

Article

Carbon Transfer from Cyanobacteria to Pelagic and Benthic Consumers in a Subtropical Lake: Evidence from a ^{13}C Labelling Experiment

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Abstract: Eutrophication of lakes often results in dominance of cyanobacteria, which may potentially lead to serious blooms and toxic water. However, cyanobacterial detritus may act as an important carbon source for aquatic organisms. Using stable isotope carbon (^{13}C) as a tracer, we assessed the carbon transfer from cyanobacteria to pelagic and benthic consumers in a 28-day outdoor mesocosm (~130 L) labelling experiment established in Lake Taihu, China, during a *Microcystis aeruginosa* bloom. The different organisms were labelled differently after addition of the labelled *Microcystis* detritus to the water. $\delta^{13}\text{C}$ of particulate organic matter and of cladoceran zooplankton peaked earlier than for larger invertebrate consumers. Among the pelagic species, *Daphnia similis* had the highest $\Delta\delta^{13}\text{C}$, while the two snail species *Radix swinhoei* and *Bellamya aeruginosa* had lower but similar $\Delta\delta^{13}\text{C}$. The bivalves showed relatively modest changes in $\delta^{13}\text{C}$. The $\delta^{13}\text{C}$ of *Anodonta woodiana* and *Unio douglasiae* showed a marginal though not significant increase, while a marked increase occurred for *Arconaia lanceolata* peaking on day 20, and *Corbicula fluminea* a slight increase peaking on day 9. Our results suggest that carbon from cyanobacteria can be incorporated by pelagic and some benthic consumers and eventually be transferred to higher trophic levels. Cyanobacterial carbon may, therefore, be considered an important carbon source supporting the entire food web during blooms, even if the cyanobacteria are not consumed directly.

Keywords: stable isotope; subtropical; shallow lake; carbon flow; zooplankton; bivalves

1. Introduction

In many lakes, phytoplankton dominates primary production [1,2] and previous food web studies have, therefore, traditionally focused on phytoplankton-based food sources [3–5]. However, benthic production can be an important contributor to the whole-lake primary and secondary production [6,7], not least in shallow lakes [8,9], so in recent years, more attention has been paid to the role of benthic processes in the energy flow and to the coupling between the pelagic and benthic systems [8–11].

Phytoplankton is utilised directly by zooplankton [12–14], mussels [15–17] and some fish [18–20]. Eutrophication often leads to an increased biomass proportion of cyanobacteria of the phytoplankton community [21–24], which may negatively affect the lake food web by hampering zooplankton

grazing [25,26]. Moreover, some cyanobacterial species produce toxins that have adverse effects on animal health [27–29] and, accordingly, cyanobacteria have commonly been considered to be of low nutritional value for zooplankton [28–31]. Yet, some studies suggest that certain zooplankton species can feed on cyanobacteria [32–34], and numerous biomanipulation experiments have shown a drastic reduction in cyanobacteria abundance following a return of large *Daphnia* after removal of plankton-benthivorous fish, indicating enhanced grazer control of the cyanobacteria [35,36].

While the use of cyanobacteria may, to some extent, be hampered by their morphology and toxicity, cyanobacterial detritus could potentially be a useful food source for zooplankton [37] and snails [38]. Hanazato and Yasuno [37] reported that *Moina micrura* was not capable of directly utilising *Microcystis* as a food source even when colonies were broken up into edible sizes, but decomposed *Microcystis* turned out to be an exploitable carbon source for this species and also for *Daphnia* [39,40]. In this way, cyanobacteria may contribute as an energy source to the higher trophic level in the food web even if they are not grazed upon directly. Cyanobacterial detritus may also be assimilated by benthic macroinvertebrates, such as *Limnodrilus* spp. and *Chironomus* spp. [38] and act as important food sources for benthivorous fish [41], with subsequent channelisation to the higher trophic levels.

