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Stoichiometry, growth, and fecundity responses to nutrient enrichment by invertebrate grazers in sub-tropical turtle grass (*Thalassia testudinum*) meadows

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Abstract Although the effectiveness of herbivores in mitigating the effects of nutrient enrichment is well documented, few studies have examined the effects of nutrient enrichment on components of consumer fitness. Enclosures were deployed in shallow turtle grass (*Thalassia testudinum*) beds in Florida Bay, Florida in fall 2003, spring 2004, and fall 2004 to measure the effects of nitrogen and phosphorous enrichment on the growth, fecundity, and stoichiometry of three invertebrate epiphyte grazers commonly associated with *T. testudinum*. The gastropod *Turbo castanea* exhibited significantly greater wet weight gain and lower C:P and N:P in enriched than in ambient treatments. Although nutrient enrichment did not have any significant effects on the growth of caridean shrimp (treatment consisted of several different caridean shrimp species), their C:N was significantly lower in enriched treatments. The final size and stoichiometry of the hermit crab *Paguristes tortugae* was not significantly affected by nutrient enrichment, nor did nutrient enrichment significantly affect the fecundity of *P. tortugae*, the only grazer in which gravid individuals or egg masses were present. Our study demonstrated that nutrient enrichment of primary producers can positively affect the growth of marine invertebrate grazers and alter their stoichiometry; however, these effects were species-specific and may be dependent upon the life stage, specific diets, and/or compensatory feeding habits of the grazers.

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Introduction

Many coastal ecosystems have been adversely affected by nutrient enrichment (e.g., Lapointe and O'Connell 1989; McGlathery 2001; Boesch 2002; Deegan 2002; Deegan et al. 2002). Seagrass meadows are particularly susceptible to the negative effects of nutrient enrichment due to their relatively high light requirements and proximity to land-derived nutrient inputs (Orth et al. 2006). In general, nutrient enrichment promotes the growth of faster growing phytoplankton, epiphytes, and/or macro-algae that can outcompete seagrasses or other submerged aquatic vegetation (SAV) for space and light (see Deegan 2002 and Duarte 2002 and references therein) and can result in subsequent decreases in SAV biomass and shoot density (e.g., Tomasko and Lapointe 1991; Tomasko et al. 1996; Deegan et al. 2002). Although the effectiveness of marine herbivores in mitigating the negative effects of nutrient enrichment on plant health has frequently been demonstrated (see reviews by Burkepile and Hay 2006; Heck and Valentine 2007), few studies have examined the effects of nutrient enrichment on the consumers themselves.

It is well known that both nutrient enrichment and limitation can alter the C:N:P ratios of marine and

freshwater primary producers (e.g., Atkinson and Smith 1983; Clark 2001), which may, in turn, alter their quality as food resources. Primary producers tend to have C:N and C:P ratios that are greater than (i.e., have a lower N and P content) those of primary consumers, resulting in a stoichiometric imbalance. As a result, primary producers with relatively high N or P content are considered high-quality foods because their N and P content is closer to that of the consumer, whereas primary producers with relatively low N or P content are considered poor quality (Russell-Hunter 1970).

Few studies have examined the effects of food quality on consumer C:N:P ratios. A major tenet of ecological stoichiometry is that the elemental ratios of consumers remain constant, regardless of the elemental ratios of the food they ingest (e.g., Elser and Urabe 1999; Sterner and Elser 2002). This consumer homeostasis can be accomplished by the adjustment of assimilation efficiencies with regard to the elemental composition of food, metabolically, or by the choice of food items and the quantity ingested (Sterner and Elser 2002). To date, studies that have investigated stoichiometric homeostasis in various organisms have had mixed results. While some of these studies found no effect of food quality on consumer C:N:P ratios and concluded that the consumer studied was homeostatic (e.g., Stelzer and Lamberti 2002; Bowman et al. 2005), others have found that enriched diets increased the P content of invertebrate grazers (e.g., Cross et al. 2003; Liess and Hillebrand 2006).

In addition to changes in consumer stoichiometry, food quality can impact consumer growth and fecundity. For example, Boersma and Kreutzer (2002) and Hessen et al. (2002) showed that cladocerans (*Daphnia magna*) fed diets of green algae low in phosphorus experienced reduced growth rates. This was also demonstrated by an experiment in which marine isopods fed nutrient-enriched *Fucus* grew faster and produced greater numbers and sizes of eggs (Hemmi and Jormalainen 2002). Other studies have also demonstrated that enriched diets can have positive effects on gonad size or index (e.g., Foster et al. 1999; Cruz-Rivera and Hay 2000) and egg production (e.g., Bonnet and Carlotti 2001; Kraufvelin et al. 2006) of primary consumers. Enriched diets can therefore result in increased consumer abundance (e.g., Schade et al. 2003; Huberty and Denno 2006).

