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SIZE DISTRIBUTION AND NUTRIENT EXCRETION OF *MELANOIDES TUBERCULATA* IN A SOUTHERN NEVADA SPRING ECOSYSTEM

Knut Mehler^{1,2} and Kumud Acharya¹

ABSTRACT.—To better understand the impact of *Melanoides tuberculata* on ecosystem processes via nutrient recycling, we quantified the body size distribution, density, and ammonia-nitrogen ($\text{NH}_4\text{-N}$) and soluble reactive phosphorus (SRP) excretion of *M. tuberculata* in Rogers Spring, which is located in southern Nevada. We examined how nutrient recycling rates were related to body size and body nutrient content. We found that small individuals dominated the size structure, density, and $\text{NH}_4\text{-N}$ and SRP excretion rates and that nutrient recycling was determined by biomass rather than by high per capita excretion rates. The $\text{NH}_4\text{-N}$ excretion rates of *M. tuberculata* are between 2 and 27 times higher than the SRP excretion rates in Rogers Spring. These results indicate that *M. tuberculata* in Rogers Spring may be P limited and rather conservative in P recycling. In contrast to stoichiometric predictions, body nutrient content was a poor predictor of excretion rates. However, there was a close correlation between the measured and modeled $\text{NH}_4\text{-N}$:SRP recycling ratio ($\text{NH}_4\text{-N}$:SRP_r), which suggests that diet N:P is more important in predicting $\text{NH}_4\text{-N}$:SRP_r than body elemental composition. Assuming that all excreted nutrients enter the water column, we determined that *M. tuberculata* contributes 17.3 mg N m⁻²d⁻¹ and 3.3 mg P m⁻²d⁻¹ to Rogers Spring. Although densities of *M. tuberculata* in the spring brook were lower than those reported in other studies, we assume that these exotic snails can have a significant impact on ecosystem processes, especially by N recycling in systems with very low ambient nutrient concentrations.

RESUMEN.—Para comprender el impacto de *Melanoides tuberculata* en los procesos de los ecosistemas a través del reciclaje de nutrientes, cuantificamos la distribución del tamaño corporal, la densidad, y el amoníaco-nitrógeno ($\text{NH}_4\text{-N}$) y fósforo soluble reactivo (SRP) en la excreción de *M. tuberculata* en Rogers Spring, localizado al sur de Nevada. Examinamos cómo las tasas de reciclaje de nutrientes se relacionan con el tamaño corporal y el contenido de nutrientes del cuerpo. Encontramos que los individuos pequeños dominaron la estructura de tamaño, densidad y las tasas de excreción de SRP y $\text{NH}_4\text{-N}$. El reciclaje de nutrientes estuvo determinado mediante la biomasa y no por las altas tasas de excreción per cápita. Las tasas de excreción de $\text{NH}_4\text{-N}$ de *M. tuberculata* son entre dos y veintisiete veces más altas que las tasas de excreción de SRP en Rogers Spring. Estos resultados indican que *M. tuberculata* en Rogers Spring puede estar limitado de P y ser más conservador en el reciclaje de P. En contraste con las predicciones estequiométricas, el contenido de nutrientes del cuerpo fue un indicador insuficiente de las tasas de excreción. Sin embargo, existe una estrecha correlación entre la proporción de reciclado $\text{NH}_4\text{-N}$:SRP medido y modelado ($\text{NH}_4\text{-N}$:SRP_r), lo que sugiere que la dieta N:P es más importante en la predicción de $\text{NH}_4\text{-N}$:SRP_r que la composición elemental del cuerpo. Asumiendo que todos los nutrientes excretados entran a la columna de agua, se determinó que *M. tuberculata* contribuye 17.3 mg N m⁻²d⁻¹ y 3.3 mg P m⁻²d⁻¹ a Rogers Spring. Aunque la densidad de *M. tuberculata* en el manantial fue inferior a la reportada en otros estudios, suponemos que estos caracoles exóticos pueden tener un impacto significativo en los procesos del ecosistema, especialmente mediante el reciclaje de N en los sistemas con concentraciones ambientales de nutrientes muy bajos.

Exotic mollusks have invaded many freshwater systems in the United States, so efforts have been made to better understand their impacts on ecosystem functions such as nutrient recycling. Ecological stoichiometry is based on the imbalance between an organism's nutrient composition and that of its diet, making stoichiometry an appropriate framework to predict nutrient recycling (Sterner and Elser 2002, Vanni 2002). Organisms assimilate the nutrients they need to maintain homeostasis and then excrete excess nutrients. The rate at

which nutrients are recycled is further dictated by allometric scaling, which is the decrease in nutrient recycling rates (per unit of body mass) in relation to body size (Elser and Urabe 1999). The released nitrogen N:P ratio is of particular interest because N and P are essential nutrients for primary producers in benthic food webs. Previous studies demonstrate that invasive gastropods can represent a significant source of N and P, particularly if they occur in high densities (Hall et al. 2003, Kerans et al. 2005).

