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Support of benthic invertebrates by detrital resources and current autochthonous primary production: results from a whole-lake ^{13}C addition

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SUMMARY

1. Secondary production of benthic invertebrates in lakes is supported by current autochthonous primary production, and by detritus derived from a combination of terrestrial inputs and old autochthonous production from prior seasons. We quantified the importance of these two resources for the dominant benthic insects in Crampton Lake, a 26 ha, clear-water system.

2. Daily additions of $NaH^{13}CO_3$ to the lake caused an increase in the stable carbon isotope ratios ($\delta^{13}C$) of the current primary production of phytoplankton and periphyton. We measured the response of four insect groups (taxon-depth combinations) to this manipulation, quantifying their current autochthony (% reliance on current autochthonous primary production) by fitting dynamic mixing models to time series of insect $\delta^{13}C$.

3. The $\delta^{13}C$ of all four groups increased in response to the manipulation, although the magnitude of response differed by taxon and by depth, indicating differences in current autochthony. Odonate larvae (Libellulidae and Corduliidae) collected at 1.5 m depth derived 75% of their C from current autochthonous primary production. Chironomid larvae collected at 1.5, 3.5 and 10 m depths derived, respectively, 43%, 39% and 17% of their C from current autochthonous primary production.

4. Both taxon-specific diet preferences and depth-specific differences in resource availability may contribute to differences in current autochthony. Our results demonstrate significant but incomplete support of insect production by current autochthony, and indicate that allochthonous inputs and old autochthonous detritus support a substantial fraction (25–83%) of insect production.

Keywords: allochthonous, aquatic insect, food web, lake, subsidy

Introduction

Food webs can be supported by both autochthonous organic matter (OM) produced within an ecosystem and allochthonous OM produced elsewhere (Polis, Anderson & Holt, 1997). In many aquatic ecosystems, inputs of allochthonous terrestrial detritus contribute substantially to the total organic carbon (C) budget (Kajak & Hillbricht-Ilkowska, 1972; Vannote *et al.*, 1980; Wetzel, 2001). Recently, researchers have quantified the contribution of these inputs to the production of lake zooplankton (Meili *et al.*, 1996; Jones *et al.*, 1999; Grey, Jones & Sleep, 2001; Karlsson *et al.*, 2003) or zooplankton plus other consumers (Carpenter *et al.*, 2005; Cole *et al.*, 2006). This research has demonstrated that allochthonous inputs can support

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a substantial portion of consumer production. However, quantitative estimates of allochthonous support of lake zoobenthos are much more rare. Given that benthic pathways often play a key role in lake production and food web dynamics (Schindler & Scheuerell, 2002; Vadeboncoeur, Vander Zanden & Lodge, 2002), understanding the extent to which zoobenthos rely on autochthonous and allochthonous production is essential for understanding energy flow at the ecosystem level.

The complexity of benthic food webs complicates efforts to quantify resource use by zoobenthos. OM ingested by zoobenthos may originate from allochthonous sources or from autochthonous sources including phytoplankton, periphyton or macrophytes. Furthermore, OM from any of these sources may be partially degraded or repackaged by bacteria and other consumers before ingestion by the organism under study. A variety of approaches have been used to understand resource use by zoobenthos, including C budgets (Wissmar, Richey & Spyridakis, 1977; Strayer & Likens, 1986), gut content analysis (Brown, 1961), correlations between growth and resource pulses (Goedkoop & Johnson, 1996), natural abundance stable isotope measurements (Rau, 1980; Hecky & Hesslein, 1995) and biomarkers, alone or in combination with stable isotopes (Goedkoop *et al*., 1998; van Oevelen *et al*., 2006a). While all of these approaches have strengths, a common weakness is difficulty in quantitatively estimating reliance on autochthonous versus allochthonous resources.

One approach that has been used successfully to quantify allochthonous and autochthonous support of lake consumers is experimental manipulation of either the stable C isotope ratio of dissolved inorganic C (DIC), or the stable N isotope ratio of dissolved inorganic N (DIN) (Cole *et al*., 2002; Pace *et al*., 2004; Carpenter *et al*., 2005; Hershey *et al*., 2006; Pace *et al*., 2007). Experimental enrichment of the ^{13}C content of the DIC pool causes an increase in the $\delta^{13}C$ of autochthonous primary producers. By measuring the rate at which the labelled, autochthonously-produced C appears in consumer tissues, it is possible to determine quantitatively the extent to which consumers are supported by autochthonous versus allochthonous resources. These experiments have revealed that terrestrial support of lake consumers can be substantial, though the extent and pathways of terrestrial support vary among lakes and consumers (Carpenter *et al*., 2005; Cole *et al*., 2006). Between 7% and 85% of the production of zoobenthos (primarily odonate larvae) in these experiments was supported by allochthonous C (Carpenter *et al*., 2005).

While powerful, such experiments have an important limitation: analyses can underestimate autochthony for organisms that are linked to detrital trophic pathways (Carpenter *et al*., 2005). Autochthonous detritus produced before the ^{13}C manipulation is not enriched in ^{13}C and may have an isotopic signal indistinguishable from that of allochthonous detritus. Consumption of this 'old' autochthonous material can therefore be misinterpreted as consumption of allochthonous material. Consequently, for organisms linked to detrital pathways it may be appropriate to consider the autochthony estimates derived from whole-lake ^{13}C manipulations not as estimates of total autochthony, but as estimates of 'current' autochthony, or the extent to which consumers are supported by autochthonous production from within the current growing season. Current autochthony estimates provide a lower-bound estimate of consumer total autochthony, and therefore an upper bound estimate on total allochthony.

