

HABITAT SPECIALIZATION AND THE EXPLOITATION OF ALLOCHTHONOUS CARBON BY ZOOPLANKTON

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Abstract. The significance of spatial subsidies depends on consumer resource interactions in the recipient habitat. Lakes are subsidized by terrestrial carbon sources, but the pathways of allochthonous carbon through lake food webs are complex and not well understood. Zooplankton vertically partition resources within stratified lakes in response to life history trade-offs that are governed by predators, the quantity and quality of food, and abiotic conditions (e.g., UV, temperature, and viscosity). We measured habitat specialization of zooplankton in an oligotrophic lake where allochthonous and autochthonous resources varied with depth. During stratification, the quantity and quality of zooplankton food was highest in the hypolimnion. We used a yearlong time series of the $\delta^{13}\text{C}$ of zooplankton and particulate organic matter (POM) to determine which zooplankton species exploited hypolimnetic rather than epilimnetic resources. Because the $\delta^{13}\text{C}$ of POM decreased with depth, we used the $\delta^{13}\text{C}$ of zooplankton to detect inter- and intraspecific variation in habitat selection. We incubated *Daphnia pulex* at discrete depths in the water column to confirm that the $\delta^{13}\text{C}$ of zooplankton can indicate habitat specialization. Zooplankton that specialized in the epilimnion relied more on allochthonous carbon sources than those that specialized in the hypolimnion. Therefore, the fate of allochthonous carbon subsidies to lakes depends on spatially explicit consumer–resource interactions.

Key words: allochthonous; allochthony; *Daphnia*; food web; habitat specialization; lake; organic carbon; spatial subsidy; stable isotope; zooplankton.

INTRODUCTION

The terrestrial subsidy of carbon to aquatic ecosystems is a classic example of a spatial subsidy (Polis et al. 1997), whereby a donor-controlled resource (dissolved organic carbon, terrestrial detritus, or prey) is supplied to a recipient habitat. This subsidy is common in streams, rivers, estuaries, and lakes (Polis et al. 1997, Sobczak et al. 2002, Carpenter et al. 2005), and can lead to reciprocal fluxes of prey (Nakano and Murakami 2001) or predators (Knight et al. 2005) from freshwater to terrestrial ecosystems. The nature and magnitude of terrestrial subsidies can strongly affect the recipient habitat's local production and community interactions (Polis et al. 1997). In lakes, dissolved organic carbon (DOC) from terrestrial sources can fuel pelagic food webs through the microbial loop (Tranvik 1992), but the physical and optical properties of DOC (e.g., bioavailability, UV attenuation) may also limit primary production, and affect both consumer–resource (Leech and Williamson 2001) and predator–prey interactions (Williamson et al. 1999a). At the ecosystem level, terrestrial carbon subsidies affect whole lake metabolism by subsidizing ecosystem respiration relative to produc-

tion (del Giorgio et al. 1999). However, the specific pathways and seasonal fate of terrestrial carbon subsidies are not well defined for lake food webs, so the general significance of allochthonous subsidies for plankton communities and upper trophic levels is still uncertain (Grey et al. 2000, 2001, Pace et al. 2004, Carpenter et al. 2005).

Abiotic gradients in the water column of lakes create substantial resource heterogeneity for zooplankton and affect how efficiently a zooplankton community can exploit terrestrial subsidies. Vertical gradients of temperature, light, and nutrients interact to determine the production, spatial location, and composition of autochthonous carbon (Fee 1976, Sterner and Hessen 1994, Park et al. 2004), as well as the bioavailability of allochthonous carbon (Sobczak et al. 2002, Obernosterer and Benner 2004). These abiotic gradients also affect predator–prey interactions and habitat selection trade-offs (Williamson et al. 1999a, Leech and Williamson 2001). Zooplankton can also indirectly modify interactions between abiotic gradients and the ecological processes that structure their food resources (Mazumder et al. 1990, Tessier and Woodruff 2002a, Pilati and Wurtsbaugh 2003). Such complex interactions lead to considerable uncertainty regarding the general significance of terrestrial subsidies for lake food webs, and highlight the importance of taking a community-wide perspective (Carpenter et al. 2005).

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Focusing on zooplankton traits, and how they seasonally respond to environmental change (Norberg et al. 2001), may help resolve how efficiently zooplankton communities can exploit terrestrial subsidies (Norberg 2004). Two important traits structure the feeding behaviors of zooplankton in fishless oligotrophic lakes that have deep chlorophyll maxima and allochthonous carbon subsidies. The first trait involves the ability to exploit subsurface autochthonous production (Williamson et al. 1996). In stratified lakes, *Daphnia* commonly face a trade-off between food abundance and temperature because high food concentrations are common in cooler subsurface waters (Fee 1976, Cullen 1982, Lampert 2006). In the short term, a population may adopt a distribution in the water column that reflects an optimization of growth and reproduction (Lampert et al. 2004), and exhibit size-based (Kessler and Lampert 2004) and individual-based (Kessler 2004) differences in the propensity to exploit subsurface resources. Over the longer term, this trade-off could lead to clone-based differences in subsurface resource exploitation (Tessier and Leibold 1997). Allochthonous subsidies can affect the temperature–food trade-off experienced by zooplankton (Lampert et al. 2004), by altering how the proportion of autochthonous and allochthonous carbon sources varies with depth (Williamson et al. 1999b). Oligotrophic lakes are commonly supported by a substantial terrestrial subsidy (Cole et al. 2000), and often have deep chlorophyll maxima (Fee 1976, Cullen 1982). However, it remains unclear how efficiently zooplankton can exploit these subsurface resources (Williamson et al. 1996, Cole et al. 2002b, Winder et al. 2003), and therefore, how much zooplankton rely on allochthonous subsidies (Grey et al. 2001).

The second important trait involves the ability to exploit resources with varying food quality (Tessier and Woodruff 2002b). Tessier and Woodruff (2002b) found that a trade-off in the ability of *Daphnia* grazers to exploit rich vs. poor quality food helped explain interlake variation in the efficiency of resource exploitation by zooplankton communities. Zooplankton species differ in their ability to select prey items of varying quality (Burns and Schallenberg 2001) and digest different biochemical constituents (Cowie and Hedges 1996). The food quality of an allochthonous subsidy can be low or high, depending on whether it is in the form of terrestrial detritus (Elser et al. 2000) or if it has been repackaged or upgraded in the microbial loop (Tranvik 1992, Vera et al. 2001). The food quality of autochthonous carbon depends on its elemental stoichiometry (Klausmeier et al. 2004) and fatty acid composition (Martin-Creuzburg et al. 2005), both of which can vary with depth in the water column of lakes (Park et al. 2004). Food quantity and quality often increase concurrently with depth (Winder et al. 2003, DeMott et al. 2004, Park et al. 2004), but this is not always the case (Cole et al. 2002b). As a consequence, taxa or individuals could specialize on a particular habitat (i.e.,

at a particular depth), or within a habitat with respect to the resource size or quality (Tessier and Woodruff 2002b). From a seasonal perspective, temporal variation of allochthonous and autochthonous resources could lead to inter- or intraspecific variation in the proportion of allochthonous carbon in zooplankton diets (i.e., zooplankton allochthony; Grey et al. 2001).

