson
Climate Impacts Research Centre (CIRC), Abisko Scientific Research Station, SE-981 07 Abisko, Sweden; Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden

Markus Meili
Institute of Applied Environmental Research (ITM), Stockholm University, SE-106 91 Stockholm, Sweden

Mats Jansson
Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden

Abstract

We compared the stable carbon isotopic composition ($\delta^{13}C$) of crustacean zooplankton with that of potential carbon sources in 15 lakes in northern Sweden with different dissolved organic carbon (DOC) concentrations (2–9 mg L^{-1}) to test the hypothesis that zooplankton depended more on allochthonous carbon in humic lakes than in clear-water lakes. Based on $\delta^{13}C$ signature, we found that the pool of organic matter in the lakes was dominated by carbon of allochthonous origin over the whole DOC gradient. Zooplankton were generally depleted in ^{13}C compared to organic matter in the catchment, particulate organic matter in the lake water, and shallow surface sediment. However, the isotopic composition of zooplankton could not be explained without a significant contribution from both allochthonous and autochthonous carbon sources in all lakes. The relative importance of these two carbon sources did not relate to the concentration of, or proportion between, allochthonous and autochthonous organic carbon in the water. Instead, the proportion between allochthonous and autochthonous carbon in the crustacean zooplankton was consistent with a rather conservative use of the energy mobilized by bacterioplankton and phytoplankton in the lakes.

Both allochthonous and autochthonous carbon sources can support secondary production in lakes (Hessen and Tranvik 1998). Photosynthesis is the dominant energy mobilization process for secondary production in many lakes, where organic carbon fixed by primary producers is consumed directly by grazing or recycled via the microbial loop (Wetzel 2001). Zooplankton thus utilize autochthonous carbon by grazing on phytoplankton or on bacteria and other organisms depending on phytoplankton production. However, bacteria can also utilize allochthonous organic matter as a source of energy (De Haan 1974, 1977; Tranvik 1988). Furthermore, allochthonous organic matter can enter the food web directly by zooplankton grazing of detrital particles (Hessen et al. 1990). Consequently, allochthonous sources may contribute a substantial portion of the zooplankton carbon in the lakes that have low primary production (Salonen and Hammar 1986; Meili et al. 1993, 1996, 2000; Grey et al. 2001).

The relative importance of allochthonous and autochthonous carbon for pelagic biota can vary among lakes. Jones (1992) suggested that allochthonous organic carbon should be relatively more important in supporting planktonic food webs in humic lakes compared with clear-water lakes. A similar difference was shown by Jansson et al. (2000) in a compilation of data from temperate unproductive lakes, where an increasing portion of the pelagic energy mobilization was covered by bacterial utilization of allochthonous organic carbon as the dissolved organic carbon (DOC) concentration of the lakes increased. In lakes with food webs fuelled by energy mobilized from allochthonous carbon (i.e., humic lakes), a large part of the zooplankton production could therefore depend on allochthonous carbon (e.g., Meili et al. 1993, 1996, 2000). No quantitative cross-lake studies have, however, been made to clarify the relative importance of allochthonous carbon versus autochthonous carbon utilization by zooplankton in humic lakes compared with clear-water lakes.

To test the hypothesis that allochthonous carbon is more important as a base for zooplankton production in humic lakes as compared with clear-water lakes, we analyzed the stable carbon isotopic composition of crustacean zooplankton and their potential carbon sources in 15 subarctic lakes in northern Sweden with different concentrations of allochthonous DOC.

Materials and methods

Investigated lakes—Fifteen lakes in subarctic northern Sweden (68°N, 18°E) were included in the study. The lakes are situated along an altitudinal gradient (270 to 1,140 m a.s.l.) from the coniferous forest to the alpine belts (Table 1) in the Scandinavian mountains. For a more detailed description of the lake catchments, see Karlsson et al. (2001). Ear-

Acknowledgments

Thanks to Ludmilla Janeck and Thomas Westin for their assistance during the field work and to Bo Edlen, Sonja Lojen, and Håkan Wallmark for the stable isotopic analyses. EU structural funds and funding from regional and national governments financially supported this study.

Table 1. Physical, chemical, and biological characteristics of 15 subarctic lakes in northern Sweden. The values represent the means (±SD, n = 3 or 4) for the summer of 1999 (DIC and CO_2 values are from the summer of 2000). Mean PEM_{het} are based on summer mean values of PP and BP assuming a BGE of 26% and that 40% of PP is available for bacteria. Alt, altitude; Area, lake surface area; Z, mean lake depth; T, water temperature; Phyto, phytoplankton biomass.

Lake	Vegetation belt	Alt (m a.s.l.)	Area (km^2)	Z (m)	T (°C)	DIC (μmol L^{-1})	CO_2 (μmol L^{-1})	DOC (mg L^{-1})	POC (mg L^{-1})	TN (μg L^{-1})	TP (μg L^{-1})	BP (μg C L^{-1} d^{-1})	PP (μg C L^{-1} d^{-1})	Phyto (μg C L^{-1})	PEM_{het} (%)
1	Coniferous forest	270	0.11	2.3	14.0±3.5	187±32	31±6	8.9±1.2	0.65±0.27	420±85	7.7±3.7	2.7±0.9	7.7±2.5	20±9	26
2		376	0.03	1.5	12.7±3.3	94±3	36±3	9.0±0.8	1.52±0.49	371±67	11.3±1.1	6.6±1.8	4.7±2.1	44±19	65
3		415	0.10	0.6	11.8±4.3	91±13	31±3	8.5±1.5	0.75±0.17	346±56	9.3±1.4	7.7±3.7	4.0±2.4	35±11	72
4		365	0.11	3.0	13.3±1.5	764±125	23±3	6.4±1.3	0.35±0.20	250±94	3.4±1.5	1.7±0.6	7.0±3.5	15±7	17
5	Subalpine	375	0.13	3.5	11.3±1.5	71±15	29±8	6.2±0.6	0.17±0.04	209±135	6.3±1.5	2.1±1.1	0.7±0.3	9±1	81
6		510	0.03	1.9	9.3±3.9	214±30	28±1	5.0±1.2	0.32±0.08	244±179	4.8±1.9	2.0±0.8	2.6±1.7	15±3	49
7	Low alpine	710	0.04	2.8	10.8±2.1	69±7	26±4	3.2±0.4	0.39±0.03	113±35	7.9±1.1	1.7±0.8	1.0±0.2	23±6	70
8		712	0.04	2.8	10.9±2.2	77±9	27±2	3.6±0.3	0.37±0.09	207±136	7.9±4.3	2.1±1.1	0.9±0.7	16±4	77
9		770	0.01	1.8	11.0±2.3	36±1	26±5	3.5±0.4	0.31±0.05	157±18	9.0±0.8	2.9±1.1	0.2±0.2	21±5	94
10	Middle alpine	850	0.02	2.2	7.9±2.0	80±16	24±1	3.3±1.1	0.20±0.03	248±103	5.9±0.8	1.1±0.5	1.3±0.4	17±4	52
11		865	0.11	4.5	8.0±1.5	147±18	24±1	3.5±1.0	0.27±0.03	187±17	6.8±2.4	1.6±0.5	1.2±0.4	26±14	64
12		993	0.17	4.7	8.0±1.1	132±10	23±3	2.7±0.8	0.25±0.01	142±34	5.5±1.0	2.0±0.6	1.2±0.5	22±8	69
13	High alpine	1,045	0.17	5.3	7.2±1.0	43±5	21±3	1.9±0.8	0.43±0.09	62±5	2.9±0.4	0.6±0.1	0.2±0.1	54±10	77
14		1,115	0.04	1.9	4.9±1.2	117±17	22±3	2.2±0.7	0.14±0.02	93±33	5.3±0.0	1.1±0.1	1.5±0.6	5±3	45
15		1,140	0.27	8.6	6.4±0.5	115±9	23±3	2.0±0.4	0.13±0.03	125±55	3.4±2.7	0.4±0.1	0.3±0.2	3±0	58

