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Terrestrial subsidies to lake food webs: an experimental approach

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Abstract Cross-ecosystem movements of material and energy are ubiquitous. Aquatic ecosystems typically receive material that also includes organic matter from the surrounding catchment. Terrestrial-derived (allochthonous) organic matter can enter aquatic ecosystems in dissolved or particulate form. Several studies have highlighted the importance of dissolved organic carbon to aquatic consumers, but less is known about allochthonous particulate organic carbon (POC). Similarly, most studies showing the effects of allochthonous organic carbon (OC) on aquatic consumers have investigated pelagic habitats; the effects of allochthonous OC on benthic communities are less well studied. Allochthonous inputs might further decrease primary production through light reduction, thereby potentially affecting autotrophic resource availability to consumers. Here, an enclosure experiment was carried out to test the importance of POC input and light availability on the resource use in a benthic food web of a clear-water lake. Corn starch (a C_4 plant) was used as a POC source due to its insoluble nature and its distinct carbon stable isotope value (δ^{13}C). The starch carbon was closely dispersed over the bottom of the enclosures to study the fate of a POC source exclusively available to sediment biota. The addition of starch carbon resulted in a clear shift in the isotopic signature of surface-dwelling herbivorous and predatory invertebrates. Although the starch carbon was added solely to the sediment surface, the carbon originating from the starch reached zooplankton. We suggest that allochthonous POC can subsidize benthic food webs directly and can be further transferred to pelagic systems, thereby highlighting the importance of benthic pathways for pelagic habitats.

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Introduction

A major concept in ecology has been that energy fluxes proceed within food webs fueled by autochthonous (within ecosystem) primary production (Polis and Strong 1996). More recently, the relevance of externally produced (allochthonous) matter for focal food webs has been recognized (reviewed in Polis et al. 1997). Aquatic food webs may be supported by autochthonous primary production and/or by allochthonous matter imported from the surrounding catchment (e.g., Pace et al. 2004; Carpenter et al. 2005; Solomon et al. 2011). These allochthonous sources can enter in either dissolved or particulate form. Many studies have demonstrated that dissolved organic carbon (DOC) can stimulate heterotrophic production considerably and that heterotrophic bacteria can utilize allochthonous DOC as a carbon source (Tranvik 1988). Its incorporation in bacterioplankton biomass might represent a major entry route of externally produced organic carbon (OC) into lake food webs (Grey et al. 2000; Karlsson et al. 2003; Jansson et al. 2007), although some studies suggest that much of the production does not reach higher trophic levels (Cole et al. 2002, 2006; Karlsson 2007). However, less is known about the incorporation of particulate organic carbon (POC). Allochthonous POC may be available to bacteria through decomposition and to other consumers through direct consumption (Cole et al. 1990, 2011; Hessen and Nygaard 1992), but there is a lack of estimates of its contribution to consumers (but see Pace et al. 2004; Carpenter et al. 2005; Cole et al. 2006).

Most of the focus on allochthonous organic matter (OM) subsidies to lake food webs has been on energy mobilization in the pelagic habitat (Jansson et al. 2007). Hence, the possibility of energy mobilization via the benthic food web has been largely neglected, although the benthic habitat might play an important role for whole lake productivity and food web dynamics (Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002). Allochthonous particulate OM is one of the major contributors of OC to the sediment (Kortelainen et al. 2004). Furthermore, flocculation of DOC has recently been identified as a major contributor to the POC pool in boreal lakes (von Wachenfeldt and Tranvik 2008). The settled OM can be buried over the long term, lost through mineralization, and/or re-enter the food web via the uptake and incorporation by bacteria or via direct consumption by meio- and macrofaunal organisms. Although there are a few examples of the allochthony (i.e., the reliance of consumers on allochthonous resources) of benthic consumers (Cole et al. 2006; Solomon et al. 2008, 2011), studies investigating the utilization of allochthonous carbon by benthic biota remain scarce.

Supplemental to the effect of providing an energy subsidy, allochthonous OM often contains colored substances, such as humic acids, that alter the light regime and reduce the light availability for photosynthesis (Klug 2005). The decrease in light penetration can discriminate against autotrophic primary production, thereby increasing the relative importance of heterotrophic pathways (Ask et al. 2009a). Any change in the ratio of heterotrophic to autotrophic basal production can also affect higher trophic consumers since most benthic organisms are dependent on attached algae for energy sustenance (France 1996). However, the combined effects of allochthonous carbon input and light penetration on benthic heterotrophic energy mobilization remain underappreciated.

In this study, we used a full-factorial design to test the energy subsidy effect of light availability and the input of a POC source to the sediment on a benthic food web. The experiment was conducted in a small, oligotrophic, clear-water lake in mesocosms that extended from the water surface into the bottom sediment. We added an isotopically distinct POC source only available to benthic biota and shaded the incoming light to independently manipulate the carbon source and light extinction effects of POC. Our results suggest that POC entered the benthic food web through sediment bacteria and detritivores, and was further transferred to predatory consumers. Furthermore, we demonstrate that the reliance on POC by benthic consumers was independent of the light availability. Finally, we also show that the effects on sediment metabolism could be transferred to the pelagic habitat.

Methods

Study site and experimental design

The study was carried out in Lake Almberga (68°19′91″N, 19°09′22″E), an oligotrophic clear-water lake located in Abisko in sub-arctic northern Sweden. The lake is small (mean depth 3.2 m, maximum depth 6 m, area 0.055 km^2) and surrounded by a sub-arctic birch forest (for further description see Ask et al. 2009b).

In the first week of June 2008, 16 mesocosms, each consisting of a sealed plastic tube with a metal ring at the top and at the bottom (diameter 1.5 m), were placed parallel to the shoreline at a depth of approximately 1.9 m. Each mesocosm was attached to four wooden poles that were anchored in the sediment such that the upper ring was fixed approximately 20 cm above the water. The bottom ring was pressed into the sediment by divers to ensure no exchange with the surrounding water body. The total volume of each mesocosm was approximately 3.5 m^3.