The composition and vertical distribution of allochthonous and autochthonous resources have important consequences for measuring zooplankton allochthony. Some studies suggest only a small fraction (<10%) of dissolved organic carbon supports zooplankton production (Cole et al. 2002a), whereas others, using stable isotopes, suggest that substantially more allochthonous carbon (up to 50%) contributes to zooplankton diets (Grey et al. 2001, Pace et al. 2004). The $\delta^{13}\text{C}$ of consumers is normally slightly higher than their food source ($\sim 0.5\%$; McCutchan et al. 2003). However, the $\delta^{13}\text{C}$ of zooplankton is typically lower than the $\delta^{13}\text{C}$ of particulate organic matter (POM; del Giorgio and France 1996), suggesting that zooplankton selectively feed on a food source that makes up a small proportion of the carbon in POM and has a low $\delta^{13}\text{C}$. The $\delta^{13}\text{C}$ of zooplankton is particularly low in oligotrophic lakes (Grey et al. 2000), supporting the idea that allochthonous carbon in POM ($\delta^{13}\text{C}$ approximately -28%) masks the lower $\delta^{13}\text{C}$ of algal carbon (Grey et al. 2001, Karlsson et al. 2003). POM is a heterogeneous mixture of algae, bacteria, and allochthonous and autochthonous detritus, and the composition and $\delta^{13}\text{C}$ of these food sources can vary with depth. No study has examined the consequences of such vertical gradients for estimating zooplankton allochthony.

In this study, we examine how zooplankton differentially exploit subsurface resources in an oligotrophic lake (Council Lake) with a deep chlorophyll maximum. In Council Lake, the $\delta^{13}\text{C}$ of POM decreases with depth in the water column, consistent with an increasing proportion of autochthonous carbon with depth. We hypothesized that zooplankton feeding deeper in the lake would have a lower $\delta^{13}\text{C}$ and rely less on allochthonous carbon. To address this, we first measured seasonal $\delta^{13}\text{C}$ patterns of various species and sizes of zooplankton that differed in their water column distribution. Second, we experimentally manipulated the feeding depth of *Daphnia pulex* (using enclosures) to confirm that $\delta^{13}\text{C}$ can indicate habitat specialization. The gradient in the $\delta^{13}\text{C}$ of POM food sources allowed us to link habitat specialization of zooplankton with their exploitation of terrestrial subsidies. We conclude that the pathways of allochthonous and autochthonous carbon through lake food webs depend on the composition, habitat selection, and size structure of the zooplankton community. More generally, the exploitation of spatial subsidies can depend on spatially explicit consumer resource interactions in the recipient habitat.

METHODS

Study site

Council Lake is a warm monomictic lake that rarely gets permanent ice cover. It is located on southern Vancouver Island, British Columbia, Canada (48°31'45" N, 123°40'16" W), in a watershed that consists of western hemlock stands interspersed with coastal Douglas-fir and western red cedar. The watershed receives most of its annual precipitation (~1200 mm/yr) in the winter months (Nowlin et al. 2004). The maximum depth of Council Lake is 17 m, the mean depth is 5.2 m, and the surface area is 17 ha. During the summer, 1% light levels often reach the lake bottom, dissolved organic carbon concentrations are ~2–3 mg C/L, and epilimnetic chlorophyll *a* concentrations are typically <1 µg/L (Davies et al. 2004).

Annual collection of plankton in Council Lake (2002–2003)

We sampled zooplankton and particulate organic matter (POM) <41 µm in Council Lake 28 times between 14 February 2002 and 17 March 2003. We collected samples at least monthly over the whole sampling period, every two weeks during lake stratification (May–November), and every 3–4 days in July. We collected zooplankton during the day with a Wisconsin net (64-µm mesh, 50 cm diameter) by vertical net tows (0–17 m). We froze bulk zooplankton samples within four hours of collections, and later sorted out composite samples from five taxonomic groups: *Daphnia pulex*, *Holopedium gibberum*, *Leptodiptomus tyrelli*, *Epischura nevadensis*, and *Chaoborus trivittatus*. Prior to isotopic analysis, we measured the average body size of each zooplankton sample using a dissecting microscope, a digital camera, and zooplankton counting software (Z-Count, unpublished software).

We used a Niskin bottle to collect POM from three depths (2, 8, 16 m) in the spring of 2002, nine depths (1, 3, 5, 7, 8, 9, 12, 14, 16 m) in July, and six depths (~2, 6, 8, 10, 12, 14 m) for the remainder of the study. For each sample, we filtered at least 1 L of lake water through a 41-µm Nitex mesh onto precombusted (550°C for 1 h) 25 mm GF-C filters (Whatman). We dried the filters overnight at 60°C and packaged them in tin cups for isotopic and elemental analysis. We measured chlorophyll *a* (chl *a*) of POM <41 µm by filtering samples through GF/Fs (Whatman), immersing the filters in 95% ethanol overnight at 4°C, and analyzing the extract on a spectrophotometer.

All stable isotope samples were analyzed on a Finnigan Delta Plus Advantage stable isotope ratio mass spectrometer (Finnigan MAT, Bremen, Germany) at the Water and Aquatic Sciences Research Laboratory, at the University of Victoria. Percentage carbon and nitrogen of organic matter on the filters was used to calculate particulate carbon concentrations. *D. pulex* samples from the cage experiment were run with a lower

level of helium dilution to obtain a sufficient carbon signal. We included a powdered *Daphnia* standard in every sample run, and its precision was <0.2‰ within and between all sample runs.

We used chl *a*, the proportion of algal carbon (α), and the $\delta^{13}\text{C}$ POM (<41 µm), to test for relationships between the autochthonous composition of POM and its $\delta^{13}\text{C}$. We estimated α using a carbon-to-chlorophyll ratio of 40 (following Kritzbeg et al. 2004). Though this ratio varies widely among lakes (Leavitt and Carpenter 1990), it only affects our estimates of the absolute proportion of algae in POM and not the slope of the relationship with POM $\delta^{13}\text{C}$ within each strata. A relationship between chl *a* and POM $\delta^{13}\text{C}$ would not be expected if algae had the same $\delta^{13}\text{C}$ as allochthonous carbon, or if algae had a lower $\delta^{13}\text{C}$ (Karlsson et al. 2003) and only made up a small fraction of the carbon in POM compared to allochthonous sources (Grey et al. 2001). Previous studies suggest the $\delta^{13}\text{C}$ of algae is lower than allochthonous carbon (Grey et al. 2001, Karlsson et al. 2003). Therefore, over a large range of α we predict a negative relationship between α and POM $\delta^{13}\text{C}$. We split our analysis by lake strata, because the slope of this relationship may decrease if the $\delta^{13}\text{C}$ of algae decreases with depth.

We estimated the $\delta^{13}\text{C}$ for zooplankton with their lipid extracted ($\delta^{13}\text{C}_{\text{LE}}$), using a lipid normalization model from a previous study (Matthews 2006). This model normalizes zooplankton to a zero lipid content based on the positive relationship between zooplankton C:N and lipid content, and measured differences in $\delta^{13}\text{C}$ between zooplankton tissue with and without lipid (Matthews 2006). Because the seasonal patterns of zooplankton $\delta^{13}\text{C}$ and $\delta^{13}\text{C}_{\text{LE}}$ are qualitatively similar (see Appendix A), we use $\delta^{13}\text{C}$ to compare feeding behaviors among zooplankton species and to calculate zooplankton allochthony.

Cage design

We constructed 36 cylindrical cages (diameter, 0.4 m; height, 0.6 m; volume, ~75 L) using stainless steel woven wire mesh (Ferrier Wire Good Company, Toronto, Canada). The diagonal diameter of the holes was ~320 µm, and there were >500 holes/cm². We made a cylindrical frame out of 16-gauge aluminum, wrapped the wire mesh around the outside, and welded the mesh to the frame. We made identical lids for both ends by welding wire mesh onto 14-gauge aluminum rings that we tightly fitted to the cylindrical frame. We surrounded each cage with nylon straps that were adjustable to fit snugly around each cage. The cages were suspended vertically at discrete depths.

