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Terrestrial organic matter support of lake food webs: Evidence from lake metabolism and stable hydrogen isotopes of consumers

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Abstract

We quantified the utilization of terrestrial organic matter (OM) in the food web of a humic lake by analyzing the metabolism and the consumers' stable isotopic (C, H, N) composition in benthic and pelagic habitats. Terrestrial OM inputs (3 g C m^{-2} d^{-1}) to the lake greatly exceeded autochthonous OM production (3 mg C m^{-2} d^{-1}) in the lake. Heterotrophic bacterial growth (19 mg C m^{-2} d^{-1}) and community respiration (115 mg C m^{-2} d^{-1}) were high relative to algal photosynthesis and were predominantly (> 85%) supported by terrestrial OM in both habitats. Consequently, terrestrial OM fueled most (85%) of the total production at the base of the lake's food web (i.e., the sum of primary and bacterial production). Despite the uncertainties of quantitatively estimating resource use based on stable isotopes, terrestrial OM clearly also supported around half the zooplankton (47%), macrozoobenthos (63%), and fish (57%) biomass. These results indicate that, although rates of terrestrial OM inputs were around three orders of magnitude greater than that of autochthonous OM production, the use of the two resources by higher trophic levels was roughly equal. The disproportionally low reliance on terrestrial OM at higher trophic levels, compared with its high rates of input and high support of basic biomass production in the lake, suggests that autochthonous resources could not be completely replaced by terrestrial resources and indicates an upper limit to terrestrial support of lake food webs.

Photosynthesis is the basis for consumers at all trophic levels in most ecosystems. Primary production in lake ecosystems takes place in benthic and pelagic habitats. Autochthonous organic matter (OM) is transferred via intermediate consumers to top consumers (i.e., fish), which often exploit both habitats depending on species characteristics and life history. Recent research has recognized that consumers in lakes, besides relying on autochthonous OM, can largely utilize OM from terrestrial primary production (i.e., allochthonous OM) via its lateral export and subsequent transformations in aquatic systems (Carpenter et al. 2005; Jansson et al. 2007; Cole et al. 2011).

The input of terrestrial OM profoundly affects the food webs of nutrient-poor lake ecosystems, serving as a substrate for heterotrophic metabolism and by negatively affecting autotrophic production. Colored terrestrial OM depresses primary production in the benthic habitat (Ask et al. 2009) and may also negatively affect pelagic primary production (Carpenter et al. 1998; Jansson et al. 2000). However, heterotrophic bacteria grow on both allochthonous and autochthonous OM (Kritzberg et al. 2004). Bacterial use of allochthonous OM means that bacterial production often equals or dominates over primary production in unproductive lake ecosystems (Ask et al. 2009; Faithfull et al. 2012). Terrestrial OM may support consumers at all trophic levels in both benthic and pelagic habitats either via bacteria and bacterial consumers or via direct consumption of terrestrial particulate OM (Karlsson et al. 2004; Cole et al. 2006; Berggren et al. 2010). Zooplankton have been demonstrated to rely greatly on terrestrial OM in both clear-water and humic lakes with low pelagic primary production (Grey et al. 2001; Carpenter et al. 2005; Cole et al. 2011). For zoobenthos and fish, the few existing estimates suggest that terrestrial support is highest in humic lakes where the poor light climate represses otherwise dominant benthic primary production (Karlsson et al. 2009; Premke et al. 2010; Solomon et al. 2011).

Despite substantial evidence of terrestrial support of lake secondary production, several aspects of the contribution of terrestrial OM to the growth of aquatic consumers (i.e., allochthony) are unclear. Much of our knowledge of allochthony derives from studies using the natural abundance of stable carbon isotopes ($\delta^{13}C$) as a tracer (Grey et al. 2001; Karlsson et al. 2003). However, this technique has limitations, as only small or insignificant differences exist in $\delta^{13}C$ between terrestrial and aquatic primary producers. Algal $\delta^{13}C$ signatures are also variable and must be measured under natural conditions where algae are difficult to physically separate from allochthonous OM (Grey et al. 2001). Thus, many estimates of allochthony include considerable methodological uncertainty. Allochthony in higher consumers has also been questioned, in part because terrestrial OM is a poor substrate for direct use by heterotrophs (Hessen 1998; Brett et al. 2009) and because the transfer of terrestrial OM to consumers via bacteria is inefficient (Jansson et al. 2000; Berglund et al. 2007).

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Furthermore, bacteria lack biochemicals essential for the growth and reproduction of consumers (Hessen 1998; Martin-Creuzburg et al. 2011). High input of terrestrial OM and a high degree of allochthony at the basal trophic level are therefore not necessarily reflected in a similar high degree of allochthony in consumers.

In this study, we tested the hypothesis that terrestrial OM supports a major part of consumer biomass production at all trophic levels in both benthic and pelagic habitats in a lake with high input of terrestrial OM. Furthermore, we tested the hypothesis that allochthony decreases in organisms that represent increasing trophic levels from the basal level of the food web (bacteria and algae) to intermediate (zooplankton, zoobenthos) and top (fish) consumers. We sampled a small humic lake in northern Sweden and measured primary production, heterotrophic bacterial production, community respiration in benthic and pelagic habitats, and the stable isotopic signatures of zooplankton, zoobenthos, and fish to quantify the utilization of allochthonous and autochthonous resources by basal producers and by intermediate and top consumers in the lake.