We manipulated POC input and light conditions in order to determine whether POC can subsidize the benthic food web and if the effects of the subsidy transfer up to non-adjacent consumers. Corn starch (Sigma-Aldrich, St Louis, MO; hereafter referred to as ‘starch carbon’) was used as the OC source. The use of starch carbon was motivated by two major requirements: our model OC source needed to be (1) insoluble and deposited rapidly so that it was only available to the benthic community, and (2) easy to distinguish using stable isotope analyses from naturally available carbon sources in the system for the purpose of being able to trace it in different food web compartments. The starch carbon was washed several times before the experiment to remove the finest fraction. Corn starch granules settled rapidly, and in our experiment the majority of particles (about 82%) should have settled within 5.2 h according to Stoke’s law of sedimentation (Dhital et al. 2010), suggesting further that potential re-suspension over the experimental duration was negligible. Porter et al. (2004) demonstrated that in typical isolated tanks similar to our mesocosms, benthic mean flow and benthic shear velocity were low. Low benthic mean flow and shear velocity likely limit re-suspension events and/or high fluxes of DOC from the sediment. Corn is a C_4 plant with a distinct isotopic $\delta^{13}C$ signature, and we measured a $\delta^{13}C$ value of −10.4 ± 0.2‰ [mean ± 1 standard deviation (SD)] for the starch used in this experiment. This isotopic signature deviated strongly from the signal of other OC sources in the mesocosms (Table 1). Starch carbon was dispersed close to the bottom of the mesocosms on three occasions during the experiment. We used a pump-up garden sprayer with a modified sprayer head to prevent lateral spraying. The starch carbon was carefully sprayed about 20 cm above the whole bottom area. We added high amounts of starch to maximize the isotopic signal and the stimulation of heterotrophic production. Initial addition (41 g m^{-2} of carbon starch) took place after the first sampling occasion in the second week of June. Further additions (25 g m^{-2} of carbon starch) were carried out in mid-July and the beginning of August. These additions were carried out to study the fate of a POC source metabolized by benthic communities. Thus, our study was similar to previous experiments in which glucose was added either to pelagic mesocosms (Ducklow et al. 1986) or in whole-lake experiments (Blomqvist et al. 2001) where the concentration and recalcitrance of the OC added were not crucial.

Light conditions were manipulated by covering and wrapping mesocosms with shading cloth, resulting in a 50% reduction of photosynthetically available radiation (PAR) at the bottom of the shaded mesocosms compared to ambient light conditions (mid-day values: 150.5 ± 37.5 and 358.0 ± 57.5 µmol m^{-2} s^{-1}, respectively). To distinguish between the effects of decreased light penetration and the carbon input, a full 2 × 2 factorial design was applied with the following treatments: no carbon and no shade; carbon and no shade; no carbon and shade; carbon and shade (hereafter referred to as −C−S, +C−S, −C+S, +C+S, respectively). Each treatment was replicated four times. The mesocosms were sampled on three occasions (9–13 June, 7–11 July, and 11–15 August 2008, respectively), except for the stable isotope samples of organisms and sediment, which were only taken on the last sampling occasion.

Sampling

Water samples were collected with a Ruttner sampler at 0.5 m depth of each mesocosm and analyzed for total phosphorus (Tot-P), total nitrogen (Tot-N), and chlorophyll *a* using standard methods. Benthic primary production in the soft-bottom sediments was determined by measuring changes in dissolved inorganic carbon (DIC) in transparent and dark plastic tubes (inner diameter 54 mm) containing the upper 5-cm sediment layer and overlying water. In each mesocosm, duplicate sediment cores were collected for the primary production and respiration measurements,

Table 1 Carbon and nitrogen isotope signatures $\delta^{13}C$ and $\delta^{15}N$ of available carbon sources in the mesocosms with and without carbon under ‘no shade’ conditions

Carbon source	No carbon and no shade		Carbon and no shade	
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Sediment	−27.4 ± 0.5***	1.1 ± 0.9	−23.8 ± 0.6***	0.4 ± 0.4
Starch	–	–	−10.4 ± 0.2	–[a]
POM	−28.9 ± 2.5	3.8 ± 0.7	−28.8 ± 2.7	3.9 ± 0.4

† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ in terms of significant differences in ^{13}C signatures between ‘no carbon, no shade’ treatment (−C−S) and ‘with carbon, no shade’ (+C−S) treatment

POM, Particulate organic matter

Data are presented as the mean ± standard deviation (SD)

[a] Isotopic signature of starch ^{15}N could not be determined because the N content of starch was below the detection limit of the stable isotope analysis (<0.3% N)

respectively. The transparent and dark tubes were placed over the bottom within the mesocosms and incubated for 24 h. Water samples collected at the start and end of the incubation period in each tube were injected into vials purged with nitrogen and subsequently acidified with 20% HCl and analyzed for DIC using a model CP4900 Varian gas chromatograph (Varian, Middelburg, The Netherlands). Respiration was calculated from the DIC increase in the dark incubation tubes (ΔDIC_{dark}) and primary production (PP) was calculated as $PP = \Delta DIC_{light} - \Delta DIC_{dark}$.

Zooplankton was sampled with a 100-µm-mesh net (diameter 25 cm), and samples were preserved with Lugol's solution. One tow was made in each mesocosm from a dept of 1.5 m to the surface at an approximate speed of 0.5 m s^{-1}. Individuals were counted, measured, and identified to lowest taxonomic level. Biomass was calculated using published mass–length relationships (Botrell et al. 1976). Macrozoobenthos was sampled with a sediment corer (core diameter 60 mm; UWITEC, Mondsee, Austria). In each mesocosm, two samples were taken to account for potential spatial variability, and only the upper 5 cm of the sediment was used for further analysis. Samples were sieved using a 0.5-mm net, preserved in 70% ethanol, and stained with rose bengal. In the laboratory, macroinvertebrates were counted, measured, and identified to the lowest possible taxonomic level. Biomass (dry weight) was calculated using published mass–length relationships (Smock 1980; Johnston and Cunjak 1999; Baumgärtner and Rothhaupt 2003).