In 2005, we conducted a ^{13}C manipulation experiment in a large, clear-water, oligotrophic lake. Here we report the response of benthic insects to this experiment. We quantify the extent to which insect production is supported by current autochthonous primary production, and offer insights into within- and among-lake patterns of resource use.

Methods

Site description and ^{13}C manipulation

Crampton Lake is an oligotrophic, clear-water system located on the Wisconsin–Michigan border, U.S.A. (89°32'W, 46°13'N). Lake area is 25.7 ha, maximum depth is 18.5 m, and mean depth is 3.5 m. The average 1% light level during this study was 9 m, and thermocline depth ranged from 2 to 6.5 m. Macrophytes (predominantly *Sparganium* spp. and *Eriocaulon aquaticum*) are present though not abundant in some parts of the littoral zone, and the moss *Fissidens* sp. is patchily abundant at depths around 4–6 m. Unconsolidated OM dominates the substrate, as a thin layer (0.5–5 cm)

overlying sand and gravel at depths *c.* <3.5 m and as a much thicker layer at greater depths.

We added $NaH^{13}CO_3$ to the mixed layer of Crampton Lake daily from 13 June to 7 August 2005 (day 164–219). As a result of this manipulation, the $\delta^{13}C$ of the DIC pool increased over the course of *c.* 3 weeks from a background value around −12‰ to a plateau between 5‰ and 15‰, then decreased again towards background after we stopped adding ^{13}C. A complete description of our ^{13}C-addition methods is available in Pace *et al.* (2007).

Statistical model to estimate current autochthony

Because the ^{13}C labelling of current autochthonous production is dynamic over time as a result of the changing $\delta^{13}C$ of DIC, static mixing models typically used in natural-abundance stable isotope studies were not applicable to our study. Instead, we estimated current autochthony using time-series models that compare changes in consumer $\delta^{13}C$ with changes in the $\delta^{13}C$ of current autochthonous primary production (Pace *et al.*, 2004; Carpenter *et al.*, 2005; Pace *et al.*, 2007). We fit the following model separately for each consumer taxon at each depth:

$$X_t = w[(1-m)P_t + mP_{t-u}] + (1-w)S_t \quad (1)$$

(Pace *et al.*, 2004). The left side of this equation (X_t) represents the $\delta^{13}C$ of the insect biomass pool (X) on day t. Insect $\delta^{13}C$ is modelled as a function of two drivers or resources: a current autochthonous resource (P_t) and a detrital resource representing old OM in the sediments (S_t). The contribution of the current autochthonous resource to the insect C pool is estimated by the parameter w ($0 \le w \le 1$). To account for time lags associated with the deposition of current autochthony on the bottom and its incorporation into consumer tissues, the contribution from the current autochthonous resource is further divided into a fraction m ($0 \le m \le 1$) from day t-u and a fraction (1-m) from day t. Previous experiments with this model demonstrated that this distinction substantially improved model fits (Pace *et al.*, 2004). We used a profile likelihood analysis to find the value of u that minimized variance (Burnham & Anderson, 1998), and then estimated w and m by least squares using an optimization routine in the R statistical package (R Foundation for Statistical Computing, Vienna, Austria).

The current autochthonous production consumed by zoobenthos may include a mixture of phytoplankton and periphyton. Furthermore, the relative contribution of these two sources probably varies with depth; at deeper sites most or all of the available current autochthonous production should be from settling phytoplankton, while the availability of periphyton should increase at shallower depths. Our goal was to quantify the total reliance of zoobenthos on this mixture, not the relative contributions of phytoplankton and periphyton. However, differences in $\delta^{13}C$ between phytoplankton and periphyton are often observed in natural abundance stable isotope studies. If these differences also exist between the time series of Crampton Lake phytoplankton and periphyton during the ^{13}C manipulation, then our current autochthony estimates could be sensitive to our assumptions about the relative contributions of phytoplankton and periphyton to zoobenthos diets. To evaluate the importance of this effect we fit the model under two different scenarios: either the autochthonous driver was completely periphyton or completely phytoplankton. This allowed us to bracket the range of possible current autochthony estimates across any periphyton–phytoplankton mixture in the diet.

Measuring consumer and resource $\delta^{13}C$ time series

To ensure continuous time series of macroinvertebrate $\delta^{13}C$ data spanning the course of the study, we aggregated taxa at the family level for $\delta^{13}C$ analyses. The taxon-depth combinations that we considered were: Chironomidae (Diptera) and Libellulidae/Corduliidae (Odonata) at 1.5 m; Chironomidae at 3.5 m; and Chironomidae at 10 m. We combined the two odonate families because they were difficult to distinguish while alive and are trophically similar (Merritt & Cummins, 1996); subsequent examination indicated that *c.* 75% of individuals were *Celithemis elisa*. A study in Crampton Lake in 2005 demonstrated that these four taxon-depth combinations (henceforth, 'groups') collectively accounted for >40% of whole-lake benthic secondary production (A.L. Babler and C.T. Solomon, unpubl. data). When all of the depth zones of the lake were considered, Chironomidae and Libellulidae/Corduliidae accounted for *c.* 66% of whole-lake benthic secondary production. At a finer taxonomic level, chironomid production was dominated at 1.5 and 3.5 m by the genera *Procladius* and

Ablabesmyia (66% and 56% of chironomid production, respectively), and at 10 m by the genus *Chironomus* (>80% of production) (A.L. Babler and C.T. Solomon, unpubl. data). We collected invertebrates with a multiple corer from several sites at each depth, approximately weekly from 2 June through 23 August and on additional occasions in September and October (days 153–282). After sieving cores through 500 μm mesh, we removed individual insect larvae, identified them to the family level (under magnification when necessary), and placed them in vials of tap water for *c.* 12 h to evacuate their gut contents. To integrate over individual-level variation in stable isotope ratios, we ran stable isotope analyses on subsamples of homogenized tissue taken from pooled samples of multiple individuals. The number of individuals in pooled samples ranged from 3 to 44 for chironomids (mean = 15) and from 1 to 5 for odonates (mean = 2), depending on individual mass and availability. Pooled samples were dried at 50–60 °C, ground to a uniform fine powder, and prepared for isotopic analysis.