Temporal cage experiment (21 July–8 August 2003)

The two goals of the temporal cage experiment were (1) to test if the differences in $\delta^{13}\text{C}$ among zooplankton that we observed in July 2002, and subsequently in July 2003, were associated with feeding depth, and (2) to

determine the rate of change of *D. pulex* $\delta^{13}\text{C}$ in response to a change in the $\delta^{13}\text{C}$ of its food source. In both years, we observed that the $\delta^{13}\text{C}$ of POM decreased with depth. We cultured *D. pulex* to have an isotopic signature significantly different from *D. pulex* in Council Lake, and then incubated them in situ at different depths in Council Lake. In June 2003, we stocked a single 1000-L mesocosm with *D. pulex* from Council Lake, and fed them with *Scenedesmus aculeatus* from a batch culture in the laboratory. Our intention was to grow *D. pulex* on an algal diet that had a significantly higher $\delta^{13}\text{C}$ than either autochthonous or allochthonous carbon in Council Lake. From another study (Perga et al. 2006), we knew the $\delta^{13}\text{C}$ of allochthonous carbon in the watershed was -27.5 (SD = 0.79). The day before the experiment, we pumped *D. pulex* from the mesocosm and used a plankton splitter to gently divide the *D. pulex* into 45 separate containers. The following day we used 36 of these containers to inoculate 36 cages with *D. pulex*, and kept nine containers to measure the initial isotopic composition of *D. pulex*. On 21 July the $\delta^{13}\text{C}$ of *D. pulex* in the mesocosm was -19.1‰ (SD = 0.38, $N = 9$ cages), the initial density was 1.3 *D. pulex*/L (SD = 0.3, $N = 9$), and the initial biomass was 7.0 $\mu\text{g/L}$ (SD = 3.0, $N = 9$).

We ran the temporal cage enclosure experiment from 21 July to 8 August 2003. Every three days after 21 July (day 0), we removed two traps from each of the three depths (4, 8, and 14 m). This gave us two replicate time series of 6–7 measurements for each depth. Upon removing each cage from the lake, we transferred *D. pulex* into a separate container and froze them until analysis. On each day of the experiment we collected zooplankton using vertical tows as described previously, and POM from six depths (2, 4, 7, 9, 12, 16 m) for isotopic and elemental analysis. On replicate filters we measured the $\delta^{13}\text{C}$ ($<41\ \mu\text{m}$) and chl *a* ($<41\ \mu\text{m}$ and $>0.7\ \mu\text{m}$) as before, and determined particulate phosphorus concentration of POM ($<41\ \mu\text{m}$) using a Lachat automated ion analyzer (Zellweger Analytics, Dorset, UK).

Profile cage experiment (29 July–8 August)

On day 9 of the temporal cage experiment (29 July), we used the 12 previously removed traps to begin the profile cage experiment. The goal of the profile cage experiment was to provide an additional test for an effect of feeding depth on the $\delta^{13}\text{C}$ of *D. pulex*. In this experiment we set two replicate cages at 2, 4, 8, 10, 12, and 14 m, and incubated them with *D. pulex* from the same stock mesocosm. The $\delta^{13}\text{C}$ of *D. pulex* at the start of this experiment was -18.2‰ (SD = 0.23, $N = 9$). The initial density and biomass of *D. pulex* was 1.3 individuals/L (SD = 0.20) and 13.8 $\mu\text{g/L}$ (SD = 2.5, $N = 9$), respectively.

Depth distribution of Council Lake zooplankton

In 2002 and 2003, we sampled the daytime and nighttime depth distribution of zooplankton for one

date in July 2002, and four dates in July 2003 using a 25-L Schindler-Patalas trap (1, 3, 5, 7, 8, 9, 12, 14, 16 m). We chose July for this part of the study because data from 2002 revealed that this was the time when the $\delta^{13}\text{C}$ gradient of POM was strongest. Because diurnal vertical migrations were minimal for all taxa, we pooled day and night depth distribution data for each taxa and calculated the depth at maximum density. We used LOWESS to visually check that this depth of maximum density was the only major peak of zooplankton density in the profile. In 2002, we separated depth distribution counts of *D. pulex* into two size classes ($<1.8\ \text{mm}$ and $>1.8\ \text{mm}$) to match the size classes of our isotopic data.

RESULTS

Annual variation in the $\delta^{13}\text{C}$ of plankton

The range in the $\delta^{13}\text{C}$ of POM₄₁ (for a given sampling date) was largest during thermal stratification (Fig. 1A). The daily average range over the water column for the $\delta^{13}\text{C}$ of POM₄₁ was 3.8‰ (min, 0.93‰; max, 7.8‰). Seasonal variation in algal biomass (chl *a*) was negatively related to the $\delta^{13}\text{C}$ of POM₄₁ in the hypolimnion ($\beta_0 = -32.1$, $\beta_1 = -1.91$, $F_{1,54} = 5.8$, $P = 0.02$, $r^2 = 0.10$), but there was no significant relationship in the epilimnion ($\beta_0 = -31.0$, $\beta_1 = -0.54$, $F_{1,55} = 1.2$, $P = 0.28$) or metalimnion ($\beta_0 = -32.5$, $\beta_1 = 0.32$, $F_{1,54} = 0.3$, $P = 0.59$). The $\delta^{13}\text{C}$ of POM₄₁ was negatively related to the proportion of algal carbon in POM₄₁ in the hypolimnion ($\beta_0 = -32.1$, $\beta_1 = -9.7$, $F_{1,54} = 10.5$, $P < 0.01$, $r^2 = 0.17$) and epilimnion ($\beta_0 = -31.0$, $\beta_1 = -4.5$, $F_{1,53} = 3.9$, $P < 0.05$, $r^2 = 0.10$), but not in the metalimnion ($\beta_0 = -32.5$, $\beta_1 = 0.93$, $F_{1,54} = 0.1$, $P = 0.76$; Fig. 2).

Throughout the stratified period the $\delta^{13}\text{C}$ of POM₄₁ typically declined with depth, but the gradients were steepest in July (Fig. 3). Despite the decline in the $\delta^{13}\text{C}$ of POM₄₁ with depth, the $\delta^{13}\text{C}$ of POM₄₁ could not entirely account for the range of zooplankton $\delta^{13}\text{C}$ in Council Lake (Fig. 1, Appendix A). Most notably, the $\delta^{13}\text{C}$ of *L. tyrelli* and large *D. pulex* was always lower than the lowest $\delta^{13}\text{C}$ of POM₄₁ measured on the same day. Normalizing the $\delta^{13}\text{C}$ of zooplankton to zero lipid content (Matthews 2006) partially explained the mismatch between the $\delta^{13}\text{C}$ of zooplankton and POM (Appendix A). Kling et al. (1992) found that lipids accounted for between 17% and 50% of the difference between zooplankton $\delta^{13}\text{C}$ and POM. In Council Lake, lipid normalization accounted for 30–100% of the difference (mean = 56%) between the $\delta^{13}\text{C}$ of large *D. pulex* and the minimum daily $\delta^{13}\text{C}$ of POM. Only *Chaoborus*, *Holopedium*, *D. pulex* ($<1.8\ \text{mm}$), and *Epischura* had lipid normalized $\delta^{13}\text{C}$ values ($\delta^{13}\text{C}_{\text{LE}}$) that were within the range of the $\delta^{13}\text{C}$ of POM₄₁ (Appendix A). Large *D. pulex* and *L. tyrelli* always had a lower $\delta^{13}\text{C}$ (and $\delta^{13}\text{C}_{\text{LE}}$) than POM₄₁. The $\delta^{13}\text{C}$ of *D. pulex* ($>1.8\ \text{mm}$) and *L. tyrelli* declined concurrently with the $\delta^{13}\text{C}$ of POM below the epilimnion (Figs. 1 and 3), and increased in the fall as the $\delta^{13}\text{C}$ gradient of POM₄₁ weakened (Fig. 3B). This indicates that zoo-

