

Stable isotope changes in freshwater shrimps (*Exopalaemon modestus* and *Macrobrachium nipponensis*): trophic pattern implications

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Abstract Trophic patterns of omnivorous freshwater shrimps, *Exopalaemon modestus* and *Macrobrachium nipponensis*, were investigated in two shallow eutrophic lakes by using stable isotope analysis. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of *M. nipponensis* and *E. modestus* increased with increasing body weight, which might be attributed to larger individuals ingesting organisms that feed higher up the food chain and/or increased assimilation of benthic food items with enriched isotopic signatures. Of the freshwater shrimps occurring in the studied lakes, those from Lake Taihu had significantly elevated $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (4.3‰ and 1.8‰, respectively) compared with those from the less eutrophic Lake Chaohu, indicating that the isotopic signature might partially reflect the trophic states of their habitats. Mixing model results suggested that the benthic food web provides the primary carbon source for both shrimp species, and that *E. modestus* assimilated

relatively more pelagic food sources than *M. nipponensis* in these lakes.

Keywords *Exopalaemon modestus* · Food web linking · Freshwater shrimps · *Macrobrachium nipponensis* · Stable isotopes

Introduction

Exopalaemon modestus and *Macrobrachium nipponensis* are common and commercially important freshwater shrimps in China. The general natural distribution of *E. modestus* ranges from the south of China to Siberia in Russia in the north, whereas *M. nipponensis* naturally occurs in China, Japan, Vietnam, and Siberia in Russia (Li et al., 2003). These species are widely distributed in the middle and lower reaches of the Yangtze River in southern and southeastern China, and have been reported in rivers, lakes, streams, reservoirs, and ponds (Guo et al., 2005). Because of its excellent flavor, in recent years *M. nipponensis* has been cultivated at a considerable scale in the middle and lower reaches of the Yangtze River in northern and northeastern China (Li et al., 2005; Miao & Ge, 2002).

E. modestus and *M. nipponensis* are considered to be the most adaptable and hardy shrimp species that are found in a series of aquatic ecosystems along a trophic gradient (Han & Shu, 1995; Oh et al., 2002)

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and have been known to successfully invade other aquatic ecosystems. For instance, *M. nipponensis* has been introduced to the Philippines and Singapore (Cai & Shokita, 2006). The introduction of *E. modestus* and other exotic species into the plateau Lake Dianchi, China is thought to be responsible for the disappearance of an endemic atyid shrimp species, *Caridina dianchiensis* (Liang & Yan, 1985). *E. modestus* has been introduced into rivers in western North America through transport in the ballast water of large-volume cargo ships from Asia (Emmett et al., 2002). Further human-mediated dispersal will transport this species to suitable habitats, including reservoirs and lakes across this region because it lives well in lakes (Oh et al., 2002). It is reasonable to presume that these freshwater shrimps compete for food and space with each other and with the native shrimps in the invaded aquatic systems when they occupy similar habitats and overlap in food items. Therefore, understanding the trophic ecology of these shrimps from aquatic systems in their native distribution will provide invaluable information on their roles in food webs, e.g., energy transfer and material cycling, and this information will be crucial, for example, in fishery and aquaculture management, and in setting realistic restoration and management targets in invaded systems. However, known studies of these freshwater shrimps mainly focus on their growth, reproductive biology, and culture performance (e.g., Oh et al., 2002; Liu et al., 2003; Li et al., 2005), and trophic studies are extremely rare in aquatic ecosystems, which limits the understanding of trophic ecology and the identification of the role of these shrimps in native and invaded systems.

Traditionally, trophic relationships have been studied by using gut content analysis, which provides snapshots of feeding information immediately prior to capture and is vulnerable to biases related to the identification of the different prey types, digested and evacuated at different rates. Recently, the use of stable carbon and nitrogen isotopes as an alternative approach to study trophic relationships has greatly increased (e.g., Vander Zanden et al., 1999; Greenwood et al., 2001; Post, 2002; Williams & Trexler, 2006; Pasquaud et al., 2007). The isotope signature of an animal reflects its assimilated diet over a period of time. Specifically, the stable nitrogen isotope ratio ($\delta^{15}\text{N}$) of consumers is enriched about 3–4‰ relative to their food sources during trophic transfer (Vander

Zanden & Rasmussen, 1999, 2001; Post, 2002; McCutchan et al., 2003; Vanderklift and Ponsard, 2003), which indicates that the trophic level can be calculated from direct measurements of the $\delta^{15}\text{N}$ of consumer, the corresponding isotope values at the base of the food web, and the enrichment of $\delta^{15}\text{N}$ per trophic level (Post et al., 1999; Vander Zanden et al., 1999). The stable carbon isotope ratio ($\delta^{13}\text{C}$) exhibits little or no trophic level enrichment (0–1‰), and is used to identify the sources of primary production for consumers. For example, differences in $\delta^{13}\text{C}$ between pelagic, benthic, and terrestrial sources could be transferred up the food chain and indicate the importance of different sources of primary production to consumers (France, 1995; Hecky & Hesslein, 1995).