On soft substrates such as those in Crampton Lake, isolating periphyton from detrital OM and recently deposited phytoplankton is extremely difficult. We chose to scrape samples from ceramic tiles suspended in the water column (0.5 m depth). While this approach is imperfect because algal communities on artificial substrates may differ from those on natural substrates (Aloi, 1990; Cattaneo & Amireault, 1992), we felt it was the best way to obtain pure samples of current periphyton production. Each week we collected and homogenized the periphyton regrowth on two tiles, dried it at 60 °C, and prepared it for isotopic analysis. Because our model for estimating insect current autochthony (eqn 1) utilizes daily data for the independent (driver) variables, we interpolated a daily periphyton δ^{13}C time series from our observed data. First, we interpolated daily values from our earliest to latest observed periphyton data by fitting the following model:

$$P_{t+1} = (1 - \lambda)P_t + \alpha(C_t - \varepsilon) \quad (2)$$

This model describes periphyton δ^{13}C (P) on day $t + 1$ as a function of periphyton δ^{13}C the previous day, modified by decreases because of losses of labelled tissue (λ), and by the daily uptake (α) of new inorganic C (C_t) that is photosynthetically fixed with fractionation term ε. We fit this model to our observed periphyton δ^{13}C time series and a daily time series of $\delta^{13}C_{CO_{2(Aq)}}$ (Pace *et al.*, 2007). The resulting predicted time series of periphyton δ^{13}C extended from day 161 to 238. We extrapolated this time series back to day 151 by assuming that periphyton δ^{13}C remained constant from day 151 to 161 (prior to the start of ^{13}C additions). Similarly, we extrapolated forward in time from day 239 to 282 by assuming that periphyton δ^{13}C continued to decline as predicted by the fitted model until it depurated to the pre-addition baseline, whereupon it remained constant until the end of the time series.

We used the same phytoplankton δ^{13}C time series in this study that we developed while analysing the response of pelagic consumers to the ^{13}C manipulation experiment (Pace *et al.*, 2007). In brief, phytoplankton δ^{13}C was measured using two approaches that minimized contamination from detrital particles that might have affected δ^{13}C values. In one approach, we used density centrifugation to physically isolate algal cells from detritus after concentrating particles from bulk water samples using a plankton centrifuge (Hamilton, Sippel & Bunn, 2005); in the other, we measured δ^{13}C in algal-specific phospholipid fatty acids (Boschker, de Brouwer & Cappenberg, 1999; Boschker, Kromkamp & Middelburg, 2005). Daily phytoplankton δ^{13}C values were interpolated by fitting a model similar to that described above for periphyton simultaneously to the δ^{13}C time series derived from the two approaches.

To indicate the δ^{13}C of the detrital (allochthonous + old-autochthonous) driver, we intended to use the δ^{13}C of sediment OM. Small cores of surficial sediments were collected by SCUBA divers by forcing modified plastic syringes (diameter = 2.6 cm) into the substrate. Samples were collected every 3 to 4 weeks at 1.5, 3.5 and 10 m near a subset of the sites used for benthic invertebrate collections. Care was taken to avoid disturbing the sediments, so that cores included the top layer of flocculent, recently-deposited material. Cores were immediately stoppered under water, then brought to the surface, where the upper 5 mm of each core was extruded. These samples were dried at 60 °C, ground to a uniform fine powder, and prepared for stable isotope analysis. After analysing these samples, we discovered that the δ^{13}C of insects collected before the ^{13}C manipulation was always lower than the δ^{13}C of sediment OM at the depth at which insects were collected (see Results).

This indicated that bulk sediment OM could not have been the true detrital isotopic end member. Instead, we used the $\delta^{13}C$ of the first observed pre-manipulation individual for each group as our best indicator of the $\delta^{13}C$ of the detrital-end member actually consumed.

Stable isotope ratios were measured using isotope ratio mass spectrometers at the University of Alaska and the University of California-Davis. Samples were acid-fumed before analysis to remove inorganic carbonates. $^{13}C/^{12}C$ ratios were standardized to internal working standards calibrated against the international Pee Dee Belemnite standard. Analytical precision (mean SD of all duplicate analyses) was 0.3‰ for periphyton, 0.1‰ for sediments and 0.5‰ for zoobenthos.

Estimating parameter uncertainty

Parameter uncertainties for fits to eqn 1 were estimated by calculating the SD of 1000 bootstrap iterations (Efron & Tibshirani, 1993). Besides estimating the uncertainty in current autochthony estimates that was associated with model errors (residuals), our bootstrap analysis also incorporated an estimate of our uncertainty about the true value of the detrital end member. We estimated the pooled SD of all pre-label insect $\delta^{13}C$ data (1.34‰; $n = 5$). With each bootstrap iteration, a random value for the $\delta^{13}C$ of the detrital end member was drawn from a normal distribution centred on the nominal value for that group and with a SD of 1.34‰. We checked that bootstrapped distributions of parameter estimates looked approximately normal and had means similar to our fitted point estimates.

