Subsidies of Organic Carbon of Terrestrial and Benthic Plants to Crustacean Zooplankton in Artificial Aquatic Ecosystems

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Abstract

Studies of zooplankton in lake pelagic ecosystems have traditionally focused on their role as grazers of phytoplankton. Using carbon stable isotopes, we reported here on the contribution of terrestrial and benthic plants to the organic carbon intake of zooplankton in artificial aquatic ecosystems. The study systems consist of 8 tanks in which submerged macrophyte Vallisneria natans grow and into which leaves of the lilytree Magnolia denudate have dropped since 2011. In 2015, lilytree leaf litter, particulate organic matters (POM), macrophytes, periphyton and zooplankton were sampled for carbon stable isotope analyses. IsoSource mixing models were then used to estimate the contribution of each component to zooplankton. The results showed that lilytree leaves provided greatest support to zooplankton, followed by POM. Submerged macrophytes and periphyton also contributed significantly to zooplankton. The supplementation of non-pelagic organic carbon is thus likely to enhance the growth of zooplankton and increase the control of phytoplankton, with important implications for lake management.

Keywords

Terrestrial Organic Carbon, Crustacean Zooplankton, Macrophytes, Periphyton, Subsidies.

1. Introduction

Zooplankton have traditionally been studied as grazers of phytoplankton in lake pelagic ecosystems. However, since the beginning of the 21st century, there is growing evidence that the growth of lake zooplankton is also subsidized to varying degrees by allochthonous input of terrestrial organic carbon from the lake catchment. Pace et al. made daily additions of $NaH^{13}CO_3$ to two lakes over 42 d and used a dynamic model to suggest that lake primary producers alone could not meet the energy requirements of lake food webs, that terrestrial systems may account for 40%–55% of particulate organic carbon in lakes, and that 22%-50% of zooplankton carbon was also derived from terrestrial systems [1]. Cole et al. used stable isotope analysis of H, C, and N to estimate terrestrial support for zooplankton in lakes and found that zooplankton comprise in the region of 20% to 40% organic material of terrestrial origin [2].

However, it is also known that terrestrial carbon inputs is generally of low nutritional quality and thus the extent to which such supplements support of zooplankton production has been the subject of debate [3-5]. Brett et al. argued that the contribution of terrestrial carbon to the zooplankton could be overestimated [3]. One of difficulties using stable isotope ratios to estimate the relative significance of different carbon sources in supporting for zooplankton is the choice of the endmember for the calculation. As inputs of terrestrial organic carbon involve a mixture of plant material from all over the catchment basin, choosing particular soils or dominant trees as the endmembers for terrestrial organic carbon to zooplankton may lead to bias [2,6].

Meanwhile, periphyton associated with submerged macrophytes are also seen to be another important source of carbon for zooplankton [7]. However, as the stable carbon isotopes signatures of periphyton cannot be distinguished from those of submerged macrophytes in the same lake, their relative contribution to the zooplankton could not be separated [7].

2. Methods

Here we estimated the contributions of terrestrial vegetation (*lilytree Magnolia denudate*), submerged macrophytes and periphyton to zooplankton via carbon stable isotope analyses in a series of artificial aquatic ecosystem. These systems consisted of 8 polyethylene plastic tanks, designed for the study of submerged macrophytes. The tanks were 150 cm height with a bottom diameter of 100 cm and 150 cm a top diameter of 150 cm. After the addition of a 20 cm layer of sediment and a further 70 cm of water the tanks were planted with the submerged macrophytes *Vallisneria natans* in 2011. Since then the only supply of terrestrial organic carbon has been in the form of leaf litter from the lilytree *Magnolia* denudate. Thus these artificial aquatic ecosystems provide an opportunity to study the contribution of different non-pelagic carbon sources to zooplankton.