Lake Taihu is an important source of water supply to the city of Wuxi (Jiangsu Province, China), which is situated on the north-eastern bank of the lake. In late May 2007, a drinking water crisis occurred in Wuxi due to a massive outbreak of *Microcystis* sp. in the lake [42]. Historical data on Lake Taihu show that cyanobacterial blooms usually occur from late spring (March) through summer and autumn [43], and in recent years blooms have become more frequent in winter as well [44]. *Microcystis* blooms in Lake Taihu are often associated with relatively high abundances of small zooplankton such as *Bosmina* [45]. Both the abundance and biomass of macroinvertebrates were much higher in the northern part of Lake Taihu, with recurrent cyanobacteria blooms, than in the southern part [46], which indicates that *Microcystis* is used as a food source, either directly or indirectly as detritus. We conducted a ^{13}C tracer mesocosm experiment to assess to what extent the cyanobacteria-derived carbon acted as a carbon source for the pelagic and benthic consumers during a *Microcystis* bloom. We hypothesised that cyanobacterial detritus constitutes a significant proportion of the carbon source for both pelagic and benthic consumers.

2. Materials and Methods

2.1. Study Area

Lake Taihu is a large shallow lake, located in a subtropical region of China (30°55'40"–31°32'58" N and 119°52'32"–120°36'10" E). The lake is ~2338 km² in area and its average depth is about 1.9 m. The lake is currently eutrophic, with recurrent cyanobacterial blooms that are dominated by *Microcystis aeruginosa* [41]. We conducted the experiment at the shore of Meiliang Bay, situated in the northern and most eutrophic part of the lake, which is characterised by almost complete *Microcystis aeruginosa* dominance of the phytoplankton biomass in summer [23].

2.2. Detritus Preparation and Labelling

Samples of cyanobacteria during a bloom dominated by *Microcystis*, mostly *Microcystis aeruginosa* (>99%), were collected from Meiliang Bay using a plankton net (mesh size 64 µm) in August 2010. The live *Microcystis* was incubated in three air-tight and magnetically stirred bottles (10 L) with pre-filtered (0.45 µm) lake water for two days under natural regimes of light and temperature. During the incubation, 6717 g living *Microcystis*, concentrated on a plankton net (64 µm), was labelled with 15 g NaH¹³CO₃ (98% ¹³C). The tracers were added to the bottles in 10 equal portions at identical time intervals from 7:00 to 16:00. After the incubation, the *Microcystis* cells were collected with a 30 µm net and washed repeatedly with deionised water to remove unassimilated ¹³C. The labelled *Microcystis* was then dried to constant weight in an oven at 60 °C for 72 h, and the detritus mass was ground into fine powder using a mortar and pestle.

2.3. Labelling Experiment

The outdoor experiments were conducted during September and October 2010 at the Lake Taihu Experimental Station, situated on the shore of Lake Taihu. Twenty-four high density polyethylene (HDPE) mesocosms (height 66 cm; ~130 L) were constructed and subsequently filled with 15 cm lake sediment, which was well-mixed and filtered on a 0.5 cm meshed sieve, and 90 L lake water pre-filtered through a plankton net (mesh size 64 μm). All mesocosms were floated in an artificial pond (6 \times 5 \times 2 m) located on the shore of Meiliang Bay. Similar-sized individuals of *Bellamya aeruginosa* ($n = 7$, 10.4 \pm 0.5 g total wet weight (TWW)), *Radix swinhoi* ($n = 4$, 1.1 \pm 0.2 g TWW), *Corbicula fluminea* ($n = 4$, 12.0 \pm 0.6 g TWW), *Anodonta woodiana* ($n = 1$, 26.9 \pm 10.2 g TWW), *Unio douglasiae* ($n = 1$, 26.8 \pm 8.3 g TWW) and *Arconaia lanceolata* ($n = 1$, 18.6 \pm 12.7 g TWW), collected from Lake Taihu, were added after four days relative to the natural abundance in Lake Taihu [47]. Zooplankton were naturally hatched from the added sediment.