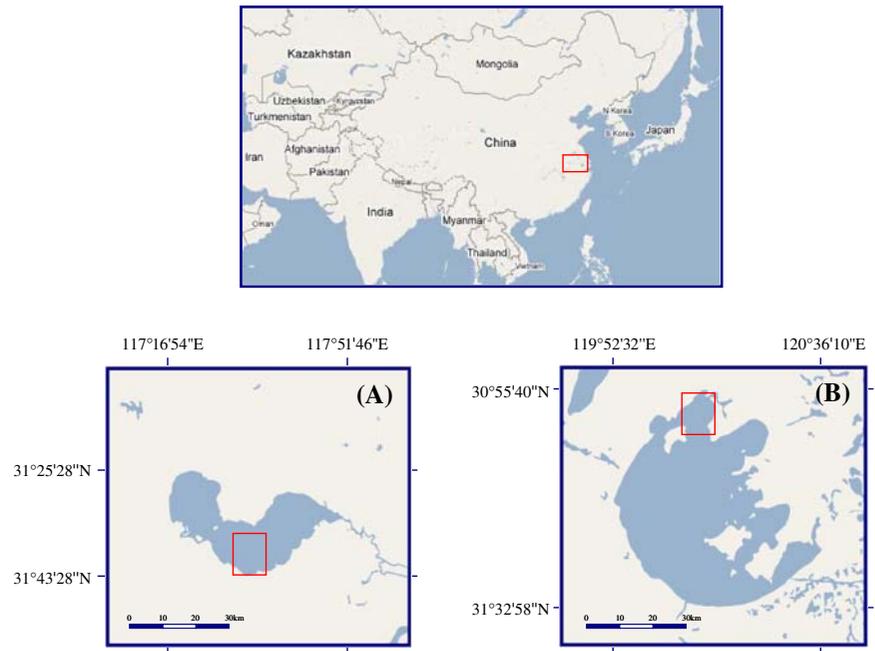
In light of these facts, stable carbon and nitrogen isotopes were used to investigate the trophic patterns of *E. modestus* and *M. nipponensis* collected from lakes in their naturally distributed region. We examined the variations in stable isotopes as a function of body weight, and the difference of stable isotopes between species and lakes. Possible reasons for the trophic patterns in the observed variations and differences are discussed, and we also utilized the distinct isotopic baselines of pelagic and benthic habitats in these lakes to estimate to what extent these shrimps relied on the pelagic and benthic food webs.

Materials and methods

Study lakes

Lakes Chaohu (117°16'54"–117°51'46" E, 31°25'28"–31°43'28" N) and Taihu (119°52'32"–120°36'10" E, 30°55'40"–31°32'58" N), the fifth and third largest freshwater lakes in China, respectively, are located in the mid–lower basins of the Yangtze River in southeastern China (Fig. 1). According to the Organisation for Economic Cooperation and Development (OECD) (1982), the lakes are all in eutrophic states in terms of total phosphorus (TP) concentrations (Table 1), and phytoplankton are the dominant flora, with a high biomass consisting of cyanobacteria (mainly *Anabaena* and *Microcystis*) (Zhang et al., 2007a, b). Aquatic macrophytes are scarce in the lake, possibly because of altered nutritional conditions and light limitation.

