



Widespread natural intraspecific variation in tissue stoichiometry of two freshwater molluscs: Effect of nutrient enrichment



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ABSTRACT

A central premise of ecological stoichiometry is that consumers maintain relatively fixed elemental composition in their bodies, a process known as elemental homeostasis. Although nutrient enrichment is a ubiquitous problem facing many freshwater lakes around the world, intraspecific variation in elemental composition of freshwater invertebrates and its relationship with nutrient loading have not been well addressed. Here, we examined carbon:nitrogen:phosphorus (C:N:P) stoichiometry of two widely distributed molluscs, *Corbicula fluminea* and *Bellamya aeruginosa*, from several subtropical shallow lakes across a nutrient gradient. Our results showed that these two species exhibited substantial natural intraspecific variation in tissue stoichiometry which can reach or even exceed the values among different freshwater taxa investigated before. Our results suggest that tissue P content presents the greatest variations, followed by N content, and lowest in C content. Tissue P content ranged about three-fold (0.56%–1.65%) and five-fold (0.41%–2.28%) for *B. aeruginosa* and *C. fluminea*, respectively. Correspondingly, N content ranged from 5.16% to 12.06% and from 6.47 to 11.36%, respectively. Tissue %P, C:P and N:P ratios were strongly correlated with $\text{PO}_4^{3-}\text{-P}$ and/or chlorophyll-*a* in the water column. Tissue N and P contents of *B. aeruginosa* and P content of *C. fluminea* increased with increasing lake trophic levels (mesotrophic to eutrophic to hypertrophic). These results suggest that the two molluscs can adjust their tissue stoichiometry in relation to nutrient enrichment. Relaxing the assumption of strict homeostasis may help them cope with potential stoichiometric constraints. The results provide additional clues to why these two species are successful invaders and widely distributed.

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1. Introduction

Ecological stoichiometry focuses on understanding how the structure and function of ecosystems are influenced by the balance of chemical elements (carbon:nitrogen:phosphorus [C:N:P] ratios) and energy between the requirements by organisms and local availability in their environment (Elser et al., 2000). A central premise of ecological stoichiometry is that consumer elemental composition is relatively independent of food resource nutrient content, a process known as elemental homeostasis. Elements consumed in excess of the consumer's requirements are excreted or respired, while those limiting in supply are retained. In this context, mismatches between the elemental requirements of a consumer and

the supply of elements in its diet can constrain its growth and reproduction, which in turn affect a range of ecological, biogeochemical and physiological processes (El-Sabaawi et al., 2012b; Elser and Urabe, 1999). A first step in understanding these influences is to identify patterns of variation in the elemental composition of the organisms that may influence ecosystem processes. It is therefore important to characterize the natural variation that exists among individuals in their body stoichiometry and to understand factors that generate it.

To date, studies of organismal stoichiometry have mostly focused on characterizing variability and drivers among taxonomic and functional groups (Cross et al., 2003; Evans-White et al., 2005; Small and Pringle, 2010). In contrast, relatively few studies have examined the extent and causes of intraspecific variability in organismal stoichiometry in natural ecosystems (Frost et al., 2005a). A growing body of evidence suggests, however, that intraspecific variability in organismal stoichiometry is greater than was previously thought (Bertram et al., 2008; El-Sabaawi et al., 2012a,b; González et al., 2011; Small et al., 2011). Therefore, consumer

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body stoichiometry can often track diet or environmental stoichiometry (Frost et al., 2005b; Goloran et al., 2015; Schade et al., 2003, 2005). For example, zooplankton C:P ratio is strongly correlated to the seston C:P ratio (Hessen et al., 2005). A field study also found that invertebrates across multiple trophic levels in the high-P stream had significantly higher P content and lower C:P compared to the low-P stream (Small and Pringle, 2010). That study found that between-stream variation in P content of a given taxon greatly exceeds in-stream variation among different taxa.

Nutrient enrichment is a ubiquitous problem in many freshwater lakes and may lead to increased N and P contents of both seston and periphyton (Frost and Elser, 2002; Qin et al., 2007; Sterner et al., 2008; Liao et al., 2014), which constitute the base of lake food webs. If deviation from strict homeostasis is a widespread phenomenon in freshwater invertebrates, then larger variations in nutrient loading could lead to extensive natural intraspecific variations in stoichiometric (C:N:P) composition of freshwater invertebrate such as molluscs. Still, it is less clear how tissue stoichiometry varies along nutrient gradient for many freshwater molluscs (Cross et al., 2005a; Naddafi et al., 2012; Small et al., 2009; Small and Pringle, 2010). One way to elucidate this question is to assess tissue C:N:P stoichiometry of freshwater molluscs among lakes with different nutrient loading (mainly P and N), as higher contents of these may affect tissue stoichiometry via altered food elemental composition (Naddafi et al., 2009).