Results

Periphyton $\delta^{13}C$ increased rapidly in response to the ^{13}C addition, from a pre-addition value of −25‰ to a maximum of −5‰ near the end of the addition (Fig. 1). Following the cessation of the addition, periphyton $\delta^{13}C$ rapidly returned towards pre-addition values. The interpolated time series of daily periphyton $\delta^{13}C$ provided a good fit to the observed data; the residual SD was 1.4‰, and the correlation of predictions with observations was 0.97. Phytoplankton $\delta^{13}C$ increased and decreased slightly more quickly than periphyton $\delta^{13}C$ in response to the beginning and end of the manipulation, but otherwise showed a very similar pattern and maximum label (Fig. 1).

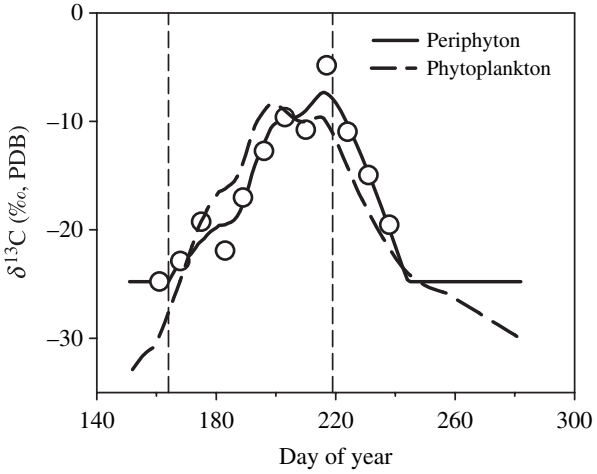

Fig. 1 Time series of periphyton and phytoplankton $\delta^{13}C$. Vertical dashed lines show the beginning and end of the ^{13}C manipulation. The daily time series of periphyton $\delta^{13}C$ (solid line) was interpolated from the observed periphyton data (circles). The daily phytoplankton $\delta^{13}C$ (dashed line) is from Pace *et al.* (2007).

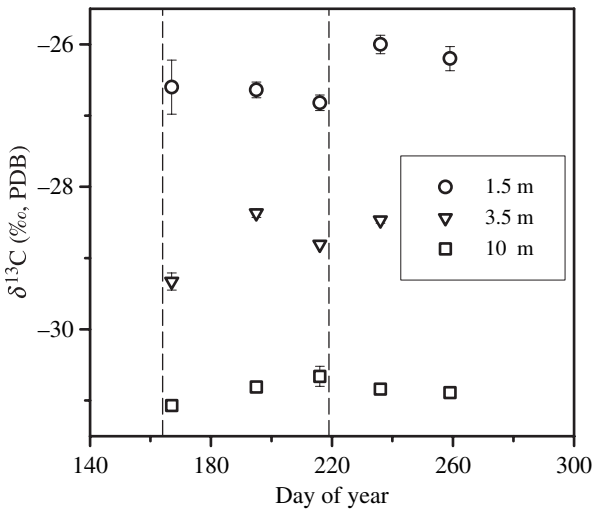

Fig. 2 $\delta^{13}C$ of sediment organic matter (upper 5 mm) at three depths. Vertical dashed lines show the beginning and end of the ^{13}C manipulation. Error bars (±1 SD) are visible in cases where the SD was >0.1‰.

In contrast to the substantial changes in primary producer $\delta^{13}C$, there was little to no response of surficial sediment $\delta^{13}C$ to the addition experiment (Fig. 2). Sediment $\delta^{13}C$ did not change appreciably

during the course of the experiment at 1.5 m depth. Temporal variability was high at 3.5 m, without apparent pattern. At 10 m sediment $\delta^{13}C$ did show a temporal pattern consistent with a response to the addition, but the magnitude of change was small. There were consistent differences in sediment $\delta^{13}C$ across depths, with lower $\delta^{13}C$ observed at deeper depths. Pre-addition zoobenthos $\delta^{13}C$ was lower than pre-addition sediment $\delta^{13}C$ for all four of the taxa that we considered. This difference was 2.0‰ for 1.5 m odonates, 3.4–3.5‰ for 1.5 and 3.5 m chironomids and 4.7‰ for 10 m chironomids.

All four time series of zoobenthos $\delta^{13}C$ clearly increased in response to the addition experiment, indicating some reliance on current autochthonous production (Fig. 3). Within-taxon variability in $\delta^{13}C$ was also apparent in all four time series, particularly for 1.5 and 3.5 m chironomids (Fig. 3a,b), which were considerably more taxonomically diverse than the other two groups that we considered. Fitted models provided good descriptions of the data despite this variability in $\delta^{13}C$. Residual SD were low, and correlations of predictions with observations were moderate to high (Table 1). Model estimates of the current autochthony of consumers ranged from 75% for odonates to 17% for chironomids at 10 m (Fig. 4). Results were similar when we used phytoplankton instead of periphyton as the current autochthonous driver; model fits were equally good, and point estimates of current autochthony were always within 2 percentage points of those derived from fitting to the periphyton time series (Table 1). For simplicity, we focus our discussion in the remainder of the paper on the results from the periphyton fits. Bootstrapped SD for these autochthony estimates were between 7 and 8 percentage points (Table 1, Fig. 4).