lier studies have shown that the lakes are ice-free for approximately 3 to 4 months per year (Karlsson et al. 2001). During 1999, the lakes varied widely in water temperature (summer mean values: 4.9–14°C), DOC (1.9–9.0 mg L^{-1}), particulate organic carbon (POC, 0.13–1.52 mg L^{-1}), and total nitrogen (TN, 62–420 μg L^{-1}). All these variables had higher values at lower altitudes than at higher altitudes (Table 1). The range was also relatively large in total phosphorus (TP, 2.9–11.3 μg L^{-1}), but there was no consistent trend with altitude (Table 1). The low nutrient content of the lakes was reflected in low pelagic net primary production (PP, 0.2–7.7 μg C L^{-1} d^{-1}) and net bacterioplankton production (BP, 0.4–7.7 μg C L^{-1} d^{-1}) in the lakes (Table 1). The low PP : BP ratio (mean 1.1, range 0.1–4.0) in the lakes was explained by the utilization of allochthonous carbon by bacteria (Karlsson et al. 2001) and that N : P ratios of the water generally favored BP over PP (Karlsson et al. 2002). Thus, bacterial mobilization of energy from allochthonous carbon (BP_{allo}) was responsible for a large part of the pelagic energy mobilization (PEM = BP_{allo} + PP) in the lakes.

Sampling and analyses—The stable carbon isotopic composition of catchment soil mor layer (O_a + O_e horizon; Soil Survey Staff 1990), dissolved organic matter (DOM), surface sediment, and the 10–30- and 30–50-μm fractions of particulate organic matter (POM) were analyzed once in midsummer in each lake. Analyses of all other parameters were carried out after samplings once a month during the ice-free period (n = 3 or 4). Composite water samples were collected using a tube-sampler (1 or 2 m long, 3.4 cm diameter) at five locations in each lake. Each 1- or 2-m layer of the water column was sampled in proportion to its relative volume of the whole lake by using depth–volume curves of the lakes based on echo-sounding surveys. Because stable thermal stratification never developed in any of the lakes (Karlsson et al. 2001), the whole lake volume was treated as a homogeneous unit, and the water samples from the five locations and from all depths were mixed to composite samples of between 15 and 20 liter. Subsamples were then taken to analyze the concentration of DOC, POC, TP, and TN; the stable carbon isotopic composition of DOM and POM; the phytoplankton biomass; and the BP. Water temperature and PP (POC + DOC) was measured along a depth profile, and concentration and stable isotopic composition of dissolved inorganic carbon (DIC) and CO_2 were determined (measured or calculated) from surface water samples, all collected over the deepest part of each lake. Methods for measurements of PP (^{14}C-method), BP ([^{3}H]-leucine method), nutrients (DOC, TN, TP), and temperature are reported in Karlsson et al. (2002).

Particulate material for POC analysis was collected on preignited GF/F filters by filtering 0.05–1.15 liters of lake water. Filters were stored frozen prior to analysis at the Umeå Marine Sciences Centre (Carlo Erba 1106 element analyzer). Samples for determination of phytoplankton biomass were preserved with Lugol's solution and counted using the Utermöhl technique and an inverted microscope. The concentration of DIC and CO_2 were determined using a headspace equilibration technique (Cole et al. 1994). Water was collected at 1 m depth using a Ruttner sampler (2 liters)

and transferred to 1-liter bottles without contact with air. Air (50 ml taken 2 m above the ground against the wind) were injected into the 1-liter glass bottles and equilibrated by shaking for 1 min. The concentration of CO_2 in the headspace gas was immediately measured using an infrared gas analyzer (EGM-3, PP-system). For determination of DIC, the water was acidified with 5 ml of 3 M HCl prior to equilibration. The concentration of DIC and CO_2 in the water was calculated according to Cole et al. (1994) using Henry's law and the CO_2 fugacity–pressure relationship presented by Weiss (1974). For isotopic analysis of DIC, water samples were collected from 0.5 m depth using a tube sampler (0.5 m long, 3.4 cm diameter). Water was transferred into a glass bottle without air contact, preserved with $HgCl_2$ (final concentration 350 mg Hg L^{-1}), then sealed in the bottle. The $\delta^{13}C$ value of CO_2 was calculated from the measured $\delta^{13}C$ value of DIC, using data on the concentration of CO_2 and HCO_3^-, and the water temperature to account for chemical fractionation according to Mook et al. (1974). POM and DOM samples for isotope analysis were extracted from the lake water by tangential flow filtration (0.2 μm). Both the concentrate (POM, 0.2–0.4 liter) and the filtrates (DOM, 2.5–5 liters, acidified to pH 2) were freeze-dried before isotopic analysis. Horizontal hauling using several plankton nets connected in a series collected POM of 10–30 and 30–50 μm. The fractions from the different nets were collected on GF/F filters and dried (65°C). Crustacean zooplankton were collected by vertical hauling using a plankton net with a mesh size of 100 μm and were stored in filtered lake water (12–24 h) for gut evacuation. The most abundant species were later separated and washed with MQ-water before drying (65°C). Surface sediment (0–1 cm sediment depth) was collected from a shallow and the deepest part of each lake. Soil humus from the mor layer of different vegetation belts (n = 5–7 per vegetation belt, Table 1) was also sampled after removing the uppermost undecomposed layer (O_i horizon). Sediments and soil matter were dried (65°C) and homogenized. Analyses of stable carbon isotopes in solid samples were carried out at the Institute of Applied Environmental Research, Stockholm University (Carlo Erba EA 1108 elemental analyzer connected to a Fison Optima isotope ratio mass spectrometer at continuous flow), and at the Department of Forest Ecology, Swedish University of Agricultural Sciences, Umeå (Europa Scientific carbon and nitrogen analyzer connected to a Europa 20–20 stable isotope analyzer). Isotopic analysis of DIC was performed at the Jozef Stefan Institute in Ljubljana, Slovenia (Europa 20–20 stable isotope analyzer with an ANCA TG trace gas separation module). Results are expressed by the $\delta^{13}C$ notation in per mil (‰) as $\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1{,}000$, where $R = {}^{13}C/{}^{12}C$. The analytical precision was 0.1‰ in all laboratories.