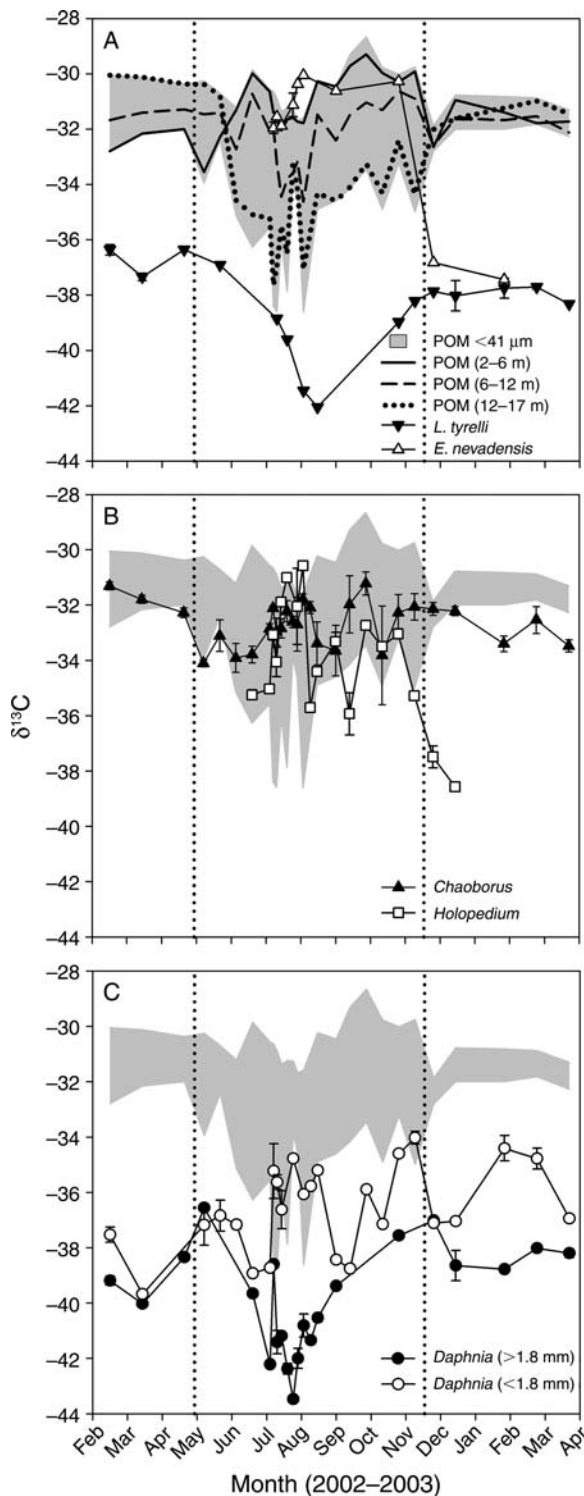


FIG. 1. Seasonal patterns in the $\delta^{13}\text{C}$ of zooplankton and particulate organic matter (POM) in Council Lake, southern Vancouver Island, British Columbia, Canada, 2002–2003. Vertical dotted lines show the period of thermal stratification. Error bars are \pm SE. The shaded region spans the maximum and minimum of the $\delta^{13}\text{C}$ of POM <41 μm collected over the entire water column.

plankton fed on a fraction of POM (probably algae) that had a lower $\delta^{13}\text{C}$ than bulk POM. Lipid normalization did not significantly affect the relative seasonal patterns of zooplankton $\delta^{13}\text{C}$ in Council Lake (Appendix A).

Seasonal patterns of zooplankton $\delta^{13}\text{C}$ depended strongly on the taxonomic grouping, and additionally on the size class for *D. pulex* (Appendix B, Fig. 1). As a result, zooplankton differentially responded to seasonal changes in the availability and distribution of allochthonous and autochthonous resources. The annual average $\delta^{13}\text{C}$ of *Epischura* was $\sim 6\text{‰}$ higher than *L. tyrelli*, but the differences for a given sampling day were greatest during stratification (Fig. 1A). Likewise, the biggest differences between the $\delta^{13}\text{C}$ of small and large *D. pulex* (SD and D, respectively) were during stratification ($\Delta_{\text{SD-D}} = -0.5\text{‰}$ to 7.8‰ ; Fig. 1C). In July, the average body size of *D. pulex* accounted for $\sim 80\%$ of the variation in both the $\delta^{13}\text{C}$ ($F_{1,31} = 149.1, r^2 = 0.82, P < 0.001$) and $\delta^{13}\text{C}_{\text{LE}}$ ($F_{1,31} = 118.8, r^2 = 0.79, P < 0.001$) of *D. pulex* (linear regression in Fig. 4).

Temporal cage experiment

The vertical distribution of resources in Council Lake was similar in July 2002 and 2003. In 2002, C:N was lowest in the hypolimnion, $\delta^{13}\text{C}$ decreased with depth (Fig. 3), and particulate carbon and chl *a* increased with depth (Matthews 2006). In July 2003, the $\delta^{13}\text{C}$, C:N, and C:P of POM decreased with depth, whereas the particulate carbon and chl *a* increased with depth (Fig. 5). Over the entire 18 days of the cage experiments, the $\delta^{13}\text{C}$ of POM₄₁ was lowest in the hypolimnion, and highest in the epilimnion (lines in Fig. 6).

The density of *D. pulex* declined significantly over the 18 day experiment ($F_{1,37} = 13.3, P = 0.001$, ANOVA

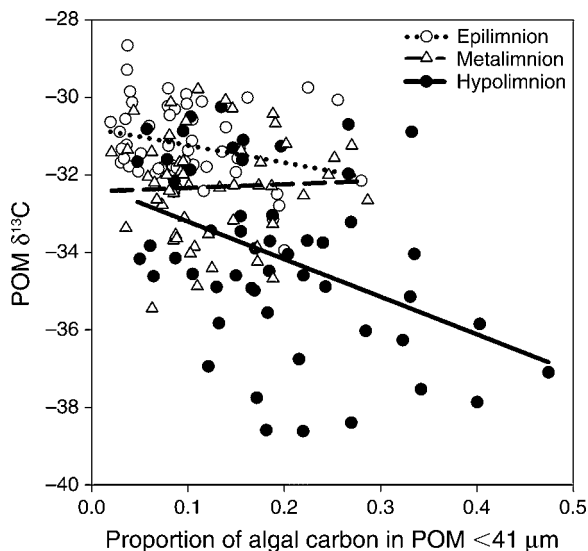


FIG. 2. Relationship between the proportion of algal carbon (α) and the $\delta^{13}\text{C}$ of POM <41 μm in Council Lake for 2002–2003.

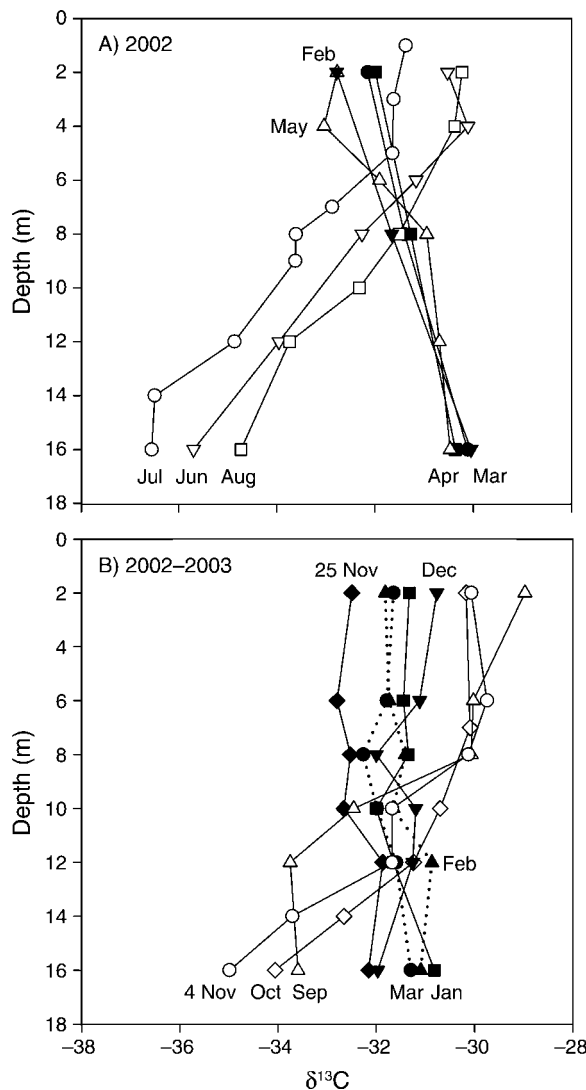


FIG. 3. Vertical gradients in the $\delta^{13}\text{C}$ of POM in Council Lake for (A) February–August 2002 and (B) September 2002–March 2003. Open symbols are for profiles during thermal stratification.