The mesocosm ecosystems were allowed to develop and stabilise for one month. The experiment was initiated by adding 7 g *Microcystis* detritus (labelled and powdered) to the 21 mesocosms on day 0, which is equivalent to 350 $\mu\text{g L}^{-1}$ chlorophyll-*a* in the natural water column (unpublished data), while the other mesocosms (3 replicates) acted as controls. The simulated concentration of chlorophyll-*a* was similar to that in the study of Chen et al. [48] but much lower than the concentration reported by Qin et al. [42] during the cyanobacteria blooming phase in Lake Taihu. The average concentration of *Chl-a* on day 0 was 25.4 \pm 4.2 $\mu\text{g L}^{-1}$. The experiment lasted for 28 days.

2.4. Sample Collection

Particulate organic matter (POM), zooplankton, two species of snails, four species of bivalves and periphyton were sampled for analyses of carbon stable isotopes on day 0, 1, 3, 5, 9, 14, 20 and 28. The control mesocosms (no addition of labelled detritus) were sampled on day 0 and the isotope values in these mesocosms were used as controls. At each sampling date, 3 random mesocosms out of the 21 originally labelled mesocosms were sampled and not used any more during the study.

During each sampling event, POM samples were prepared by filtering 1–2 L of water from the mesocosms onto pre-weighed and pre-combusted GF/C filters followed by oven drying at 60 $^{\circ}\text{C}$. Zooplankton were collected and concentrated by filtering about 30 L of water through a bolting silk plankton net with a mesh size of 64 μm . At least 40 individuals of each zooplankton species (*Daphnia similis*, *Diaphanosoma* sp., *Scapholeberis kingi*, *Sinocalanus dorrii* and *Cyclops* sp.) were collected for analysis, and the animals were kept in filtered lake water, allowed to empty their guts and then removed and dried at 60 $^{\circ}\text{C}$. Snails (*B. aeruginosa* and *R. swinhoi*) and bivalves (*C. fluminea*, *A. woodiana*, *U. douglasiae* and *A. lanceolata*) were picked directly after the mesocosms were emptied. About 5 g fresh abdominal muscle tissue of each species was dried at 60 $^{\circ}\text{C}$ in the oven. After emptying and removing the sediments left in the mesocosms, followed by careful cleaning, periphyton was sampled by brushing the walls and transferring the samples to deionised water, which was then filtered over pre-combusted and pre-weighed GF/C filters. The filters with periphyton were dried at 60 $^{\circ}\text{C}$.

2.5. Stable Isotope Analysis

All samples were analysed to determine $^{13}\text{C}/^{12}\text{C}$ ratios using a SerCon 20-20 isotope ratio mass spectrometer at the Department of Ecology and Institute of Hydrobiology, Jinan University, Guangzhou, China. Isotope abundance was expressed using the conventional delta notation against the Vienna-PeeDee Belemnite standard:

$$\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$$

where R is the $^{13}\text{C}/^{12}\text{C}$ ratio. The precision of repeated measurements was ca. $\pm 0.3\text{‰}$.

2.6. Data and Statistical Analyses

The maximum ^{13}C uptake by consumers was calculated as $\Delta\delta^{13}\text{C} = \delta^{13}\text{C}_{\text{peak sample}} - \delta^{13}\text{C}_{\text{background}}$, representing the enriched carbon uptake by consumers.

Due to the sampling design with day 0 as being our control, we first conducted an unpaired t -test, with Welch's correction, where we analysed which of the days a given taxa differed in $\delta^{13}\text{C}$ from its starting level (control, day 0). We then conducted a one-way Analysis of Variance (one-way ANOVA) to compare the differences in $\delta^{13}\text{C}$ values between peak values (i.e., $\Delta\delta^{13}\text{C}$) of, respectively, five zooplankton species (each species as one level) and four bivalves (each species as one level). If significant, a post hoc multiple comparisons were carried out by Tukey's least significant difference (Tukey LSD) procedure. Unpaired t -test, with Welch's correction, was also used to examine the differences in $\Delta\delta^{13}\text{C}$ between the two snail species and the differences of their peaking means on day 14 and $\Delta\delta^{13}\text{C}$ differences between the cladoceran (three species) and copepod (two species) group. All these comparisons were performed with the statistical package SPSS version 22.0.