Assumptions and calculations—A major shortcoming in plankton research is the difficulty of obtaining isotopic signatures on the autotrophic phytoplankton community, as phytoplankton is difficult to separate from the POM of the lake water. Moreover, the fractionation can vary among systems and species, and caution is required when estimating the $\delta^{13}C$ values of phytoplankton from the inorganic carbon source. Often the $\delta^{13}C$ values of phytoplankton are approximated from values found in pelagic consumers. However, the carbon isotope fractionation in phytoplankton is increasingly well understood and can for some systems be estimated from the CO_2 concentration ($[CO_2]$) of the water and the specific growth rate (μ) of the phytoplankton (Goericke et al. 1994; Laws et al. 1997). In order to obtain realistic estimates of the $\delta^{13}C$ values of organic carbon from pelagic primary production, we combined the two approaches by using $\delta^{13}C$ values of pelagic consumers to construct an algal fractionation model. In the model, we estimated the $\delta^{13}C$ of autotrophic phytoplankton for the ice-free period by using the $\delta^{13}C$ values of CO_2 and a fractionation factor (ε_p) varying with μ and the $[CO_2]$ in the lakes. The μ was calculated using data on PP and phytoplankton biomass. Because PP in our study lakes were nutrient limited (Jonsson et al. unpubl. data), the fractionation should depend on μ (Burkhardt et al. 1999). Also, considering the high $[CO_2]$ (Table 1) relative to the low μ (mean 0.13 d^{-1}, range 0.01–0.45 d^{-1}) in the lakes, we assumed that CO_2 was the only carbon source. Thus, the conditions in the lakes seem suitable for estimating $\delta^{13}C$ values of phytoplankton by using a fractionation model of the type reported by Laws et al. (1995) and Popp et al. (1998), even though it was developed from studies of laboratory systems. The ε_p was estimated by assuming a linear dependence on the ratio between μ and $[CO_2]$ (Laws et al. 1995; Popp et al. 1998). The maximum ε_p during CO_2 fixation by ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and β-carboxylase carboxylation can be obtained when $\mu/[CO_2]$ approaches zero and is likely to be ~25.4–28.3‰ (Goericke et al. 1994); we adopted a midrange value of 26.85‰. The minimum ε_p was set equal to the ε_p necessary to obtain the lowest zooplankton $\delta^{13}C$ value in the lake with the highest $\mu/[CO_2]$ in the absence of any allochthonous contribution (18.8‰, Fig. 1).

The allochthonous fraction of carbon assimilated by zooplankton (Zoo_{allo}) was estimated by assuming that zooplankton ($\delta^{13}C_{zoo}$) is a mixture of phytoplankton carbon ($\delta^{13}C_{phyto}$) consumed directly and of allochthonous carbon ($\delta^{13}C_{mor}$) having passed bacteria (fractionation assumed to be negligible, Coffin et al. 1994), taking into consideration a trophic fractionation (F) between zooplankton and its diet.

$$Zoo_{allo} = \frac{(\delta^{13}C_{zoo} - F - \delta^{13}C_{phyto})}{(\delta^{13}C_{mor} - \delta^{13}C_{phyto})} \quad (1)$$

For the trophic fractionation, we adopted a value of 0.43‰ derived from studies on zooplankton in a low-productivity lake, Loch Ness (Grey et al. 2001). The influence of differences in fractionation factors was tested by assuming F values ranging from 0.2 to 1‰ (Michener and Schell 1994; del Giorgio and France 1996) and maximum ε_p values ranging from 25.4 to 28.3‰ (*see above*).

The PEM available to zooplankton was calculated as the sum of BP_{allo} plus the PP fraction available for zooplankton (PP_z). Bacterial carbon demand was calculated using a growth efficiency (BGE) of 26% (the median of published values in freshwaters, del Giorgio and Cole 1998) and was assumed to be primarily covered by PP, with the residual covered by allochthonous organic carbon. The fraction of PP

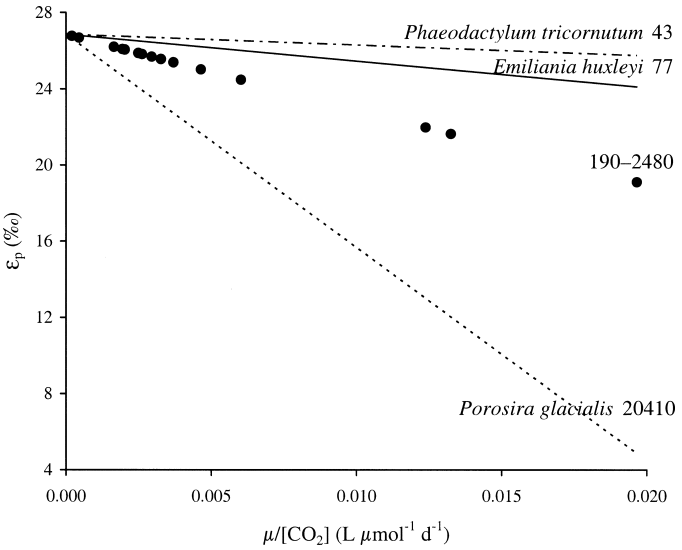

Fig. 1. Model used to compute phytoplankton fractionation (ε_p) as a function of the ratio between the phytoplankton specific growth rate and the lake water CO_2 concentration (μ/[CO_2]) in 15 subarctic lakes in northern Sweden. Included are the regression lines obtained when using the slope from the models for three marine species (named at each respective regression line) from Popp et al. (1998). Numbers denote the cell volume (μm^3) for the three species and the range for the phytoplankton community in the study lakes.