Discussion

Few studies have measured seasonal change in the $\delta^{13}C$ of lake insects (but see Grey *et al.*, 2004b; Hershey *et al.*, 2006). We observed that insect $\delta^{13}C$ time series were variable (Fig. 3), probably due both to seasonal changes in the relative abundance of species and ontogenetic stages, and to ontogenetic, individual, and species-level variation in diet preferences. Despite

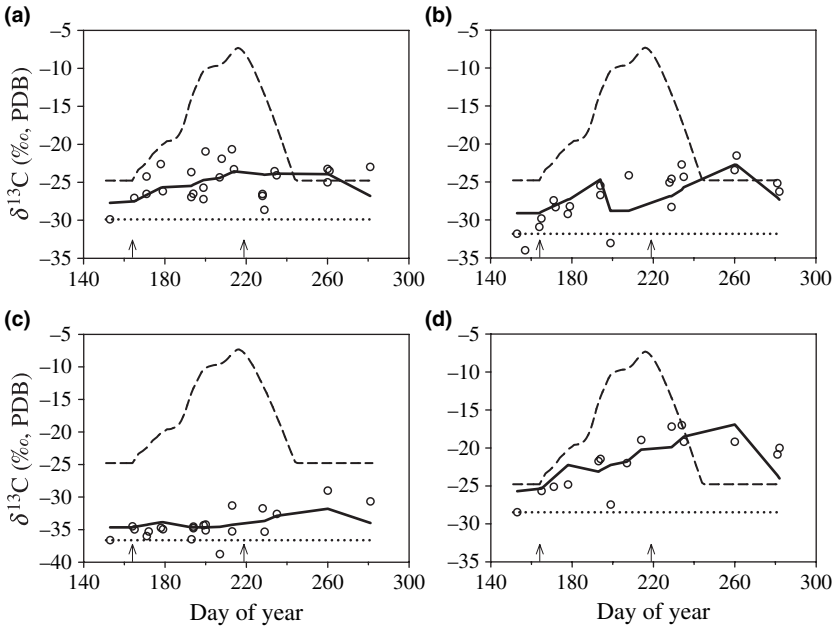

Fig. 3 Time series of zoobenthos $\delta^{13}C$ for four taxon-depth combinations: (a) Chironomidae, 1.5 m; (b) Chironomidae, 3.5 m; (c) Chironomidae, 10 m; (d) Odonata (Libellulidae and Corduliidae), 1.5 m. In each case the circles show observed zoobenthos $\delta^{13}C$ (pooled sample of multiple individuals) and the solid line shows predictions from the fitted model of zoobenthos current autochthony. The other lines show daily $\delta^{13}C$ values of potential C sources used as drivers in these models: the dashed line represents periphyton and the dotted line represents the 'detrital' (allochthonous + old autochthonous) end member. Arrows show the beginning and end of the ^{13}C manipulation.

Table 1 Summary of model fits for estimates of insect current autochthony

Autochthonous driver	Consumer and depth (m)	*u*	*m*	*w*	Mean error	*r*
Periphyton	Chironomidae 1.5	42 ± 6.4	0.51 ± 0.12	0.43 ± 0.08	2.16	0.37
	Chironomidae 3.5	44 ± 2.6	0.95 ± 0.12	0.39 ± 0.07	2.34	0.73
	Chironomidae 10	42 ± 6.9	1.00 ± 0.16	0.17 ± 0.07	1.79	0.66
	Odonata 1.5	42 ± 3.0	0.68 ± 0.10	0.75 ± 0.08	2.43	0.72
Phytoplankton	Chironomidae 1.5	41 ± 9.4	0.45 ± 0.18	0.44 ± 0.08	2.33	0.29
	Chironomidae 3.5	43 ± 2.8	1.00 ± 0.11	0.37 ± 0.07	2.14	0.77
	Chironomidae 10	41 ± 7.0	0.99 ± 0.16	0.17 ± 0.08	1.87	0.50
	Odonata 1.5	41 ± 6.8	0.62 ± 0.14	0.75 ± 0.09	3.13	0.69

Time series of consumer $\delta^{13}C$ were fit to eqn 1, using time series of either periphyton or phytoplankton $\delta^{13}C$ as the autochthonous driver. Least-squares parameter estimates (± bootstrapped SD), mean error (‰) and correlation of predictions and observations (*r*) are given. The parameter *w* describes the proportion of insect C that is derived from current autochthonous primary production.

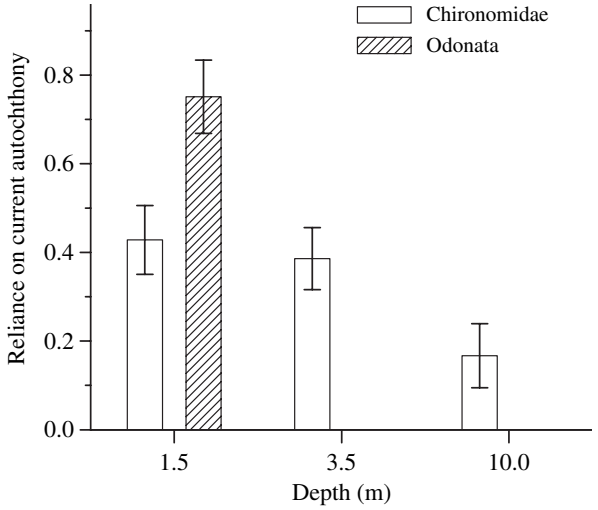

Fig. 4 Proportion of zoobenthos production derived from current autochthonous primary production, as estimated by model fits shown in Fig. 3. Error bars show ±1 bootstrapped SD.

this variability, model fits were reasonably good and current autochthony estimates were well constrained (Figs 3 & 4). Nonetheless, it is useful to consider how two assumptions inherent in our analysis may have biased those estimates.