Methods

Sampling and analyses—We sampled Upper Bear Lake, a small (area: 0.05 km^2, max. depth: 8 m) humic headwater lake in boreal northern Sweden (64°07′22″N, 18°46′47″E). The lake catchment consists of coniferous forest (pine, spruce) and open *Sphagnum*-dominated mires. The fish community comprises a single fish population of Eurasian perch (*Perca fluviatilis*). Sampling for fish stable isotopes, sediment stable isotopes, benthic primary and bacterial production (both previously presented in Ask et al. 2009 and Karlsson et al. 2009), and benthic respiration was carried out in 2006 (once in June), whereas sampling for pelagic primary and bacterial production, pelagic respiration, and stable isotopes in zooplankton and zoobenthos was carried out in 2009 (every second to third week between April and October). The vertical attenuation coefficient (K_d; 3.8 and 3.7 m^{-1}), dissolved organic carbon (DOC; 16.8 and 18.3 mg L^{-1}), and total phosphorus (29.8 and 27.6 $\mu g\ L^{-1}$) values were similar in June 2006 and 2009.

We estimated the runoff for the study catchment using daily means of specific discharge from the nearby Krycklan catchment (50 km northeast of Upper Bear Lake), where stream water levels were recorded continuously using a pressure transducer and a 90° V-notch weir housed in a heated shed (Laudon et al. 2011). Discharge was calculated from the stream water level and established height–discharge rating curves. Discharge measured at the Upper Bear Lake inlet, 1996–1998 (Jansson et al. 2001), indicated that the mean specific discharge (approximately 10 L s^{-1} km^{-2}) was not significantly different from that recorded in the Krycklan catchment over the same period (Köhler et al. 2008). Moreover, registered water levels at the inlet of Upper Bear Lake on a total of 18 dates, 2007–2009, demonstrated a strong correlation with the water level in the Krycklan stream ($r^2 = 0.85$, $n = 18$, $p < 0.01$).

Water temperature and photosynthetically active radiation (PAR) were measured using an LI-250 light meter equipped with an LI-193 SA quantum sensor (LI-COR) every 0.5 m throughout the water column. The K_d was calculated from the slope of the linear regression of the natural logarithm of PAR vs. depth. Water samples for analysis of DOC, stable hydrogen isotopes (δ^2H) in water, heterotrophic bacterioplankton production, and community respiration were collected from the mid-epilimnion and upper hypolimnion. DOC was also measured in the inlet stream, estimated to drain > 90% of the lake catchment area (Berggren et al. 2009). Analyses of DOC followed standard procedures described by Karlsson et al. (2002). Terrestrial DOC input was calculated by multiplying DOC concentration in the inlet by discharge after linear interpolation of DOC concentrations between sampling dates. The total organic carbon input (TOC) was calculated by assuming that particulate organic carbon constituted 5% of the terrestrial DOC export (Ivarsson and Jansson 1994). The input is expressed per unit of lake area.

Pelagic net primary production was measured at five depths throughout the trophogenic layer, from the surface down to 2.3 m, for 4 h around noon according to the standard ^{14}C incorporation method described by Schindler et al. (1972). Measured primary production was converted to daily whole-lake values following the method of Karlsson et al. (2002). Pelagic community respiration was estimated by analyzing the change in O_2 as measured using a fiber-optic transmitter system (FIBOX 3; PreSens GmbH) during dark incubation for 24 h at in situ temperatures in cooling incubators at the laboratory. Optical O_2 readings were performed from the outside of top-filled 22-mL incubation bottles with sensor spots attached to the inside wall. Respiration rates were calculated from the absolute difference in O_2 concentrations over 24 h, assuming a respiratory quotient of 1. All respiration rates were measured in five replicate bottles. From each set of five replicates, those displaying the highest and lowest respiration rates were discarded; the final respiration estimates were calculated as the mean of the remaining three replicates. Pelagic bacterial production was measured using a slightly modified version (Karlsson et al. 2002) of the [^3H]-leucine incorporation method (Smith and Azam 1992). Benthic gross primary production and community respiration were measured by collecting soft sediment cores in airtight transparent or dark plastic tubes from six depths (i.e., 1, 1.5, 2, 3, 5, and 7 m). Rates were calculated as the change in dissolved inorganic carbon (analyzed using gas chromatography) in the water above the sediment during 24 h of in situ incubation. Benthic bacterial production was measured at depths of 1, 3, and 7 m using a modified version of the [^3H]-leucine incorporation technique (Ask et al. 2009). For detailed descriptions of the benthic carbon flux estimates, see Ask et al. (2009). Area-weighted whole-lake mean values of benthic primary production, bacterial production, and respiration were calculated for the lake.

For analysis of δ^2H signatures of allochthonous OM, we sampled OM from the humus layer of the dominant vegetation types (i.e., spruce, pine, and mire vegetation). For the δ^2H of the autochthonous OM, we collected periphyton (in August and October) from a rope floating in

Table 1. Stable hydrogen isotopes (mean ± 1 SD) of water and organic matter in Upper Bear Lake and catchment.