model with log density as response variable, lake strata as a fixed factor, and experiment day as the covariate), but the rate of decline was not significantly different among strata (ANOVA interaction term, $F_{2,37} = 0.39$, $P = 0.68$). Similarly, the rate of decline of *D. pulex* biomass did not depend on the strata (ANOVA interaction term, $F_{2,37} = 0.58$, $P = 0.57$). At the end of the experiment, the average density and biomass of *D. pulex* was 0.15 individuals/L ($SD = 0.06$, $N = 4$), and 2.4 $\mu\text{g/L}$ ($SD = 0.72$, $N = 4$), respectively. Unfortunately, neither epilimnetic trap had enough *D. pulex* remaining on day 18 for $\delta^{13}\text{C}$ measurements (Fig. 6).

We used a nonlinear least squares analysis to test if the rate of decline in the $\delta^{13}\text{C}$ of *D. pulex* was significantly different among strata. We found that the $\delta^{13}\text{C}$ of *D.*

pulex in all strata decreased over time, but more rapidly in the hypolimnion, followed by the epilimnion, and metalimnion (Appendix C). The rate of change in the $\delta^{13}\text{C}$ of *D. pulex* in Council Lake (0.045–0.094‰/d) was slightly lower than for *D. hyalina* (0.090–0.13‰/d) in a laboratory-based diet switch experiment (Grey 2000). We cannot determine if the $\delta^{13}\text{C}$ of *D. pulex* reached equilibrium with its food source, because we do not know the $\delta^{13}\text{C}$ of the fraction (algal or bacterial) of POM that was consumed. However, because the rate of decline in the $\delta^{13}\text{C}$ of *D. pulex* is significantly different among depths, this indicates a strong effect of feeding depth on the $\delta^{13}\text{C}$ of *D. pulex*.

Profile cage experiment

After nine days the average density and biomass of *D. pulex* declined to 0.26 *D. pulex/L* ($SD = 0.21$, $N = 12$ cages) and 2.8 $\mu\text{g/L}$ ($SD = 2.0$, $N = 12$), respectively. By the end of the experiment, there was no effect of lake strata on the density (ANOVA, $F_{2,9} = 0.69$, $P = 0.53$) or biomass (ANOVA, $F_{2,9} = 0.71$, $P = 0.52$) of *D. pulex*. However, we did find a significant effect of feeding depth on *D. pulex* $\delta^{13}\text{C}$ (ANOVA, $F_{2,9} = 48.4$, $P < 0.001$; Fig. 7). The $\delta^{13}\text{C}$ of *D. pulex* in the metalimnetic (*M*) cages (7, 9 m) was higher than *D. pulex* in both epilimnetic (*E*) and hypolimnetic (*H*) cages ($E = -30.2\text{‰}$, $N = 4$ cages; $M = -27.9\text{‰}$, $N = 4$; $H = -33.6\text{‰}$, $N = 4$).

The average lake density of *D. pulex* for July was 0.19 *D. pulex/L* ($SD = 0.13$, $N = 7$ sampling dates), and the biomass was 2.2 $\mu\text{g/L}$ ($SD = 0.84$, $N = 7$). This density and biomass is similar to the density (0.15–0.26 *D. pulex/L*) and biomass (2.4–2.8 $\mu\text{g/L}$) of *D. pulex* remaining in the cages at the end of the temporal and profile cage experiments.

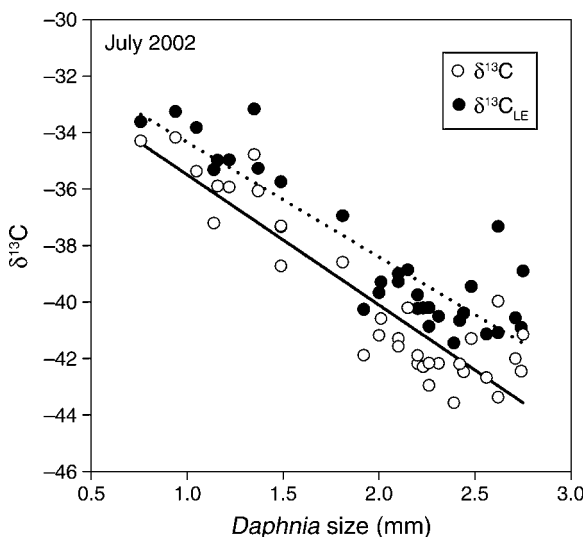


FIG. 4. Relationship between the average *Daphnia pulex* body size and $\delta^{13}\text{C}$ during July 2002; $\delta^{13}\text{C}_{LE}$ is the $\delta^{13}\text{C}$ of *D. pulex* following lipid normalization (Matthews 2006).