Samples for stable carbon isotope analysis were collected in May 2015 from 8 tanks. Other measured water parameters included a range of total phosphorus from 0.04 to 0.11mg·L^{-1}, total nitrogen from 0.44 to 2.47 mg·L^{-1} and chlorophyll a from 5.88 to 49.36 μg·L^{-1}. Water samples were collected from each tank using a 5-L water sampler. Particulate organic matter (POM) was measured by filtering 2L to 5L water through precombusted (500℃, 4h) and preweighted Whatman (GF-F) glass-fiber filters (pore size 0.7 μm). Filters were then dried to a constant weight at 60℃. Macrophyte samples were collected using a quantitative iron clamp with an area of 0.2 m^2, then sorted into species, rinsed with distilled water, and dried at 60℃ for 48 h. Periphyton was collected from macrophytes with a wire or nylon brush and rinsed into a plastic container filled with distilled water. All visible particles of non-periphyton material were removed manually and the periphyton samples were then filtered through a 100 μm mesh sieve, followed by filtration onto precombusted GF/F filters which were subsequently dried at 60℃ for 48 h. Leaf litter was also from the quantitative iron clamp when it was used for collecting macrophyte samples, and likewise rinsed with distilled water and dried at 60℃ for 48 h. The dried samples of macrophytes, periphyton and filters were then ground with mortar and pestle for stable isotope analyses. Zooplankton were collected with a 64μm mesh-size net. Upon return to the lab, zooplankton (mainly crustaceans *Moina macrocopa* and *Thermocyclops taihokuensis*) were transferred to beakers with demineralized water to empty their guts for two hours and then sorted into genera, handpicked and transferred to precombusted tin cups, which were subsequently freeze-dried.

All samples were analyzed carbon stable isotope ratios on an EA 1112 elemental analyzer coupled to a Hydra 20-20 isotope ratio mass spectrometer at Jinan University [8]. Stable isotope ratios are expressed in the delta (δ) notation, defined as parts per thousand (per mil, ‰) deviation from a certified standard; $\delta^{13}C=(R_{sample}/ R_{standard} - 1) \times 1000$, and R is the ratio$^{13}C$:$^{12}C$. The analytical precision was 0.1‰ in all laboratories. The standard for $\delta^{13}C$ was Vienna Pee Dee Belemnite. We applied the IsoSource mixing model to estimate contributions of POM, macrophytes, periphyton, and lilytree leaf litter to zooplankton from the 8 tanks [9]. The differences in mean contribution among the potential carbon sources were compared with one-way ANOVAs.

3. Results

Lilytree leaf litter had the lowest $\delta^{13}C$ value with a mean of -29.5‰. POM showed a mean value of -23.97‰ for $\delta^{13}C$. The $\delta^{13}C$ of macrophytes averaged -20.35‰, and periphyton had the greatest $\delta^{13}C$ value at -14.81‰, with high variation as indicated by high standard deviation. Zooplankton showed a moderate carbon stable isotope ratio averaging -24.50‰, well within the range of the four basic food sources (Figure 1). The $\delta^{13}C$ values of lilytree leaf litter distinguished it from other food sources available in the tanks and allowed us to estimate the proportion of organic carbon incorporated by zooplankton that was derived from terrestrial plants.

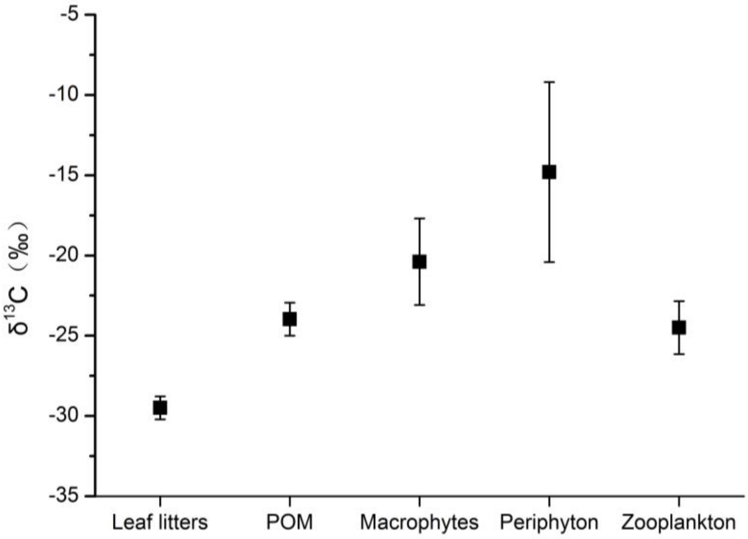

Figure1. Carbon stable isotopes of leaf litter, POM, macrophytes, periphyton and zooplankton (mean ± SD)

