STABLE ISOTOPES INDICATE INDIVIDUAL LEVEL TROPHIC DIVERSITY IN THE FRESHWATER GASTROPOD *LYMNAEA STAGNALIS*

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ABSTRACT

In lacustrine ecosystems, benthic grazers are generally thought to feed on sediment detritus and microalgae, although there is a paucity of information on food resource use within populations. In this study, we investigated individual level trophic signatures for grazing snails, *Lymnaea stagnalis*, along with primary consumers and producers in the same habitat, using carbon and nitrogen stable-isotope analyses. In addition, we tested whether ontogeny and parasite presence influence food resource use. The large variation in δ^{13}C and δ^{15}N isotopic signatures indicated that individuals within a population feed on different food sources. Snails appear to have much greater individual variance in trophic behaviour than the other lacustrine species sampled (larval chironomid *Chironomus plumosus*, amphipods, *Gammarus lacustris*, zooplankton *Ceriodaphnia* sp. and *Simocephalus vetulus*). Moreover, variation among snails was not explained by shell length or the presence of parasitic infections. Habitat heterogeneity and resource availability at the microhabitat level may be the primary factors determining individual food sources.

INTRODUCTION

Resource diversity supports species co-existence, high biodiversity and resistance to food-web disturbance (e.g. Hori & Noda, 2001; Kondoh, 2003). Food source diversity exists not only among species, but also among individuals within populations (Leite *et al*., 2002; Bolnick *et al*., 2002, 2003). For instance, intrapopulation feeding diversity in blue tilapia has been estimated using stable isotopes, revealing that their food sources were obtained both from the water column and from benthic habitats (Gu, Schelske & Hoyer, 1997).

In lacustrine ecosystems, food source diversity of benthic animals is poorly understood, although benthic invertebrate grazers are generally thought to feed on generalized mixtures of sediment detritus and microalgae (Reavell, 1980; Merritt & Cummins, 1996; Wetzel, 2001). However, recent studies have reported that chironomid larvae and snails feed on chemoautotrophic bacteria and vascular plants in addition to detritus and microalgae (Elger, Barrat-Segretain & Amoros, 2002; Grey, Kelly & Sleep, 2004; Doi *et al*., 2006a, Arakelova & Michel, 2009). The food sources of lymnaeid snails have been extensively studied because these snails are common in lakes and provide a large contribution to benthic and pelagic food webs (e.g. Reavell, 1980; Leite *et al*., 2002; Vander Zanden & Vadeboncoeur, 2002). Lymnaeids provide an important food source for fishes (Vander Zanden & Vadeboncoeur, 2002). Therefore, the intrapopulation food source diversity of benthic animals is important to fully understand the feeding dynamics at higher trophic levels. Like other benthic invertebrates, lymnaeids have generally been considered to be surface grazers that feed on detritus and microalgae in lake sediments (Reavell, 1980). However, lymnaeids can also feed on vascular plants, carrion, the carcasses of other snails and insects, amphibian eggs and even their own offspring (Kolodziejczyk & Martynuska, 1980; Zikhon-Lukonina, 1987; Monakov, 1998; Elger *et al*., 2002). Therefore, we set out to test quantitatively the hypothesis that lymnaeids have large intrapopulation diversity in food resource use.

Trophic ontogeny has been observed with changes in body size and age, mainly in fish (e.g. Gorokhova & Hansson, 1998; Scharf, Juanes & Rountree, 2000; Céréghino, 2006). Benthic invertebrates may also have trophic ontogeny related to body size, due to changes in available food sources related to their mouth size (e.g. Céréghino 2006), movement rates (Monakov, 1998), territoriality, metabolic changes and other physiological changes with body size. To our knowledge, quantitative tests for trophic ontogeny are lacking for lacustrine snails.

Parasites have also been shown to modify the feeding patterns of their intermediate snail hosts (e.g. Barnard & Behnke 1990; Thompson, 1990; De Jong-Brink *et al*., 2001; Michel, McIntyre & Chan, 2007). Parasite-modified behaviour of hosts often results in an increased success of transmission of parasites to subsequent hosts (De Jong-Brink *et al*., 2001), and changes the spatial distribution (Yurlova, Vodyanitskaya & Glupov, 2000) and ecological niche of the host population (Barnard & Behnke 1990; Miura *et al*., 2006). Moreover, hosts may try to compensate for the increased nutritional demands imposed by parasites with increased foraging (Barnard & Behnke, 1990).

