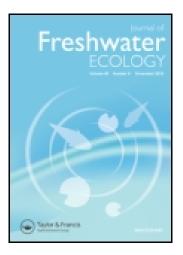
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Contributions of Pelagic and Benthic Dietary Sources to Freshwater Mussels: Evidence from Stable Carbon Isotope Analysis

Zhourui Wen^{a,b,c}, Ping Xie^{a,d}, and Jun Xu^a

ABSTRACT

In Gonghu Bay of Lake Taihu, tissue of five mussel species showed δ^{13} C values similar to or slightly below that of pelagic suspended particulate organic matter (SPOM). This indicated that mussels in this area either fed non-selectively and so reflected available carbon in the pelagic habitat or selected for phytoplankton. The situation was the same for Anodonta woodiana woodiana and Cristaria plicata in Meiliang Bay; however, for the remaining three species, Hyriopsis cumingii, Arconaia lanceolata, and Lamprotula rochechouarti, tissue had intermediate δ^{13} C values, falling between those for pelagic SPOM and benthic sediment organic matter (SOM), suggesting a possible preferential selection of phytoplankton from the pelagic SPOM but more likely reflecting local differences in pelagic SPOM and benthic SOM composition and available organic carbon sources. The mixing model showed that pelagic SPOM accounted for over 98% of carbon incorporated by all mussels in Gonghu Bay and two mussels in Meiliang Bay, suggesting the dietary importance of pelagic food sources for mussels. Less than 50% of the assimilation in H. cumingii, A. lanceolata, and L. rochechouarti came from the pelagic carbon sources in Meiliang Bay, which suggested that these species consumed a mix of benthic and pelagic derived carbon sources.

INTRODUCTION

Mussels, as filter feeders, have received attention for their potential role as time-integrated bioindicators of aquatic habitat character and shifts because they record chronically, through food web transfer via short-lived producer organisms, the more ephemeral isotopic signatures of the sources associated with anthropological nutrient loads (Cabana and Rasmussen 1996, McKinney et al. 1999, Raikow and Hamilton 2001, Post 2002). Their longevity, limited movement, relative ease of collection, and low trophic position also make them suitable candidates for estimation of baseline isotopic signatures.

It has long been suggested that both estuarine and marine bivalves assimilate most of their dietary carbon through the uptake of phytoplankton (Widdows et al. 1979, Asmus and Asmus 1991, Dame and Prins 1998). Recently however, with the introduction of stable isotope analysis, it has been possible to trace the flow of organic matter directly from source to consumer (Kaehler et al. 2000). The application of this technique has led to the suggestion that uptake of benthic carbon sources, such as macroalgal, by filter feeders through detrital food webs in benthic and pelagic communities has been underestimated (e.g., Dunton and Schell 1987, Duggins et al. 1989, Bustamante and Branch 1996). It is therefore reasonable to expect that filter feeders in a given habitat experience differences not only in the benthic vs. pelagic source contributions but also the species-specific food habit (Gannes et al. 1997, Lorraine et al. 2002, O'Reilly et al. 2002, Post 2002, Rubenstein and Hobson 2004).

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The aim of this study was to investigate the variation in percentage of pelagic and benthic food resources of freshwater mussels in shallow eutrophic Lake Taihu by means of stable carbon isotope analysis, examining the δ^{13} C ratios from freshwater mussels, suspended particulate organic matter (SPOM), and surface sediment organic matter (SOM).

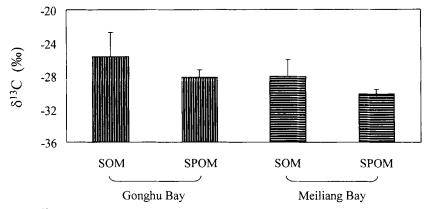
MATERIALS AND METHODS

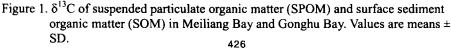
In 2005, mussels were collected from Meiliang Bay and Gonghu Bay of Lake Taihu (30°5'-32°8'N and 119°8'- 121°55'E) (Wen et al. 2009). Three to twelve individuals of each species, including Hyriopsis cumingii, Arconaia lanceolata, Anodonta woodiana woodiana, Cristaria plicata, and Lamprotula rochechouarti, were sampled depending on the availability. SPOM and SOM samples were obtained from 5-L surface water and 1-3 cm surface sediment samples at three sites in each bay.

Water samples were vacuum-filtered through pre-combusted (500°C, 6 h) GF/C (Whatman®) filters (1.2 µm pore size) and then dried at 60°C for 24h. Surface sediment (1-3 cm) was rinsed in distilled water and dried (60°C, 48 h). Mussel adductor muscle tissue was removed, rinsed in distilled water, and dried (60°C, 48 h). Adductor muscle tissue was used in this study, as muscle tissue has low turnover rates (Gorokhova and Hansson 1999) and is therefore representative of a time-integrated diet. All samples were ground to a fine powder with a mortar and pestle and then stored in a desiccator with a silica gel desiccant for subsequent stable isotope analysis.

Stable carbon isotope ratios were analyzed with a Delta Plus (Finnigan) continuous-flow isotope ratio mass spectrometer directly coupled to an NC2500 elemental analyzer (Carlo Erba). The isotopic compositions of samples were expressed as parts-per-thousand (‰) differences from a standard reference material using the equation: δ^{13} C (‰) = (R_{sample}/R_{standard} - 1) × 1000, where R is 13 C/ 12 C. The standard reference material was VPDB belemnite. International reference material was carbonatite (IAEA-NBS18) for δ^{13} C. More than 20% of the samples were analyzed two or more times, and the standard errors of replicate analyses were approximately ± 0.2 %.