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The red-rimmed melania (*Melanoides tuberculata*) is native to subtropical Asia, Africa, and Australia (Duggan 2002). This snail was introduced into the United States by the aquarium trade in the mid-1960s (Murray 1964) and has infested many freshwater ecosystems. It primarily prefers a shallow, freshwater water body with a low velocity, warm temperature (21–30 °C), and muddy to sandy substrate (de Kock and Wolmarans 2009). Concerns arise because *M. tuberculata* has direct impacts on native snails through food competition and egg predation (Ladd and Rogowski 2012). It is also a host for trematodes, which are detrimental to fish and humans (Mitchell et al. 2005). *Melanoides tuberculata* is also parthenogenetic, which can result in tremendous population growth. Once established, this snail species can reach densities between 2000 and 16,000 snails m⁻² (Freitas et al. 1987, Freitas and Santos 1995), and maximum densities of 50,000 snails m⁻² have also been reported (Roessler et al. 1977). Based on its diet, *M. tuberculata* is considered a generalist herbivore and detritivore. It feeds on diatoms, periphyton, and detritus (Pointier et al. 1991). Despite the growing recognition of the impact of this snail on native fauna (Rogowski 2012, Ladd and Rogowski 2012), there is no available information regarding its contribution to ecosystem processes based on nutrient recycling.

Previous studies have shown that body size and the elemental composition of the consumer and its food are important factors that dictate nutrient recycling (Torres and Vanni 2007, Devine and Vanni 2002, Vanni 2002). However, little is known about how these factors determine nutrient recycling rates and ratios in *M. tuberculata*. The objective of this study was to quantify the mass-specific areal ammonium (NH₄-N) and soluble reactive phosphorus (SRP) excretion rates of *M. tuberculata* among a wide range of body sizes in a spring brook in southern Nevada. Additionally, the body N and P content of the snails and their potential diet were measured to determine if N and P excretion rates reflect body size and body elemental composition. Finally, the mass-specific excretion rates were multiplied by snail biomass to determine if *M. tuberculata* contributes to N and P fluxes by high per capita and mass-specific excretion rates or by high abundances.

METHODS

Study Site

Nutrient excretion experiments were conducted in the spring brook of Rogers Spring, which is located in the discharge area of the carbonate-rock aquifer system within the Lake Mead National Recreation Area in southern Nevada. Old carbonate rocks are displaced by younger, less permeable evaporite rocks along the Rogers Fault, which forces the groundwater to flow upward to the surface and form a pool. The source of the spring is near the center of the pool, and water flows out into the spring brook, which is between 0.75 m and 1 m wide. Rogers Spring is hyperoligotrophic with total dissolved nitrogen and total phosphorus concentrations of 220 µg L⁻¹ and 4 µg L⁻¹, respectively. Several invasive species have been introduced or transplanted into Rogers Spring, such as convict cichlids (*Amatitlania nigrofasciata*), spotted tilapia (*Tilapia mariae*), goldfish (*Carassius auratus*), sailfin mollies (*Poecilia latipinna*), golden shiners (*Notemigonus crysoleucas*), and mosquitofish (*Gambusia affinis*) (Courtenay and Deacon 1982). However, these fish species were restricted to the spring source and were not found in the spring brook. *Melanoides tuberculata* was most likely introduced into Rogers Spring through intentional release from fish tanks and they are the dominant benthic invertebrate in the spring brook.

The spring brook of Rogers Spring is a representative *M. tuberculata* habitat because the water is shallow (0.05–0.3 m) and warm (30.6 °C) with a low flowing velocity (range 0.7–1.9 m s⁻¹) and a muddy to pebbly substrate. The ambient NH₄-N and SRP concentrations are both 0.003 mg L⁻¹. Unlike other springs in southern Nevada, the groundwater is rich in K⁺, Na⁺, Ca⁺, Mg²⁺, and SO₄²⁻ ions, which cause a very high electrical conductivity of 3180 µS cm⁻¹.

Snail and Periphyton Sampling and Nutrient Excretion Experiments

Because previous studies reported juvenile recruitment coinciding with warmer months (Dudgeon 2009), we expected to have access to the entire range of *M. tuberculata* size classes by early fall. Therefore, we conducted density and biomass estimations and nutrient experiments in October 2012. For density and biomass estimations, snails were collected

from 5 transects that were oriented perpendicular to the channel along a 20-m stretch of the spring brook (with 5-m between each transect). At each transect, 3 samples were taken from the left bank, the right bank, and the center of the spring brook (15 total samples) by pressing a 0.019-m² sampling frame 5 cm into the substrate. The bottom of the frame was closed and the trapped substrate was transferred to a sorting tray. The 3 frames from each transect were pooled together into one composite sample. All live snails were picked by hand, counted, and separated into 4 size classes (<5 mm, 5–10 mm, 11–15 mm, and >15 mm) based on their shell length range (the distance between the tip of the apex and the edge of the bottom lip). In the laboratory, the snails were dried at 60 °C, and the density and biomass for each size class were scaled up to the spring brook bottom area of 1 m².