Ultimately, changes in primary producers due to nutrient enrichment, and their subsequent effects on primary consumers, can alter community structure. For example, Tewfik et al. (2007) observed increased consumer density and shifts in functional groups, and decreased consumer diversity, macrodetrital biomass, and seagrass canopy density along a gradient of nutrient loading in Caribbean seagrass beds. Along this gradient, primary consumer diversity was greatest, and primary consumer density least, at intermediate levels of nutrient enrichment. In another example, nutrient-driven changes in the refuge value of the macrophyte canopy and in the food resources of epifaunal grazers led to significantly greater total epifaunal biomass and density in enriched plots, compared to ambient plots at a severely P-limited site in Florida Bay (Gil et al. 2006). These changes in the relative abundance of herbivores due to nutrient enrichment may also alter competitive interactions. When food is limiting, competition between and within consumers may restrict growth and fecundity and thus keep densities and biomass low. Overall, herbivores are more strongly affected by competition than plants and carnivores; however, the strength of competitive effects varies greatly among herbivores (Gurevitch et al. 1992). Additionally, intraspecific competition is usually stronger than interspecific effects among herbivores (Gurevitch et al. 1992). An increase in the quantity or quality of food resources due to nutrient enrichment may release consumers from interspecific and intraspecific competition. This, in turn, could allow their densities and biomass to increase. Conversely, high resource availability can result in lowered consumer species diversity due to the proliferation of opportunistic species (Valiela 1995; Singer and Battin 2007).

In this study, we examined the effects of nutrient enrichment on the growth, fecundity, and stoichiometry of three invertebrate grazers common to *Thalassia testudinum* Banks *ex* König communities in Florida Bay, Florida. Specifically, we addressed the following questions: (1) Do seagrass-associated invertebrate grazers of epiphytes exposed to intense, short-term nutrient enrichment experience greater growth and fecundity compared to those in ambient conditions? (2) Does intense, short-term nutrient enrichment of epiphytic algae lead to changes in the C:N:P ratios of seagrass-associated invertebrate grazers?

Methods

Study sites and experimental organisms

Experiments were performed at sites in both the eastern and western portions of Florida Bay, a largely oligotrophic (Fourqurean and Robblee 1999) estuarine system dominated by *Thalassia testudinum* (turtle grass) meadows. During the fall (October to November) of 2003 and 2004, experiments were performed near Peterson Key (fall 2003: N24°54′48″, W80°44′30″; fall 2004: N24°55′9.18″, W80°44′38.88″) in an area of western Florida Bay that may be subjected to either N- or P-limitation (Armitage et al. 2005). Experiments were performed near Bob Allen Keys (N25°01′50.28″, W80°41′14.1″) during the spring (April to May) of 2004 in an area of eastern Florida Bay that is