3. Results

After addition of the labelled *Microcystis detritus* ($\delta^{13}\text{C} = 6.42\text{‰}$) to the mesocosms, ^{13}C in the POM increased significantly (unpaired t -test, $t = 13.31$, $df = 2.15$, $p < 0.01$) and reached its maximum on day 1 (-0.81‰), followed by a weak decline until the end of the experiment (Figure 1A). $\delta^{13}\text{C}$ of periphyton also showed a significant increase peaking on day 9 (-9.15‰) and then decreased gradually until the end of the experiment (Figure 1A). The $\delta^{13}\text{C}$ signatures of POM and periphyton were similar at the end of the experiment, being -18.73‰ and -18.79‰ , respectively, and were not by then significantly different from the starting levels (day 0) (Figure 1A).

As for the zooplankton, $\delta^{13}\text{C}$ of cladocerans increased rapidly and significantly during the first three days, after which it slowly declined until the end of the experiment, by then not being significantly different from the starting levels (Figure 1B). For *Daphnia similis*, *Scapholeberis kingi* and *Diaphanosoma* spp., the observed ^{13}C enrichment peaked on day 3, with mean values of, respectively, -6.59‰ , -7.52‰ and -9.44‰ ; *D. similis* showed significantly higher maximum values than *Diaphanosoma* sp. (one-way ANOVA, $F_{2,6} = 8.15$, $n = 3$, $p < 0.05$), while no marked differences were detected between *D. similis* and *S. kingi* ($p > 0.05$) (Figure 1B). Moreover, for copepods, a fast and significant increase of $\delta^{13}\text{C}$ was found for both *Sinocalanus dorrii* and cyclopoid copepods during the first three days, *S. dorrii* reaching its maximum value on day 3 (-14.68‰), while cyclopoid copepods peaked on day 14 (-12.34‰) (Figure 1C).

The $\delta^{13}\text{C}$ in *R. swinhoi* increased rapidly from day 0 to day 14 (from -17.29 to -10.86‰), peaking on day 14 (unpaired t -test, $t = 8.58$, $df = 3.20$, $p < 0.01$), and then showed a sharp decrease until the end of the experiment (Figure 1D). For *B. aeruginosa*, no significant enrichment in ^{13}C was found during the first nine days, after which it increased until day 14, followed by a slight decline towards the end of the experiment (Figure 1D). The $\delta^{13}\text{C}$ values of both *R. swinhoi* (-10.86‰) and *B. aeruginosa* (-17.36‰) peaked on day 14, the peak of *R. swinhoi* being much higher than that of *B. aeruginosa* (unpaired t -test, $t = 11.26$, $df = 3.90$, $p < 0.001$). At the end of the experiment, however, the two species of snails had similar $\delta^{13}\text{C}$ signature, which did not differ significantly from the starting levels on day 0 (Figure 1D).

The $\delta^{13}\text{C}$ patterns of bivalves showed relatively modest changes compared with the other organisms. A strong and significant ^{13}C enrichment was traced for *A. lanceolate*, with a gradual increase in $\delta^{13}\text{C}$ after the addition of labelled detritus peaking on day 20 (-22.05‰) (unpaired t -test, $t = 7.81$, $df = 3.15$, $p < 0.01$), after which it declined slightly until the end of the experiment (Figure 1E). *Corbicula fluminea* had a significantly (unpaired t -test, $t = 4.99$, $df = 2.44$, $p < 0.05$) higher $\delta^{13}\text{C}$ on day 9 than on day 0 (changing from -25.5 to -24.1‰), but neither *A. woodiana* nor *U. douglasiae* showed values differing significantly from those on day 0, though tended to show the highest values also on day 9 (Figure 1E).