Carbon and nitrogen stable-isotope ratios (δ^{13}C and δ^{15}N) have been increasingly used to quantify the food resources used

by macroinvertebrates in various ecosystems (McCutchan *et al.*, 2003). Because carbon stable isotopes typically become enriched by 0.8 (France and Peters, 1997) and ^{15}N is enriched by 3.4 (Post, 2002) relative to an individual's prey, stable-isotope techniques can provide information on food source diversity (Gu *et al.*, 1997; Leite *et al.*, 2002). To test whether there is significant individual variation, and whether this is explained by ontogenetic and parasitic influences on food consumption, we examined the degree of intrapopulation diversity in food sources within a natural population of freshwater snails (*Lymnaea stagnalis* (L.)) by analysing carbon and nitrogen stable isotopes.

MATERIAL AND METHODS

Study site

Samples were collected in Lake Fadikha (54°35′N, 78°12′E), part of the Lake Chany complex in the Barabinskaya lowland of western Siberia. All samples were collected within an area of 140 m^2, in water depths ranging from 0.1 to 0.5 m. The sample site had high microhabitat heterogeneity with sediment, vegetation of macroalgal beds (dominated by *Cladophora* spp.) and vascular plants (mainly *Phragmites australis*). Substrates varied between detritus and vascular plants growing on predominantly silt and clay sediments.

Study species

Lymnaea stagnalis is a dominant gastropod in the Lake Chany complex (Yurlova & Vodyanitskaya, 2005). This snail is an obligatory first intermediate (primary) host as well as the second intermediate host for a number of digenean trematode parasites. The larval stages of the trematode parasite are located in the hepatopancreas, gonad or mantle, depending on the parasite and the host (Esch *et al.*, 2001, 2002). Some trematode species possess larval stages that castrate the snail host, either chemically or directly. Previous studies have shown that *L. stagnalis* is the first intermediate host for 15 trematode species and the second intermediate host for 18 trematode species (Yurlova, 2003; Yurlova *et al.*, 2006). In a previous paper on larval trematodes in western Siberia, we reported the effects on the snail host, including behavioural changes (Yurlova *et al.*, 2000) and reproduction (Yurlova, 2003). We determined that 75–100% (in different years) of infected snails were castrated by the trematode parasites (Yurlova, 2003).

Comparative samples used for isotope analysis included the dominant components of the habitat: benthic invertebrates (chironomid larvae *Chironomus plumosus* and amphipods *Gammarus lacustris*), zooplankton species (*Ceriodaphnia* sp. and *Simocephalus vetulus*), macroalgae *Cladophora* spp., the vascular plant *Phragmites australis*, sediment organic matter (SOM, mainly in silt and clay) and particulate organic matter (POM).

Sample collection and preparation

We collected *L. stagnalis* (total 39 individuals) at depths of 0.1–0.5 m in August 2002 randomly by hand, across various substrates including sediment, detritus and macrophytes. The snails were measured (length of shell from apex to aperture) with a sliding calliper, dissected and examined for the presence of trematodes using a microscope in the laboratory. The 23 individuals of *L. stagnalis* with infections of *Plagiorchis* species (90.5% of the observed trematodes) and 16 uninfected snails were processed for stable-isotope analysis. The foot was dissected from each snail, since the foot is primarily muscle. Because lipids have lower $\delta^{13}C$ values and therefore affect the ecological interpretation of carbon isotope data (Kurata, Minami & Kikuchi, 2001), lipids were removed using a chloroform–methanol mixture (2:1 by weight).

Sediment grab samples were collected (three replicates, see Doi *et al.*, 2004) in August 2002. Isotope samples were taken from (as specified above) SOM, *Cladophora* species, chironomid and amphipod benthic invertebrates. In a previous study (Doi *et al.*, 2006b) we sampled zooplankton (*Ceriodaphnia* sp. and *S. vetulus*), a vascular plant (*P. australis*) and POM at the same study site and during the same season (August) and therefore we incorporated the carbon and nitrogen isotope data from that study.