For nutrient excretion experiments, 5 snails from each size class were chosen (20 samples total) by haphazardly picking them from each transect. They were measured to the nearest 0.1 mm, and then rinsed with prefiltered (0.45- μ m pore size) spring water (shell length ranges within size classes: <5 mm: 3.1–4.8 mm; 5–10 mm: 7.6–9.7 mm; 11–15 mm: 11.1–14.5 mm; >15 mm: 16.8–24.7 mm). The snails were then placed individually into acid-washed plastic tubes containing 45 mL of prefiltered spring water. The plastic tubes with snails were kept at an ambient temperature by securing each tube to a rack and placing the racks back into the spring brook. Five control tubes without snails were used to account for ambient NH₄-N and SRP in the spring water. After 1 h, the water was immediately filtered through a 0.7- μ m filter and analyzed for NH₄-N and SRP using the phenol-hypochlorite technique (Solozarno 1969) and the molybdate blue ascorbic acid technique (APHA 1992), respectively. Per capita excretion rates were calculated as the differences between the initial and final nutrient concentrations in each tube after incubation. After the excretion experiments were completed, the snails were removed from the tubes, immediately frozen, and transported to the laboratory. Mass-specific excretion rates were calculated after standardizing the body size by dividing the per capita excretion rates by the body mass. Areal N and P excretion were scaled up for the entire spring brook by multiplying per capita

and mass-specific excretion rates by the average snail biomass per m² for each size class ($n = 4$) and in each transect ($n = 5$).

Periphyton was collected from a minimum of 10 haphazardly selected cobbles from each frame (150 cobbles total) by brushing it into acid-washed plastic bottles. The suspension was filtered through pre-ashed filters (0.7- μ m pore size), and then the filters were frozen, and later dried and ground for N and P analysis.

Elemental Analysis of Snails and Periphyton

In the laboratory, the body tissue of thawed snails was separated from the shells using sterilized forceps and then ground to a fine powder. Snails and periphyton were analyzed for P using the ascorbic acid method. The samples were digested in potassium persulfate and sulfuric acid for 1 h at 121 °C, and a spectrophotometer (UV PharmaSpec-1700, UV-VIS spectrophotometer, Shimadzu, Columbia, MD, USA) was used to determine P concentration. Apple leaves were used as a P standard reference (1515 Apple Leaves, National Institute of Standards and Technology, U.S. Department of Commerce). Snails and periphyton were analyzed for C and N by dry combustion at 960 °C using an elemental analyzer (Perkin-Elmer 2400 Series II CHNS/O Analyzer, Waltham, MA, USA) at Goldwater Environmental Laboratory at Arizona State University. Carbon, N, and P concentrations were calculated as a percentage per unit dry mass (DM), and C:N, C:P, and N:P ratios were calculated based on molar units.

To estimate the role of body N:P and food N:P on the NH₄-N:SRP excretion ratio (hereafter NH₄-N:SRP_r) for individuals used in the excretion experiments, we used the Sterner (1990) stoichiometric model, which estimates fluxes of N and P in and out of zooplankton as follows:

$$s = f/(1 - L) - bL/(1 - L), \text{ when } f > b \quad (1)$$

and

$$s = f(1 - L)/(1 - Lf/b), \text{ when } f < b, \quad (2)$$

where s is the nutrient ratio excreted by the consumer, f is the N:P ratio of the producer, b is the N:P ratio of the consumer, and L is the maximum assimilation efficiency for the limiting nutrient. Assimilation efficiencies for aquatic herbivores were assumed to be 0.75

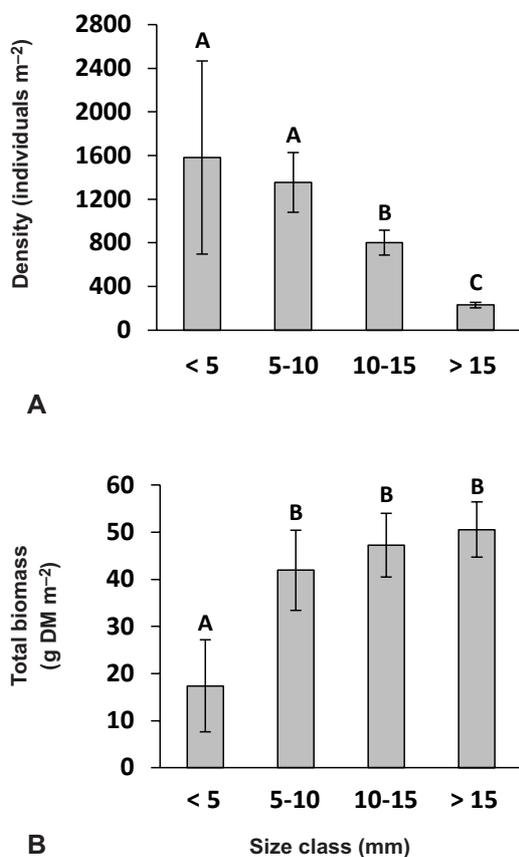


Fig. 1. Density (A) and mean (\pm SE) total biomass (B) among the 4 size classes of *Melanoides tuberculata* in Rogers Spring. The different letters above the bars indicate significant differences among snail size classes ($P < 0.05$).

for all calculations, according to Sterner and Hessen (1994).