The results of IsoSource mixing models showed that the contribution of leaf litter to crustacean zooplankton was on average 39.2%, making it the principal contributor among the four basal food sources investigated, with a significantly (one-way ANOVA, $P<0.05$) input than that of POM, macrophytes or periphyton. The contribution of POM to crustacean zooplankton averaged 26%. The average contribution of macrophytes and periphyton is 18% and 15% respectively. However, there was no significant differences between the contributions of POM, macrophytes and periphyton (one-way ANOVA, $P>0.05$) (Figure 2).

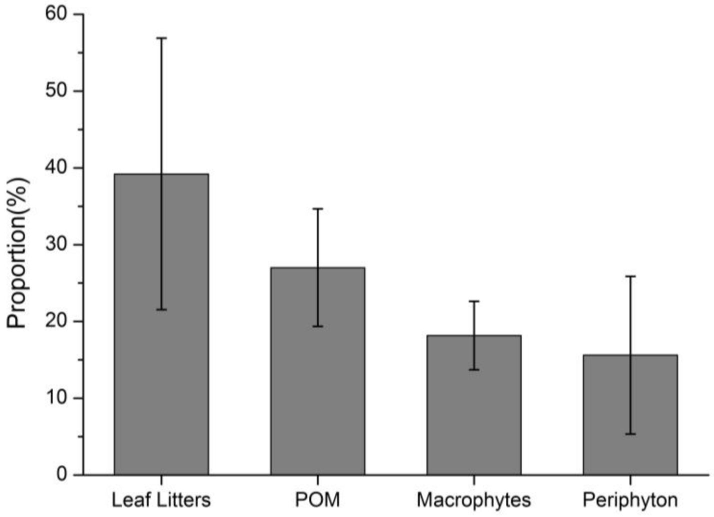

Figure 2. Percentage proportion of zooplankton supported by leaf litter, POM, macrophytes and periphyton (mean ± SD)

4. Discussion

The reported proportion of zooplankton organic carbon derived from terrestrial origins varies widely. For instance, Wilkinson et al. reported that terrestrial sources contributed anything from 1 to 74% of the organic carbon incorporated by crustacean zooplankton [10]. Based on a study of 15 lakes in northern Sweden Karlsson et al. found that, based on ^{13}C signatures, mean contribution of allochthonous organic carbon to zooplankton was within the range of 9%–77% [6]. Meanwhile Lau et al. identified autochthonous resources as a main driver of secondary production, even in dystrophic lakes where allochthonous organic matter dominates quantitatively over that derived from photosynthetic autotrophs [5]. Our study showed a high proportion of lilytree leaf litter carbon in crustacean zooplankters, although the pathways from leaf litter to zooplankton require further study. Our study also showed that pelagic consumers depend significantly on carbon sources of benthic origin, in this case submerged plants and periphyton. On average, POM contributed a relatively modest 27% of organic carbon assimilated by planktonic crustaceans. Considering that POM in this case comprised a mixture of phytoplankton, macrophytes, periphyton and lilytree leaf litter, the true contribution of pelagic primary producer phytoplankton zooplankton growth may be even lower than the results suggest. In eutrophic lakes management plans often focus heavily on the control of phytoplankton. Crustacean zooplankton is a main limiting factor on phytoplankton growth, and thus elevated zooplankton to phytoplankton ratios are of potentially crucial importance [11,12]. Supplementation of organic carbon by non-pelagic sources, i.e. plant material of terrestrial and benthic, will likely enhance zooplankton production and thus lead to increased grazing pressure on phytoplankton. Thus terrestrial organic carbon inputs and abundant submerged macrophytes may play an important role supporting lake management.

5. Conclusion

Our study demonstrated that lilytree leaves provided greatest support to zooplankton. Submerged macrophytes and periphyton also contributed significantly to zooplankton. The supplementation of non-pelagic organic carbon (derived from terrestrial plants and benthic plants such as submerged plants or periphyton) is thus likely to enhance the growth of zooplankton and increase the control of phytoplankton, with important implications for lake management.

Acknowledgements

Natural Science Foundation.

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