Stable-isotope analysis

All samples were oven-dried at 60°C for at least 24 h and stored in a freezer at −20°C until stable-isotope analyses were completed. The carbon and nitrogen isotope ratios of the samples were measured with a mass spectrometer (DELTA plus, Finnigan MAT). The results are presented using common delta notation calculated as: $\delta^{13}C$ or $\delta^{15}N = (R_{sample}/R_{standard} - 1) \times 1{,}000$ (‰); where R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio for $\delta^{13}C$ or $\delta^{15}N$, respectively. Pee Dee Belemnite and atmospheric nitrogen were used as $\delta^{13}C$ and $\delta^{15}N$ world standards, respectively. Analysis error was within ± 0.2 for $\delta^{13}C$ and $\delta^{15}N$. Doi *et al.* (2008) showed that there were no significant differences among carbon and nitrogen isotope values of tissues (foot, gonad and hepatopancreas). Thus, the isotopic values taken from a single component of somatic tissue are representative for the whole body in *L. stagnalis*.

Data analysis

We compared snail $\delta^{13}C$ and $\delta^{15}N$ values to the values of primary producers and primary consumers, including zooplankton and benthic invertebrates (amphipods and chironomids), to estimate the food sources of snails, since isotope values of primary producers indicate potential food sources, and primary consumers provide an isotope baseline for the food web (Post, 2002). We used Pearson's correlation coefficient to determine relationships between body size and isotope values, and analysis of covariance (ANCOVA) to test the effect of infection on tissue isotope values (shell lengths as covariance). To test the differences among consumer species, we used one-way ANOVAs. All statistical analyses were performed using R v. 2.7.0 (R Development Core Term, 2008). Since we could not discriminate between infected and uninfected *L. stagnalis* in the field, sample sizes were different between infected and uninfected snails.

RESULTS

The foot tissue of *Lymnaea stagnalis* demonstrated a broad range of $\delta^{13}C$ and $\delta^{15}N$ values. These ranges were much larger than those of other invertebrates (Table 1, Fig. 1). Isotope results suggest that the food sources of zooplankton, especially cladoceran species (*Ceriodaphnia* sp. and *Simocephalus vetulus*) and amphipods (*Gammarus lacustris*), were mainly derived from POM while the food sources of chironomids (*Chironomus plumosus*) were derived from both POM and surface sediments (Doi *et al.*, 2006b). The results of the ANOVAs for carbon and nitrogen isotopes among consumer species indicate that the variances differed significantly among consumers ($F_{(4,46)} = 1.74$ for carbon, $F_{(4,46)} = 6.37$ for nitrogen, $P < 0.01$). The SD, coefficients of variation (CVs) and the ranges of isotopic values for *L. stagnalis* were notably larger than those of other invertebrates (Table 1), and the sample sizes of *L. stagnalis* ($n = 39$) were substantially larger than those of other invertebrates and potential food sources ($n = 3$–4), although the CVs for the

Table 1. δ^{13}C and δ^{15}N values (mean ± SE), CVs and the ranges of isotope values, and sample size (n) in benthic and planktonic invertebrates from Lake Fadikha in the Lake Chany complex.

	δ^{13}C (‰)			δ^{15}N (‰)			
Species	Mean ± SE	CV	Range	Mean ± SE	CV	Range	*n*
Lymnaea stagnalis	−28.6 ± 0.4	8.5	11.6	7.7 ± 0.3	23.1	7.4	39
Gammarus lacustris	−29.6 ± 0.1	0.4	0.2	8.0 ± 0.2	6.2	1.0	4
Chironomus plumosus	−27.1 ± 0.3	2.1	1.1	7.3 ± 0.1	4.2	1.2	4
Simocephalus vetulus	−30.6 ± 0.2	0.5	0.5	4.7 ± 0.3	12.6	1.2	3
Ceriodaphnia sp.	−30.6 ± 0.2	1.1	0.3	4.6 ± 0.3	10.6	0.9	3