Fig. 1 Maps of Lake Chaohu (A) and Lake Taihu (B), southeastern China. The boxes represent the approximate areas used for the freshwater shrimp samples in this study



Limnological characteristics of these lakes are summarized in Table 1 (data from Geng, 2006; Yang, 2006; Zhang et al., 2006; Xu et al., 2007a). In these

lakes, *E. modestus* and *M. nipponensis* are two important freshwater shrimps, which are popularly used as food for people in this region; these shrimps

Table 1 Average values and ranges for selected limnological parameters in Lake Chaohu from August 2002 to July 2003 and in Lake Taihu from August 2004 to July 2005 (data from Geng, 2006; Yang, 2006)

Parameter	Lake Chaohu*		Lake Taihu*	
	Range	Average	Range	Average
Surface area (km ²)	No data	770	No data	2428
Storage capability (m ³)	No data	2.1 × 10 ⁹	No data	4.8 × 10 ⁹
Depth (m)	1.5–6.5	3.4	No data	2.2
Oxygen saturation (mg l ⁻¹)	7.2–16.0	11.7	2.7–13.8	7.93
Secchi depth (cm)	17.6–106.5	51.2	10.5–60.4	29.29
pH	6.4–10.1	8.1	7.2–9.0	8.1
Conductivity (μS cm ⁻¹)	122–472	244	46–67	55
Temperature (°C)	3.6–30.9	19.3	16.5–29.8	25.7
Algal density (10 ⁹ ind. l ⁻¹)	0.1–61.9	13.2	0.1–79.6	16.0
Total algal biomass (mg l ⁻¹)	5.2–22.7	11.4	No data	No data
Chlorophyll <i>a</i> (μg l ⁻¹)	9.4–47.9	17.1	10.0–36.3	84.1
TP (mg l ⁻¹)	0.06–0.23	0.11	0.06–0.29	0.14
Ortho-P (mg l ⁻¹)	0.002–0.05	0.02	0.03–0.08	0.05
TN (mg l ⁻¹)	0.9–6.1	2.23	0.2–5.2	2.28
NO ₃ -N (mg l ⁻¹)	0.17–3.09	1.26	0.4–1.7	0.89
NH ₄ -N (mg l ⁻¹)	0.12–0.67	0.39	0.05–3.43	0.63

* Limnological parameters were not the average and range of whole-lake, but of the areas where the freshwater samples were collected, i.e., middle area in Lake Chaohu and the Meiliang Bay in Lake Taihu

TN, total nitrogen

have accounted for 10–40% of the total annual fishery catch in recent years.

Field collection and lab processing

Freshwater shrimps, *E. modestus* and *M. nipponensis*, were collected in Lakes Chaohu and Taihu in September 2003 and October 2004, respectively, by net casting and from fishermen (Fig. 1). Shrimps were dissected and the tail muscle tissues were taken for stable isotope analysis because shell material is enriched in ^{13}C and does not reflect what is actually assimilated by these consumers (Mitchell et al., 1996; Stenroth et al., 2006).

After collection and transport to the laboratory, the samples were either processed immediately or kept frozen for processing later. Before analysis, samples were rinsed with distilled water and dried in a dry oven at 60°C to constant weight. Samples were then ground to a fine homogeneous powder with a mortar and pestle. The mortar and pestle were washed and dried to prevent cross contamination between samples. Powder from the samples was kept in Eppendorf tubes and sealed in desiccators with silica gel for later analysis.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements

Stable carbon and nitrogen isotope ratios were analyzed with a Delta Plus (Finnigan) continuous flow isotope ratio mass spectrometer (CF-IRMS) directly coupled to an NA2500 elemental analyzer (Carlo Erba). The isotopic compositions of samples were expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ notation using the equations as follows:

$$\delta^{13}\text{C} (\text{‰}) = \left(\frac{\left(\frac{^{13}\text{C}}{^{12}\text{C}} \right)_{\text{sample}}}{\left(\frac{^{13}\text{C}}{^{12}\text{C}} \right)_{\text{standard}}} - 1 \right) \times 10^3,$$

$$\delta^{15}\text{N} (\text{‰}) = \left(\frac{\left(\frac{^{15}\text{N}}{^{14}\text{N}} \right)_{\text{sample}}}{\left(\frac{^{15}\text{N}}{^{14}\text{N}} \right)_{\text{standard}}} - 1 \right) \times 10^3,$$

where ‰ is parts per thousand and $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ are the atomic ratios of the number of atoms in the sample or standard, and higher δ values denote a greater proportion of the heavy isotope. The

international standards are Vienna Pee Dee Belemnite (VPDB) and the Earth's atmospheric nitrogen, for C and N, respectively. International reference materials were carbonatite (IAEA-NBS18) for $\delta^{13}\text{C}$, and ammonium sulfate (IAEA-USGS25) for $\delta^{15}\text{N}$. On a daily basis, an internal working standard, urea ($\delta^{13}\text{C} = -49.44\text{‰}$ and $\delta^{15}\text{N} = -1.53\text{‰}$), was used for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. More than 20% of the samples were analyzed two or more times. Average standard deviations of duplicate measurements were 0.2‰ and 0.3‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