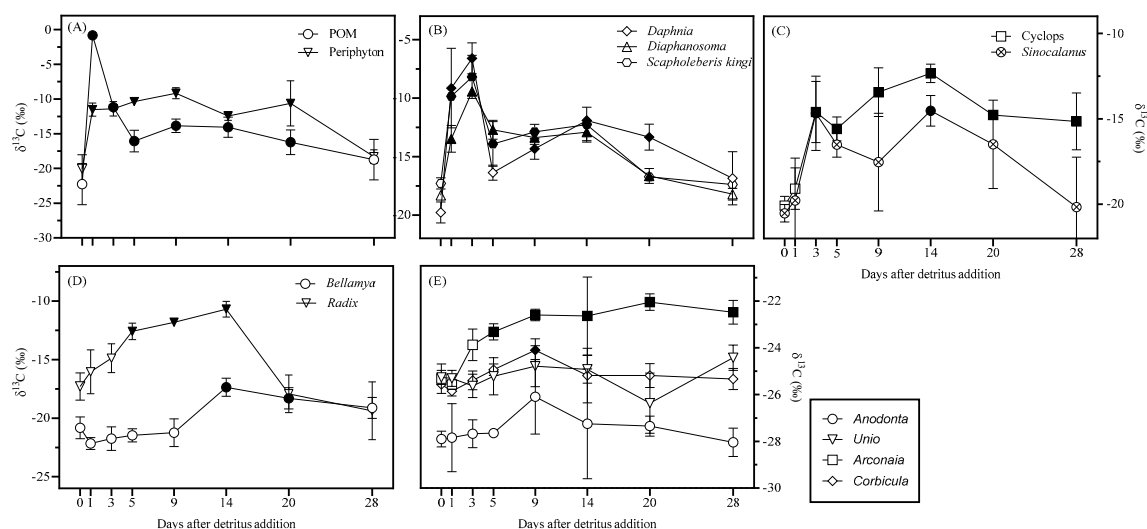


Figure 1. Variations in $\delta^{13}\text{C}$ signatures of pelagic and benthic organisms following addition of labelled *Microcystis* detritus to the water column of the mesocosms during the 28-day experiment. Error bars represent the standard deviation (SD) for three replicate mesocosms. **(A)** Periphyton (sampled from the inside wall of the mesocosm), POM (particulate organic matter); **(B)** cladocerans (*Daphnia similis*, *Diaphanosoma* spp. and *Scapholeberis kingi*); **(C)** copepods (*Sinocalanus dorrii* and cyclopoid copepods); **(D)** snails (*Radix swinhoei* and *Bellamya aeruginosa*) and **(E)** bivalves (*Anodonta woodiana*, *Unio douglasiae*, *Arconaia lanceolata* and *Corbicula fluminea*). Note the different scales on the y-axes. The filled symbols represent the $\delta^{13}\text{C}$ of a given species on days where it was significantly different from the control's values (on day 0).

Among the pelagic species, *D. similis* had the highest $\Delta\delta^{13}\text{C}$ (12.34 ± 1.33) (one-way ANOVA, $F_{4,10} = 13.07$, $n = 5$, $p < 0.001$) (Figure 2A), while the average $\Delta\delta^{13}\text{C}$ was similar for *Diaphanosoma* sp. (8.89 ± 0.19) and *S. kingi* (8.81 ± 1.84). Cladocerans tended to have higher $\Delta\delta^{13}\text{C}$ values than copepods, the difference being insignificant, though (unpaired *t*-test, $t = 2.17$, $df = 2.99$, $p > 0.05$) (Figure 2A), whereas the mean values for *S. dorrii* and cyclopoid copepods were 6.00 and 7.74, respectively.