Stable isotopes

Surface sediment (0–3 cm) was sampled, acidified (10% HCl), and dried (60°C). Zooplankton was sampled from each mesocosm and pooled by treatment to cumulate enough material for isotopic analyses. Samples were separated into two dominant metazooplankton groups [calanoid copepods and cladocerans (primarily *Bosmina* sp.)], collected on GF/F-filters, and dried (60°C). Macroinvertebrate samples were taken with an Ekman dredge (2–6 per mesocosm). All organisms were picked out from the sediment while alive and kept alive for 48 h in GF/F-filtered lake water for gut evacuation. The macroinvertebrates were subsequently rinsed with Milli-Q water, dried (60°C) for 48 h, and ground. Small individuals were pooled (2–10 individuals) to obtain sufficient mass for the isotopic measurements and homogenized. For mollusks, only the soft body tissue was analyzed. All solid samples were stored in tin capsules until analysis.

Stable isotope analyses of organisms and sediment were carried out at the Stable Isotope Facility of the University of California at Davis (CA). Measurements were made on a continuous-flow isotope ratio mass spectrometer (model 20-20; PDZ Europa, Cheshire, UK). The results are expressed using the delta (δ) notation in ‰ as $\delta = (R_{sample}{:}R_{standard} - 1) \times 1{,}000$, where $R = {}^{13}C{:}{}^{12}C$ or ${}^{15}N{:}{}^{14}N$. The standards used were Pee Dee belemnite (PDB) for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$. A quarter of the samples were analyzed in duplicate or triplicate, and the analytical error was 0.3‰ for $\delta^{15}N$ and $\delta^{13}C$. Sample analyses also yielded percentage carbon and nitrogen from which stoichiometric C:N ratios (by weight) were derived.

Statistical analyses

The lipid content of animals varies strongly within and among groups. Lipids are depleted in ${}^{13}C$ relative to carbohydrates and proteins (DeNiro and Epstein 1977) and variation in lipid content causes variation in $\delta^{13}C$. Lipids are composed mainly of carbon and the C:N ratio of animals is strongly correlated to their lipid content (Post et al. 2007). The $\delta^{13}C$ of zooplankton was therefore normalized following Smyntek et al. (2007):

$$L = \frac{93}{1 + (0.246 \times (C:N_{atom}) - 0.775)^{-1}}$$

$$\delta^{13}C = \delta^{13}C_{bulk} + D\left(-0.2068 + \frac{3.9}{1 + 287.1\,L^{-1}}\right)$$

where $C{:}N_{atom}$ is the atomic ratio of carbon:nitrogen used to calculate a lipid factor (L). $\delta^{13}C_{bulk}$ is the measured $\delta^{13}C$ signature and D is the average difference between $\delta^{13}C$ values of proteins and lipids in the samples, often given as 6‰ (McConnaughey and McRoy 1979). Benthic macroinvertebrate $\delta^{13}C$ signatures were not normalized, as recommended by Kiljunen et al. (2006).

Time series data (nutrient, chlorophyll, and biomass) were analyzed with repeated-measures analyses of variance (ANOVAs), and responses in individual benthic invertebrate taxa were analyzed with two-way ANOVAs. These statistical analyses were performed in R 2.12.0 (R Foundation for Statistical Computing, Vienna, Austria). We used circular statistics (Zar 1996) to quantify the overall effects of carbon addition and light condition on the stable isotope values of benthic and pelagic communities in a two-dimensional space. Compared to conventional statistical approaches based on traditional $\delta^{13}C$ and $\delta^{15}N$ bi-plots, circular statistics allow a quantitative understanding of complex isotopic changes at the community and food web levels in time and/or space (Schmidt et al. 2007). Here, the procedure consisted of calculating the mean position of each taxon ($n = 9$ taxa per treatment for benthic communities; $n = 2$ and $n = 3$ taxa for pelagic communities in no shade and shade treatments, respectively) in the isotopic niche space ($\delta^{13}C$–$\delta^{15}N$) and then measuring position distance between treatments with and without carbon addition in both the no shade and shade conditions. The difference in the positions of any given taxon was characterized by a single vector composed of an angle (θ) and a length (λ). For each group (i.e., benthic and pelagic community), the mean vector of change between treatments with and without carbon addition, defined by its angle (μ) and length (r), was calculated. All vectors were represented in arrow diagrams where increased δ^{13}C values corresponded to right-directed vectors, and increased δ^{15}N values corresponded to top-orientated vectors (e.g., Schmidt et al. 2007, 2009). Rayleigh's tests were used to assess whether the distribution of the angles of change departed from uniformity (Zar 1996), i.e., testing for a significant effect of carbon addition on the community. Watson–William's two-sample tests of homogeneity were then used to determine whether light condition modified the changes in stable isotope values induced by the addition of carbon, i.e., testing for significant differences in the isotopic shifts (vectors) caused by different light conditions. Further details on circular statistics are available in Zar (1996) and Schmidt et al. (2007). Circular statistics were performed using Oriana 3.11 (Kovach Computing Services, Anglesey, Wales, UK).