	δ^2H (‰)	1 SD (‰)	*n*
Mire soil	−147.5	11.5	3
Pine soil	−127.9	5.2	2
Spruce soil	−128.2	5.2	3
Phytoplankton	−233.7	16.7	4
Periphyton	−237.6	14.1	3
Sediment	−129.2	2.3	5
Water (epi)	−94.3	8.2	9
Water (hypo)	−97.9	5.7	9

the surface water. Phytoplankton for analysis of δ^2H signatures were cultured at constant temperature (17°C) with a 16 : 8 light : dark cycle according to the following procedure. A 20% volume of lake water inoculum was cultured in 1-L beakers (four replicates) containing L16 medium (Lindstrom 1991) and Milli-Q water for 3 weeks. The δ^2H of the local tap water (which has the same δ^2H value as does the Milli-Q water; H. Laudon and J. Karlsson unpubl. data) was estimated to be −92.3 ± 1.6‰ (n = 280, mean ±1 SD; M. Bergvall and H. Laudon unpubl. data) over 1.5 years of measurements between the spring of 2007 and the autumn of 2008, implying that the cultured algae and the algae in the lake water have very similar isotopic compositions of source H (Table 1). To collect the algae, the water was centrifuged, and the resulting algal pellets were stored in the freezer.

Crustacean zooplankton were sampled by vertically hauling a plankton net through the top 4 m of the water column. The zooplankton, which were stored in filtered lake water for gut evacuation 12–24 h before separation (24 samples in total), were comprised of calanoid copepods (*Eudiaptomus* sp.), cyclopoid copepods (*Cyclops* sp.), and cladocerans (dominated by *Cerodaphnia* sp. and *Daphnia* sp. as well as a small fraction, < 5%, of *Bosmina* sp.). Soft surface sediment was collected from the sediment cores after incubation for benthic primary production by removing the surface organic layer (0–1 cm) of the sediment into a container. Common zoobenthos (chironomids, n = 5) were collected at shallow depths (1–2 m, three locations) in midsummer, separated, and washed with distilled water. Fish were sampled in benthic and pelagic habitats using multimesh gill nets (two to four nets per habitat). Part of the fish dorsal muscle was used for isotopic analysis (n = 15). Water for δ^2H analysis was filtered (0.2 μm) and stored in airtight glass bottles without air bubbles until analysis. Solid material for isotopic analysis was freeze-dried or dried at 65°C, homogenized when necessary and stored frozen until analysis. Analyses of the δ^2H of nonexchangeable H were carried out at the Colorado Plateau Stable Isotope Laboratory, Northern Arizona University, following Doucett et al. (2007).

Organic matter samples and standards were equilibrated with local water vapor to correct for exchangeable H. Solid samples were analyzed by means of pyrolysis, and the isotopic composition of H^2 gas was measured using isotope ratio mass spectrometry. The δ^2H of water samples was analyzed by means of headspace equilibration with H_2 gas and a platinum catalyst using isotope ratio mass spectrometry. The δ^2H data are expressed in per mil (‰) notation relative to Vienna Standard Mean Ocean Water.

Calculations—The relative contribution of allochthonous OM (i.e., allochthony) to the rates of total OM input (i.e., terrestrial input + primary production), community respiration (R), bacterial production (BP), and total basal production (i.e., sum of autotrophic production and heterotrophic bacterial production based on allochthonous OM) was calculated by dividing the rates based on allochthonous OM by the total rates.

Community respiration (measured by means of dark incubations) based on allochthonous OM was estimated after subtracting the share based on autochthonous primary production (R_{auto}) and assuming that the remaining respiration was supported by terrestrial OM:

$$\text{Allochthony } R = 100 \times (R - R_{auto})/R \quad (1)$$

where R_{auto} is the sum of autotrophic dark respiration and heterotrophic respiration (presumably dominated by bacteria) based on autochthonous OM. Autotrophic dark respiration was set to 20% of net primary production (Graham et al. 1996). Minimum and maximum values of allochthony, R, were estimated by assuming that 0% or 100% of the net primary production was used for heterotrophic respiration. Allochthony of bacterial growth was estimated after subtracting the bacterial use of net primary production (BP_{auto}):

$$\text{Allochthony } BP = 100 \times (BP - BP_{auto})/PB \quad (2)$$

BP_{auto} was calculated by multiplying the primary production (PP) available to bacteria (PP_b) by the bacterial growth efficiency on autochthonous OM (BGE_{auto}). PP_b was set to 0% and 100% of net primary production to obtain maximum and minimum estimates of the allochthony of bacterial production. Literature values were used for BGE_{auto} in the pelagic (53%; Del Giorgio and Cole 1998) and benthic (54%; Ask et al. 2009) habitats. Allochthony of the total basal production was calculated as the bacterial production based on allochthonous OM divided by total basal production:

$$\text{Allochthony basal production} = 100 \times (BP - BP_{auto})/(BP - BP_{auto} + PP) \quad (3)$$

The allochthony of consumers was estimated using a mixing model, including the δ^2H signatures of consumers ($\delta^2H_{consumer}$), allochthonous OM (δ^2H_{allo}, mean of all soils), autochthonous OM (δ^2H_{auto}, mean of in-lake-produced and cultured algae), and water (δ^2H_{water}, mean of all samples) as

$$\text{Allochthony} = 100 \times ((\delta^2H_{consumer} - \omega_{tot} \times \delta^2H_{water})/(1 - \omega_{tot}) - \delta^2H_{auto})/(\delta^2H_{allo} - \delta^2H_{auto}) \quad (4)$$