available to the bacteria (PP_b) was set equal to the sum of the phytoplankton exudate production (assumed to be 30%, Baines and Pace 1991; Arvola et al. 1996) plus the DOC released from zooplankton grazing on the phytoplankton (assumed to be 10%, Lampert 1978). Thus, BP_{allo} can be expressed as Eq. 2.

$$BP_{allo} = ([BP/BGE] - PP_b) \times BGE \quad (2)$$

The PP_z was calculated assuming that bacterial respiration of PP_b was not available to the zooplankton (Eq. 3).

$$PP_z = PP - PP_b \times (1 - BGE) \quad (3)$$

Thus, the fraction of PEM available to zooplankton that was covered by heterotrophic bacterioplankton energy mobilization using external carbon sources (PEM_{het}) can be expressed as Eq. 4.

$$PEM_{het} = BP_{allo}/(PP_z + BP_{allo}) \quad (4)$$

The influence of uncertainties associated with the assumptions was tested by assuming BGE values ranging from 20 to 37% (lower and upper quartiles of published values in freshwaters, del Giorgio and Cole 1998) and PP_b values ranging from 30 to 50% (Baines and Pace 1991).

For an assessment of zooplankton use of potential carbon sources, we used data covering a whole ice-free period (Tables 1, 2), because both the zooplankton food preferences and diet $\delta^{13}C$ values can vary seasonally (Meili et al. 2000; Grey et al. 2001) and because consumer isotopic signals carry a memory of previous diets.

Table 2. Stable carbon isotopic composition ($\delta^{13}C$, ‰) of different components of 15 subarctic lakes in northern Sweden. The values for the mor layer represent the mean (±SD, n = 5–7) for samples from the different vegetation belts (*see text*). The values for DIC, calculated CO_2, POM (>0.2 μm), and zooplankton represent the means (±SD, n = 3 or 4) for the summer of 1999 (DIC and CO_2 are from the summer of 2000). The $\delta^{13}C$ of autotrophic phytoplankton (Phyto) was estimated using summer mean values of ε_p and $\delta^{13}C$ of CO_2 (*see text*). n.a., not analyzed.

	$\delta^{13}C$ composition (‰)											
Lake	Mor Layer	Shallow sediment	Deep sediment	DOM	DIC	CO_2	POM >0.2 μm	POM 10–30 μm	POM 30–50 μm	Phyto	Cladocera	Copepoda
1	−27.7±0.9	−25.1	−28.4	−27.7	−8.0±0.9	−16.4±0.6	−28.9±0.4	−31.7	−32.6	−38.4	−34.8±2.0	−33.7±0.7
2	−27.7±0.9	−27.3	−29.6	−29.6	−11.0±1.1	−17.6±0.8	−29.2±0.4	−30.5	−28.2	−43.2	n.a.	−33.8±0.7
3	−27.7±0.9	−25.8	−29.7	−28.4	−9.8±2.1	−16.7±1.6	−29.0±0.4	−30.6	−28.5	−42.1	−30.9±0.5	−30.1±0.4
4	−27.7±0.9	−26.7	−34.1	−29.9	−8.4±0.6	−18.6±0.6	n.a.	−30.2	−30.0	−37.7	−35.8±1.2	−37.0±1.6
5	−27.2±1.0	−25.2	−27.6	−28.8	−11.5±1.7	−17.7±1.3	−29.8±0.2	−32.1	−32.2	−43.6	−32.1±0.7	−32.9±0.8
6	−27.2±1.0	−23.0	−28.1	−28.6	−8.8±1.7	−18.2±1.3	−28.3±1.0	−30.5	−30.7	−42.4	−34.0±0.6	−34.8±0.5
7	−26.8±0.5	−25.5	−29.5	−27.6	−8.3±3.5	−15.2±2.5	−30.5±0.9	−31.2	−30.0	−41.3	−32.4±0.1	−32.8±0.4
8	−26.8±0.5	−24.3	−28.8	−27.7	−11.0±3.8	−18.1±3.2	−28.9±1.0	−29.2	−27.4	−44.1	n.a.	−31.3±0.9
9	−26.8±0.5	−25.3	−28.8	−28.3	−16.6±2.4	−19.5±1.7	−29.8±0.6	−27.2	−27.4	−46.2	n.a.	−31.7±0.6
10	−26.7±0.5	−22.7	−29.6	−28.4	−9.0±4.2	−16.7±3.3	−28.4±1.0	−28.0	−28.0	−42.3	−32.4±0.0	−32.5±0.4
11	−26.7±0.5	−24.7	−26.4	−28.7	−5.6±0.9	−15.0±0.6	−29.6±0.6	−28.5	−27.3	−41.0	−31.5±0.6	−33.5±0.2
12	−26.7±0.5	−23.4	−25.6	−28.5	−4.1±0.3	−13.2±0.2	−28.5±1.2	−27.3	−26.2	−39.1	n.a.	−31.0±0.7
13	−25.3±0.7	−21.1	−23.5	n.a.	n.a.	n.a.	−30.7±1.1	−29.3	−28.3	n.a.	n.a.	−30.9±0.8
14	−25.3±0.7	−20.7	n.a.	n.a.	−2.6±0.7	−11.9±0.5	−28.1±0.1	n.a.	−25.7	−33.5	−31.0±1.1	n.a.
15	−25.3±0.7	−19.1	n.a.	n.a.	−4.7±3.6	−13.8±3.3	−26.7±0.8	−26.3	−25.1	−38.8	−33.4±0.8	−32.3±1.3

Results and discussion

Isotopic signals—The lake catchment mor $\delta^{13}C$ value ranged from −27.7 to −25.3‰ (Table 2) with less depleted values at higher altitudes, consistent with findings of terrestrial plants along altitudinal gradients from other mountain regions (Körner et al. 1988, 1991). We assumed that the mor layer $\delta^{13}C$ values can be used as an adequate proxy for the $\delta^{13}C$ value of allochthonous matter draining from the catchments to the lakes. The $\delta^{13}C$ in shallow sediment (range −27.3 to −19.1‰) in the lakes was higher compared with that of deep sediment, mor layer (except for Lake No. 2), and POM (Table 2). The relatively high isotopic signal of the shallow sediment, where light climate in contrast to the deep sediment permit significant photosynthesis (Jonsson et al. unpubl. data), can be attributed to benthic primary production, which is known to be significant in arctic and subarctic lakes (Björk-Ramberg and Ånell 1985; Welch and Kalff 1974). $\delta^{13}C$ values are often relatively high in benthic algae, where CO_2 uptake is diffusion limited because of the thick boundary layers, resulting in low discrimination against ^{13}C (France 1995*a*). The $\delta^{13}C$ of DOM (range −29.9 to −27.6‰) was generally close to the catchment mor value but clearly separated from the $\delta^{13}C$ of sediment, as well as pelagic POM and zooplankton, indicating a predominance of allochthonous matter in the lakes' DOM pool. The POM $\delta^{13}C$ values were clearly depleted compared with the shallow sediment, and in general, the values were also slightly depleted compared with the mor layer.