Data Analysis

One-way analysis of variance (ANOVA) was used to test for significant differences in snail density and snail biomass among the 4 size classes. One-way ANOVA was used to compare the areal and per capita $\text{NH}_4\text{-N}$ and SRP excretion rates among the 4 size classes to determine if nutrient excretion rates were related to snail size. Simple linear regressions were fitted to determine the slope and intercept relationships between body size (DM including shells) and the mass-specific $\text{NH}_4\text{-N}$ and SRP excretion rates, as well as the $\text{NH}_4\text{-N}$:SRP excretion ratio. To test if body elemental composition of *M. tuberculata* dictates excretion rates and ratios, simple linear

regressions were fitted to determine the slope and intercept relationships between mass-specific body %N, %P, and N:P ratios and mass-specific $\text{NH}_4\text{-N}$ and SRP excretion rates. Differences were considered significant if $P < 0.05$. Before analyses were performed, data were tested for normality and equal variances using the Kolmogorov–Smirnov test and Levene’s test, respectively. All statistical analyses were done in SAS version 8.2 for Windows (SAS Institute, Cary, NC).

RESULTS

Snail Density and Biomass

In Rogers Spring, densities of *M. tuberculata* decreased significantly with body size (ANOVA: $F = 1.67$, $df = 3$, $P = 0.0$; Fig. 1A). In the size class >15 mm, mean densities reached 229 snails m^{-2} . In the size class <5 mm mean densities reached 1581 snails m^{-2} with a maximum value of 5098 snails m^{-2} . Snail biomass (DM, including shells m^{-2}) differed significantly among size classes (ANOVA: $F = 5.03$, $df = 3$, $P = 0.012$). In the size class <5 mm, the mean biomass was 17.4 g DM m^{-2} , but a maximum value of 51.3 g DM m^{-2} was reached in the size class 10–15 mm (Fig. 1B).

Snail Nutrient Excretion Rates

Per capita $\text{NH}_4\text{-N}$ excretion rates were highly variable among size classes. The $\text{NH}_4\text{-N}$ excretion rates were positively related to body size in the size classes <5 mm, 5–10 mm, and 10–15 mm (ANOVA: $F = 0.832$, $df = 3$, $P < 0.001$; Fig. 2A). No differences in the $\text{NH}_4\text{-N}$ excretion rates were found between the size classes 10–15 mm and >15 mm. In contrast, the excreted SRP did not differ significantly among size classes (ANOVA: $F = 2.34$, $df = 3$, $P = 0.23$; Fig. 2B).

The differences among the size classes were also reflected in the areal $\text{NH}_4\text{-N}$ and SRP excretion rates, but in a different pattern. The mean areal $\text{NH}_4\text{-N}$ excretion rate was a significant function of body size (ANOVA: $F = 2.60$, $df = 3$, $P = 0.01$). The mean areal $\text{NH}_4\text{-N}$ excretion rate was 0.24 mg N $\text{m}^{-2}\text{h}^{-1}$ for the size class >15 mm and 0.97 mg N $\text{m}^{-2}\text{h}^{-1}$ for the size class 5–10 mm (Fig. 3A). The mean areal SRP excretion rate was also a significant function of body size (ANOVA: $F = 9.664$, $df = 3$, $P < 0.001$). The size class >15 mm had the lowest mean areal SRP excretion rate

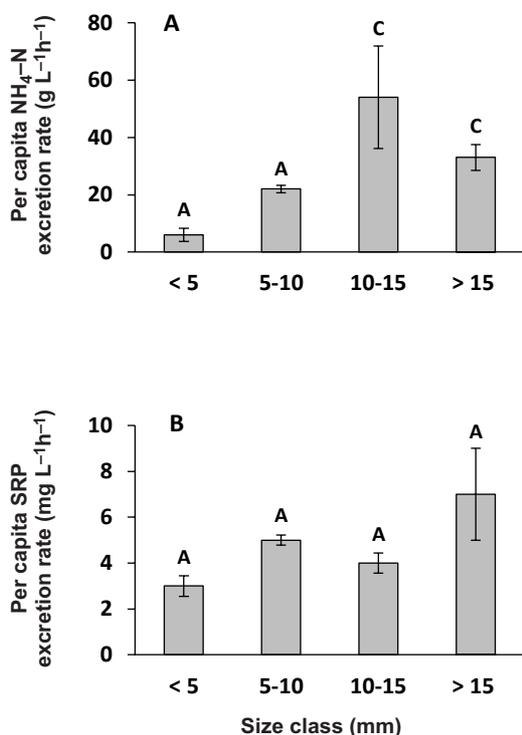


Fig. 2. Mean (\pm SE) per capita $\text{NH}_4\text{-N}$ excretion rate (A) and snail SRP excretion rate (B) among the 4 size classes of *Melanoides tuberculata* in Rogers Spring. The different letters above the bars indicate significant differences among snail size classes ($P < 0.05$).

value, $0.007 \text{ mg P m}^{-2}\text{h}^{-1}$, and the size class $<5 \text{ mm}$ had the highest mean areal SRP excretion rate value, $0.24 \text{ mg P m}^{-2}\text{h}^{-1}$ (Fig. 3B).