Stable isotope mixing model

We used IsoError 1.04 (Phillips and Gregg 2001) to calculate the fraction of macroinvertebrates and zooplankton composed of starch carbon. IsoError uses linear mixing models to quantify the contribution of two sources (end-members) to a mixture. In contrast to other two-source mixing models, it accounts for variability in the isotopic signature of both the mixture and the sources (details available in Phillips and Gregg 2001). As end-members for the two-source mixing model, we used carbon starch (−10.4 ± 0.2‰) and shallow surface sediment (−27.4 ± 0.7‰) for macroinvertebrates. For pelagic consumers, we used carbon starch and the mean signature reported for autotrophic phytoplankton (40.2‰) from forest lakes in northern Sweden (Karlsson et al. 2003). Source estimates were corrected for trophic fractionation using a fractionation factor of 0.4‰ (Post 2002). We assumed a trophic position of 2 for macroinvertebrates, and 2 and 3 for cladocerans and copepods, respectively (Karlsson et al. 2004). The effect of uncertainty in the calculation of reliance on starch carbon was estimated as 95% confidence intervals (CIs) for macroinvertebrates. For zooplankton, we varied the autochthonous end-member to between −37.5 and −43.0‰ (range of literature values). We assumed that zooplankton reached isotopic equilibrium with the isotopic signal of their food sources during the experiment, while this was probably not the case for macroinvertebrates. For all measurements, values are given as mean ± 1 SD unless stated differently.

Results

Water samples

Total nutrient concentrations and sediment chlorophyll *a* did not differ among treatments (Table 2). Chlorophyll *a* in the water column was generally low in all treatments but was significantly lower in the carbon treatments (Table 2); chlorophyll *a* of periphyton from the enclosure walls was higher in the shaded treatments, but was not affected by starch addition (Table 2). Benthic primary production decreased in the shaded treatments, although this decrease was only marginally significant (Table 2).

Community composition and biomass of zooplankton and benthic macroinvertebrates

Zooplankton was dominated by copepods, which represented 85.3 ± 7.8% of the total metazoan biomass, whereas cladocerans only accounted for 13.4 ± 7.9%. Copepods were dominated by calanoids, whereas cladocerans were dominated by *Bosmina* sp. (83.0 ± 14.2 and 39.8 ± 18.7%, respectively). Total biomass of crustacean zooplankton did not change over the duration of the experiment ($F_{3,44} = 0.016$, $P = 0.90$) and was not affected by the addition of carbon or shading ($F_{3,44} = 0.148$, $P = 0.70$, and $F_{3,44} = 1.679$, $P = 0.21$, respectively). Benthic macroinvertebrate community composition was highly variable between sampling occasions and also among and within treatments but was dominated by chironomids, oligochaetes, and Sphaeriidae (range 34.1–100.0, 0.0–60.1, and 0.0–20.1% of total biomass, respectively). Total biomass of benthic macroinvertebrates did not change over time ($F_{3,44} = 0.113$, $P = 0.75$) and was not affected by carbon addition and shading ($F_{3,44} = 0.81$, $P = 0.376$ and $F_{3,44} = 2.170$, $P = 0.15$, respectively).

Stable isotope signatures

Most of the benthic and pelagic taxa responded to the treatments. Carbon addition induced enrichment in most benthic invertebrate taxa compared to treatments without carbon (Fig. 1; Table 3). In the no shade treatments, the strongest enrichments were observed in Sphaeriidae and amphipods (Fig. 1d, i), whereas in the shade treatments, ^{13}C-enrichment of Hydracarina, amphipods, and Planorbidae was most pronounced (Fig. 1d, g, j). Due to low densities, we pooled the zooplankton of all four replicates from each treatment to accumulate enough material for the isotopic analyses. Only in the +C−S treatment were enough cladocerans available to allow replicated analyses. Therefore, data for individual zooplankton taxa could not be evaluated statistically with ANOVA. Zooplankton showed

Table 2 Mean concentrations of chlorophyll *a* in the water column, sediment, and periphyton from the enclosure walls, of nutrients in the water column, and of benthic autochthonous primary production in relation to carbon, shade, and carbon × shade treatment effects

Variables	Mean[a]	Carbon	Shade	Carbon × shade
Chl *a* water (μg L^{-1})		<0.001***	0.59	0.86
−C−S	0.65 ± 0.05			
−C+S	0.70 ± 0.04			
+C−S	0.51 ± 0.18			
+C+S	0.57 ± 0.15			
Chl *a* sediment (μg g^{-1} dry weight)		0.22	0.53	0.32
−C−S	126.4 ± 32.0			
−C+S	125.1 ± 35.2			
+C−S	132.3 ± 22.8			
+C+S	137.9 ± 16.3			
Chl *a* periphyton (mg m^{-2})		0.99	0.028*	0.34
−C−S	38.6 ± 10.3			
−C+S	49.3 ± 18.8			
+C−S	31.5 ± 12.7			
+C+S	56.3 ± 13.5			
Total phosphorus (P) (μg L^{-1})		0.15	0.12	0.78
−C−S	10.8			
−C+S	10.6			
+C−S	11.2			
+C+S	10.9			
Total nitrogen (N) (μg L^{-1})		0.26	0.17	0.82
−C−S	201.3			
−C+S	196.9			
+C−S	201.9			
+C+S	192.5			
Benthic PP (mg C day^{-1} m^{-2})		0.27	0.057†	0.88
−C−S	129 ± 49.9			
−C+S	81 ± 59.4			
+C−S	162 ± 44.5			
+C+S	104 ± 48.6			

† $P < 0.1$, * $P < 0.05$, *** $P < 0.001$

Chl *a* water, concentration of chlorophyll *a* in the water column; Chl *a* sediment, concentration of Chl *a* in the sediment; Chl *a* periphyton, concentration of Chl *a* in the periphyton from the enclosure walls; benthic PP, benthic autochthonous primary production

Data are presented as mean concentrations ± 1 SD

[a] Chl *a* water and Chl *a* sediment represent average values over June, July, and August (measured once per month); Chl *a* periphyton represent August values (average over treatments); total P and total N represent average values over June and July (measured once per month); benthic PP represents August values (average over treatments)

similar or stronger shifts in the δ^{13}C signature than benthic invertebrates (Fig. 1). Shifts in the δ^{13}C signature of cladocerans were generally stronger than those in copepods (Fig. 1a, b). Shading did not affect benthic invertebrates (Table 3), but it did induced depletion in ^{15}N in cladocerans (Fig. 1a). The change in isotopic signatures of benthic invertebrates was also affected by light conditions (carbon × shade interaction effect). Seven taxa showed ^{15}N depletion in the +C−S treatments and ^{15}N enrichment in the +C+S treatments (Fig. 1), although the difference was only significant for oligochaetes (Table 3).