The contribution of PP to different DOM and POM pools can be assessed from the $\delta^{13}C$ in organic matter from PP, as estimated by the algal fractionation model. A problem with this fractionation model is that differences in the cell size of phytoplankton can cause differences in fractionation (Popp et al. 1998; Burkhardt et al. 1999), as illustrated by the slope from the model for three species from Popp et al. (1998) applied on our data (Fig. 1). The differences in the slope of the obtained ε_p–$\mu/[CO_2]$ relationship between these species were suggested to result from the large differences in the ratio of volume to surface area, as reflected by the different volumes (*Phaeodactylum tricornutum,* 43 μm^3; *Emiliania huxleyi,* 77 μm^3; *Porosira glacialis,* 20,410 μm^3). The phytoplankton communities in our study lakes were dominated by small species (Jonsson et al. unpubl. data), with a biomass-weighted mean volume of the phytoplankton community of 820 μm^3 (range 190–2,480 μm^3). The minimum fractionation determining the slope of our relationship between ε_p and $\mu/[CO_2]$ is constrained by the observed $\delta^{13}C$ difference between CO_2 and zooplankton in the lake with the highest $\mu/[CO_2]$ and is unlikely to be much higher since this would be inconsistent with the observed phytoplankton community volume. Thus, we assume that the obtained ε_p values (mean 24.8‰, range 18.8–26.8‰, Fig. 1) are valid for the purpose of this study. The ε_p and the $\delta^{13}C$ of CO_2 (Table 2) resulted in a mean $\delta^{13}C$ of −41‰ (range −46.2 to −33.4‰, Table 2) in organic matter produced by autotrophic phytoplankton. The results agree reasonably well with reports of phytoplankton fractionation relative to DIC ($\delta^{13}C$ of CO_2 is ~9–11‰ lighter than $\delta^{13}C$ of HCO_3^-) in other unproductive lakes: Meili et al. (1996) reported a fractionation of between 23 and 27‰ in a humic lake, Rau (1978) found net plankton $\delta^{13}C$ values of −46.9‰ in a subarctic lake corresponding to a fractionation of about 30‰, and Hecky and Hesslein (1995) suggested a fractionation of 35–37‰ for phytoplankton in three arctic lakes.

Comparisons of the $\delta^{13}C$ in organic matter from PP in our lakes to that of other potential sources of organic carbon show that allochthonous matter clearly dominated both DOM and POM, even in clear-water lakes. The estimated allochthonous contribution was, on average, 90% (range 78–99%) to the DOM pool and 85% (range 65–93%) to the POM pool (POM_{allo}), which is consistent with the low PP and autotrophic biomass in the lakes (Table 1). Thus, the range of organic carbon concentrations found in the lakes also represents a range in allochthonous organic carbon concentrations.

The crustacean zooplankton were divided into cladocerans and copepods. No data on protozoans and rotifers are included in the zooplankton of this study. In each lake, the species that dominated the crustacean biomass were analyzed. For cladocerans, this procedure included one to three species for each lake (*Daphnia galeata, Daphnia longispina, Bosmina coregoni, Holopedium gibberum*). For copepods, either *Eudiaptomus graciloides* or *Cyclops scutifer* were analyzed, but in three of the lakes, both species were included. The $\delta^{13}C$ values of cladocerans and copepods (Table 2) did not differ significantly from each other in the lakes (paired *t*-test, $p = 0.406$), and the two groups were therefore pooled when evaluating the $\delta^{13}C$ data.

Zooplankton use of different carbon sources—Zooplankton were depleted in ^{13}C by up to 6‰ compared to total POM (>0.2 μm) when means for the whole season were compared (paired *t*-test, $p < 0.001$), which is similar to values reported from other lakes (del Giorgio and France 1996; Jones et al. 1999). Zooplankton were also depleted in ^{13}C compared to POM (10–30 μm) and POM (30–50 μm) (paired *t*-test, $p < 0.001$, single sampling occasion), which have size fractions that better represent the preferred food particle size for the crustaceans (Sterner 1986; Bern 1994). These results show that the crustacean zooplankton utilized an isotopically lighter food source than any of the POM fractions we have analyzed. Both allochthonous and benthic particulate carbon were always isotopically heavier than zooplankton, suggesting that zooplankton selectively fed on isotopically light carbon from PP (Fig. 2). There was no trend in zooplankton $\delta^{13}C$ values with the concentration of DOC or POC or the POM_{allo} in the lakes (Table 3). Instead, zooplankton was generally more depleted in ^{13}C in lakes where PEM_{het} was low (Fig. 3A, $r^2 = 0.50$, $p = 0.003$, $n = 15$). Also, the ^{13}C depletion in zooplankton relative to total POM (>0.2μm, $r^2 = 0.44$, $p = 0.01$, $n = 14$) and mor ($r^2 = 0.46$, $p = 0.005$, $n = 15$) generally increased as PEM_{het} decreased (Fig. 3B), suggesting that differences in zooplankton ^{13}C depletion is attributable to the relationship between autotrophic and heterotrophic PEM. The mean contribution of allochthonous carbon to zooplankton (Zoo_{allo}) was 53% (range 9–77%). The relative importance of allochthonous carbon was not related to the concentration of DOC or POC or to

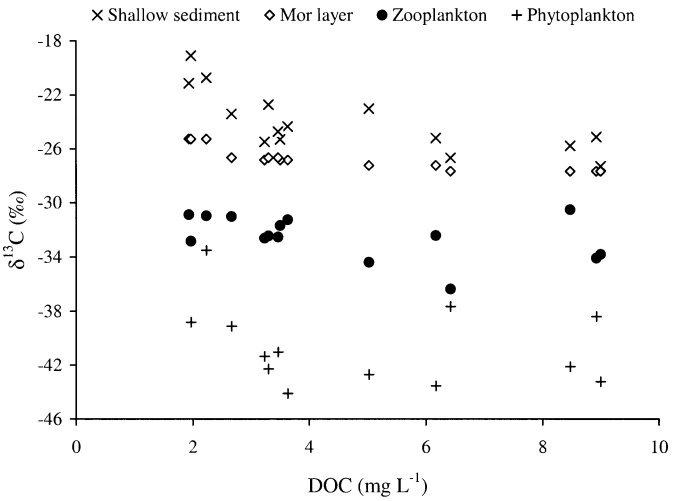

Fig. 2. $\delta^{13}C$ values of shallow sediment, catchment mor layer, zooplankton, and autotrophic phytoplankton (estimated) in 15 subarctic lakes in northern Sweden.