Body mass was a poor predictor of per capita $\text{NH}_4\text{-N}$ and SRP excretion rates ($\text{NH}_4\text{-N}$: $r^2 = 0.18$, $P = 0.08$; SRP: $r^2 = 0.02$, $P = 0.12$). However, the mass-specific $\text{NH}_4\text{-N}$ and SRP excretion rates decreased significantly with body mass ($\text{NH}_4\text{-N}$: $r^2 = 0.63$, $P < 0.01$; SRP: $r^2 = 0.69$, $P < 0.01$; Fig. 4A, 4B). Body mass had no effect on the $\text{NH}_4\text{-N}$:SRP_r ($r^2 = 0.003$, $P = 0.67$; Fig. 4C). Excretion rates for $\text{NH}_4\text{-N}$ were $0.17 \mu\text{g N (mg DM)}^{-1}\text{h}^{-1}$ in the size class $>15 \text{ mm}$ and $0.72 \mu\text{g N (mg DM)}^{-1}\text{h}^{-1}$ in the size class 5–10 mm. Excretion rates for SRP were $0.03 \mu\text{g P (mg DM)}^{-1}\text{h}^{-1}$ in the size class $>15 \text{ mm}$ and $0.27 \mu\text{g P (mg DM)}^{-1}\text{h}^{-1}$ in the size class $<5 \text{ mm}$.

Snail and Periphyton Elemental Composition

Body size had no significant effect on either body N and P content or body N:P ratio (%N: r^2

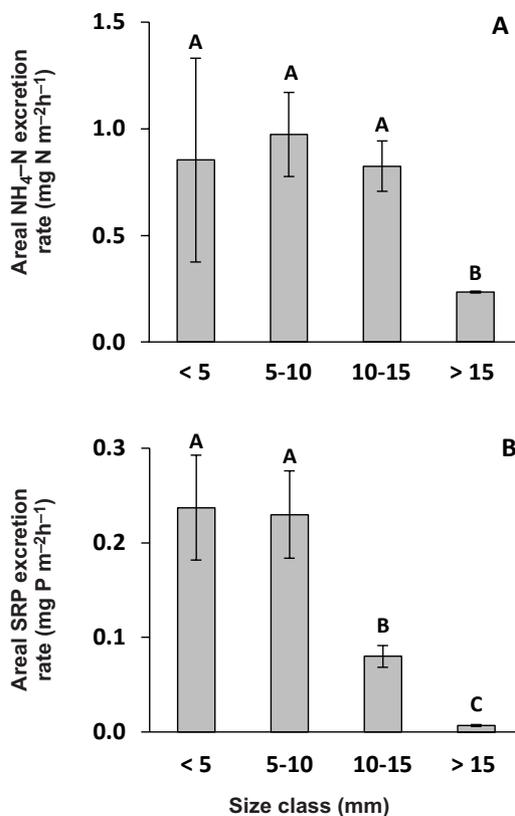


Fig. 3. Mean (\pm SE) areal $\text{NH}_4\text{-N}$ excretion rate (A) and areal SRP excretion rate (B) among the 4 size classes of *Melanoides tuberculata* in Rogers Spring. The different letters above the bars indicate significant differences among snail size classes ($P < 0.05$).

$= 0.02$, $P > 0.1$; %P: $r^2 = 0.004$, $P > 0.1$; N:P: $r^2 = 0.01$, $P > 0.1$). However, both body N content and the N:P ratio slightly decreased with body size. Mean body C content was 40% and N content was 9%. Mean body P content varied only slightly ($\pm 0.6\%$) despite a wide range of body sizes (11–377 mg DM), which resulted in a mean N:P ratio of 33. Periphyton P content was very low (range 0.04%–0.09%), whereas N content ranged from 1.7% to 1.92% and resulted in a very high N:P ratio that ranged from 82 to 95.