For the snail species, $\Delta\delta^{13}\text{C}$ of *R. swinhoei* (5.93 ± 1.46) tended to be higher than for *B. aeruginosa* (3.46 ± 1.73), but the difference was not significant (unpaired *t*-test, $t = 1.90$, $df = 3.89$, $p > 0.05$) (Figure 2B). The bivalve *A. lanceolata* (3.28 ± 0.64) showed a higher potential of utilising *Microcystis*-derived carbon ($\Delta\delta^{13}\text{C}$) than *A. woodiana* (1.33 ± 0.71), *U. douglasiae* (0.84 ± 0.68) and *C. fluminea* (1.50 ± 0.65) (one-way ANOVA, $F_{3,8} = 7.64$, $n = 4$, $p < 0.01$) (Figure 2C), but no clear differences were found among the three species (one-way ANOVA, $F_{2,6} = 0.76$, $n = 3$, $p > 0.05$) (Figure 2C).

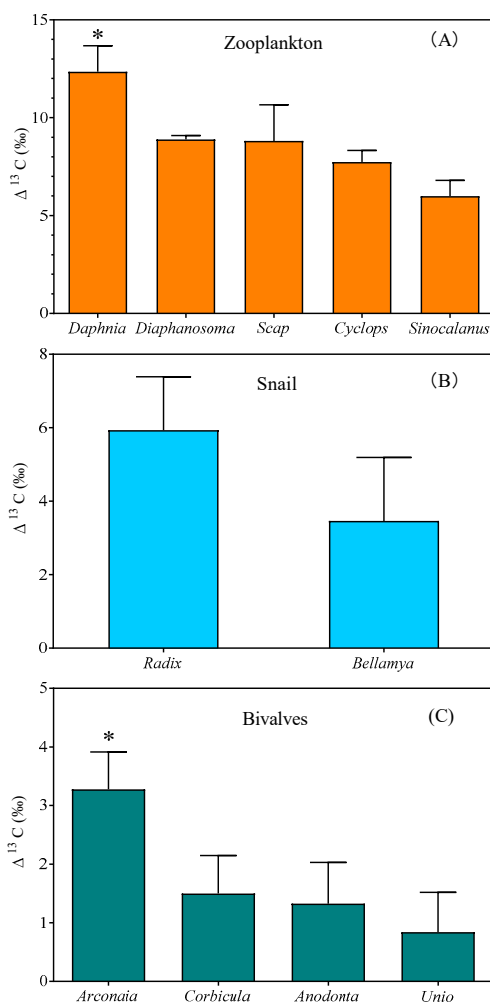


Figure 2. Comparison of ^{13}C enrichment ($\Delta\delta^{13}\text{C}$) of the different species of cladocerans, copepods, snails and bivalves on $\delta^{13}\text{C}$ peak days during the experiment. Data are presented as averages with SD error bars ($n = 3$). Note: * indicate significant differences than other species in each group. (A) cladocerans (*Daphnia similis*, *Diaphanosoma* spp. and *Scapholeberis kingi*) and copepods (*Sinocalanus dorrii* and cyclopoid copepods); (B) snails (*Radix swinhoei* and *Bellamya aeruginosa*) and (C) bivalves (*Anodonta woodiana*, *Unio douglasiae*, *Arconaia lanceolata* and *Corbicula fluminea*).

4. Discussions

We found that addition of ^{13}C -labelled *Microcystis* detritus to the water column led to increasing $\delta^{13}\text{C}$ in both pelagic and benthic consumers. This indicates that detritus from cyanobacteria may be used as a carbon source in both the pelagic and the benthic food web in eutrophic lakes with extensive growth and blooming of cyanobacteria, such as Lake Taihu.

In our study, $\delta^{13}\text{C}$ of POM was highest on day 1 (just after addition of the labelled detritus) and periphyton peaked on day 9. The enrichment of $\delta^{13}\text{C}$ in periphyton may reflect both uptake of detritus-derived- ^{13}C from the water column and of labelled detritus settled on the walls. Among the pelagic filter feeders, both cladocerans and calanoid copepods had elevated $\delta^{13}\text{C}$, and especially *Daphnia* showed higher $\delta^{13}\text{C}$ values than calanoid copepods (Figure 2A). This difference may reflect their different feeding modes, although variations in growth rate may also have contributed. Calanoid copepods are selective feeders and discriminate between high- and low-quality foods under optimal food conditions [49], while daphnids are non-selective mechanical sievers [50,51]. However, the typically higher growth rate and tissue turnover rate of cladocerans will also lead to higher maximum $\delta^{13}\text{C}$ labelling values than for copepods, because $\delta^{13}\text{C}$ in the food resources (POM)

declined after day 1, which may partially be due to the sinking of undecomposed detritus to the bottom. Other experimental studies also indicate that cyanobacteria detritus is a useful food source for crustacean zooplankton [39,52–54].