First, we assumed that periphyton collected from tiles at 0.5 m depth provided a good indicator of the $\delta^{13}C$ of natural epipelic periphyton at multiple depths. We are not aware of studies that compare periphyton $\delta^{13}C$ between natural and artificial substrates, or between multiple depths in a lake. Both of these factors could influence periphyton $\delta^{13}C$, via effects on community composition, growth rates and sources of DIC (Aloi, 1990; Cattaneo & Amireault, 1992; Vadeboncoeur & Lodge, 1998). For instance, periphyton $\delta^{13}C$ probably decreases with increasing depth as a result of decreasing light intensity and productivity (MacLeod & Barton, 1998); on the other hand, the potential importance of this bias also decreases with depth, as the availability of periphyton relative to deposited phytoplankton decreases. We suspect that, were it possible to isolate pure samples of epipelic periphyton, their $\delta^{13}C$ time series might differ from the tile time series that we measured. However, as demonstrated by the similarity between model fits to the periphyton and phytoplankton time series (Table 1), the strong signal introduced by the ^{13}C manipulation means that differences of even a few per mil in driver $\delta^{13}C$ have relatively little impact on estimates of zoobenthos current autochthony. Nonetheless, future studies of benthic processes, including estimates of autochthony, would greatly benefit from new methods for isolating epipelic periphyton.

Secondly, we assumed that resource use during the May–October period that we studied accurately represents annual resource use. If seasonal pulses of resources to the benthic community occur outside the May–October bounds of our study (e.g. from spring or autumn phytoplankton blooms or autumn leaf fall) and translate to pulses in insect production, our autochthony estimates could be biased. We doubt that this is likely to be a major source of bias in our estimates, for two reasons. We have not observed seasonal phytoplankton blooms in Crampton Lake despite >10 years of field work there. Furthermore, low water temperatures throughout much of the year and protracted incorporation of resource pulses into

food webs both probably dampen the connection between resource pulses and insect production in this system.

High current autochthony of odonates

Over 70% of the production of libellulid and corduliid odonates was derived from current autochthonous primary production. This high reliance on autochthony is probably not due to direct consumption of primary producers, as odonates are widely reported to be obligate predators that ingest plant material only incidentally (Merritt & Cummins, 1996; Corbet, 1999). Instead, odonate diets must include a significant proportion of organisms that are themselves heavily reliant on current autochthonous production. Given that insect production at 1.5 m is dominated by chironomids (A.L. Babler and C.T. Solomon, unpubl. data), which as a group have fairly low current autochthony (Fig. 4), odonates must be feeding selectively on some less dominant but highly autochthonous prey. One possibility is that odonates prey on zooplankton that live in or migrate to the littoral zone. The autochthony of Crampton Lake zooplankton is quite high (92% for a biomass-weighted composite of the dominant pelagic species; Pace *et al.*, 2007) and odonate larvae have been reported to consume zooplankton (Pritchard, 1964; Corbet, 1999). Alternatively, odonates could be feeding selectively on benthic invertebrates that are highly reliant on current autochthony, potentially even including some subset of highly autochthonous chironomids. Further research is necessary to understand the pathways by which odonates incorporate substantial current autochthonous production.

Detrital pathways, bacteria and chironomids

In contrast to odonates, chironomids rely heavily (57–83%) on detrital pathways. Detritus is a heterogeneous resource, and our study was not designed to resolve insects' reliance on alternate detrital pathways. Nonetheless, our results do provide some insights into the nature of this trophic link. At each depth, we observed that the $\delta^{13}C$ of pre-manipulation chironomids was lower than that of bulk sediment OM. A similar pattern has been observed for chironomid, trichopteran and ephemeropteran insects in a number of lakes (Grey *et al.*, 2004b; Karlsson & Bystrom, 2005; Hershey *et al.*, 2006). While it is possible that these organisms use some completely separate, low $\delta^{13}C$ resource not associated with the benthos (as suggested above for odonates preying on zooplankton), this explanation seems unlikely for consumers such as chironomids that are tied more tightly to the benthos by their foraging styles and limited mobility. Instead, the low $\delta^{13}C$ of these organisms probably indicates selective assimilation of some ^{13}C-depleted component of the sediment OM (Doi *et al.*, 2006).

At least three mechanisms could make low-$\delta^{13}C$ OM available to chironomids. First, heterotrophic respiration by aerobic bacteria produces ^{13}C-depleted DIC, which may become available to benthic consumers after subsequent fixation by chemo- or photoautotrophs (France, delGiorgio & Westcott, 1997; Lennon *et al.*, 2006). This mechanism is probably most important below the thermocline, where respired C may come to dominate the DIC pool because of limited atmospheric exchange. Limited $\delta^{13}C$ data for hypolimnetic DIC and particulate organic carbon (POC) do suggest such an effect in Crampton Lake: mean $\delta^{13}C$ of DIC at 9 m was $-19.8‰$ ($\pm 2.6‰$ SD, $n = 2$), and mean $\delta^{13}C$ of pooled hypolimnetic POC was $-32.6‰$ ($\pm 1.3‰$ SD, $n = 3$). Secondly, methanogenesis in anoxic sediments produces extremely ^{13}C-depleted methane which insects may incorporate via methanotrophic or chemoautotrophic bacteria (Grey, Kelly & Jones, 2004a; Kohzu *et al.*, 2004; Grey & Deines, 2005; Deines & Grey, 2006). Methanogenesis is probably limited in Crampton Lake, as the intensity, extent and duration of hypoxic conditions is limited [dissolved oxygen (DO) < 1 mg L^{-1} below 10 m for *c.* 2 months]; Grey *et al.* (2004b) did not observe substantial seasonal effects of methanotrophy on chironomid $\delta^{13}C$ in a lake with similar DO characteristics. Nonetheless, the extreme ^{13}C depletion characteristic of methane-derived OM means that even minor contributions to insect diets from this pathway could result in insect $\delta^{13}C$ lower than bulk sediment $\delta^{13}C$. Thirdly, lipids tend to be ^{13}C-depleted relative to bulk OM (DeNiro & Epstein, 1977). Given that benthic consumers may encounter low quality food (low fatty acid composition) during some periods of the year (Goedkoop *et al.*, 2000), they might selectively assimilate lipids from ingested OM.