We used equation 1 in the Sterner model because diet N:P is much greater than snail N:P, and the results showed a close correlation between the modeled and measured $\text{NH}_4\text{-N}$:SRP_r. On average, the modeled $\text{NH}_4\text{-N}$:SRP_r was 1.7 times higher than the measured $\text{NH}_4\text{-N}$:SRP_r. However, the mass-specific body N and P content, as well as the body N:P ratio,

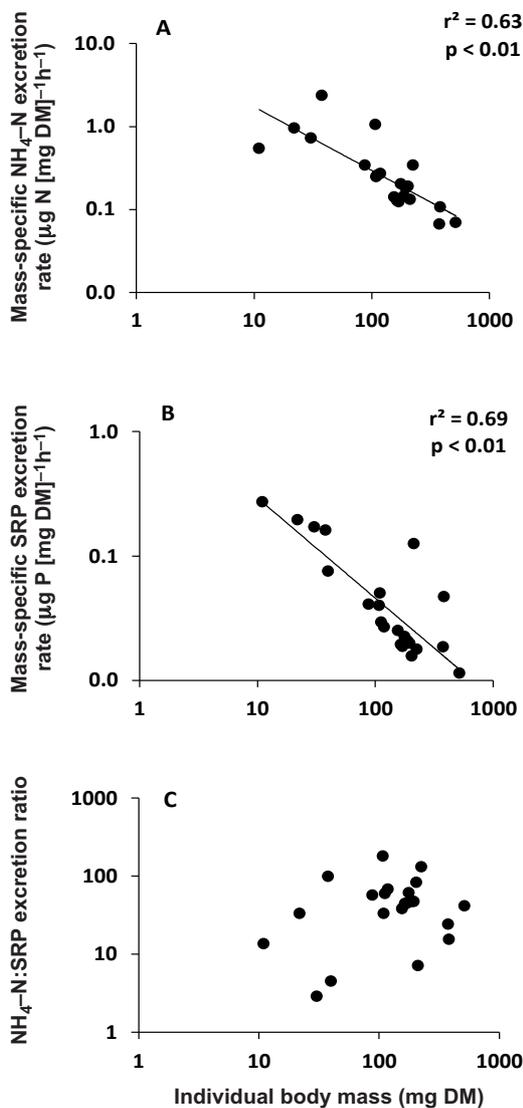


Fig. 4. Linear regressions between individual body dry weight (DM including shell) and mass-specific $\text{NH}_4\text{-N}$ excretion rate (A), mass-specific SRP excretion rate (B), and $\text{NH}_4\text{-N}:\text{SRP}$ excretion ratio of *Melanoides tuberculata* (C). Each point represents the excretion rate and ratio of an individual snail. Regressions not shown when $P > 0.05$.

did not explain the mass-specific $\text{NH}_4\text{-N}$ and SRP excretion rates and the $\text{NH}_4\text{-N}:\text{SRP}_r$ (Fig. 5A–C).

DISCUSSION

Snail Density and Biomass

The size distribution of *M. tuberculata* is important for gaining a better understanding

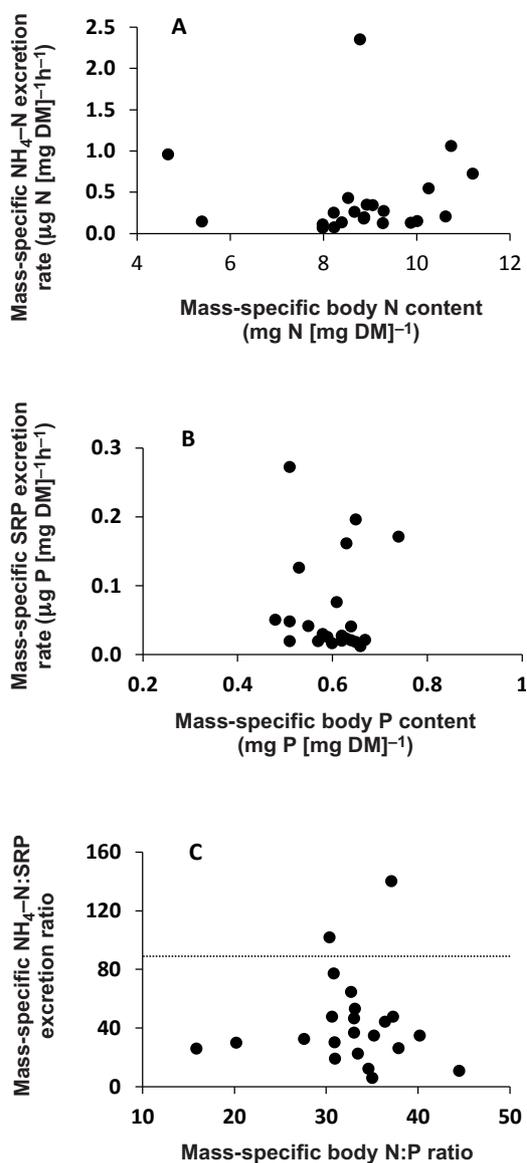


Fig. 5. Mass-specific body N content and mass-specific $\text{NH}_4\text{-N}$ excretion rate (A), mass-specific body P content and mass-specific SRP excretion rate (B), and mass-specific body N:P ratio and $\text{NH}_4\text{-N}:\text{SRP}$ excretion ratio (C) of *Melanoides tuberculata*. Each point represents the excretion rate and ratio of an individual snail. Regressions not shown when $P > 0.05$. The dashed line represents the diet N:P ratio.

of $\text{NH}_4\text{-N}$ and SRP recycling in aquatic ecosystems. Higher areal $\text{NH}_4\text{-N}$ and SRP excretion rates reflected the aggregation of small individuals (size classes <5 mm and 5–10 mm), even though the larger size classes (10–15 mm and >15 mm) had a greater areal biomass.