Mixing model

To calculate the contribution of pelagic and benthic food webs to the nutrition of *E. modestus* and *M. nipponensis*, a mass balance mixing model was used to estimate the contribution of benthic secondary production to these freshwater shrimps by using the formula:

$$\text{percent benthic} = \frac{\delta^{13}\text{C}_{\text{shrimp}} - \delta^{13}\text{C}_{\text{pelagic}}}{\delta^{13}\text{C}_{\text{benthic}} - \delta^{13}\text{C}_{\text{pelagic}}} \times 100,$$

where $\delta^{13}\text{C}_{\text{shrimp}}$, $\delta^{13}\text{C}_{\text{pelagic}}$, and $\delta^{13}\text{C}_{\text{benthic}}$ are the mean $\delta^{13}\text{C}$ values for shrimp, the pelagic baseline, and the benthic baseline, respectively. For trophic fractionation of $\delta^{13}\text{C}$, the calculation demonstrated that the mean difference in benthic fraction between the assumptions of 0‰ and 1‰ was only 7–10%. Therefore, we used 0‰ as the fractionation factor for carbon (Post, 2002). Primary producers, e.g., algae, at the base of food chains have been documented to vary considerably in $\delta^{13}\text{C}$ temporally and spatially in Lakes Chaohu and Taihu (Xu et al., 2005; Zhou et al., submitted to Ecological Engineering). Owing to the fact that these baseline variations are preserved at higher trophic levels, it was not possible to compare the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of the freshwater shrimps directly. As a means to adjust for temporal and lake-specific variations in the $\delta^{13}\text{C}$ values of the primary producers, we used long-lived primary consumers, surface-grazing snails and filter-feeding mussels, to represent the benthic and pelagic food web baseline, respectively, in order to calculate the contribution of the pelagic and benthic food webs to the nutrition of *E. modestus* and *M. nipponensis* (Vander Zanden & Rasmussen, 1999; Post, 2002), because these long-lived macroinvertebrates are

considered to be less sensitive to seasonal fluctuations of isotopic compositions of primary producers, and can reflect the base of the benthic and pelagic food webs, respectively, in lake ecosystems (Vander Zanden et al., 1999; Post, 2002).

Statistical analysis

Differences in the isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) between *E. modestus* and *M. nipponensis* were analyzed with one-factor analyses of variance (ANOVA), with variance estimates at each lake as replicates. When significant differences among treatments and their interactions were found, Student–Newman–Keuls (SNK) tests were undertaken as a posteriori comparisons. The relationships between the body size of the shrimps and the isotopic composition in their tissues was analyzed with one-way analysis of covariance with lakes as a factor, the proportion of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as variables, and body size as a covariate. First, a linear regression model was tested separately for each lake. If there were significant regressions ($P < 0.05$) among stable isotopes and body size in the lakes samples, the homogeneity of b (the slopes of the linear regression) was tested. Although significant regressions were sometimes found in the lakes, b values were not homogeneous and the analysis of covariance was not carried any further. Therefore, the relationships between the body size of the shrimps and isotopic

composition in their tissues was analyzed with linear regression analysis.

Results

Isotope composition in muscle tissues of the sampled shrimps, *E. modestus* and *M. nipponensis*, ranged from -26.7% to -20.5% for $\delta^{13}\text{C}$, and from 18.6% to 10.5% for $\delta^{15}\text{N}$; the standard deviation of both nitrogen and carbon isotope values within shrimp populations from the lakes varied from 0.5 to 1.5 per mil. The number of freshwater shrimps analyzed for each species per lake varied between 9 and 24. The average, maximum, and minimum values of body weight, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ were compared for *E. modestus* and *M. nipponensis* in the two lakes (Table 2). For nitrogen, the signatures were on average 2.1‰ and 0.5‰ higher in *M. nipponensis* than in *E. modestus* samples in Lake Chaohu ($P < 0.001$) and in Lake Taihu ($P < 0.05$), respectively; for carbon, the signatures were on average 0.8‰ and 1.3‰ higher in *M. nipponensis* than in *E. modestus* samples in Lake Chaohu ($P = 0.08$) and in Lake Taihu ($P < 0.001$), respectively. Between-lake comparison of the isotope signatures of shrimps showed significant enrichment in both nitrogen and carbon signatures (up to 1.8‰ for $\delta^{13}\text{C}$ and 4.3‰ for $\delta^{15}\text{N}$) in Lake Taihu with regard to those in Lake Chaohu (*M. nipponensis*, nitrogen, $P < 0.001$; *M. nipponensis*, carbon, $P < 0.001$; *E. modestus*, nitrogen, $P < 0.001$; *E. modestus*, carbon, $P < 0.01$).