POM_{allo}, but to PEM_{het} in the lakes (Table 3; Fig. 4, $r^2 = 0.78$, $p < 0.001$, $n = 14$). This trend did not change when accounting for uncertainties in different parameters (i.e., BGE, maximum ε_p, F, PP_b), and introducing possible errors gave surprisingly small effects on the results (Fig. 4). The small effect of varying ε_p and F is expected because of the large difference in $\delta^{13}C$ between allochthonous and autochthonous organic matter in the lakes (Vander Zanden and Rasmussen 2001).

The lack of correlation between the concentration of DOC and the relative utilization of allochthonous carbon by zooplankton could have been due to utilization of carbon sources other than allochthonous carbon and PP. Benthic primary production could be responsible for a major part of total primary production in arctic and subarctic lakes (Welch and Kalff 1974; Björk-Ramberg and Ånell 1985) and also can be a potentially important carbon source for pelagic consumers. Benthic primary produced carbon can enter pelagic food chains by zooplankton grazing either in the sediment, on resuspended particulate matter, or through bacterioplankton that utilize DOC released from benthic algae. However, our results do not indicate benthic primary production as a significant source of carbon for the zooplankton we have studied. The crustaceans included are planktonic and were not found when analyzing the fauna of the surface sediment in three of the lakes (lake Nos. 7, 8, and 12, Byström pers. comm.). There were no signs of any significant resuspension of sediments contributing to the POM pool since POM was clearly depleted relative to the sediment in all of the lakes (−2.0 to −9.5‰, Table 2), including the shallow wind-exposed lakes most susceptible to resuspension. Other results from the lakes in this study show that the shallow sediments probably are net heterotrophic with higher respiration than carbon fixation (Jonsson et al. in press) and that allochthonous organic carbon rather than benthic primary produced carbon (in addition to PP) support bacterial growth in the pelagic zone of the lakes (Karlsson et al. 2002). Finally, the deviation in $\delta^{13}C$ values between sediment and zooplankton

Table 3. Correlation (Pearson product–moment correlation coefficients) between different fractions of organic matter and Zoo_{allo} and zooplankton $\delta^{13}C$ based on summer mean values for 15 subarctic lakes in northern Sweden.

	DOC (mg L^{-1})	POC (mg L^{-1})	POC_{allo} (%)	PEM_{het} (%)
Zooplankton $\delta^{13}C$ (‰)	−0.475	−0.179	−0.371	0.705*
Zoo_{allo} (%)	0.052	0.202	0.453	0.880**

DOC, POC, and POC_{allo} are log transformed to obtain normality (n = 13–15, *see* Tables 2, 3). The significance levels are * $p < 0.01$, ** $p < 0.001$. No asterisk means that there is no significant ($p > 0.01$) relationship between the two variables.

was highest in the clear-water lakes, suggesting that zooplankton did not rely significantly on benthic primary produced carbon, even in the clearest lakes where benthic contribution to the overall lake production is expected to be highest. In this respect, our results agree with data from other lakes (France 1995*b*) and indicate that the studied zooplankton mainly utilize allochthonous carbon and pelagic autochthonous carbon.

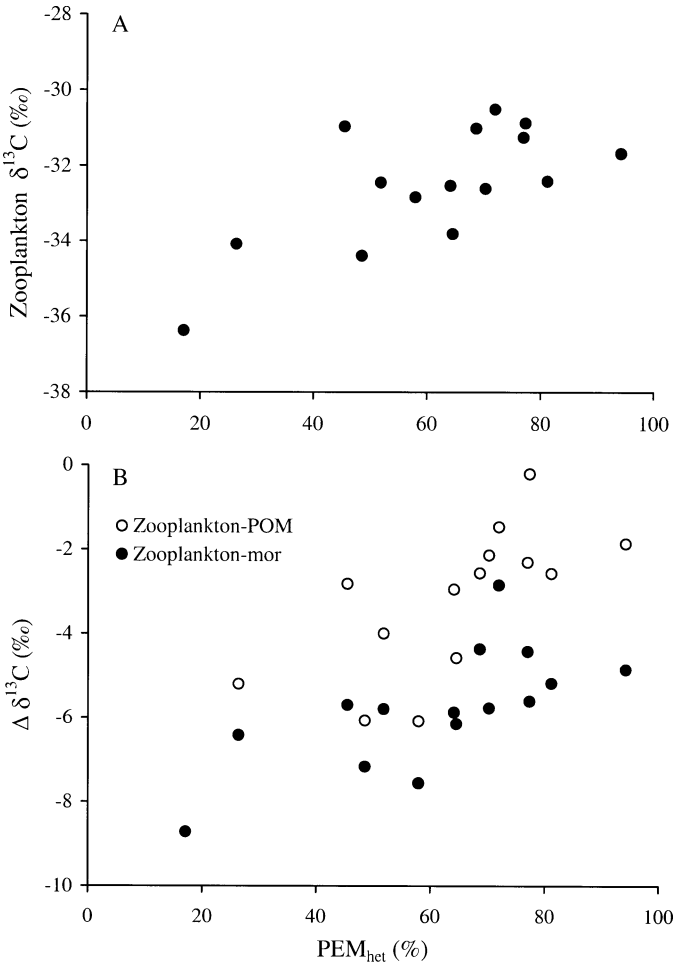

Fig. 3. (A) $\delta^{13}C$ values of zooplankton and (B) $\delta^{13}C$ values of zooplankton relative to that of POM (>0.2μm) and the catchment mor layer plotted against the PEM_{het} in 15 subarctic lakes in northern Sweden.