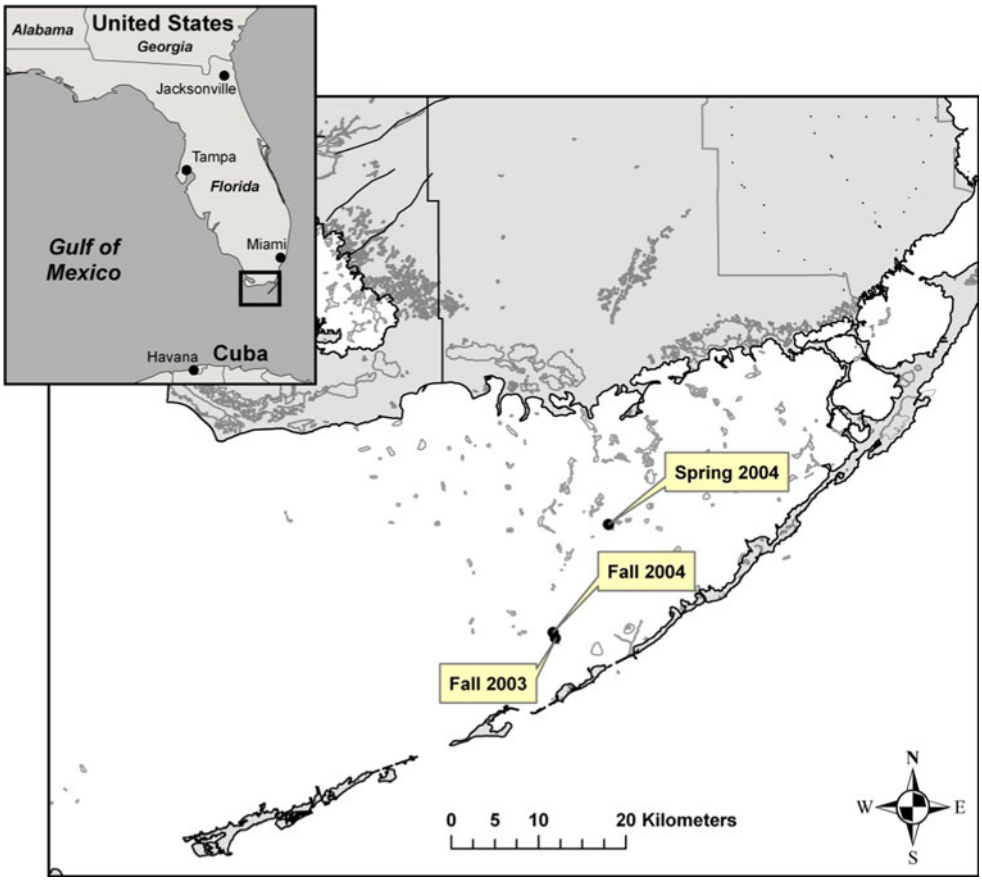

Fig. 1 Map showing location of study sites in Florida Bay, Florida, USA

severely P-limited (Fourqurean and Zieman 2002; Armitage et al. 2005) (Fig. 1).

For our grazer treatments, we chose three locally common epiphyte grazers: the gastropod *Turbo castanea* Gmelin, the hermit crab *Paguristes tortugae* Schmitt, and a combination of the caridean shrimp *Thor manningi* Chace, *Thor floridanus* Kingsley, and *Hippolyte* spp., which could not be reliably identified to species level while alive. All of these grazers are common in the areas in which our experiments were performed (Holmquist et al. 1989; Frankovich and Zieman 2005). Both caridean shrimp (e.g., Quiñones-Rivera and Fleeger 2005) and *T. castanea* (e.g., Frankovich and Zieman 2005) are known to be epiphyte grazers. In general, hermit crabs are thought to be omnivorous detritivores (Hazlett 1981), but some such as *Pagurus* spp. (e.g., Ruesink 2000), and *Paguristes* spp. (e.g., Petersen et al. 2005) are herbivorous. Average natural densities of these organisms ranged from an average of 6.7 to 27.5 individuals m^{-2} (Frankovich and Zieman 2005) for the gastropod *Turbo castanea*, 15–130 individuals m^{-2} for caridean shrimp (*Thor* spp.) (Robblee and Daniels 2003) and 1–12 individuals m^{-2} for the hermit crab *Paguristes tortugae* (Gil et al. 2006). For ease, *T. castanea* will be hereafter referred to as gastropod, *P. tortugae* will be referred to as hermit crab, and the mixture of caridean shrimp species will be referred to as caridean shrimp.

Experimental design

This study was part of a larger effort that examined the combined and separate effects of nutrient enrichment and grazer species composition on epiphyte communities and seagrass condition (Baggett et al. 2010). The design for this portion of the study had two factors: nutrient level and grazer composition. Nutrient level had two nutrient treatments (ambient and enriched), and grazer composition had two single-species grazer treatments (caridean shrimp and gastropods) in fall 2003 and spring 2004 and three single-species grazer treatments (caridean shrimp, gastropods, and hermit crabs) in fall 2004. An experimental duration of 4 weeks was chosen based on previous studies that have shown effects of food quality on consumer growth (e.g., Hemmi and Jormalainen 2002; Stelzer and Lamberti 2002; Kraufvelin et al. 2006; Liess and Hillebrand 2006), fecundity (e.g., Hemmi and Jormalainen 2002; Kraufvelin et al. 2006), and elemental content (e.g., Liess and Hillebrand 2006) in experiments with durations ranging from 14 to 34 days. An additional consideration in choosing the experimental duration was the concern that a longer

experimental duration would result in increased mortality of grazers, particularly the caridean shrimp due to their relatively short life spans. Increased mortality of the grazers would have not only caused a lower recovery of grazers, but also possibly led to the recovery of grazers of lower condition (i.e., one more representative of a dying organism rather than a healthy adult organism) because they were nearing the end of their life span.