Table 2 Comparison of the average, maximum, and minimum values of body weight, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ observed in the tail muscle of freshwater shrimps, *Exopalaemon modestus* and *Macrobrachium nipponensis*, collected in Lakes Chaohu and Taihu

	<i>E. modestus</i>			<i>M. nipponensis</i>		
	Weight (g)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Weight (g)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Lake Chaohu						
Average	2.1	-24.5	12.6	4.2	-23.7	14.7
Standard deviation	1.0	1.1	1.5	1.9	1.5	0.6
Maximum	3.6	-22.5	14.8	6.2	-22.0	15.9
Minimum	0.7	-26.3	10.5	0.7	-26.7	13.3
Number	16	16	16	15	15	15
Lake Taihu						
Average	1.1	-23.2	16.9	2.2	-21.9	17.4
Standard deviation	0.6	1.1	0.5	1.8	0.9	0.5
Maximum	2.1	-21.7	17.6	6.0	-20.5	18.6
Minimum	0.2	-25.1	16.1	0.2	-23.8	16.5
Number	9	9	9	24	24	24

Simple linear regression analysis was used to examine if there was any correlation between the isotopic signatures and body weight of *E. modestus* and *M. nipponensis* and between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Muscle $\delta^{15}\text{N}$ of *E. modestus* showed positive trends with the individual body mass (Lake Chaohu, $r = 0.47$, $P = 0.06$, $n = 16$; Lake Taihu, $r = 0.84$, $P < 0.01$, $n = 9$), and $\delta^{15}\text{N}$ values of *M. nipponensis* also showed positive trends with body weight (Lake Chaohu, $r = 0.49$, $P = 0.06$, $n = 15$; Lake Taihu, $r = 0.54$, $P < 0.01$, $n = 24$) (Fig. 2A). Muscle $\delta^{13}\text{C}$ of *E. modestus* also showed positive trend with the individual body mass (Lake Chaohu, $r = 0.62$, $P < 0.01$, $n = 16$; Lake Taihu, $r = 0.60$, $P = 0.08$, $n = 9$), and the $\delta^{13}\text{C}$ values of *M. nipponensis* also showed a significant positive correlation with body weight (Lake Chaohu, $r = 0.75$, $P < 0.01$, $n = 15$; Lake Taihu, $r = 0.59$, $P < 0.01$, $n = 24$) (Fig. 2B). Positive trends between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of shrimps were found in Lake Chaohu ($r = 0.65$, $P < 0.001$, $n = 16$ for *E. modestus*; $r = 0.46$, $P = 0.08$, $n = 15$ for *M. nipponensis*) and in Lake Taihu ($r = 0.34$, $P = 0.38$, $n = 9$ for *E. modestus*; $r = 0.40$, $P = 0.05$, $n = 24$ for *M. nipponensis*) (Fig. 3).

Plotting the carbon and nitrogen signatures for *E. modestus* and *M. nipponensis*, compared with the isotope signature of the primary consumers in Lake Chaohu and Lake Taihu, including long-lived filter-feeding mussels and surface-grazing snails, and short-lived zooplankton and chironomidae larvae, suggested that the benthic food web provides the primary carbon source for these shrimp species (Table 3, Fig. 4). The mixing model showed that 71% and 82% of the assimilation in *E. modestus* and *M. nipponensis*, respectively, came from the benthic food web in Lake Chaohu; 95% and 100% of the assimilation in *E. modestus* and *M. nipponensis*, respectively, came from the benthic food web in Lake Taihu.