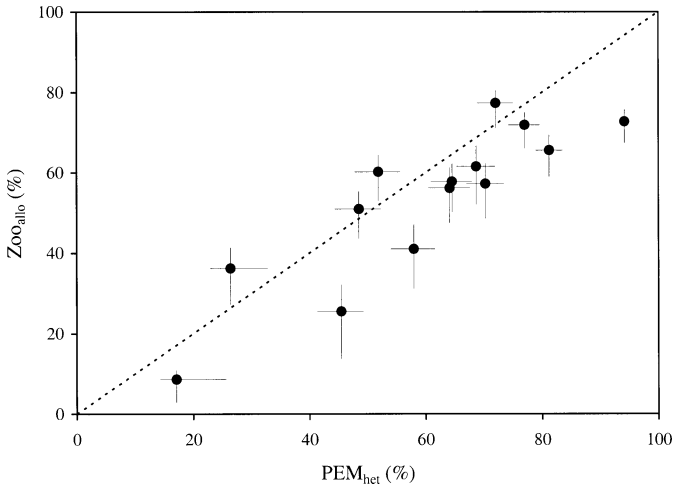

Fig. 4. Estimated allochthonous carbon in zooplankton (Zoo_{allo}) plotted against PEM_{het} in 14 subarctic lakes in northern Sweden. Lake No. 13 is not included because $\delta^{13}C$ of DIC is missing. Error bars for PEM_{het} show the minimum and maximum values obtained when using a BGE of 20–37% (del Giorgio and Cole 1998) and a utilization of PP by bacteria of 30–50% (Baines and Pace 1991) in the calculation of PEM. Error bars for Zoo_{allo} show the minimum and maximum values when using an F of 0.2–1‰ (Michener and Schell 1994; del Giorgio and France 1996) and a maximum ε_p of 25.4–28.3‰ (Goericke et al. 1994).

Our results strongly indicate that zooplankton utilization of allochthonous versus autochthonous carbon sources was not related to the proportion of allochthonous to autochthonous carbon in the lake water (Table 3). Allochthonous carbon dominated the particulate pool but the investigated zooplankton were generally depleted in ^{13}C compared to POC (Table 2). We can also conclude that the availability of allochthonous DOC was not reflected in a direct relation between allochthonous DOC and the relative amount of allochthonous carbon in the investigated zooplankton. Instead, the share of allochthonous carbon in zooplankton was related to the proportions between bacterioplankton production (based on allochthonous carbon) and primary production available for zooplankton (Fig. 4). Thus, in the lakes where a large share of the energy mobilization was from bacterial use of allochthonous carbon we also found a high share of allochthonous carbon in zooplankton, whereas in lakes where energy mobilization was dominated by primary production, we found a high share of autochthonous carbon in zooplankton. It was, therefore, not the concentration of allochthonous organic carbon that was critical to the extent in which allochthonous carbon supported zooplankton growth, but the use of allochthonous carbon by bacterioplankton in relation to the generation of autochthonous carbon by phytoplankton. It must be pointed out that we cannot say to what extent bacterioplankton and phytoplankton were consumed directly or to what extent they were transferred to zooplankton via other organisms in the food web, only that the assimilation of carbon in zooplankton was proportional to the energy mobilization from PP and BP. In several of the lakes in Fig. 4, it seems as if the crustacean zooplankton incorporated more autochthonous carbon than its proportion of the total energy mobilization (points below the 1 : 1 line). This might have been the result of active selection of autochthonous food sources as well as the loss of bacterial carbon by the grazing and respiration of other organisms (e.g., flagellates or ciliates) before entering the crustacean zooplankton. However, the possible preference for autochthonous carbon by crustacean zooplankton or a difference between copepods and cladocerans in this respect cannot be resolved with the data available and is of secondary importance compared to the general relationship between Zoo_{allo} and PEM_{het}. Instead, given the large range of uncertainties taken into account (Fig. 4), the data demonstrate a rather conservative use by zooplankton of the food sources supported by heterotrophic and autotrophic energy mobilization.

The results did not support our hypothesis that zooplankton use allochthonous carbon to a higher degree in humic lakes than in clear-water lakes. Instead, it was in the lakes where the energy mobilization was based primarily on bacterial use of allochthonous carbon that we found the highest share of allochthonous carbon in zooplankton. Our original hypothesis failed because the importance of the bacterial energy mobilization from allochthonous carbon in the study lakes was not proportional to the concentration of allochthonous DOC as suggested by Jansson et al. (2000). Instead, the relationship between BP (based on allochthonous carbon) and PP appeared to be governed by the availability of nitrogen and phosphorus (Karlsson et al. 2002). Lakes with high N : P ratios were thus dominated by PP, whereas lakes with low N : P ratios were dominated by BP independent of the DOC concentration. We can then conclude that zooplankton is more dependent on allochthonous carbon in lakes with a large heterotrophic base for the total pelagic energy mobilization, as was similarly suggested by Jones (1992), but that this dependence is not necessarily related to a high content of allochthonous carbon in the lake water. Even extremely clear lakes can be dominated by heterotrophic energy mobilization and have zooplankton populations that rely on allochthonous carbon.

References

ARVOLA, L., P. KANKAALA, T. TULONEN, AND A. OJALA. 1996. Effects of phosphorus and allochthonous humic matter enrichment on the metabolic processes and community structure of plankton in a boreal lake (Lake Pääjärvi). Can. J. Fish. Aquat. Sci. **53:** 1646–1662.

BAINES, S. B., AND M. L. PACE. 1991. The production of dissolved organic matter by phytoplankton and its importance to bacteria: Patterns across marine and freshwater systems. Limnol. Oceanogr. **36:** 1078–1090.

BERN, L. 1994. Particle selection over a broad size range by crustacean zooplankton. Freshw. Biol. **32:** 105–112.

BJÖRK-RAMBERG, S., AND C. ÅNELL. 1985. Production and chlorophyll concentration of epipelic and epilithic algae in fertilized and nonfertilized subarctic lakes. Hydrobiology **126:** 213–219.

BURKHARDT, S., U. RIEBESELL, AND I. ZONDERVAN. 1999. Stable carbon isotope fractionation by marine phytoplankton in response to daylength, growth rate, and CO_2 availability. Mar. Ecol. Prog. Ser. **184:** 31–41.

COFFIN, R. B., L. A. CIFUENTES, AND P. M. ELDERIDGE. 1994. The use of stable carbon isotopes to study microbial processes in

estuaries, p. 222–240. *In* K. Lajtha and R. H. Michener [eds.], Stable isotopes in ecology and environmental science. Blackwell.

COLE, J. J., N. F. CARACO, G. W. KLING, AND T. K. KRATZ. 1994. Carbon dioxide supersaturation in the surface waters of lakes. Science **265:** 1568–1570.

DE HAAN, H. 1974. Effect of fulvic acid fraction on the growth of a *Pseudomonas* from Tjeukemeer (The Netherlands). Freshw. Biol. **4:** 301–310.

———. 1977. Effect of benzoate on microbial decomposition of fulvic acids in Tjeukemeer (The Netherlands). Limnol. Oceanogr. **22:** 38–44.

DEL GIORGIO, P. A., AND J. J. COLE. 1998. Bacterial growth efficiency in natural aquatic systems. Ann. Rev. Ecol. Syst. **29:** 503–541.

———, AND R. L. FRANCE. 1996. Ecosystem-specific patterns in the relationship between zooplankton and POM or microplankton δ^{13}C. Limnol. Oceanogr. **41:** 359–365.