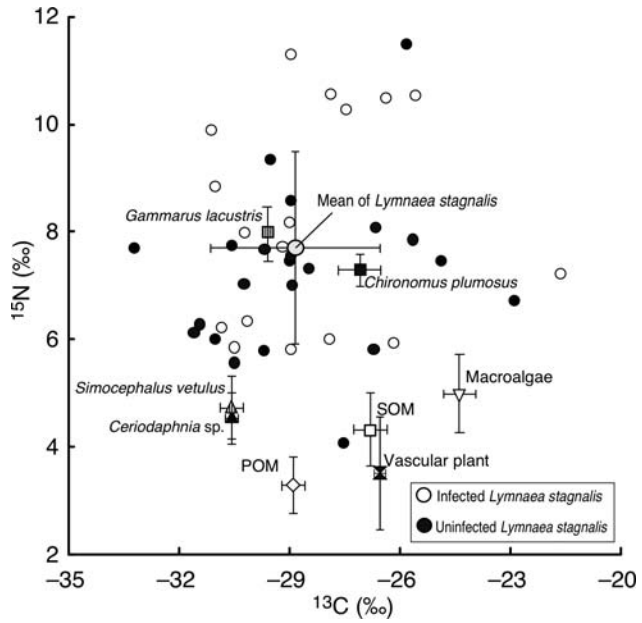

Figure 1. Carbon and nitrogen stable-isotope ratios of the snail *Lymnaea stagnalis*, SOM, macroalgae (*Cladophora* spp.), chironomid larvae (*Chironomus plumosus*), amphipods (*Gammarus lacustris*), zooplankton (*Ceriodaphnia* sp. and *Simocephalus vetulus*), POM and a vascular plant (*Phragmites australis*). Open and filled circles for isotope ratios of *L. stagnalis* indicate trematode-infected and -uninfected individuals, respectively. Error bars indicate ±1 SD.

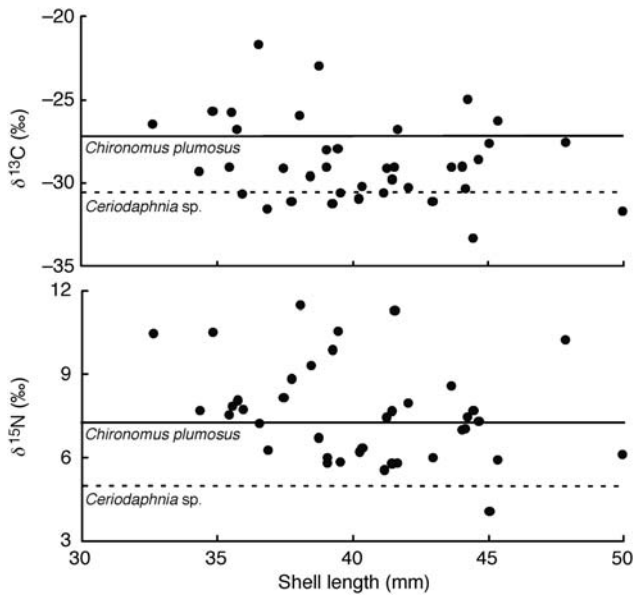

Figure 2. Relationships between shell length (mm) and carbon and nitrogen stable-isotope ratios of *Lymnaea stagnalis*. The lines indicate the mean carbon and nitrogen isotope values of chironomid larvae as the dominant deposit feeder (solid line) and *Ceriodaphnia* species as the dominant filter feeder (dotted line).

isotope data decreased with increasing sample size because of a corresponding reduction in variation (Lancaster & Waldron, 2001).

The shell length of *L. stagnalis* in our sample ranged from 32.6 to 49.9 mm. There were no significant correlations between shell length (mm) and isotope values ($r = -0.289$, $P = 0.06$ for δ^{13}C; $r = -0.247$, $P = 0.13$ for δ^{15}N, $n = 39$; Fig. 2). Trematode-infected and -uninfected individuals also did not differ significantly in δ^{13}C and δ^{15}N values (ANCOVA; $F_{(3,36)} = 1.04$, $P = 0.365$ for δ^{13}C; $F_{(3,37)} = 2.95$, $P = 0.05$ for δ^{15}N; Fig. 1).

DISCUSSION

Our results showed that δ^{13}C and δ^{15}N values in the foot tissue of *Lymnaea stagnalis* varied remarkably among individuals. The differences in isotope signatures indicate that individual snails were using distinctive food sources, since the typical isotope enrichment from diet is smaller than the variation in isotope values observed in the population. However, other potential factors causing variation in isotope signatures also exist and are considered below.

First, the isotope values of the consumers may vary with temporal isotope changes in the primary producers (Zohary *et al.*, 1994; Post, 2002). However, isotope ratios of long-lived animals reflect the mean values of long-term isotope dynamics of primary producers (Post, 2002). The life span of *L. stagnalis* snails in Lake Chany is 2–2.5 years (Yurlova, 2003), and isotope values of mature snails reflect an average of the long-term isotope dynamics of primary producers (Post, 2002). Thus, isotope values of *L. stagnalis* may not reflect the temporal isotope dynamics of primary producers, whereas shorter-lived consumers, including zooplankton and benthic invertebrates, will display this temporal variation.