Discussion

E. modestus and *M. nipponensis* play a key role in trophic links as both consumer and prey. The diets of these freshwater shrimps have traditionally been determined through the analysis of gut contents, which has indicated that these shrimps are omnivorous, exploiting a large range of food sources from benthic to pelagic food webs (Shi et al., 1995; Hu

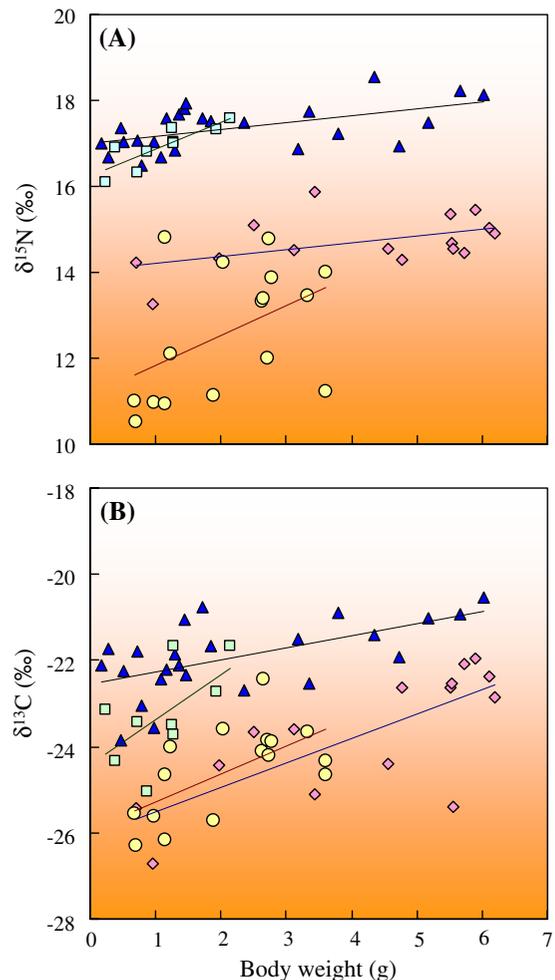


Fig. 2 $\delta^{15}\text{N}$ (A) and $\delta^{13}\text{C}$ (B) values as a function of body weight of the freshwater shrimps, *Exopalaemon modestus* and *Macrobrachium nipponensis*, collected in Lakes Chaohu and Taihu. Circles and diamonds represent *E. modestus* and *M. nipponensis*, respectively, sampled from Lake Chaohu; squares and triangles represent *E. modestus* and *M. nipponensis*, respectively, sampled from Lake Taihu. Solid lines are trend lines that best describes the relationship between the isotope ratio values and the body weight of the shrimps. For $\delta^{15}\text{N}$: $y = 11.1 + 0.7x$ ($r = 0.47$, $P = 0.06$, $n = 16$) and $y = 14.0 + 0.2x$ ($r = 0.49$, $P = 0.06$, $n = 15$) for *E. modestus* and *M. nipponensis*, respectively, in Lake Chaohu, and $y = 16.2 + 0.6x$ ($r = 0.84$, $P < 0.01$, $n = 9$) and $y = 17.0 + 0.2x$ ($r = 0.54$, $P < 0.01$, $n = 24$) for *E. modestus* and *M. nipponensis*, respectively, in Lake Taihu. For $\delta^{13}\text{C}$: $y = -25.9 + 0.6x$ ($r = 0.62$, $P < 0.01$, $n = 16$) and $y = -26.1 + 0.6x$ ($r = 0.75$, $P < 0.01$, $n = 15$) for *E. modestus* and *M. nipponensis*, respectively, in Lake Chaohu, and $y = -24.4 + 1.0x$ ($r = 0.60$, $P = 0.08$, $n = 9$) and $y = -22.5 + 0.3x$ ($r = 0.59$, $P < 0.01$, $n = 24$) for *E. modestus* and *M. nipponensis*, respectively, in Lake Taihu. Note the difference in the ranges of isotopic data between shrimp species and lakes