To better understand how nutrient loading affects freshwater invertebrate stoichiometry, the natural variation in elemental (C, N and P) stoichiometry is quantified in two molluscs, the deposit feeder *Bellamyia aeruginosa* (Gastropoda) and the suspension feeder *Corbicula fluminea* (Bivalvia), from several lakes that vary widely in nutrient concentrations. *C. fluminea* mainly feeds on phytoplankton and particulate organic matter (Sousa et al., 2008) while *B. aeruginosa* grazes on periphyton off sediments and macrophytes (Chen and Sung, 1975). We chose these two species because they are widely distributed in Chinese lakes, rivers and reservoirs, suggesting that they have a wide variation in habitats and environmental conditions. In addition, *C. fluminea* is an invasive species for many freshwater ecosystems in North America, South America and Europe (Sousa et al., 2008), indicating this species is able to change tissue stoichiometry in response to the variation in elemental composition of their food in different environments (Naddafi et al., 2009, 2012).

In this study, we measured tissue elemental stoichiometry of *B. aeruginosa* and *C. fluminea* collected from subtropical shallow lakes across a nutrient gradient. We attempted to address the following questions: (1) What is the natural variation in tissue C:N:P stoichiometry of these two molluscs in lakes with different nutrient loading? (2) Whether tissue C:N:P stoichiometry is related to nutrient gradient of the lakes? We predicted that increases in nutrient concentrations in the medium they live in would result in increased body tissue N and P contents, and decreased tissue C:N and C:P ratios. Besides, according to their feeding habit, we hypothesized that elemental composition of *B. aeruginosa* is significantly correlated with nutrients in surface sediment, while elemental

composition of *C. fluminea* will show a significant correlation with nutrients in the water column.

2. Methods

2.1. Sample collection and laboratory analysis

Specimens of *B. aeruginosa* and *C. fluminea* were collected from 34 subtropical freshwater lakes in China (Table S1). These lakes are all shallow but vary greatly in surface area. Nutrients and chlorophyll a (Chl-*a*) concentrations in water column showed substantial variations among lakes (Table 1). The studied lakes ranged from mesotrophic to hypertrophic. For each lake, one to nine sites located in the pelagic zone were sampled in summer (July or August) from 2007 to 2009. Molluscs were collected by modified Peterson grab and were kept in water for 12 h without food to allow clearance of guts. Shell length of *B. aeruginosa* and *C. fluminea* were measured using a vernier caliper. To reduce the effect of body size on tissue stoichiometry, we selected similar sized *B. aeruginosa* and *C. fluminea* (Table 2 and Fig. S1). Specimens were then stored separately (individually) in a freezer (-20°C) prior to further analyses.

Foot-muscle tissue samples were separated from each specimen with a scalpel and then freeze-dried to constant weight. To prepare for elemental analysis, muscle tissue samples were ground to fine powder with a mortar and pestle. Subsample masses of 500–2000 μg were used for elemental analysis. C and N contents of each specimen were measured with an elemental analyzer (EuroVector EA3000, Italy), and P content was measured as phosphate after hot hydrolysis with potassium persulfate (Naddafi et al., 2012). C:N, C:P, and N:P ratios were reported on molar units, and C, N, and P content were calculated as per gram dry mass.

2.2. Measurement of environmental parameters

In our study lakes, phosphorus often was the limiting factor for primary production (Wang and Wang, 2009). Hence, we considered Chl-*a*, total phosphorus (TP) and orthophosphate ($\text{PO}_4^{3-}\text{-P}$) in water column as proxies for pelagic productivity, while total phosphorus in surface sediment (TPs) as proxy for benthic productivity. Total nitrogen in water column (TN) and surface sediments (TNs) and other water physicochemical parameters were also measured (Table 1). Concurrent to the collection of molluscs, a 2-L water sample was taken about 25 cm above the lake bed at each sampling site to measure TN, TP and Chl-*a* based on the standard methods (APHA, 2012). Conductivity and transparency were measured in situ using YSI 6600 sensor and Secchi disk, respectively. Also, a short sediment core at each site was collected using a gravity sampler equipped with a perspex tube (11 cm in diameter). The upper 3 cm of the cores was extruded and transferred into polyethylene bags. Sediment samples were freeze dried and then ground with a mortar and pestle. TPs and TNs in sediments were determined by subsampling approximately 30 mg of the dried sediment from each site. Next, 25 ml of distilled water was added and the samples were analyzed, using a combined persulphate digestion followed by spectrophotometric analysis (Ebina et al., 1983).

Table 1
Descriptive statistics of environmental parameters for the 34 studied lakes.

Environmental variables	Mean \pm SD	Min	Max	CV (%)
Conductivity ($\mu\text{s}/\text{cm}$)	266.6 \pm 171.3	61.5	696.0	64.26
Secchi depth (m)	0.76 \pm 0.64	0.20	3.10	84.22
TN (mg/L)	1.04 \pm 0.64	0.36	3.12	61.61
TP (mg/L)	0.066 \pm 0.051	0.013	0.314	76.10
Chl- <i>a</i> ($\mu\text{g}/\text{L}$)	12.92 \pm 14.67	1.22	77.30	113.56
TSI	57.6 \pm 7.5	40.2	75.1	13.02
TNs (mg/kg)	2281.0 \pm 1673.1	223.7	8251.3	73.35
TPs (mg/kg)	688.9 \pm 483.9	101.5	3645.2	70.24

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