Experimental set-up and treatment factors

Experimental enclosures consisted of transparent cylindrical enclosures (0.50 m tall, 0.30 m internal diameter, 0.07 m^2 footprint) deployed 2 m apart in beds of *Thalassia testudinum* at a depth of approximately 0.40 m. The cylinders were covered with mesh tops (0.50 mm) to prevent grazers from escaping and to deter bird predation. Six small holes (5 cm diameter) spaced at regular intervals in the cylinder walls and covered with 0.50 mm mesh allowed water exchange between the cylinders and the outside environment. Nutrients were added to enriched treatment cylinders by suspending a perforated PVC tube filled with 250 g of the controlled-release fertilizer Osmocote™ (18 % N, 6 % P). Approximately halfway through the experimental period (i.e., at the 2-week point), the fertilizer was replaced before it completely dissolved. Fertilizer remaining in the tubes at the halfway point and at the end of the experiments was dried and weighed. These values were then subtracted from the original deployment weight (250 g) to determine fertilizer losses during the course of the experiment, and the resulting values were divided by the number of days of deployment to determine the weight of fertilizer lost per day for each tube. This value was multiplied by 0.18 to determine the nitrogen loading rate (g N day^{-1}) and by 0.06 to determine the phosphorous loading rate (g P day^{-1}). These rates were then converted to mmol N m^{-2} day^{-1} and mmol P m^{-2} day^{-1}, respectively.

In an effort to offset grazer mortality during the course of the experiments, we used initial grazer densities that were considerably higher than reported natural densities. Five gastropods (71 individuals m^{-2}), seventy caridean shrimp (1,000 individuals m^{-2}), and five hermit crabs (71 individuals m^{-2}) were added to their respective treatments. Although we were unable to determine reproductive status of the gastropods and hermit crabs at the beginning of the experiments, care was taken to avoid using gravid caridean shrimp.

Experimental procedure and laboratory analyses

Before being added to the appropriate treatment cylinder, gastropod and hermit crab grazers were blotted dry for 30 s to remove excess water and marked with an identifying number using numbered plastic bee tags adhered with cyanoacrylate glue, and their initial in-shell wet weights were obtained. Before weighing, the aperture lip of the gastropods was also marked with nail polish. In the case of caridean shrimp, we did not mark or obtain initial weight measurements for fear of damaging the shrimp during the process. We also did not obtain initial carapace and total length of individual hermit crabs not only for fear of damaging them, but also out of concern that the hermit crabs would exchange shells, either with each other or with empty shells present in the shell hash substrate, during the course of the experiment. Before experimental grazers were added, we attempted to remove existing grazers from all cylinders using a suction sampling technique modified from Orth and van Montfrans (1987). Four replicates of each nutrient-grazer treatment combination were then randomly assigned to the cylinders.

After 4 weeks, all cylinders were suction sampled to remove grazers and any additional organisms that may have entered the cylinders during the course of the experiment or escaped collection at their beginning (see Table 1 for grazer recovery data). All samples were transported on ice to the laboratory and frozen until further analysis. Upon analysis, the samples were thawed and then sorted using a magnifying lamp and grazers were enumerated. Final in-shell wet weight and lip growth of the gastropods were determined. After these measurements, gastropods were removed from their shells for later stoichiometric analysis by gently tugging the protruding anterior ends of their bodies using forceps; however, if this method proved difficult for certain organisms, their shell was crushed in order to remove the organism in one whole piece rather than risk tearing it in half with the forceps. Hermit crabs were removed from their shells using the same methods as for gastropods. Care was taken to ensure that no pieces of crushed shell were included in any of the weight measurements or stoichiometric analyses. The final carapace length and dry weight of the caridean shrimp and the final in-shell wet weight, carapace length, and total length of hermit crabs were measured. When possible, the females of each grazer species were checked for eggs, and if present, the average diameter of the eggs and average clutch dry weight were determined.

After all measurements were taken, grazers from each treatment replicate were dried for at least 24 h in an 80 °C drying oven and ground to a powder with a mortar and pestle for C:N:P analysis. Following the technique of Sharp (1974), nitrogen and carbon content of the grazers were measured using a Costech 4010 CNS analyzer. Phosphorus content was determined using the standard wet chemical technique of Solorzano and Sharp (1980) and Fourqurean et al. (1992) with samples being analyzed on a Skalar Autoanalyzer.