Responses on the community level (benthic and pelagic) showed clear patterns to carbon and shade treatments. Carbon addition induced a significant overall enrichment of δ^{13}C signatures in the benthic community (Rayleigh's test, $Z > 6.27$, $P < 0.001$; Fig. 2; Table 4). Similarly, carbon addition induced an overall enrichment in ^{13}C in pelagic communities; however, this was only significant in shaded conditions (Rayleigh's test, no shade: $Z = 1.98$, $P = 0.14$; shade: $Z = 2.85$, $P = 0.043$). In no shade conditions, only cladocerans and copepods were found in the mesocosms, which restricted the analysis to two taxa (*Chaoborus* sp. were not caught in the no shade treatments). The mean direction of change in the benthic community differed between +C−S and +C+S treatments [mean ± SD: 104.7 ± 30.2° and 62.8 ± 34.4°, respectively (Table 4); Watson–William's test, $F = 6.74$, $P = 0.019$]. Overall, the addition of carbon induced a ^{15}N-depletion in the +C−S treatments (Fig. 2a), whereas it induced an enrichment in ^{15}N in the +C+S treatments (Fig. 2c). The change in pelagic invertebrates was light independent; i.e., the mean direction of change was not significantly different between +C−S and +C+S treatments [96.3 ± 6.1° and 96.0 ± 13.1°, respectively (Table 4); Watson-William's test, $F < 0.001$, $P = 0.98$]. The addition of carbon induced a slight ^{15}N-depletion of zooplankton in both light conditions (Fig. 2b, d).

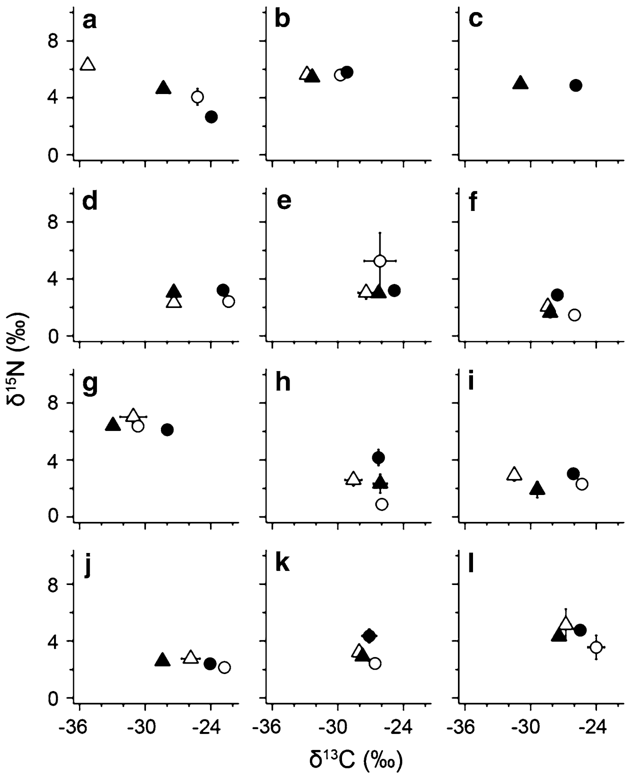

Fig. 1 Isotope signatures [mean ± 1 standard error (SE)] of pelagic and benthic invertebrates in Lake Almberga, Sweden under the four treatment conditions, i.e., no carbon, no shade (*open triangles*); no carbon, with shade (*filled triangles*); with carbon, no shade (*open circles*); with carbon, with shade (*filled circles*): **a** Cladocera, **b** Copepoda, **c** *Chaoborus* sp., **d** Amphipoda, **e** Ceratopogonidae, **f** Chironomidae, **g** Hydracarina, **h** Oligochatea, **i** Sphaeriidae, **j** Planorbidae, **k** *Sialis* sp., **l** Trichoptera. Samples for *Choaborus* sp. in the no carbon, no shade treatment and in the carbon, no shade treatment were not available

Starch carbon reliance

Reliance on starch carbon ranged between 0.6 and 28.2% for chironomids and amphipods, respectively, but did not differ between the +C−S and +C+S treatments within macroinvertebrate groups (Fig. 3). The reliance of zooplankton on starch carbon was similar or higher than of benthic macroinvertebrates. The reliance of cladocerans on starch carbon was considerably higher than that of copepods.

Discussion

Several studies have highlighted that terrestrial-derived OC can subsidize lake metabolism (Jansson et al. 2007; Cole et al. 2011). While the importance of DOC to lake food webs is well studied, studies on POC are rare. Our results show that POC can subsidize lake food webs and further that benthic and pelagic consumers benefit from POC subsidies. The added starch carbon was traced in almost all benthic primary and secondary consumers, indicated by an overall enrichment of ^{13}C in all major macroinvertebrate taxa independent of light conditions. We identified group-specific differences in responses to the addition of starch carbon. Our experiment was designed to introduce a POC subsidy exclusively to the sediment, with no carbon added to the water column. However, we still found pronounced effects on zooplankton, suggesting that the effects on the benthic system were transferred to the pelagic system.