Further evidence that some or all of these processes may play an important role in the benthic food web

comes from the observation, made in this and several other recent studies, that sediment $\delta^{13}C$ decreases with depth (Karlsson *et al*., 2003; Karlsson & Bystrom, 2005; Hershey *et al*., 2006). A variety of factors influence sediment $\delta^{13}C$, including both the $\delta^{13}C$ of OM sources and the microbial processes associated with diagenesis (Meyers & Ishiwatari, 1993). As periphyton are generally ^{13}C-enriched relative to other autochthonous and allochthonous OM sources, it has been hypothesized that declining contributions of periphyton to the OM pool with depth could contribute to the observed relationship between depth and sediment $\delta^{13}C$ (Karlsson & Bystrom, 2005). At least in Crampton Lake, however, this mechanism cannot be solely responsible for the depth-$\delta^{13}C$ relationship, because by 10 m sediment $\delta^{13}C$ is lower that the $\delta^{13}C$ of all autochthonous and allochthonous OM sources. Additional mechanisms for a depth-$\delta^{13}C$ relationship might include (i) increases, because of changing DO conditions, in the quantity of OM derived from respired C and methanogenesis; (ii) progressive decreases in $\delta^{13}C$ during early sediment diagenesis because of factors including preferential bacterial degradation of carbohydrates and proteins relative to lipids (Meyers & Ishiwatari, 1993; Lehmann *et al*., 2002). Taken together, the decrease in sediment $\delta^{13}C$ with depth and the consistent difference between sediment $\delta^{13}C$ and natural-abundance insect $\delta^{13}C$ suggest that bacteria play an important role in the degradation and trophic transfer of detrital OM. While researchers have begun to quantify the trophic significance of bacteria in benthic food webs (Hall & Meyer, 1998; van Oevelen *et al*., 2006a,b), further research is needed to elucidate these pathways, particularly in lakes.

Mechanisms for within- and among-lake differences in current autochthony

We observed an interesting relationship between chironomid current autochthony and depth, whereby current autochthony remained nearly constant between 1.5 and 3.5 m but declined considerably by 10 m. At least two mechanisms may contribute to this relationship. First, taxon-specific differences in diet preferences could drive differences in current autochthony. Chironomid production is dominated by similar taxa at 1.5 and 3.5 m, where the two genera *Procladius* and *Ablabesmyia* make up *c*. 66% and 56% of production, respectively (A.L. Babler and C.T. Solomon, unpubl. data). In general, organisms in these genera are primarily predators on protozoans and larger organisms (Merritt & Cummins, 1996). In contrast, at 10 m >80% of chironomid production derives from the genus *Chironomus*, which are generally either detritivores or filter feeders (Merritt & Cummins, 1996). While omnivory, ontogenetic change and opportunism are characteristic of chironomid feeding (Berg, 1995), such broad differences in general diet preferences probably contribute to the patterns of autochthony that we observed. Similarly, Hershey *et al*. (2006) used a whole-lake ^{15}N addition and static mixing models to calculate that the reliance of chironomid taxa (genus to family level) on current pelagic production varied between 0% and 35% for three taxa in one lake, and between 15% and 31% for three taxa in another lake.

Changes in chironomid autochthony with depth might also result simply from changes in the relative availability of autochthonous and allochthonous resources; that is, resource use may be driven by resource availability. Periphyton production is often high in the littoral, but declines with depth because of light limitation. Phytoplankton production declines similarly with depth, but accumulation of phytoplankton on the bottom may increase with depth as a result of reduced turbulence and the depth-integrated nature of phytoplankton deposition. At the deepest sites, accumulating detritus may be disproportionately composed of terrestrial particles, because most of the smaller particles (including phytoplankton) can be decomposed before they reach the bottom (Bloesch & Uehlinger, 1990; Baines & Pace, 1994). Two observations support the idea that the deposition of current autochthonous production on the bottom at 10 m is limited. First, there was relatively little temporal change during our study in the $\delta^{13}C$ of material collected from sediment traps suspended at 9 m depth. The $\delta^{13}C$ of sedimenting material did show a clear response to the ^{13}C manipulation, similar to the phytoplankton and periphyton time series: it increased from a pre-manipulation value of $-30‰$ to a maximum $-23‰$, and then decreased after the end of the manipulation (N.D. Preston and S.R. Carpenter, unpubl. data). However, given that peak phytoplankton $\delta^{13}C$ was approximately $-5‰$, these results suggest that current autochthonous particles comprised < 30% of sedimenting material at 9 m.