We assume that δ^2H_{water} from 2009 is representative of the δ^2H_{water} experienced by fish sampled in 2006. This assumption is supported by δ^2H_{water} data from the

Krycklan stream (*see* above), in which δ^2H_{water} for the 1997–2007 period was −99.1 ± 9.7‰ (n = 121; H. Laudon unpubl. data). The ω_{tot} is the total contribution of dietary water to consumer H and was calculated for each trophic level from the trophic level of the consumer (t) and from the dietary contribution (ω) to consumer H (0.173; Solomon et al. 2009) as

$$\omega_{tot} = 1 - (1 - \omega)^t \quad (5)$$

We assumed that cladocerans and chironomids occupy trophic position 2 (Karlsson et al. 2004; Karlsson and Byström 2005) and estimate the trophic position of copepods and fish from their $\delta^{15}N$ data (not shown) in relation to the $\delta^{15}N$ of cladocerans and a trophic fractionation (ΔN) of 3.42‰ (Post 2002). The use of zooplankton and not zoobenthos as the reference level in calculating trophic positions introduces a potential error into the estimated allochthony of fish; however, we assume this potential error to be minor given that the pelagic habitat dominates the benthic habitat in terms of basal production (Ask et al. 2009), biomass of intermediate consumers (P. Byström unpubl. data), and fish resource use (Karlsson et al. 2009). Previous data from the lake, indicating 2‰ higher $\delta^{15}N$ in chironomids than in cladocerans (Karlsson unpubl. data) and that fish on average rely up to 22% on benthic resources (Karlsson et al. 2009), suggest that the present study underestimates allochthony by approximately one percentage unit; if we assume that fish rely up to 100% on benthic resources, we would underestimate allochthony by approximately seven percentage units.

We compared allochthony estimated from δ^2H data with allochthony estimated from $\delta^{13}C$ data for zooplankton and for surface (0–1 cm) sediments (>1.5-m water depth) containing no benthic algae (Ask et al. 2009) collected in 2006. The sampling of zooplankton (three occasions, June–October) and sediments (once in June) followed the same procedure as described above (for details, see Karlsson et al. 2009). Allochthony based on $\delta^{13}C$ data was calculated using the $\delta^{13}C$ signatures of allochthonous OM (−27.7‰) and autochthonous OM (−41.2‰) for forest lakes in northern Sweden (lakes 1–6 in Karlsson et al. 2003) and a trophic fractionation factor for carbon of 0.4‰ (Post 2002). We estimated the uncertainty in allochthony by using the full range of allochthonous and autochthonous end members for δ^2H (this study) and $\delta^{13}C$ (forest lakes 1–6 in Karlsson et al. 2003) and by varying ΔN (2.42–4.42; Post 2002) and ω (0.10–0.22; Cole et al. 2011).

Where possible, the data are presented as seasonal averages (± 1 SD). The results presented are based on the 2009 sampling, but for some parameters we include data from 2006 (as described above).

Results

The lake ice disappeared in early May and the water column was stratified from late May until mid-September. The lake water DOC concentration was 21.8 ± 5.4 mg L^{-1} in the epilimnion and 24.3 ± 4.1 mg L^{-1} in the hypolimnion. The catchment export of TOC (per unit of lake area) to the lake during the study period (75% of annual water discharge) was 3.0 g C m^{-2} d^{-1}. PAR decreased rapidly in the lake water column, and K_d was estimated to be 4.6 ± 1.2 m^{-1}. Primary production decreased rapidly over depth; it was under detection below 1.5-m water depth in the benthic habitat and averaged only 5.8% of surface (0.3 m) values at 2.3-m water depth in the pelagic habitat. Whole-lake primary production (3.4 mg C m^{-2} d^{-1}) was low relative to heterotrophic bacterial production (19.4 mg C m^{-2} d^{-1}) and community respiration (115.4 mg C m^{-2} d^{-1}; Fig. 1).

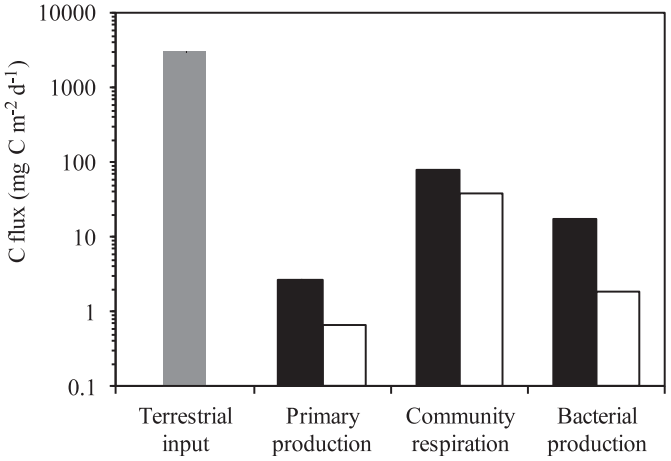

Fig. 1. Carbon fluxes in Upper Bear Lake including the terrestrial organic carbon input and the primary production, community respiration, and heterotrophic bacterial production in benthic (open bars) and pelagic (closed bars) habitats.