Earlier studies have challenged the importance of terrestrial subsidies to lake food webs (Brett et al. 2009; Francis et al. 2011). In particular, the question whether allochthonous POC can contribute to aquatic consumer production has largely remained unresolved (but see Cole et al. 2006; Caraco et al. 2010). Our study adds to the growing literature that emphasizes the importance of allochthonous carbon for benthic and pelagic consumers (Cole et al. 2006, 2011; Solomon et al. 2011). The clear ^{13}C enrichment and high reliance of benthic macroinvertebrates indicates substantial incorporation of starch carbon into faunal biomass. There are two potential entry routes for the starch carbon into invertebrate biomass: direct use, i.e., the primary consumption of starch by zoobenthos, and indirect use, i.e., the uptake of carbon via the consumption of benthic bacterial biomass supported by starch. Although it is likely that starch carbon was taken up directly by zoobenthos, our results suggest that starch carbon was also consumed indirectly via the incorporation into bacterial biomass and subsequently transferred to benthic consumers. Bacteria have been shown to discriminate strongly against ^{15}N (Hoch et al. 1994; McGoldrick et al. 2008) and to have low δ^{15}N values compared to benthic algae (Karlsson and Säwström 2009). Indeed, in the +C−S treatments, δ^{15}N signatures of benthic macroinvertebrates were slightly depleted. Thus, both bacterial uptake and direct consumption of starch carbon likely occurred. A previous study estimated that terrestrial POC can represent the dominant carbon source for zoobenthos (Cole et al. 2006). However, allochthony varied substantially with benthic and pelagic primary production. Our estimates were lower than those reported by Cole et al. (2006) for lakes with low primary production. This difference might be caused by two factors. First, direct comparison of the two studies is limited since our calculations are based on the uptake of starch carbon, while Cole et al. (2006) addressed allochthonous carbon in general. Second, benthic primary production in our study system was high. Cole et al. (2006) reported comparable benthic primary production from two lakes out of the four lakes they studied. These lakes also showed the lowest allochthony in macroinvertebrates (6 and 60%, respectively). Thus, the higher allochthony

Table 3 Results from two-way analysis of variance for δ^{13}C and δ^{15}N of benthic macroinvertebrates

Taxa	*df*	Carbon	Light	Carbon × light[a]
δ^{13}C				
Amphipods	1, 7	110.35***	0.27	–
Ceratopogonidae	1, 7	1.17	0.79	–
Chironomids	1, 11	7.06*	0.80	2.70
Hydracarina	1, 4	2.80	0.06	–
Oligochaeta	1, 10	$3.50^{\dagger}$	1.62	3.22
Sphaeriidae	1, 8	53.70***	1.51	–
Planorbidae	1, 5	11.51*	$4.95^{\dagger}$	–
Sialis sp.	1, 10	4.99*	0.62	0.01
Trichoptera	1, 8	16.57**	1.90	–
δ^{15}N				
Amphipods	1, 7	0.02	$4.16^{\dagger}$	–
Ceratopogonidae	1, 7	0.77	0.50	–
Chironomids	1, 11	0.55	1.43	0.87
Hydracarina	1, 4	2.71	1.06	–
Oligochaeta	1, 10	0.04	$3.35^{\dagger}$	8.28*
Sphaeriidae	1, 8	0.13	0.21	–
Planorbidae	1, 5	2.43	0.01	–
Sialis sp.	1, 10	0.13	1.78	3.08
Trichoptera	1, 8	0.61	>0.01	1.75

† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

[a] Interaction effects could not be determined for all taxa due to insufficient numbers of organisms for replication

reported by Cole et al. (2006) may be caused by (1) natural allochthonous sources being more efficiently used in the food web compared to starch carbon, and (2) lower benthic autochthonous production.

Autotrophic primary production was marginally reduced in our shaded treatments. This is analogous to situations in which an increase in colored DOC can repress photosynthesis in benthic habitats by changing the light availability for benthic algae (Jones 1992; Carpenter et al. 1998). A recent study reported an increased utilization of terrestrial resources and a simultaneous decreased utilization of benthic resources of zoobenthos with reduced light availability (Solomon et al. 2011). In contrast, we found a similar dependence on starch carbon of macroinvertebrates at low and high light availability. Macroinvertebrates were ^{15}N depleted in the +C–S treatments, whereas they were ^{15}N enriched in the +C+S treatments, suggesting that the use of resources other than starch carbon or starch-mediated pathways differed, although such an assessment was beyond the scope of our study. The similar reliance on starch carbon in the no shade and shade treatments, however, indicates that the uptake of starch carbon was not hampered when the access to autochthonous resources was limited.

The magnitude of the responses in terms of δ^{13}C and δ^{15}N signatures and of starch carbon reliance differed considerably between zoobenthic taxa. We observed a relatively low reliance of chironomids and oligochaetes on starch carbon. Solomon et al. (2008) reported a high reliance of chironomids on detrital pathways (57–83%), although the allochthony of chironomids was likely lower because these authors could not discriminate between autochthonous and allochthonous detritus. We could not determine the utilization of resources other than starch carbon and thus likely underestimated allochthony in these taxa. Inter-individual variability of isotopic signatures within oligochaetes and chironomids was high, reflecting the fact that these taxa are composed of different groups, including herbivores, detritivores, and strict carnivores (Schmid-Araya and Schmid 2000). This high inter-individual variability suggests that reliance on starch carbon was likely high in some groups, such as detritivores, but low in others, such as carnivores. In addition, oligochaetes and chironomids generally live buried in the sediment and therefore might only have partly used the surface layer where we distributed the starch. In contrast, surface-dwelling consumers, such as amphipods and snails (Planorbidae), showed a high reliance on starch carbon.