Second, isotope turnover rate of individuals could have affected the isotope variations. If isotope turnover rates are high, then isotopes provide no more integrated a picture than a single scan of consumer stomach contents. However, isotope turnover time for snails is relatively long, from months to years (Post, 2002). Thus, the isotope variation of the snails may be a result of long-term signal to assimilate food sources rather than the stochastic variation.

Finally, the isotope composition of animals can be affected by dietary shifts during growth (Gu *et al.*, 1997; Gorokhova & Hansson, 1998; Post, 2003). However, in this study we could not detect significant correlations between isotope values and *L. stagnalis* shell length. Therefore, growth and life stage at the

sizes we examined were not the primary factors determining food sources for the adult snails.

We also estimated the effect of parasite infection on the food sources of the snails. Our results suggest that if there are any parasite-induced changes in feeding patterns, they did not affect the δ^{13}C signature of *L. stagnalis*. However, the δ^{15}N signature of *L. stagnalis* was marginally (but not significantly) different between parasite-infected and -uninfected snails. Because δ^{15}N of parasite tissues is generally higher than that of host tissue (Doi *et al*., 2008) as it indicates differences in trophic position (Post, 2002), this would explain the δ^{15}N enrichment in the infected snails.

Since these alternative factors could not explain all of the variation in δ^{13}C and δ^{15}N values, we conclude that variation is a result of snail intrapopulation food source diversity. The isotope signatures indicate that individual snails fed directly and indirectly (i.e. as detritus) on different food sources, such as sediment, microalgae, macroalgae and phytoplankton. Some studies have reported that the food sources for lymnaeids consist not only of detritus and microalgae but also include vascular plants, carrion, the carcasses of other snails and insects, eggs of amphibians and their own fry (Kolodziejczyk & Martynuska, 1980; Monakov, 1998; Elger *et al*., 2002); however, these studies were based on feeding observations. Thus, our study is the first to estimate the assimilation of various food sources of snails using stable isotopes.

We found the intrapopulation variation in food source to be very high among lymnaeids compared with other benthic and planktonic invertebrates in this study and also in comparison with findings from previous studies on chironomid larvae and zooplankton (e.g. Zohary *et al*., 1994; Gu *et al*., 1997; Post, 2002; Doi *et al*., 2004, 2006a, b). The reported intrapopulation variations in these studies (e.g. Doi *et al*., 2004, 2006a, b), are less than $\pm$1.1 (SD). Moreover, Gu *et al*. (1997) showed large intrapopulation variation in stable isotopes of bluegill fish, but the intrapopulation variation in invertebrates in that study was less than $\pm$1.1 (SD), and less than that of the bluegill. However, we should caution that the logistical limitations of that study meant that different sample sizes and methods among taxa made these comparisons difficult to interpret. As our results have indicated that individual variation among snails was considerably higher than expected, it would be fruitful to address future work on individual variation across additional taxa.

Habitat heterogeneity and individual flexibility in habitat preference is likely to underlie the high intrapopulation food source diversity documented here for lymnaeids. The littoral zone of Lake Fadikha contains a variety of microhabitats including soft and hard substrates, macrophytes and vascular plants. We found *L. stagnalis* distributed on a variety of microhabitats, including sediments and submerged and emergent plants, and individuals can move to the water surface and through the water column (Reavell, 1980; N.I.Y., personal observation). This variety of microhabitats may provide various food sources such as phytoplankton, insects, SOM, microalgae, macrophytes and vascular plants. In contrast, *Chironomus plumosus* inhabit only sediments, creating a fixed tube and feeding on surrounding surface sediments (Otto & Svensson, 1980).

In aquatic ecosystems, food sources for benthic invertebrates such as snails and insects have previously been considered to be limited to detritus and microalgae in the sediment. However, here we have demonstrated a more diverse use of food sources within a population of common snails, which was independent of body size and trematode parasite infection. This is an initial step; further study is needed to document the prevalence and test the mechanisms of these findings. We anticipate greater understanding of the fine-scale differences in resource use among lacustrine invertebrates by means of field and laboratory experiments with specific food items and alternative habitat choices.

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