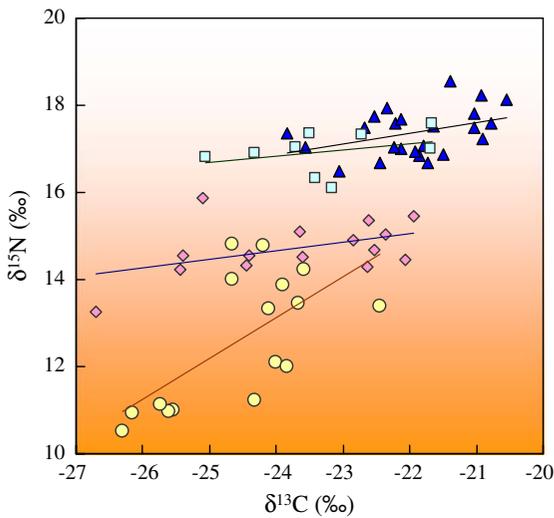


Fig. 3 Relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for freshwater shrimps, *Exopalaemon modestus* and *Macrobrachium nipponensis*, collected in Lakes Chaohu and Taihu. Circles and diamonds represent *E. modestus* and *M. nipponensis*, respectively, sampled from Lake Chaohu; squares and triangles represent *E. modestus* and *M. nipponensis*, respectively, sampled from Lake Taihu. Solid lines are trend lines that best describe the relationships between the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of freshwater shrimps with linear equations of $y = 35.6 + 0.9x$ ($r = 0.65$, $P < 0.001$, $n = 16$) and $y = 19.4 + 0.2x$ ($r = 0.46$, $P = 0.08$, $n = 15$) for *E. modestus* and *M. nipponensis*, respectively, in Lake Chaohu, and $y = 20.3 + 0.1x$ ($r = 0.34$, $P = 0.38$, $n = 9$) and $y = 22.8 + 0.2x$ ($r = 0.40$, $P = 0.05$, $n = 24$) for *E. modestus* and *M. nipponensis*, respectively, in Lake Taihu. Note the difference in the ranges of isotopic data between shrimp species and lakes

et al., 2001; Liu et al., 2005), including algae, fresh macrophytes, aquatic insects, protozoans, crustaceans, rotifers, oligochaetes, copepod, crustaceans, chironomid larvae, detritus, and inorganic material (e.g., sand grains). Since *E. modestus* and *M. nipponensis* are omnivores living in an extremely heterogeneous environment, it is difficult for

ecologists to identify and distinguish between the ingested and assimilated food sources through traditional gut content analysis. It is generally recognized that isotopic composition of an animal reflects its assimilated diet over a period of time. In this study, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of *M. nipponensis* and *E. modestus* increased with increasing body weight. It is unlikely that isotope fractionation would change during growth of shrimps, because Minagawa & Wada (1984) found that marine invertebrates fed with the same diet showed consistent isotopic ratios with age. One possible explanation is that older and larger individuals may ingest organisms that feed higher on the food chain, such as drifting invertebrates. This assumption has recently been demonstrated in *M. nipponensis* through gut content analysis (Liu et al., 2005), where large individuals ingested more aquatic insect larvae and less protozoans than small ones. Another possible explanation is that these shrimps increased assimilation of benthic food items as they became larger and older, since benthic algae was found to be higher in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ relative to phytoplankton in Lake Chaohu and Taihu (Xu et al., 2007a; Zhou et al., submitted to Ecological Engineering) and the benthic secondary consumers were also highly enriched in heavy isotopes compared with those of pelagic consumers (Table 3). This was also supported by the positive correlation between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of *M. nipponensis* and *E. modestus*, respectively. Variations in stable isotopes with animal size have also been found in other invertebrates (e.g., Rau et al., 1991; Gu et al., 1997; Rossi et al., 2004). For example, Rau et al. (1991) reported the changes in diet during the growth of *Euphausia superba* using stable isotope analysis and found that intermediate-sized individuals (ca. 30–40 mm) displayed the lowest $\delta^{15}\text{N}$, with higher values present in some of the smaller and larger individuals. Rossi

Table 3 Average and standard deviation (SD) values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in the secondary consumers collected from Lakes Chaohu and Taihu

	Lake Taihu			Lake Chaohu						
	$\delta^{13}\text{C}$ (‰)	SD	$\delta^{15}\text{N}$ (‰)	SD	<i>N</i>	$\delta^{13}\text{C}$ (‰)	SD	$\delta^{15}\text{N}$ (‰)	SD	<i>N</i>
Chironomid larvae	-23.7	1.3	16.2	0.6	2	-23.0	0.4	13.7	1.7	4
Bulk zooplankton	-27.7	1.1	13.9	1.2	3	-26.8	0.6	10.5	0.7	2
Grazing snails	-23.0	0.8	15.7	0.8	31	-22.4	0.6	10.5	0.6	3
Filter-feeding mussels	-28.0	2.1	8.0	3.1	36	-29.9	0.5	9.0	0.8	3