The δ^2H values of terrestrial OM derived from the various parts of the catchment were similar (analysis of variance, p = 0.062), with an average δ^2H of −134.5‰ (Table 1). The δ^2H of water displayed little variation over time or between shallow (−94.3‰) and deep (−97.9‰) water (Table 1). The δ^2H of periphyton (−237.6‰) collected in the epilimnion of the lake was similar (t-test, t = 0.322, df = 5, p = 0.761) to that of phytoplankton cultured in the laboratory (−233.7‰; Table 1). The δ^2H of surface sediments (average −129.2‰; Table 1) was similar to that of terrestrial OM, with little variation across depths (1 m: −126.7‰; 3 m: −128.9‰; 5 m: −132.3‰; and 7 m: −128.8‰). The δ^2H of the various consumers was strongly correlated to corresponding $\delta^{13}C$ signatures (r = 0.95, p = 0.004; Fig. 2).

Comparing the organic carbon input at the inlet with indigenous primary production indicates that the organic carbon input was totally (99.9%) dominated by allochthonous sources (Fig. 1). Allochthony in various metabolic processes and at all levels of the food web was estimated from data on carbon fluxes (Fig. 1) or stable isotopes (Table 1). The lake metabolism was to a small extent fueled by lake primary production, and allochthony was calculated at between 92% (minimum estimate) and 100% (maximum estimate) for bacterial production, at 96–99% for community respiration, and at 84–85% for basal production in the lake, with little variation between pelagic

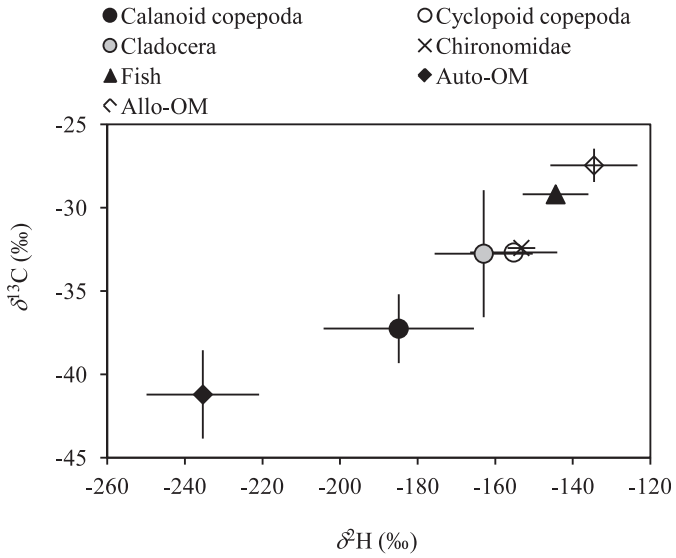

Fig. 2. Stable carbon ($\delta^{13}C$) isotopes of consumers and allochthonous (Allo-OM) and autochthonous (Auto-OM) end members plotted against stable hydrogen isotopes ($\delta^{2}H$) in Upper Bear Lake. Error bars indicate ± 1 SD of variation across season (for zooplankton) or replicates (for zoobenthos, fish, and end members).

and benthic habitats (Fig. 3). Despite the high allochthony, only a small share (3%) of the terrestrial OM input was metabolized, and most (77%) of the metabolized terrestrial OM was respired (Fig. 1). Allochthony in zooplankton averaged 47% and varied between groups, ranging from 23% in calanoid copepods to 58% in cladocerans and 60% in cyclopoid copepods. Allochthony was estimated at 63% in benthic macroinvertebrates and 57% in fish top consumers (Fig. 3). Comparing the $\delta^{2}H$ and the $\delta^{13}C$ allochthony estimates indicated good agreement between the two techniques, a pattern that largely persisted after accounting for uncertainties in end member isotopic values,

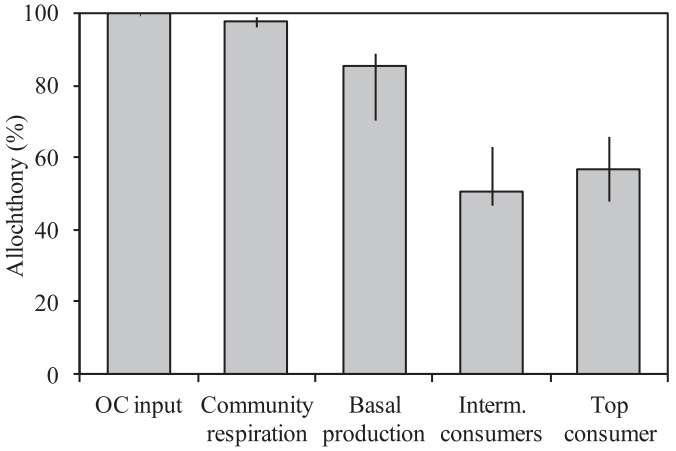

Fig. 3. The relative contribution of allochthonous OM (i.e., allochthony) to various carbon fluxes and food web components in Upper Bear Lake. Error bars indicate range in values between habitats for community respiration and basal production, between species for intermediate consumers, and between individuals for fish top consumers.