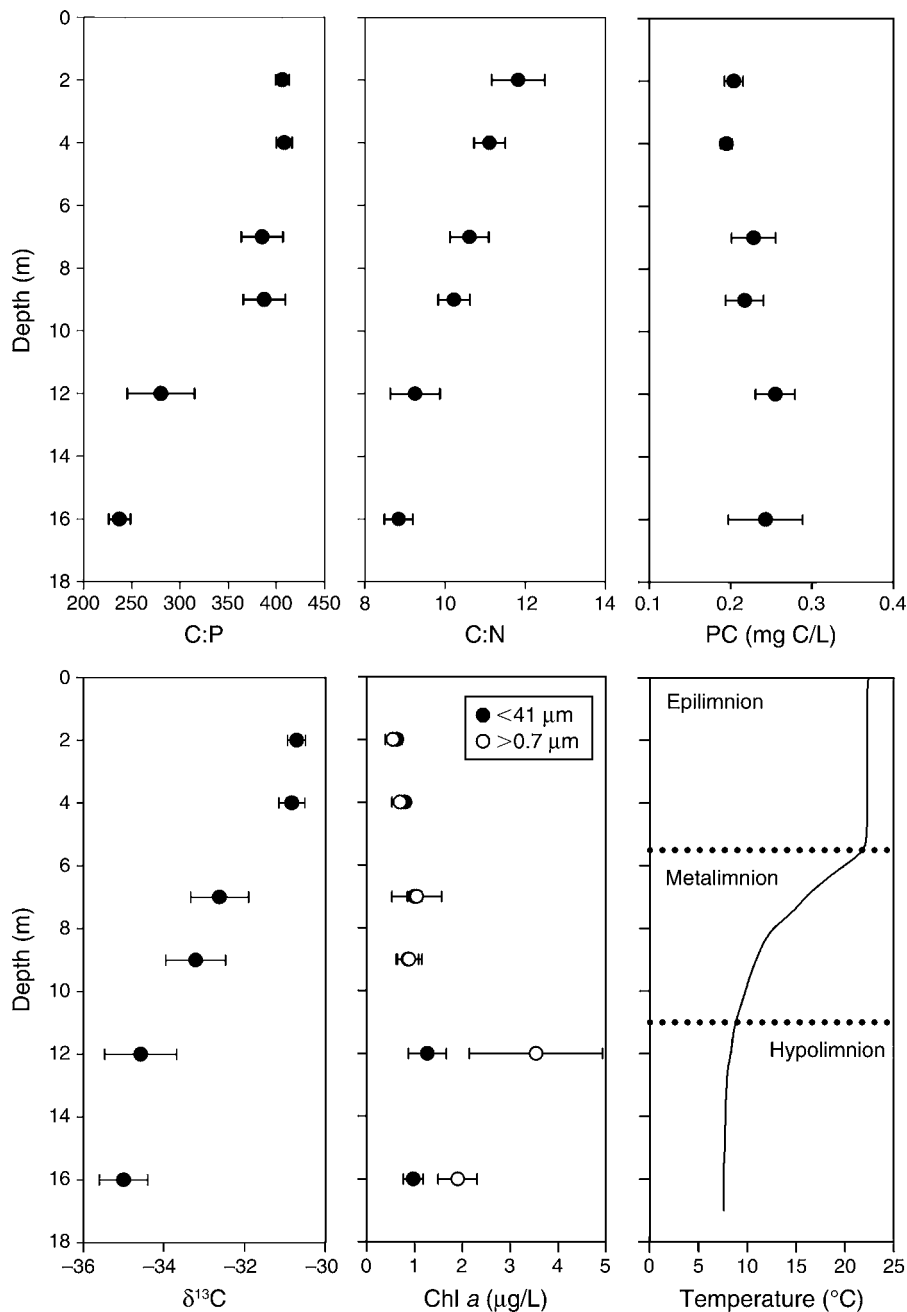


FIG. 5. Profiles of $\delta^{13}\text{C}$, C:N, C:P, particulate carbon (PC), chlorophyll *a* (chl *a*) and temperature during the cage experiments in July–August 2003. All the closed symbols are for POM <41 μm .

Depth distribution of zooplankton

In July, the depth at maximum density (DMD) for all zooplankton decreased at night by an average of 2.3 m (SE = 0.86), but this upward nighttime migration did not vary among species. In an ANOVA with sampling time (day or night) and zooplankton taxa as fixed factors (see Fig. 8), the DMD was significantly different among taxa ($F_{5,29} = 12.7, P < 0.001$) and between day and night ($F_{1,29} = 7.08, P = 0.013$), but the difference between day

and night did not depend on the taxa ($F_{5,29} = 1.04, P = 0.42$). Because there was no significant difference in migration patterns among taxa, we averaged all the night and daytime DMDs for each taxa and compared it to the $\delta^{13}\text{C}$ of each zooplankton category. Using a randomization procedure we found that the $\delta^{13}\text{C}$ of zooplankton was significantly negatively correlated with average DMD ($r = -0.88, P = 0.002, N = 1000$, Fig. 8). Zooplankton taxa that had maximum densities at deeper depths also had a lower $\delta^{13}\text{C}$.

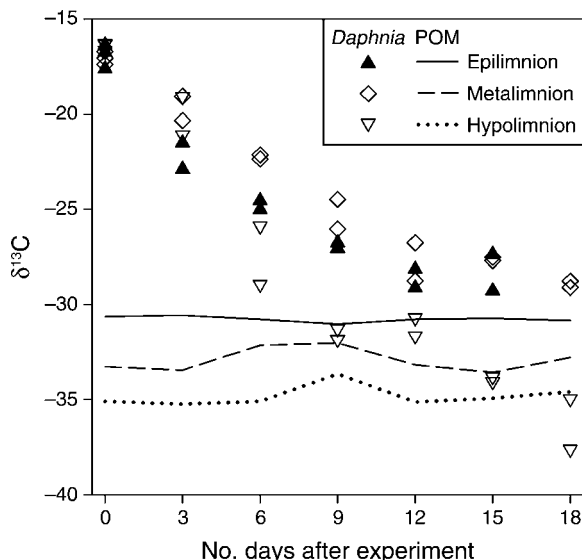


FIG. 6. The figure shows $\delta^{13}\text{C}$ of *D. pulex* in the temporal cage experiment. Symbols are for *D. pulex* for traps in the epilimnion, metalimnion, and hypolimnion, and the lines are for POM <math><41\ \mu\text{m}</math> collected at the same depths as the traps.

DISCUSSION

Our study reveals that the fate of a spatial subsidy can depend on spatially explicit consumer–resource interactions in the recipient habitat. Allochthonous carbon subsidies to lakes can affect vertical gradients in the quantity and quality of resources and lead to complex consumer resource interactions. Stable isotope analysis helped us differentiate between terrestrial (high $\delta^{13}\text{C}$) and aquatic carbon sources (low $\delta^{13}\text{C}$), and determine

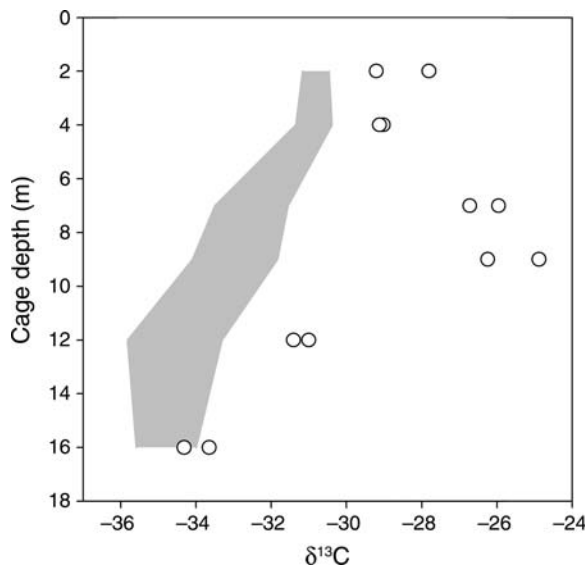


FIG. 7. The figure shows $\delta^{13}\text{C}$ of *D. pulex* in the profile cage experiment. The shaded region spans the maximum and minimum of the $\delta^{13}\text{C}$ of POM <math><41\ \mu\text{m}</math> based on the cage depth.

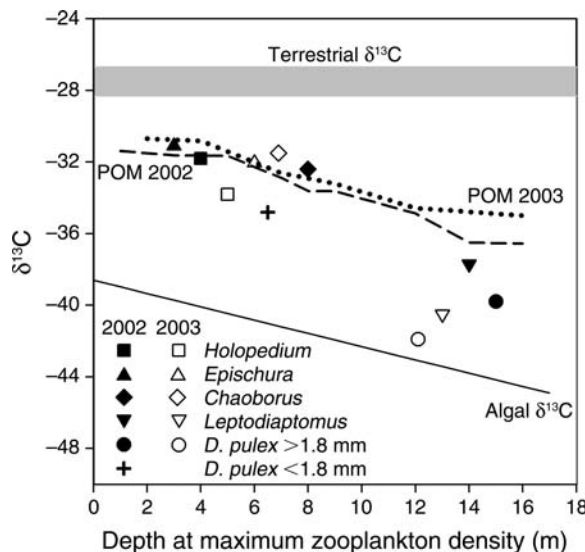


FIG. 8. Relationship between the $\delta^{13}\text{C}$ of different zooplankton taxa and sizes and their depth at maximum density. The gray region is the mean \pm SD ($N = 44$ needle samples) of terrestrial carbon (Douglas-fir needles) from a previous study (Perga et al. 2006). The dashed and dotted lines are the $\delta^{13}\text{C}$ values of POM in midsummer for 2002 and 2003, respectively. The solid line is an estimate for the change in the $\delta^{13}\text{C}$ of algae with depth (see Appendix D).

how these carbon sources varied with depth (Fig. 2). Experimental manipulations of *D. pulex*'s feeding depth confirmed that the $\delta^{13}\text{C}$ of zooplankton can indicate habitat specialization (Figs. 6 and 7), provided the $\delta^{13}\text{C}$ of food sources varies with depth (Figs. 3 and 5). Therefore, we could match variation in zooplankton $\delta^{13}\text{C}$ with inter- and intraspecific variation in habitat selection (Figs. 4 and 8), and conclude that different taxa and sizes of zooplankton differentially exploit the allochthonous carbon subsidy.