FRANCE, R. L. 1995*a*. Carbon-13 enrichment in benthic compared to planktonic algae: Foodweb implications. Mar. Ecol. Prog. Ser. **124:** 307–312.

———. 1995*b*. Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. Limnol. Oceanogr. **40:** 1310–1313.

GOERICKE, R., J. P. MONTOYA, AND B. FRY. 1994. Physiology of isotopic fractionation in algae and cyanobacteria, p. 187–221. *In* K. Lajtha and R. H. Michener [eds.], Stable isotopes in ecology and environmental science. Blackwell.

GREY, J., R. I. JONES, AND D. SLEEP. 2001. Seasonal changes in the importance of the source of organic matter to the diet of zooplankton in Loch Ness, as indicated by stable isotope analysis. Limnol. Oceanogr. **46:** 505–513.

HECKY, R. E., AND R. H. HESSLEIN. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. J. N. Am. Benthol. Soc. **14:** 631–653.

HESSEN, D. O., AND L. J. TRANVIK [EDS.]. 1998. Aquatic humic substances—ecology and biogeochemistry. Springer-Verlag.

———, T. ANDERSEN, AND A. LYCHE. 1990. Carbon metabolism in a humic lake: Pool sizes and cycling trough zooplankton. Limnol. Oceanogr. **35:** 84–99.

JANSSON, M., A.-K. BERGSTRÖM, P. BLOMQVIST, AND S. DRAKARE. 2000. Allochthonous organic carbon and phytoplankton/bacterioplankton production relationships in lakes. Ecology **81:** 3250–3255.

JONES, R. I. 1992. The influence of humic substances on lacustrine planktonic food chains. Hydrobiology **229:** 73–91.

———, J. GREY, D. SLEEP, AND L. ARVOLA. 1999. Stable isotope analysis of zooplankton carbon nutrition in humic lakes. Oikos **86:** 97–104.

JONSSON, A., J. KARLSSON, AND M. JANSSON. In press. Sources of carbon dioxide supersaturation in clearwater and humic lakes in northern Sweden. Ecosystems.

KARLSSON, J., A. JONSSON, AND M. JANSSON. 2001. Bacterioplankton production in lakes along an altitude gradient in the subarctic north of Sweden. Microb. Ecol. **42:** 372–382.

———, M. JANSSON, AND A. JONSSON. 2002. Similar relationships between pelagic primary and bacterial production in clearwater and humic lakes. Ecology **83:** 2902–2910.

KÖRNER, CH., G. D. FARQUHAR, AND Z. ROKSANDIC. 1988. A global survey of carbon isotope discrimination in plants from high altitude. Oecologia **74:** 623–632.

———, ———, AND S. C. WONG. 1991. Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. Oecologia **88:** 30–40.

LAMPERT, W. 1978. Release of dissolved organic carbon by grazing zooplankton. Limnol. Oceanogr. **23:** 831–834.

LAWS, E. A., B. N. POPP, R. R. BIDIGARE, M. C. KENNICUTT, AND S. A. MACKO. 1995. Dependence of phytoplankton carbon isotopic composition on growth rate and $[CO_2]_{aq}$: Theoretical considerations and experimental results. Geochim. Cosmochim. Acta **59:** 1131–1138.

———, R. R. BIDIGARE, AND B. N. POPP. 1997. Effect of growth rate and CO_2 concentration on carbon isotopic fractionation by the marine diatom *Phaeodactylum tricornutum*. Limnol. Oceanogr. **42:** 1552–1560.

MEILI, M., B. FRY, AND G. W. KLING. 1993. Fractionation of stable isotopes (^{13}C, ^{15}N) in the food web of a humic lake. Verh. Int. Ver. Limnol. **25:** 501–505.

———, G. W. KLING, B. FRY, R. T. BELL, AND I. AHLGREN. 1996. Sources and partitioning of organic matter in a pelagic microbial food web inferred from the isotopic composition (δ^{13}C and δ^{15}N) of zooplankton species. Arch. Hydrobiol. Spec. Issues Adv. Limnol. **48:** 53–61.

———, A. JONSSON, AND M. JANSSON. 2000. Seasonal dynamics of plankton and carbon stable isotopes (δ^{13}C) in a large humic lake (Örträsket, N. Sweden). Verh. Int. Ver. Limnol. **27:** 1940–1942.

MICHENER, R. H., AND D. M. SCHELL 1994. Stable isotope ratios as tracers in marine aquatic food webs, p. 138–157. *In* K. Lajtha and R. H. Michener [eds.], Stable isotopes in ecology and environmental science. Blackwell.

MOOK, W. G., J. C. BOMMERSON, AND W. H. STAVERMAN. 1974. Carbon isotope fractionation between dissolved bicarbonate and gaseous carbon dioxide. Earth Planet. Sci. Lett. **22:** 169–176.

POPP, B. N., E. A. LAWS, R. R. BIDIGARE, J. E. DORE, K. L. HANSON, AND S. G. WAKEHAM. 1998. Effect of phytoplankton cell geometry on carbon isotopic fractionation. Geochim. Cosmochim. Acta **62:** 69–77.

RAU, G. 1978. Carbon-13 depletion in a subalpine lake: Carbon flow implications. Science **20:** 901–902.

SALONEN, K., AND T. HAMMAR. 1986. On the importance of dissolved organic matter in the nutrition of zooplankton in some lake waters. Oecologia **68:** 246–253.

SOIL SURVEY STAFF. 1990. Keys to soil taxonomy, 4th ed. SMSS Technical Monograph 6.

STERNER, R. W. 1986. The role of grazers in phytoplankton succession, p. 107–170. *In* U. Sommer [ed.], Plankton ecology. Springer-Verlag.

TRANVIK, L. J. 1988. Availability of dissolved organic carbon for planktonic bacteria in oligotrophic lakes of different humic content. Microb. Ecol. **16:** 311–322.

VANDER ZANDEN, M. J., AND J. RASMUSSEN. 2001. Variation in δ^{15}N and δ^{13}C trophic fractionation: Implications for aquatic food web studies. Limnol. Oceanogr. **46:** 2061–2066.

WEISS, R. F. 1974. Carbon dioxide in water and seawater: The solubility of a non-ideal gas. Mar. Chem. **2:** 203–215.

WELCH, H. E., AND J. KALFF. 1974. Benthic photosynthesis and respiration in Char Lake. J. Fish. Res. B. Can. **31:** 609–620.

WETZEL, R. G. 2001. Limnology, 3rd ed. Academic Press.

Received: 31 December 2001
Accepted: 3 September 2002
Amended: 11 September 2002