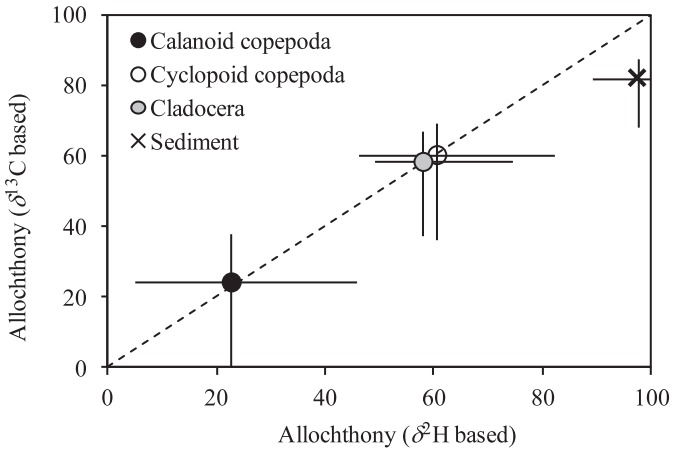

Fig. 4. Allochthony based on $\delta^{13}C$ plotted against allochthony based on $\delta^{2}H$ for consumers and sediment in Upper Bear Lake. Error bars indicate uncertainties introduced by variation in stable isotopic signatures of allochthonous and autochthonous OM, trophic fractionation of N, and contribution of dietary water to consumer H (*see* Methods).

trophic fractionation of N, and diet water contribution to consumer H (Fig. 4).

Discussion

Using a combination of carbon flux and stable isotopic data, we demonstrate that terrestrial allochthonous OM largely supported community respiration and secondary production at all trophic levels of the food web. We also demonstrate that autochthonous OM was preferentially passed to intermediate and top consumers in the lake. The degree of allochthony was therefore lower among these consumers than in the basal production.

We were unable to collect all the data in 2009 and therefore used data from 2006 for benthic metabolism and fish and for calculating allochthony from $\delta^{13}C$ data (to compare with $\delta^{2}H$-based allochthony). As light conditions, DOC, and phosphorus (major factors likely to control production and resource use in the lake) displayed similar values in the 2 yr, we assume that the results from 2006 and 2009 are comparable and that the overall patterns found are valid and robust. In addition, when calculating terrestrial C input to the lake, we used continuously recorded discharge data from the nearby Krycklan catchment because discharge and water level measurements indicated that the catchments had similar hydrological characteristics (*see* Methods). The variability in discharge among streams in the area, including the Krycklan stream, was previously reported to be under approximately 12% (Agren et al. 2007). Considering that terrestrial C input was estimated to be approximately 900 times higher than lake primary production in our study, potential errors in discharge and calculated terrestrial carbon input would not change the general pattern and conclusions of this article.

In accordance with recent studies in other regions, we found a distinct $\delta^{2}H$ separation between allochthonous and autochthonous OM. Cultured phytoplankton and periphyton collected in the lake had similar $\delta^{2}H$ values, and given

the stable δ^2H of water, we expected low temporal variation in δ^2H of autochthonous OM in the lake. Furthermore, δ^2H of terrestrial OM was similar across vegetation types, implying that variation in the source of exported terrestrial OM had minor effects on the δ^2H of allochthonous OM in the lake. Altogether, the use of δ^2H therefore permits more accurate and detailed quantification of allochthony than does the standard and more common approach based on δ^{13}C data. In particular, δ^2H avoids the problem of determining δ^{13}C composition of autotrophic phytoplankton, which still remains a strong limitation of using δ^{13}C data to quantify allochthony in pelagic food webs. The δ^{13}C of phytoplankton used here includes assumptions as to photosynthetic fractionation, and although the δ^{13}C corresponds to estimates from a nearby lake (Meili et al. 2000), it remains uncertain. Nevertheless, allochthony estimates from δ^2H data closely matched those from δ^{13}C data (Fig. 4), suggesting that δ^{13}C-based allochthony estimates for zooplankton are reliable, especially in unproductive lakes with ^{13}C-depleted phytoplankton-generated OM (Grey et al. 2001; Karlsson et al. 2003).

Only a small fraction (3%) of terrestrial OM input was metabolized in the lake food web. Still, consumers in both benthic and pelagic habitats and at all trophic levels (Fig. 3) relied on terrestrial OM, likely reflecting the high input of terrestrial OM and its dual role of both reducing primary production (Ask et al. 2009) and subsidizing heterotrophic metabolism in the lake (Jansson et al. 2007). Clearly, primary production sustained only a small fraction of the heterotrophic bacterial production, most of which was instead subsidized by terrestrial OM. High terrestrial support of bacterial metabolism has been verified for other lakes in this region from measurements of the δ^{13}C of respired carbon (Karlsson 2007). However, the very high allochthony (85%) at the basal trophic level (i.e., primary production + bacterial production) was not fully reflected in the allochthony of zooplankton (23–60%), zoobenthos (63%), or fish (57%). Consequently, algal contribution to animal production was higher than predicted based on the availability of autochthonous to allochthonous OM at the base of the food web. This difference could be due to the high quality of autochthonous vs. allochthonous OM (Brett et al. 2009), selective assimilation of autochthonous OM (Hessen 1998), or the fact that autochthonous OM is more efficiently transferred through the food web than is bacterial OM (Jansson et al. 2000; Berglund et al. 2007). Of particular importance could be the fact that consumers, by feeding on autochthonous OM, obtain essential compounds, such as fatty acids (Brett et al. 2009), that are unavailable in allochthonous OM or bacteria. This has major implications for patterns of allochthony at various trophic levels in lakes. In contrast to the mismatch in allochthony between the basal and metazoan levels, we found that allochthony at the metazoan zooplankton and zoobenthos levels was similar to that of fish top consumers, indicating a proportional transfer of allochthonous OM from intermediate to top consumers. Consequently, intermediate consumers appear to constitute a critical level not only for mass transfer of OM from basal producers to top consumers but also for adjusting the allochthony of top consumers.