Depth-based variation in carbon resources

The composition of POM varies widely among lakes, partly due to the multiple sources of carbon that fuel pelagic production (Hessen et al. 2003, Pace et al. 2004). In a survey of 109 Norwegian lakes, Hessen et al. (2003) found that the proportion of live algal carbon in POM (α) rarely exceeded 50%, and decreased with decreasing total particulate carbon. Our estimates of α for Council Lake are consistent with these previous studies (Hessen et al. 2003, Pace et al. 2004). The negative relationships between the $\delta^{13}\text{C}$ of POM and α in the epilimnion and hypolimnion (Fig. 2) suggest POM is a mixture of terrestrial carbon with a high $\delta^{13}\text{C}$ and algal carbon with a low $\delta^{13}\text{C}$. The increase in algal biomass and α with depth (increasing food quantity), as well as the decrease in the C:N and C:P of POM with depth (increasing food quality), all support the conclusion that depth-based variation in the $\delta^{13}\text{C}$ of POM partially results from an increasing proportion of algal carbon relative to allochthonous carbon. Therefore, we can use the

seasonal variation in the $\delta^{13}\text{C}$ of zooplankton and POM to detect inter- and intraspecific variation in the exploitation of allochthonous carbon by zooplankton.

Seasonality of zooplankton allochthony

The $\delta^{13}\text{C}$ of plankton can increase or decrease following lake stratification due to biogeochemical processes that alter the $\delta^{13}\text{C}$ of dissolved inorganic carbon (Quay et al. 1986, Zohary et al. 1994). In some lakes, seasonal patterns of zooplankton $\delta^{13}\text{C}$ roughly follow the $\delta^{13}\text{C}$ of POM (Zohary et al. 1994), whereas in other lakes the $\delta^{13}\text{C}$ of POM and zooplankton are seasonally decoupled (Grey et al. 2001, Matthews and Mazumder 2005). This suggests inter-lake variation in the seasonal reliance of zooplankton on algal carbon sources. Two previous studies have estimated zooplankton allochthony from seasonal patterns of zooplankton $\delta^{13}\text{C}$ (Grey et al. 2001, Pace et al. 2004). Grey et al. (2001) found that the $\delta^{13}\text{C}$ of mixed zooplankton declined at the onset of stratification despite little seasonal or depth-based variation in the $\delta^{13}\text{C}$ of POM. Pace et al. (2004) experimentally increased the $\delta^{13}\text{C}$ of dissolved inorganic carbon (DIC) during stratification in order to increase the difference between the $\delta^{13}\text{C}$ of algal carbon relative to allochthonous carbon. Pace et al. (2004) found that the seasonal increase in the $\delta^{13}\text{C}$ of *Daphnia* was less than expected based solely on an algal diet, and concluded that up to 50% of *Daphnia* carbon came from allochthonous sources. Our study builds on these previous studies by measuring allochthony in multiple zooplankton species while accounting for seasonal variation in lipid content (Appendix A), body size (Fig. 4), and depth-based variation in the $\delta^{13}\text{C}$ of zooplankton food sources (Fig. 3).

In Council Lake, the seasonal patterns of plankton $\delta^{13}\text{C}$ suggest differential exploitation of allochthonous carbon by zooplankton (Fig. 1). Previously we reported that variation in zooplankton lipid content helps explain seasonal variation in zooplankton $\delta^{13}\text{C}$ (Matthews and Mazumder 2005). In Council Lake, the $\delta^{13}\text{C}$ of POM decreases strongly with depth and masks the effect of the lipids, leading to similar seasonal patterns in the $\delta^{13}\text{C}$ of zooplankton and lipid normalized zooplankton (Appendix A). This supports our hypothesis that inter- and intraspecific variation in the $\delta^{13}\text{C}$ of Council Lake zooplankton reflects variation in food sources (i.e., allochthonous and autochthonous carbon) rather than lipid content (see also Fig. 4). During the stratified period, the $\delta^{13}\text{C}$ of *L. tyrelli* declined concurrently with the $\delta^{13}\text{C}$ of POM in the hypolimnion, and by midsummer the $\delta^{13}\text{C}$ of *L. tyrelli* and *E. nevadensis* differed by as much as 10‰. Because the low $\delta^{13}\text{C}$ of POM in the hypolimnion is directly associated with a higher proportion of algal biomass (Fig. 2), our data indicate that *L. tyrelli* exploits subsurface resources to a greater degree than *E. nevadensis* in Council Lake. In Council Lake, *L. tyrelli* likely specializes in the hypolimnion to exploit the higher concentration and

quality of food (Fig. 6). Interestingly, the seasonal $\delta^{13}\text{C}$ pattern of *L. tyrelli* is very similar to *D. pulex*, so differences in their ability to selectively feed cannot explain the observed $\delta^{13}\text{C}$ patterns in Council Lake.

The $\delta^{13}\text{C}$ of *D. pulex* and *Holopedium* diverged following thermal stratification, indicating habitat specialization in the water column and a greater reliance of *Holopedium* on allochthonous carbon (Figs. 1 and 8). *Holopedium* and small *D. pulex* specialize on food resources above the hypolimnion, whereas large *D. pulex* only feed in the hypolimnion. Their coexistence in Council Lake may involve a trade-off between the ability to exploit high quality food (subsurface algae with a low C:P; Fig. 5) and the minimum resource requirement needed to persist (Tessier and Woodruff 2002b). In the epilimnion, *Holopedium* is faced with a low abundance (~ 0.2 mg C/L) of poor quality food (C:N > 10, C:P > 300) that has a large contribution of terrestrial carbon (i.e., higher $\delta^{13}\text{C}$, Figs. 2 and 8). *Holopedium* can readily ingest bacteria sized particles (0.5–5 μm ; Hessen 1985), and *Holopedium* dominated communities graze a smaller size range of algae than *Daphnia* dominated communities (Cyr and Curtis 1999). *Holopedium* may persist in the epilimnion if they can exploit low quality food and survive at low food concentrations (Tessier and Woodruff 2002b). *Holopedium* is common in oligotrophic lakes (Hessen 1985), and likely has a lower minimum resource requirement than hypolimnetic populations of *Daphnia* (Tessier and Woodruff 2002b). The consequence of this habitat specialization is that *Holopedium* relies more on allochthonous carbon sources than *D. pulex* (Fig. 8).

Intraspecific variation in zooplankton allochthony

Different sizes of *D. pulex* in Council Lake also specialize on different habitats, and differentially rely on allochthonous carbon. The negative relationship between *D. pulex* body size and $\delta^{13}\text{C}$ suggests size-based habitat selection (Fig. 4). Indeed, smaller *D. pulex* were most abundant in the epi- and metalimnion, whereas large *D. pulex* were always found below the epilimnion. Alternatively, the relationship in Fig. 4 could result from an ontogenetic diet shift within the same habitat (e.g., from bacteria to algae), but our experimental results support size-based habitat selection (Figs. 6–8). Other studies have detected habitat specialization of *Daphnia*, but the reasons for the patterns are generally attributed to trade-offs between food abundance and predators (Leibold and Tessier 1991, Tessier and Leibold 1997, Winder et al. 2004). In Council Lake, there is no vertebrate predation, though invertebrate predation (e.g., by *Chaoborus*) might contribute to habitat specialization of zooplankton.

Intraspecific variation in the habitat selection of *D. pulex* may result from the interaction between food quality and temperature. Warmer temperatures in the epilimnion increase development rates of *Daphnia*, but the high C:P (~ 400) of epilimnetic POM likely limits *D.*

pulex growth (Anderson et al. 2005). Based on the profiles of temperature, food quantity and quality, we might expect all sizes of *D. pulex* to exploit the high quality and quantity of algal carbon in the hypolimnion. However, Lampert (2006) suggests that intraspecific competition can lead to a population distribution where smaller individuals are displaced from a deep water habitat that has the highest food quality and quantity. Such size-based differences in competitive ability could be associated with either lower food thresholds for growth (Lampert 2006), or differences in the ability to exploit food in the hypolimnion (Abrusan 2004). Mesh size of filtering combs is a phenotypically plastic trait that is directly related to grazing efficiency (Lampert 1994), and may be particularly important in the high viscosity environment of the hypolimnion (Abrusan 2004). *Daphnia* are known to increase their mesh size in response to food concentrations that are as low as in the epilimnion of Council Lake (Fig. 5; Lampert 1994). We speculate that young *Daphnia* could modify their mesh size when they are small and feeding in the epilimnion, leading to more efficient exploitation of resources in the hypolimnion as they get bigger.