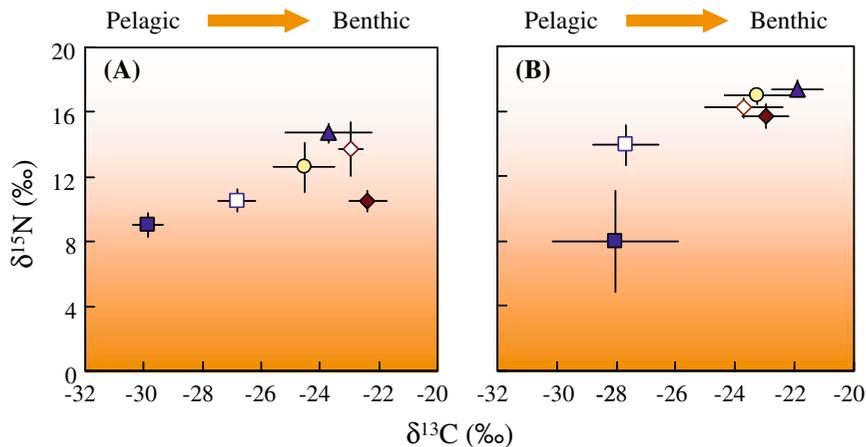


Fig. 4 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ plot for freshwater shrimps, *Exopalaemon modestus* and *Macrobrachium nipponensis*, pelagic and benthic primary consumers collected in Lake Chaohu (A) and Lake Taihu (B). Squares refer to pelagic primary consumers, with closed squares representing filter-feeding mussels and open squares representing bulk zooplankton; diamonds refer to benthic primary consumers, with closed diamonds representing

surface-grazing snails and open diamonds representing chironomidae larvae. Freshwater shrimps, *E. modestus* and *M. nipponensis*, are shown as circles and triangles, respectively. Data on primary consumers are from Xu et al. (2007a) and Zhou et al. (unpublished data). Error bars represent one standard deviation

et al. (2004) found that values of $\delta^{13}\text{C}$ depended significantly on body size in *Macoma balthica*, providing evidence of ontogenetic variation in diet with small juveniles feeding entirely on microphytobenthos, while there was a gradual tendency for larger sizes to feed more on microphytoplankton.

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of *M. nipponensis* showed significant enrichment compared with *E. modestus* in both lakes, indicating markedly different food habits of these shrimps. By comparing with the isotope signature of the primary consumers in Lakes Chaohu and Taihu, including long-lived filter-feeding mussels and surface-grazing snails, and short-lived zooplankton and chironomidae larvae (Fig. 4), we suggest that the benthic food web provides the primary carbon sources for these shrimp species. Results of the mixing model estimation provide further confirmation that both shrimps derived most of their energy from benthic food web, while *E. modestus* assimilated relatively more pelagic food sources (about 5–11%) than *M. nipponensis* in the studied lakes. This argument, however, is in disagreement with traditional analyses. For example, no differences in frequency of occurrence were found between pelagic (algae, protozoans, crustaceans) and benthic (detritus, chironomid larval, oligochaetes) food items of *M. nipponensis* by gut content analysis (Liu et al., 2005),

and there is still no detailed gut content analysis of *E. modestus* available.

Supplies of nutrients often limit phytoplankton growth (Klausmeier & Litchman, 2004). In eutrophic lakes, increasing anthropogenic waste input (commonly enriched in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) increases primary productivity and correspondingly enriches heavy isotopes in primary producers (Gu et al., 1996; Xu et al., 2005; Benson et al., 2007). Since consumers at the higher trophic levels reflect the isotopic composition of their assimilated diets, the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of consumers can be expected to reflect the trophic states of their habitats in eutrophic lakes (Xu et al., 2007b). In this study, the range of limnological parameters is broadly comparable between the lakes (Table 1), for example, TP, TN, and algal density in Lake Taihu were higher than those in Lake Chaohu. Primary consumers that derive their essential food sources from the benthic food web, including snails and chironomidae larvae, also showed relatively enriched ^{15}N and ^{13}C in Lake Taihu than in Lake Chaohu. Thus, enrichment in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of shrimps from Lake Taihu could hypothetically result from shrimp deriving ^{15}N - and ^{13}C -enriched prey items in Lake Taihu compared with those in the less eutrophic Lake Chaohu. However, there are plenty of other factors as well as anthropogenic influences

which determine the stable isotope signature within a lake food web. These variables include, but are not limited to, the isotopic signatures and concentrations of dissolved inorganic carbon and nitrogen, algal species composition (e.g., N-fixing cyanobacteria) and growth rate, percentage of fertilizer input, and the geochemistry of nutrient recycling in the lake (Yoshioka & Wada, 1994; Gu et al., 1996; Xu et al., 2007c).

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