To conclude, our results indicate that terrestrial OM was of major importance to lake function by controlling metabolic fluxes at all trophic levels. High input of colored terrestrial OM resulted in low primary production and basal production dominated by heterotrophic bacteria. Despite the fact that most of the imported terrestrial OM was not metabolized and that most of the metabolized fraction was allocated to respiration, a significant part of the zooplankton, zoobenthos, and fish growth was still supported by terrestrial OM. Our data strengthen previous suggestions (Grey et al. 2001; Karlsson et al. 2003; Cole et al. 2011) that the carbon metabolism of unproductive lake food webs relies largely on resources from terrestrial surroundings. However, the results also indicate that autochthonous OM, even though it may contribute little to the OM supply of the lake, is crucial for the growth of higher consumers in lakes. We therefore suggest that autochthonous resources supporting the growth of consumers cannot be fully replaced by allochthonous resources and that there is an upper limit to allochthony in lake food webs.

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References

Agren, A., I. Buffam, M. Jansson, and H. Laudon. 2007. Importance of seasonality and small streams for the landscape regulation of dissolved organic carbon export. J. Geophys. Res. Biogeosci. **112:** G03003, doi:03010.01029/02006jg000381

Ask, J., J. Karlsson, L. Persson, P. Ask, P. Bystrom, and M. Jansson. 2009. Terrestrial organic matter and light penetration: Effects on bacterial and primary production in lakes. Limnol. Oceanogr. **54:** 2034–2040, doi:10.4319/lo.2009.54.6.2034

Berggren, M., H. Laudon, and M. Jansson. 2009. Aging of allochthonous organic carbon regulates bacterial production in unproductive boreal lakes. Limnol. Oceanogr. **54:** 1333–1342, doi:10.4319/lo.2009.54.4.1333

———, and others. 2010. Lake secondary production fueled by rapid transfer of low molecular weight organic carbon from terrestrial sources to aquatic consumers. Ecol. Lett. **13:** 870–880, doi:10.1111/j.1461-0248.2010.01483.x

Berglund, J., U. Muren, U. Bamstedt, and A. Andersson. 2007. Efficiency of a phytoplankton-based and a bacteria-based food web in a pelagic marine system. Limnol. Oceanogr. **52:** 121–131, doi:10.4319/lo.2007.52.1.0121

Brett, M. T., M. J. Kainz, S. J. Taipale, and H. Seshan. 2009. Phytoplankton, not allochthonous carbon, sustains herbivorous zooplankton production. Proc. Natl. Acad. Sci. USA **106:** 21197–21201, doi:10.1073/pnas.0904129106

Carpenter, S. R., J. J. Cole, J. F. Kitchell, and M. L. Pace. 1998. Impact of dissolved organic carbon, phosphorus, and grazing on phytoplankton biomass and production in experimental lakes. Limnol. Oceanogr. **43:** 73–80, doi:10.4319/lo.1998.43.1.0073

———, and others. 2005. Ecosystem subsidies: Terrestrial support of aquatic food webs from ^{13}C addition to contrasting lakes. Ecology **86:** 2737–2750, doi:10.1890/04-1282

Cole, J. J., S. R. Carpenter, J. Kitchell, M. L. Pace, C. T. Solomon, and B. Weidel. 2011. Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen. Proc. Natl. Acad. Sci. USA **108:** 1975–1980, doi:10.1073/pnas.1012807108

———, ———, M. L. Pace, M. C. Van De Bogert, J. L. Kitchell, and J. R. Hodgson. 2006. Differential support of lake food webs by three types of terrestrial organic carbon. Ecol. Lett. **9:** 558–568, doi:10.1111/j.1461-0248.2006.00898.x

Del Giorgio, P. A., and J. J. Cole. 1998. Bacterial growth efficiency in natural aquatic systems. Annu. Rev. Ecol. Syst. **29:** 503–541, doi:10.1146/annurev.ecolsys.29.1.503

Doucett, R. R., J. C. Marks, D. W. Blinn, M. Caron, and B. A. Hungate. 2007. Measuring terrestrial subsidies to aquatic food webs using stable isotopes of hydrogen. Ecology **88:** 1587–1592, doi:10.1890/06-1184

Faithfull, C. L., A. K. Bergstrom, and T. Vrede. 2012. Effects of nutrients and physical lake characteristics on bacterial and phytoplankton production: A meta-analysis. Limnol. Oceanogr. **56:** 1703–1713.

Graham, J. M., P. Arancibiaavila, and L. E. Graham. 1996. Physiological ecology of a species of the filamentous green alga Mougeotia under acidic conditions: Light and temperature effects on photosynthesis and respiration. Limnol. Oceanogr. **41:** 253–262, doi:10.4319/lo.1996.41.2.0253

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, doi:10.4319/lo.2001.46.3.0505

Hessen, D. O. 1998. Food webs and carbon cycling in humic lakes, *In* L. J. Tranvik and D. O. Hessen [eds.], Aquatic humic substances: Ecology and biochemistry. Springer-Verlag.