The snails in our experiment, *R. swinhoei* and *B. aeruginosa*, were also affected by the labelled detritus early in the experiment but to a rather different degree, likely reflecting their different feeding habits and growth rates. *B. aeruginosa* generally feeds on the organic-rich surface sediment, whereas *R. swinhoei* mainly exploits periphyton [55,56]. The sediment was expected to be less enriched in $\delta^{13}\text{C}$, not least in the beginning of the experiment, due to the presence of an unlabelled pool of organic matter, which dilutes the $\delta^{13}\text{C}$ signal (unfortunately, we did not measure it), while periphyton was quickly enriched to a high value that persisted for 20 days. Moreover, small-sized snails show a much higher consumption rate per unit of biomass than large-sized snails [57,58] as well as higher tissue turnover rates. We therefore expected that the smaller *R. swinhoei* ($0.3 \pm 0.1 \text{ g}\cdot\text{ind}^{-1}$) would be more strongly affected by the labelled detritus than *B. aeruginosa* ($1.6 \pm 0.1 \text{ g}\cdot\text{ind}^{-1}$) early in the experiment, and this was confirmed by the observations.

Suspended particulate organisms (POM, including algae and detritus) have been reported to be the main food source for filter-feeding benthic bivalves, and some species have even proved to control cyanobacteria in laboratory studies [16,59], mesocosm experiments [60] and field investigations [61]. In our study, the $\delta^{13}\text{C}$ of all the bivalve species increased gradually after addition of the labelled *Microcystis* detritus (though not significantly for all species), indicating that the ^{13}C -detritus was assimilated. The effect of the labelled detritus on the bivalves was modest compared with that on the other taxa studied and not significantly different from the control (day 0) for two species (*A. woodiana* and *U. douglasiae*), likely reflecting their higher initial biomass and lower growth rate than the other taxa studied, leading to a slower turnover of unlabelled tissue. The $\delta^{13}\text{C}$ increase differed among the taxa, the highest values being recorded for *A. lanceolate*, which in our study was smaller ($18.6 \pm 12.5 \text{ g}\cdot\text{ind}^{-1}$) than *A. woodiana* ($26.9 \pm 10.2 \text{ g}\cdot\text{ind}^{-1}$) and *U. douglasiae* ($26.8 \pm 8.3 \text{ g}\cdot\text{ind}^{-1}$), though larger than *C. fluminea* ($12.0 \pm 0.7 \text{ g}\cdot\text{ind}^{-1}$), which had the second highest $\delta^{13}\text{C}$ values. Former studies have demonstrated that the filtration rate per unit of biomass is generally higher for small-sized *A. woodiana* than for larger-sized individuals of this species [62,63], whereas there were no significant differences in the filtration rate between the similar-sized *A. woodiana* and *U. douglasiae* [62]. Consequently, our results indicate that some (perhaps all) of the common filter-feeding bivalves in Lake Taihu can utilise cyanobacterial detritus-derived carbon, and this is to some extent supported by field studies showing that the highest biomass of bivalves occurs in the more eutrophic parts of the lake exhibiting frequent cyanobacteria blooms [46].

In conclusion, our results suggest that carbon from cyanobacteria detritus can be incorporated by both pelagic and some benthic consumers and eventually be transferred to higher trophic levels. Cyanobacterial carbon may thus be considered an important carbon source that supports not only the pelagic but also the benthic food web during periods with cyanobacteria blooms in eutrophic lakes, even if the cyanobacteria are not consumed directly. Our study is, however, of too short duration to elucidate potential toxic effects of feeding on cyanobacteria detritus.

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