Experimental evidence of habitat specialization

Multiple sources of carbon fuel pelagic production in lakes and contribute to complex relationships between consumers and their resources. The low $\delta^{13}\text{C}$ of zooplankton compared to POM has motivated many researchers to find the “missing carbon sources” that contribute to zooplankton production (e.g., methane, allochthonous, autochthonous). There are three main explanations for why the $\delta^{13}\text{C}$ of zooplankton is typically lower than the $\delta^{13}\text{C}$ of POM (del Giorgio and France 1996), none of which are mutually exclusive. First, zooplankton may selectively feed on algal carbon that has a lower $\delta^{13}\text{C}$ (del Giorgio and France 1996), and whose signature is masked by other carbon sources that have a higher $\delta^{13}\text{C}$ (e.g., terrestrial carbon; Grey et al. 2001). In this case, differences in $\delta^{13}\text{C}$ among zooplankton taxa might result from different abilities to exploit autochthonous algal carbon in the epilimnion. Second, zooplankton might accumulate lipids (which have a low $\delta^{13}\text{C}$) from their food, and thereby lower their whole body $\delta^{13}\text{C}$ relative to their food source (Matthews and Mazumder 2005). Using a lipid normalization procedure developed in a previous study (Matthews 2006), we determined that variation in lipid content cannot solely explain seasonal $\delta^{13}\text{C}$ differences among taxa in Council Lake (Appendix A). Third, zooplankton might feed on carbon produced deeper in the water column. Stratified lakes often show a decrease of POM $\delta^{13}\text{C}$ with depth (Quay et al. 1986, del Giorgio and France 1996), which may help explain why isotopic differences between zooplankton taxa are more common during thermal stratification (Karlsson et al. 2003, Matthews and Mazumder 2003). Our cage experiments were designed to distinguish between the first and third

hypothesis, i.e., whether zooplankton selectively feed on autochthonous production in a single habitat or whether they specialize on different habitats. Our experiments confirmed that zooplankton feeding at deeper depths have a lower $\delta^{13}\text{C}$ (Figs. 6 and 7), such that inter- and intraspecific variation in zooplankton $\delta^{13}\text{C}$ is directly associated with habitat specialization.

Challenges in quantifying zooplankton allochthony

There is some uncertainty about the isotopic composition and the carbon sources of POM in Council Lake, mainly because we were unable to measure the $\delta^{13}\text{C}$ of different food sources within POM (Pel et al. 2003, Pace et al. 2004). The $\delta^{13}\text{C}$ of phytoplankton can vary with species, size structure, and growth rate (Zohary et al. 1994, Pel et al. 2003), and vary with depth following vertical gradients in the $\delta^{13}\text{C}$ of dissolved inorganic carbon (Quay et al. 1986). In addition, bacteria in the hypolimnion may contribute to the low $\delta^{13}\text{C}$ of *L. tyrelli* and *D. pulex* (Jones et al. 1999). However, the hypolimnion of Council Lake did not become anoxic during stratification so it is unlikely that methanotrophs made a significant contribution to the diet of zooplankton (Grey et al. 2004). The $\delta^{13}\text{C}$ of allochthonous carbon may also overlap with autochthonous carbon produced in the littoral zone of lakes (Post 2002), possibly leading to a positive bias in our calculations of zooplankton allochthony (Appendix D). In addition, decomposition could change the $\delta^{13}\text{C}$ of organic matter and mask the origin of the carbon source (Lehmann et al. 2002). Isotopic variation within POM may explain some of the unexpected results from our cage experiments. The $\delta^{13}\text{C}$ of *D. pulex* in metalimnetic cages was higher than in epilimnetic cages for both experiments (Figs. 6 and 7). In the profile experiment (Fig. 7), we suspect the $\delta^{13}\text{C}$ of *D. pulex* did not reach equilibrium with its food sources. However, it is also possible that algae had a higher $\delta^{13}\text{C}$ in the metalimnion than the epilimnion, which is consistent with the lack of relationship between α and POM $\delta^{13}\text{C}$ in the metalimnion (Fig. 2).

Quantifying the extent of zooplankton allochthony is an ongoing challenge (Grey et al. 2001, Karlsson et al. 2003, Pace et al. 2004). In Council Lake, we suggest that zooplankton with a higher $\delta^{13}\text{C}$ (closer to the $\delta^{13}\text{C}$ of terrestrial carbon sources) rely more on allochthonous carbon (Figs. 2 and 8). To estimate allochthony we can use data on the $\delta^{13}\text{C}$ of algae from Karlsson et al. (2003), and a simple mixing model (Appendix D; Karlsson et al. 2003). In 12 northern Sweden Lakes (below a 1000 m altitude), the $\delta^{13}\text{C}$ of algae varies from -37.7‰ to -46.2‰ . Using this range of algal $\delta^{13}\text{C}$, we conclude that *L. tyrelli* and large *D. pulex* rely substantially less on allochthonous carbon than *Epischura*, *Chaoborus*, or *Holopedium* (Appendix D). Though our estimates are not specifically calibrated for Council Lake, they generally agree with previous studies

of zooplankton allochthony (Grey et al. 2001, Karlsson et al. 2003, Pace et al. 2004).

No previous study has considered the consequences of a vertical gradient in the $\delta^{13}\text{C}$ of POM for quantifying zooplankton allochthony. Estimates of zooplankton allochthony fundamentally depend on the $\delta^{13}\text{C}$ gradient of algae and the degree of habitat specialization of zooplankton. In Appendix D, we have included estimates of zooplankton allochthony for two cases. In the first case we assume the average $\delta^{13}\text{C}$ of algae is -41.8 over the entire water column (Appendix D; Karlsson et al. 2003). In the second case, the average is the same but we assume the $\delta^{13}\text{C}$ of algae decreases with depth at the same rate as POM (as in Fig. 8). In general, we found that a model that does not include changes in the $\delta^{13}\text{C}$ of POM with depth will overestimate allochthony in epilimnetic zooplankton and underestimate allochthony in hypolimnetic zooplankton (Appendix D).

Conclusions

This study demonstrates there are multiple carbon pathways leading from allochthonous and autochthonous sources, through the zooplankton community, and up to higher trophic levels. Despite uncertainties in the isotopic heterogeneity of POM in Council Lake, we showed that the large vertical gradients in the $\delta^{13}\text{C}$ of POM were the dominant source of variation that led to inter- and intraspecific variation in the zooplankton $\delta^{13}\text{C}$. Vertical variation in the composition of POM with respect to algal biomass (Figs. 2 and 5) supports the link between isotopic variation and variation in zooplankton allochthony. Therefore, we conclude that differences in habitat selection among zooplankton in Council Lake (Fig. 8) led to differential exploitation of allochthonous and autochthonous resources. Therefore, the exploitation of allochthonous subsidies to lakes depends on spatially explicit consumer–resource interactions.

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APPENDIX A

Seasonal patterns of lipid normalized zooplankton $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_{\text{LE}}$) (*Ecological Archives* E087-170-A1).

APPENDIX B

Summary isotopic data for zooplankton in Council Lake (*Ecological Archives* E087-170-A2).

APPENDIX C

Parameter estimates for rate of change in *Daphnia* $\delta^{13}\text{C}$ (*Ecological Archives* E087-170-A3).

APPENDIX D

Allochthony estimates for zooplankton in Council Lake (*Ecological Archives* E087-170-A4).