Ivarsson, H., and M. Jansson. 1994. Regional variation of dissolved organic matter in running waters in central northern Sweden. Hydrobiologia **286:** 37–51, doi:10.1007/BF00007279

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, doi:10.1890/0012-9658(2000)081[3250:AOCAPB]2.0.CO;2

———, ———, S. Drakare, and P. Blomqvist. 2001. Nutrient limitation of bacterioplankton and phytoplankton in humic lakes in northern Sweden. Freshw. Biol. **46:** 653–666, doi:10.1046/j.1365-2427.2001.00703.x

———, L. Persson, A. M. De Roos, R. I. Jones, and L. J. Tranvik. 2007. Terrestrial carbon and intraspecific size-variation shape lake ecosystems. Trends Ecol. Evol. **22:** 316–322, doi:10.1016/j.tree.2007.02.015

Karlsson, J. 2007. Different carbon support for community respiration and secondary production in unproductive lakes. Oikos **116:** 1691–1696, doi:10.1111/j.0030-1299.2007.15825.x

———, and P. Byström. 2005. Littoral energy mobilization dominates energy supply for top consumers in subarctic lakes. Limnol. Oceanogr. **50:** 538–543, doi:10.4319/lo.2005.50.2.0538

———, ———, J. Ask, P. Ask, L. Persson, and M. Jansson. 2009. Light limitation of nutrient-poor lake ecosystems. Nature **460:** 506–509, doi:10.1038/nature08179

———, M. Jansson, and A. Jonsson. 2002. Similar relationships between pelagic primary and bacterial production in clear-water and humic lakes. Ecology **83:** 2902–2910, doi:10.1890/0012-9658(2002)083[2902:SRBPPA]2.0.CO;2

———, A. Jonsson, M. Meili, and M. Jansson. 2003. Control of zooplankton dependence on allochthonous organic carbon in humic and clear-water lakes in northern Sweden. Limnol. Oceanogr. **48:** 269–276, doi:10.4319/lo.2003.48.1.0269

———, ———, ———, and ———. 2004. d^{15}N of zooplankton species in subarctic lakes in northern Sweden: Effects of diet and trophic fractionation. Freshw. Biol. **49:** 526–534, doi:10.1111/j.1365-2427.2004.01208.x

Kritzberg, E. S., J. J. Cole, M. L. Pace, W. Granéli, and D. L. Bade. 2004. Autochthonous versus allochthonous carbon sources of bacteria: Results from whole-lake ^{13}C addition experiments. Limnol. Oceanogr. **49:** 588–596, doi:10.4319/lo.2004.49.2.0588

Köhler, S. J., I. Buffam, H. Laudon, and K. H. Bishop. 2008. Climate's control of intra-annual and interannual variability of total organic carbon concentration and flux in two contrasting boreal landscape elements. J. Geophys. Res. Biogeosci. **113:** G03012, doi:03010.01029/02007jg000629

Laudon, H., and others. 2011. Patterns and dynamics of dissolved organic carbon (DOC) in boreal streams: The role of processes, connectivity, and scaling. Ecosystems **14:** 880–893, doi:10.1007/s10021-011-9452-8

Lindstrom, K. 1991. Nutrient requirement of the dinoflagellate *Peridinium gatunense*. J. Phycol. **27:** 207–219, doi:10.1111/j.0022-3646.1991.00207.x

Martin-Creuzburg, D., B. Beck, and H. M. Freese. 2011. Food quality of heterotrophic bacteria for *Daphnia magna*: Evidence for a limitation by sterols. FEMS Microbiol. Ecol. **76:** 592–601, doi:10.1111/j.1574-6941.2011.01076.x

Meili, M., 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. Verein. Limnol. **27:** 1940–1942.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology **83:** 703–718, doi:10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Premke, K., J. Karlsson, K. Steger, C. Gudasz, E. Von Wachenfeldt, and L. J. Tranvik. 2010. Stable isotope analysis of benthic fauna and their food sources in boreal lakes. J. North Am. Benthol. Soc. **29:** 1339–1348, doi:10.1899/10-002.1

Schindler, D. W., R. V. Schmidt, and R. A. Reid. 1972. Acidification and bubbling as an alternative to filtration in determining phytoplankton production by the ^{14}C method. J. Fish. Res. Board Can. **29:** 1627–1631, doi:10.1139/f72-250

Smith, D. C., and F. Azam. 1992. A simple, economical method for measuring bacterial protein synthesis rates in seawater using ^{3}H-leucine. Mar. Microb. Food Webs **6:** 107–114.

Solomon, C. T., J. J. Cole, R. R. Doucett, M. L. Pace, N. D. Preston, L. E. Smith, and B. C. Weidel. 2009. The influence of environmental water on the hydrogen stable isotope ratio in aquatic consumers. Oecologia **161:** 313–324, doi:10.1007/s00442-009-1370-5

———, and others. 2011. Terrestrial, benthic, and pelagic resource use in lakes: Results from a three-isotope Bayesian mixing model. Ecology **92:** 1115–1125, doi:10.1890/i0012-9658-92-5-1115

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