Mean densities of *M. tuberculata* in this study were far below maximum values reported in other studies (see Freitas et al. 1987, Pointier and McCullough 1989). One reason might be an increase in adult mortality, which reduces density. The water temperature in Rogers Spring is 30.6 °C, which is the upper tolerance limit of this species (Mitchell et al. 2005). However, Bradstreet and Rogowski (2012) showed that density variations of *M. tuberculata* in a Texas spring ecosystem over one year depended on the habitat. Another explanation for densities far below maximum values may be due to the extremely low quality of food in terms of P content. A conservative estimate of the threshold C:P ratio (threshold elemental ratio [TER], Urabe and Wanatabe 1992), based on *M. tuberculata* body C:P ratio of 172 (SD 28) and a maximal growth efficiency for C of 0.5 and for P of 1, yields a C:P ratio of 345 (SD 56), which is far below the value of the potential food source (1335) for *M. tuberculata*. Therefore, we assume that *M. tuberculata* in Rogers Spring is strongly P limited. Periphyton C:N, C:P, and N:P ratios in Rogers Spring were among the highest reported for freshwater ecosystems (e.g., Tibbets et al. 2010—algae C:P: 1119; Cross et al. 2003—stream epilithon C:P: 1741, N:P: 318) and were exceeded only by extremely nutrient-depleted stromatolites found in a spring system in Mexico (Elser et al. 2005). The extremely low food quality at Rogers Spring might be a reason for the very conservative SRP recycling rate compared to that of $\text{NH}_4\text{-N}$. However, *M. tuberculata* may actively search for areas with a higher-quality diet to meet its N:P requirements (see Fink and von Elert 2006), so a diet N:P of 82 may not represent the food they are actually eating.

Relationships between Body Size,
Body Elemental Composition,
and Nutrient Excretion

The results only partially support ecological stoichiometric theory. A positive relationship between body size (in terms of body mass) and the mass-specific $\text{NH}_4\text{-N}$ and SRP excretion rates was observed, which is in accordance with allometric theory and the prediction that smaller individuals have higher metabolic rates (Peters 1983, West et al. 1997). Previous studies also suggest that temperature can indirectly affect excretion rates by altering

metabolic rates (Devine and Vanni 2002, Postolache et al. 2006). Therefore, we believe that the high water temperature in Rogers Spring (30.6 °C) may be an additional factor that affects excretion rates of *M. tuberculata*.

In contrast, body elemental composition alone was a poor predictor of *M. tuberculata* excretion rates. Unlike results of Vanni et al. (2002), no significant relationship was found between mass-specific body N and P content and $\text{NH}_4\text{-N}$ and SRP excretion rates, or between body N:P and the excreted $\text{NH}_4\text{-N}$:SRP ratio. There was only a slightly positive relationship between body N content and the per capita $\text{NH}_4\text{-N}$ excretion rate, whereas body P content and the per capita SRP excretion rate were negatively related. The relatively constant body P content (0.6, SD 0.06) also contradicts results from other studies on invertebrates throughout their ontogeny (see Villar-Argaiz et al. 2002, Sterner and Elser 2002), even though snails in this study varied over a broad size range. It is possible that both young and adult *M. tuberculata* have similar P demands, but for different reasons, such as the high growth rates of young snails and the low P regeneration, and consequently low SRP excretion, of adult snails. Furthermore, body P content of *M. tuberculata* in this study was lower compared to other mollusks (e.g., Jurkiewicz-Karnkowska 2002, Tibbets et al. 2010). This may be an evolutionary adaption of low body demands for P (e.g., Hessen et al. 2004) or an adaptive strategy to successfully survive and develop in newly invaded ecosystems with low dietary P content. This would make *M. tuberculata* a strong competitor that can outpace native snails, particularly in P-limited ecosystems.

Mass-specific $\text{NH}_4\text{-N}$ excretion rates of *M. tuberculata* ($0.7\text{--}1.1 \mu\text{g N (mg DM)}^{-1}\text{h}^{-1}$) were slightly higher than those of *Potamopyrgus antipodarum* in an N-limited Rocky Mountain stream ($0.1\text{--}0.46 \mu\text{g N (mg AFDM)}^{-1}\text{h}^{-1}$; Hall et al. 2003) and higher than those of *Tarebia granifera* in tropical streams ($0.02\text{--}0.76 \mu\text{g N (mg AFDM)}^{-1}\text{h}^{-1}$; Moslemi et al. 2012). The mass-specific $\text{NH}_4\text{-N}$ excretion rates of *M. tuberculata* were twice as high as the upper limit of the N excretion range of zebra mussels ($0.045\text{--}0.32 \mu\text{g N mg}^{-1}\text{h}^{-1}$; Arnott and Vanni 1996), except for the largest size class (>15 mm). The mass-specific excretion rates of *M. tuberculata* in this study might be even higher

because we used DM instead of AFDM. By taking an average of 21.7% of AFDM in DM calculated for several snail species (Zhang et al. 2009), we expect the mass-specific $\text{NH}_4\text{-N}$ and SRP excretion rates of *M. tuberculata* to be about 20% higher than those presented above.