A strong shift in isotopic signature was also observed in the predator *Sialis*. Oligochaetes and chironomids, both potential prey organisms of *Sialis*, were the most dominant taxa in our study system. In addition to their numerical abundance, they presumably have faster growth rates and higher turnover than other macroinvertebrates and thus might be effectively consumed by predators. Hence, despite their relatively low reliance on starch carbon, oligochaetes and chironomids might represent a facile channel of POC to higher trophic levels within the benthic food web. Selective predation on taxa that showed strong ^{13}C

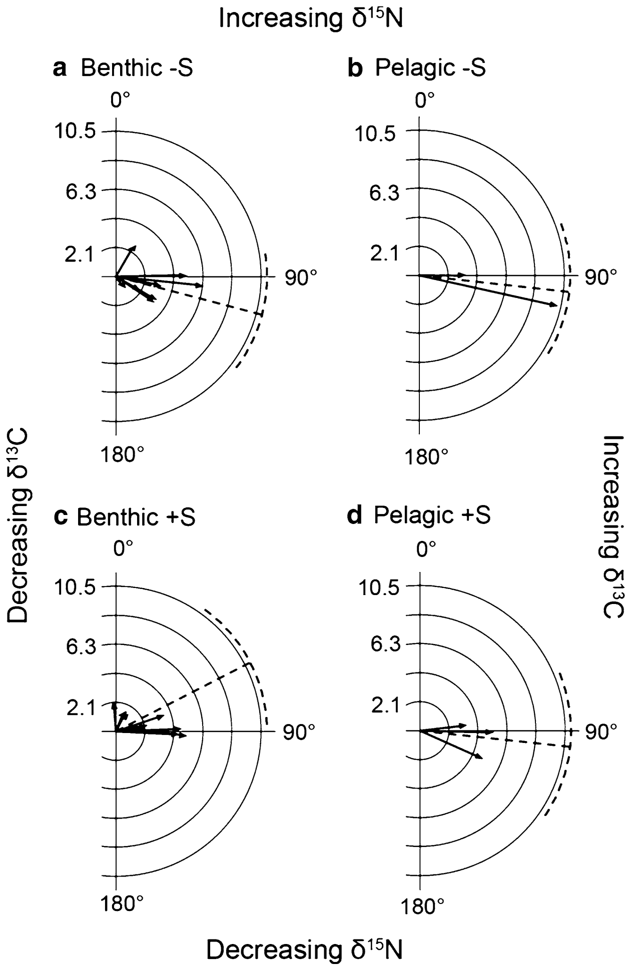

Fig. 2 Arrow diagram of the isotopic changes between treatments with and without carbon addition for benthic (**a**, **c**) and pelagic (**b**, **d**) invertebrates in no shade conditions (−*S*; **a**, **b**) and shade conditions (+*S*; **c**, **d**). Each *arrow* represents the change in δ^{15}N and δ^{13}C between the no carbon and carbon treatments, expressed as a vector in polar coordinates. *Concentric circles* Magnitude of change, *length of the solid arrow* magnitude of change for a particular taxon. Increased δ^{13}C values correspond to *right-directed vectors*, and increased δ^{15}N values correspond to *top-orientated vectors*. *Dashed line* mean angle of change (μ), *curved dashed line* 95% confidence interval (CI) around the mean angle. Circular statistics are provided in Table 4

enrichment, such as amphipods or trichopterans, might also result in a high enrichment of predators. Solomon et al. (2008) showed that obligate predators (odonates) were relatively dependent on autochthonous resources, although the most abundant prey (chironomids) heavily relied on allochthonous resources. Surface-dwelling organisms, such as amphipods and trichopterans, are likely more conspicuous to predators than organisms that inhabit the sediment, such as oligochaetes and chironomids, and might therefore be selectively preyed upon.

Although our experiment was designed to introduce the carbon source exclusively to the sediment, we observed several effects of the carbon addition transferred to the pelagic system. Potential mechanisms resulting in the observed effects on pelagic biota are (1) the re-suspension of POC from the sediment, (2) the direct grazing of pelagic biota on the sediment, and (3) the increased release of OC by benthic biota from the sediment. Although water movements inside the mesocosms were likely not completely absent, we suggest that they were very low (Porter et al. 2004). The mesocosms were comparably deep and narrow and, therefore, re-suspension was presumably negligible. Crustacean zooplankton can consume benthic OM by grazing directly on the sediment or on re-suspended particles (Hansson and Tranvik 2003; Rautio and Vincent 2007). We found evidence that the release of OC via benthic organisms (point 3 above) contributed to the observed patterns. First, we found decreased chlorophyll *a* concentrations in the water column in conjunction with carbon addition to the sediment. Previous studies have found that the increased input of DOC to the pelagic habitat negatively affected primary production and/or chlorophyll *a* concentration in the water (Klug 2005; Stets and Cotner 2008) due to the inferior competitiveness of algae in nutrient allocation compared to bacteria. Second, zooplankton was depleted in δ^{15}N signatures. The uptake of terrestrial DOC by zooplankton through bacteria has been suggested to contribute only a minor fraction to the overall reliance of zooplankton on terrestrial OC (Cole et al. 2006). We suggest that both the microbial transfer of released OC and direct grazing accounted for the high reliance on starch carbon in zooplankton (sensu Cole et al. 2006). Interestingly, the reliance of cladocerans on starch carbon was substantially higher than that of copepods. Karlsson (2007) reported that allochthony was on average 6.9% higher for cladocerans than for copepods. Similarly, Caraco et al. (2010) demonstrated that *Bosmina* sp. was supported more strongly by aged OC subsidies than copepods in the Hudson River. As non-selective filer feeders, cladocerans are likely to be more reliant on allochthonous OC than copepods. Furthermore, cladocerans can directly feed on bacteria, whereas copepods selectively feed on larger phytoplankton, flagellates, and ciliates (Sommer and Sommer 2006). Allochthonous-derived energy from bacteria to cladocerans therefore represents a two-link chain, whereas copepods likely derive energy from bacteria through a three-link chain. These different mechanisms suggest that transfer efficiency of allochthonous-derived energy might be more efficient for cladocerans than for copepods (Jansson et al. 2007). In our study, the cladocerans demonstrated a higher reliance on starch carbon than all macroinvertebrates, while the reliance of copepods on starch carbon, although lower than that of cladocerans, was at least similarly high as that of macroinvertebrates. Thus, our results verify those of previous studies that showed