Secondly, increases in sediment $\delta^{13}C$ at 10 m were minimal (Fig. 2) despite favourable depositional conditions for detecting recently-deposited current autochthonous detritus. Thus, it may be reasonable to expect that the availability of current autochthonous resources in Crampton Lake sediments mirrors the current autochthony of the chironomids: fairly high at 1.5 m due to contributions of periphyton; about the same at 3.5 m because increased accumulation of phytoplankton detritus balances reduced periphyton production; and much lower at 10 m, where the sediments are composed mostly of terrestrial and/or old phytoplankton detritus. We cannot assess the relative importance of this mechanism and the diet preference mechanism discussed above, but it is possible that both contribute to the observed relationship between chironomid autochthony and depth.

Comparing results from this experiment with those from previous ^{13}C manipulations in three smaller, nearby lakes provides some intriguing evidence that resource availability may also drive variation in resource use at the landscape scale. These previous experiments quantified, in four lake-years, the autochthony (actually, the current autochthony) of littoral zoobenthos samples dominated by odonate larvae (Carpenter *et al.*, 2005). Current autochthony was correlated with the ratio of lake water colour to chlorophyll concentration, an indicator of the relative availability of allochthonous and autochthonous OM. To determine whether the current autochthony of Crampton Lake odonates also fit this relationship between resource availability and resource use, we plotted all five current autochthony estimates together, against two different predictors. First, we plotted current autochthony against colour : chlorophyll, and observed that the current autochthony of Crampton Lake odonates did appear to relate to colour : chlorophyll in a similar way (Fig. 5a). Secondly, we plotted current autochthony against the proportion of each lake's C budget that was derived from autochthonous primary production (Fig. 5b). We calculated this quantity as gross primary production (GPP) divided by the sum of GPP and terrestrial inputs (I_T). GPP and I_T data were taken from Pace *et al*. (2007) and unpublished data (N.D. Preston and S.R. Carpenter, unpubl. data) for Crampton Lake, and from Cole *et al*. (2006) for the other lakes. Again, the current autochthony of zoobenthos was correlated with the availability of autochthonous primary production (Fig. 5b).

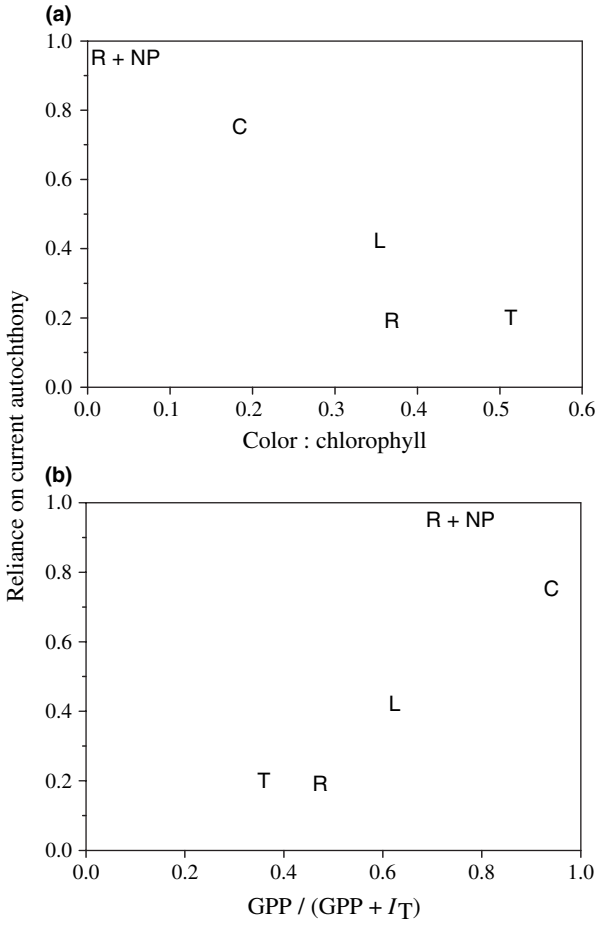

Fig. 5 Current autochthony of odonate larvae from this study and from four prior whole-lake ^{13}C manipulations performed in other lakes, plotted against (a) colour : chlorophyll ratio, an indicator of the relative availability of allochthonous and autochthonous resources; (b) the proportion of the lake C budget derived from autochthonous sources, calculated as gross primary production (GPP) divided by the sum of GPP plus terrestrial inputs (I_T). Symbols indicate lake names: C, Crampton; L, Paul; R, Peter; R + NP, Peter with added N and P; T, Tuesday. Data from Carpenter *et al*., 2005; Cole *et al*., 2006, this study, and unpublished.

Contemporary insect production is not supported primarily by contemporary autochthonous primary production in Crampton Lake; allochthonous inputs and old autochthonous detritus supported a substantial fraction (25–83%) of the production of the dominant benthic insect taxa. While detrital pathways have long been recognized as central to lake food webs (Lindeman, 1942), quantitative estimates of the carbon sources supporting benthic food webs have

emerged only recently (Peterson, 1999; Kelly, Jones & Grey, 2004; Carpenter *et al*., 2005; Hershey *et al*., 2006), and the estimates presented here are among the best constrained to date. Our results demonstrate substantial variability in the current autochthonous support of zoobenthos as a function of taxon and depth, and suggest that the relative availability of autochthonous and allochthonous resources may drive within and among-lake variation in the use of autochthonous OM. Further understanding of these patterns and their causes will be necessary as ecologists continue to integrate terrestrial and benthic pathways into models for understanding and managing lake ecosystems.

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