Although excretion rates of *M. tuberculata* (240–973 $\mu\text{g N m}^{-2}\text{h}^{-1}$ and 6.9–237 $\mu\text{g P m}^{-2}\text{h}^{-1}$) were slightly higher compared to those of *Tarebia granifera* (0–900 $\mu\text{g N m}^{-2}\text{h}^{-1}$; Moslemi et al. 2012). The mean per capita $\text{NH}_4\text{-N}$ and SRP excretion rates were within the range of *Corbicula fluminea* (Lauritsen and Mozley 1989). However, areal excretion rates were much lower than those of *Corbicula fluminea* (270–6480 $\mu\text{g N m}^{-2}\text{h}^{-1}$ and 630–15,500 $\mu\text{g P m}^{-2}\text{h}^{-1}$; Lauritsen and Mozley 1989). Therefore, the results confirm that high areal excretion rates of *M. tuberculata* in this study were caused by biomass, rather than individual excretion rates (see also Hall et al. 2003). Nutrient excretion rates for *M. tuberculata* from other freshwater ecosystems could not be compared with these results because previous studies have not been conducted on this species.

A close correlation was found between the modeled and measured $\text{NH}_4\text{-N:SRP}_r$. Due to the lack of a significant relationship between body N:P and $\text{NH}_4\text{-N:SRP}_r$, as well as the very narrow body N:P ratio among the snails, we assumed that food N:P dictates the nutrient excretion rates of *M. tuberculata* in Rogers Spring. This conforms with the findings of Elser and Urabe (1999), who concluded that nutrient release by zooplankton is a function of dietary N:P rather than body N:P. The measured $\text{NH}_4\text{-N:SRP}_r$ of *M. tuberculata* was lower than predicted by the Sterner model (Sterner 1990). To reduce the differences between the measured and modeled $\text{NH}_4\text{-N:SRP}_r$, the assimilation efficiency was adjusted to 0.9 for the limiting nutrient. Although this value seems high considering the extremely low diet P content and the probability of a high P demand due to increased growth rates related to water temperature, *M. tuberculata* may achieve these high assimilation efficiencies in Rogers Spring. However, assimilation efficiencies in the Sterner model (Sterner 1990) provide only a rough estimate of how the limiting nutrient is assimilated. The lack of a tight relationship between body N:P and $\text{NH}_4\text{-N:SRP}_r$ was most likely due to differences in

assimilation efficiencies, even among the same species, or differences in diet N:P ratios. Periphyton N:P can range between 10 and 112 in spring ecosystems throughout Nevada (Mehler unpublished data), so assimilation efficiencies may range between 0.4 and 0.9 (Valiela 1995).

CONCLUSION

This study provides estimates of density, biomass, and excretion rates for *M. tuberculata* in southern Nevada spring ecosystems that have not been previously reported. The nutrient recycling of *M. tuberculata* is of particular interest because once these mollusks invade an ecosystem they can become the dominant snail species and may monopolize the nutrient recycling (Guimaraes et al. 2001, Rader et al. 2003). However, we assume that areal $\text{NH}_4\text{-N}$ and SRP excretion were far below maximum values due to relatively low densities of *M. tuberculata* in Rogers Spring. Additional to fluxes from bacterial production (Hotchkiss and Hall 2010), the influence of *M. tuberculata* on primary production due to nutrient recycling may be dependent on temporal variability in population size. Additionally, nutrient excretion experiments were based on a one-time sampling event in early fall, and the C:N:P ratios of food sources may change temporally. To what extent the size structure, and consequently the areal excretion rates, of *M. tuberculata* changes over the period of one year should be investigated further. A study of this nature would be particularly interesting because the temporal variability of water temperatures in spring ecosystems is usually much lower than that of lotic and lentic ecosystems. Although there are no data on the N and P uptake by primary producers in Rogers Spring, we believe that *M. tuberculata* can affect nutrient recycling in ecosystems with very low ambient N and P levels. We determined that *M. tuberculata* contributes 17.3 $\text{mg N m}^{-2}\text{d}^{-1}$ and 3.3 $\text{mg P m}^{-2}\text{d}^{-1}$ to Rogers Spring nutrient loads. Considering the high $\text{NH}_4\text{-N:SRP}_r$, *M. tuberculata* may be able to increase P limitation for primary producers (also see Hall et al. 2003). To better understand the effect of *M. tuberculata* on ecosystem processes, the contribution of this mollusk to N and P recycling in freshwater systems should be determined under different ambient nutrient concentrations and size structures.

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