Differences between mussel δ^{13} C signatures were analyzed by t-test using Statistica v7 (StatSoft 2004). A linear two-source mixing model (Bustamante and Branch 1996) was used to determine the percentage of organic carbon contributed to mussel diet by pelagic SPOM as follows: % Isotope = $[(\delta^{13}C_{mussel} - \delta^{13}C_{benthic} - e) / (\delta^{13}C_{pelagic} - \delta^{13}C_{benthic})] \times 100$, where e is the average fractionation of $\delta^{13}C$ per trophic level. We considered the average fractionation value to be 1‰ for δ^{13} C (DeNiro and Epstein 1978, Fry and Sherr 1984).





RESULTS AND DISCUSSION

The mean (\pm SD) δ^{13} C ratios of SPOM and SOM were respectively -28.1 \pm 0.9‰ and -25.7 \pm 3.0‰ in Gonghu Bay and -30.2 \pm 0.6‰ and -28.1 \pm 2.0‰ in Meiling Bay (Fig. 1). The mean (\pm SD) δ^{13} C ratios of mussels ranged from -27.1 \pm 0.6‰ (*L. rochechouarti* in Meiliang Bay) to -31.0 \pm 0.7‰ (*C. plicata* in Meiliang Bay) (Fig. 2). In Meiliang Bay, δ^{13} C ratios of mussel species differed significant (P < 0.01) from one another (P < 0.01), but no significant variations were observed in Gonghu Bay. Between-bay comparison of the isotope signatures of mussels showed significant differences (P < 0.01) in three mussel species -A. woodiana woodiana, *C. plicata*, and *L. rochechouarti*. The mixing model showed that percentage of pelagic dietary carbon was greater than 98% for all mussel species in Gonghu Bay and for *A. woodiana woodiana* and *L. rochechouarti* in Meiliang Bay. The assimilations from the pelagic carbon sources for *H. cumingii*, *A. lanceolata*, and *C. plicata* in Meiliang Bay were 62.8%, 31.1%, and 1.8%, respectively (Fig. 3).

As filter-feeders, mussels remove and assimilate algae, detritus, and microorganisms from the water column generally, but they are unlikely to depend on a single food source, relying instead on the changing sources of carbon available in the water column and filtering selectively (Bougrier et al. 1997, Ward et al. 1998). In this study, we hypothesized that mussels eating pelagic dietary sources would reflect $\delta^{13}C$ values of the pelagic SPOM, while those eating benthic dietary sources would have similar δ^{13} C values to benthic SOM. In Gonghu Bay, muscle tissue of each species showed δ^{13} C values similar to or slightly below those of pelagic SPOM. This indicated that mussels in this bay either fed non-selectively and so reflected available carbon in the pelagic habitat or selected for phytoplankton. The situation was the same for A. woodiana woodiana and C. plicata in Meiliang Bay. However, for the remaining three species, H. cumingii, A. lanceolata, and L. rochechouarti, muscle tissue had intermediate δ^{13} C values, falling between those for pelagic SPOM and benthic SOM, which suggested a possible preferential selection of phytoplankton (Bougrier et al. 1997, Rouillon and Navarro 2003) from the pelagic SPOM. More likely this reflected local differences in pelagic SPOM and benthic SOM composition and available organic carbon sources.

The application of a linear mixing model allowed us to determine the percentage contribution of benthic and pelagic dietary sources to the overall δ^{13} C signatures for each mussel species. Surprisingly, pelagic SPOM accounted for over 98% of carbon

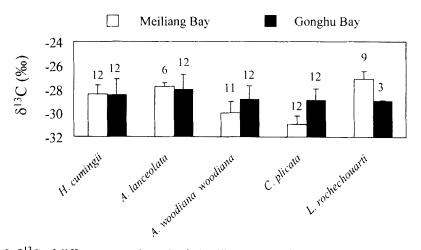


Figure 2. δ^{13} C of different mussel species in Meiliang Bay and Gonghu Bay. Values are means ± SD. Numbers above the bars indicate the number of mussels sampled.

incorporated by all mussels in Gonghu Bay and two mussels in Meiliang Bay. This overall reliance on pelagic primary production suggested that mussels were feeding nonselectively and emphasized the dietary importance of pelagic food sources for mussels. However, SPOM samples in this study could not be expected to reflect only the phytoplankton signature because SPOM contained mixed species of phytoplankton with other minute organisms and some amount of detritus; consequently the links between mussel diet and SPOM remain unclear. Less than 50% of the assimilation in H. cumingii, A. lanceolata, and L. rochechouarti came from pelagic carbon sources in Meiliang Bay, which suggested that these mussels were possibly consuming food sources derived from a variety of habitats. Alternatively, these results might indicate that mussels were consuming a mixture of benthic- and pelagic-derived carbon sources. However, given that algal productivity was highest in Meiliang Bay during the summer months, it was quite possible that mussel δ^{13} C values preferentially reflected selective feeding for the algal component in seston (Raikow and Hamilton 2001). This will need to be further investigated to establish the relationship between time-integrated mussel tissues and the instantaneous nature of the SPOM sample in eutrophic conditions, which may be masked by the differences in time-scale integration (Goschen and Schumann 1990).

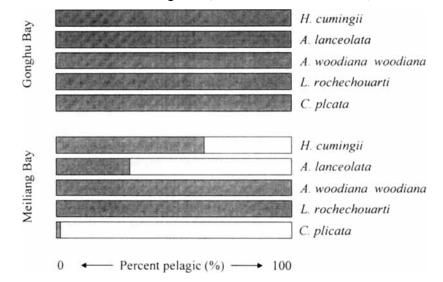


Figure 3. Percentage of pelagic dietary carbon contributed to each mussel species in Meiliang Bay and Gonghu Bay.

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