Table 4 Circular statistics quantifying changes in isotopic values (δ^{13}C and δ^{15}N) of benthic and pelagic invertebrates between treatments with and without starch carbon in no shade and shade conditions

Light condition	Organisms	n^{a}	Mean vector		Circular SD	Rayleigh's test	
			Angle (μ)	Length (r)		Z	P
No shade	Benthic	9	104.7	0.87	30.2	6.82	<0.001***
	Pelagic	2^{b}	96.3	0.99	6.1	1.98	0.14
Shade	Benthic	9	62.8	0.84	34.4	6.27	<0.001***
	Pelagic	3	96.0	0.97	13.1	2.85	0.043*

*** $P < 0.001$

[a] Number of benthic and pelagic taxa included in the analysis

[b] Sample of *Chaoborus* sp. was not available

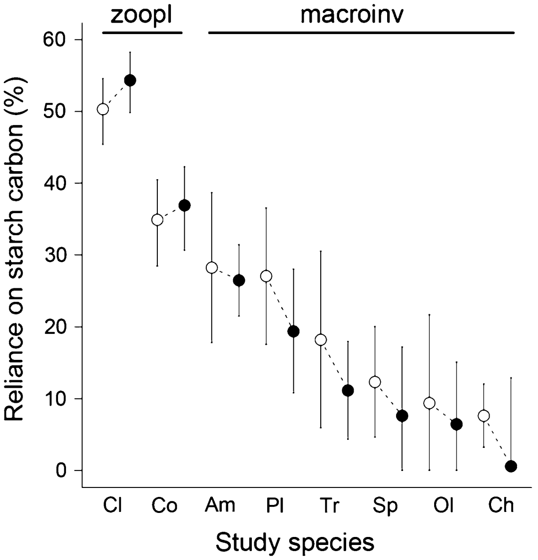

Fig. 3 Reliance on starch carbon (%) of zooplankton (*zoopl*) and benthic macroinvertebrates (*macroinv*) with and without shade. *Cl* Cladocera, *Co* Copepoda, *Am* Amphipoda, *Pl* Planorbidae, *Tr* Trichoptera, *Sp* Sphaeriidae, *Ol* Oligochaeta, *Ch* Chironomidae. Treatments shown are with carbon, no shade (*open circles*), and with carbon, with shade (*filled circles*). V*ertical bars* Uncertainty in estimated reliance by range in δ^{13}C (for zooplankton) and 95% CI (for macroinvertebrates)

substantial contribution of allochthonous carbon for zooplankton (reviewed in Cole et al. 2011). Furthermore, pelagic productivity in our study system was generally low (Karlsson et al. 2008). Our results suggest that the input of POC to benthic food webs can subsidize pelagic secondary production in the case of low pelagic primary production (Grey et al. 2000, 2001) and thus emphasize the importance of benthic pathways for pelagic production (Hecky and Hesslein 1995).

Although our estimates for reliance on POC are within the range reported in other studies (Cole et al. 2006; Caraco et al. 2010), they should be interpreted with caution. Several reasons might have led to an over- or underestimation of reliance on starch carbon. The added amount of starch carbon was relatively high. Estimates of natural input rates of terrestrial POC are rare. Preston et al. (2008) reported a mean airborne deposition of 14 mg C m^{-2} day^{-1}, but temporal and spatial variation was large in their study (1–52 and 1.5–105 mg C m^{-2} day^{-1} for <153 and >153-μm-sized fractions, respectively). Although our input was higher (approx. 1.5 g C m^{-2} day^{-1}), flocculation of DOC can contribute substantially to the POC pool in boreal lakes (von Wachenfeldt and Tranvik 2008), and thus POC availability might be considerably higher than that reported by Preston et al. (2008). Furthermore, the bioavailability of starch carbon, in particular to bacteria, is high. Terrestrial-derived OC is generally recalcitrant and likely represents a poor quality resource for consumers (Brett et al. 2009); it might therefore be only partly available to aquatic consumers. Thus, high input rates and high bioavailability might have resulted in an overestimation of the starch carbon reliance of consumers. The reliance of zooplankton might have been higher if phytoplankton was labeled with starch carbon. Phytoplankton may have taken up labeled carbon from mineralization processes of starch and subsequently been consumed by zooplankton. Although this represents an indirect reliance of zooplankton on starch carbon, it differs from our proposed mechanisms. However, our observed δ^{13}C signatures of POM from mesocosms that received starch carbon indicate that this was not likely. In contrast, macroinvertebrates may not have reached isotopic equilibrium with their food sources within the duration of our study, resulting in an underestimation of starch reliance in the benthic community.

Many studies have demonstrated the importance of allochthonous DOC for aquatic ecosystems; however, studies on the utilization of allochthonous POC are scarce. Our study adds to the growing literature showing that POC can subsidize lake ecosystems. In addition, many studies focus on the effects of allochthonous matter on pelagic communities, whereas we show that benthic communities also benefit from allochthonous inputs. Similar to experiments with glucose in the pelagic (Ducklow et al. 1986; Blomqvist et al. 2001), we used starch carbon as a model substrate for allochthonous carbon in a benthic system. Although the quantitative estimates of carbon reliance are likely not representative of natural ecosystems (as discussed above), we have highlighted potential pathways of particulate allochthonous carbon in benthic food webs. Furthermore, our results indicate that carbon utilized in the benthic habitat can be transferred further to the pelagic habitat. We suggest that these pathways might play a considerable role in lakes characterized by low primary production. We encourage future research to investigate the described mechanisms further and to quantify to which extent these pathways affect food webs in natural ecosystems.

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