Table 1 Average grazer recovery (percent, individuals per cylinder, individuals per m^2)

Treatment	Fall 2003	Spring 2004	Fall 2004	Overall average
Average % recovery (±1 SD)				
Gastropod-ambient	30.00 ± 14.14	45.00 ± 34.16	64.00 ± 40.99	50.91 ± 35.06
Gastropod-enriched	0 ± 0	28.00 ± 26.83	53.33 ± 11.55	25.00 ± 27.14
Caridean shrimp-ambient	37.62 ± 21.21	34.29 ± 19.85	34.64 ± 17.86	35.43 ± 17.21
Caridean shrimp-enriched	31.43 ± 28.54	10.48 ± 10.72	33.21 ± 16.59	25.86 ± 20.29
Hermit crabs-ambient			65.00 ± 47.26	65.00 ± 47.26
Hermit crabs-enriched			70.00 ± 47.61	70.00 ± 47.61
Average recovered individuals per cylinder (±1 SD)				
Gastropod-ambient	1.5 ± 0.71	2.25 ± 1.71	3.2 ± 2.05	2.55 ± 1.75
Gastropod-enriched	0 ± 0	1.4 ± 1.34	2.67 ± 0.58	1.25 ± 1.36
Caridean shrimp-ambient	26.33 ± 14.84	24 ± 13.89	24.25 ± 12.5	24.8 ± 12.04
Caridean shrimp-enriched	22 ± 19.97	7.33 ± 7.5	23. 25 ± 11.62	18.1 ± 14.20
Hermit crabs-ambient			3.25 ± 2.36	3.25 ± 2.36
Hermit crabs-enriched			3.5 ± 2.38	3.5 ± 2.38
Average recovered individuals per m^2 (±1 SD)				
Gastropod-ambient	21.43 ± 10.10	32.14 ± 24.40	45.71 ± 29.28	36.36 ± 25.04
Gastropod-enriched	0 ± 0	20.00 ± 19.17	38.10 ± 8.25	17.86 ± 19.38
Caridean shrimp-ambient	376.19 ± 212.05	342.86 ± 198.46	346.43 ± 178.57	354.29 ± 172.06
Caridean shrimp-enriched	314.29 ± 285.36	104.76 ± 107.22	332.14 ± 165.93	258.57 ± 202.87
Hermit crabs-ambient			46.43 ± 33.76	46.43 ± 33.76
Hermit crabs-enriched			50.00 ± 34.01	50.00 ± 34.01

Statistical analyses

For in-shell wet weight of gastropods and hermit crabs, the difference between final measurements and initial measurements was computed for each individual and then averaged for each grazer treatment by cylinder. Final measurements of caridean shrimp carapace length and individual dry weight, hermit crab total length and carapace length, and gastropod shell lip growth were averaged for each grazer treatment by cylinder. For stoichiometric analysis, individuals of each grazer treatment were pooled by cylinder and dried and ground together to produce one C:N:P sample for the appropriate grazer treatment in each cylinder. In a few cases, there was not enough ground material remaining in a sample after C and N analysis to perform P analysis, resulting in a few cylinders having C:N, but not C:P and N:P data for its respective grazer. While C:N:P data were collected for gastropods and caridean shrimp in all three experiments (fall 2003, spring 2004, and fall 2004), morphometric data were not. Gastropod shell and weight measurements were only collected in spring and fall 2004, and caridean shrimp length and weight measurements were only collected in fall 2004. Hermit crab C:N:P and morphometric data exist for fall 2004 only, since that was the lone experiment in which hermit crabs were used. Unfortunately due to wave action and grazer mortality, several replicates were lost each season, resulting in low numbers of replicates of some nutrient-grazer treatments in some seasons. As such, we performed two-way Analyses of Variance (ANOVA) ($\alpha = 0.05$) on variables with data from multiple seasons (gastropod and caridean shrimp stoichiometry and gastropod growth), with the two fixed factors being nutrient enrichment level and season, to determine whether data from the different seasons could be pooled. When necessary, data were transformed using a $\log_{10}(x + 1)$ transformation to meet the assumptions of ANOVA. There was no significant nutrient * season interaction for any of the parameters tested, meaning that the grazers' stoichiometric and growth responses to nutrient enrichment did not differ by season (Table 2). Based on this result, data from all seasons were pooled for gastropod stoichiometry and growth, and caridean shrimp growth, respectively. To ensure that nutrient loading did occur during the course of the study, *Thalassia testudinum* and epiphyte C:N:P ratios were determined using the methods described in Baggett et al. (2010). Again, we performed two-way ANOVAs ($\alpha = 0.05$) to determine whether data from the different seasons could be pooled. Only one significant nutrient * season interaction was found (epiphyte C:P) (Tables 2, 3), and as such, resulting stoichiometric data from all seasons were pooled for *T. testudinum* (C:N, C:P, and N:P) and epiphytes (C:N and N:P), respectively. All organism growth, fecundity, and stoichiometric data as

Table 2 Univariate results of two-way ANOVAs

	df	*F*	*p*
Caridean shrimp C:N			
Season	1, 15	1.777	0.202
Nutrient	1, 15	4.806	0.045
Season * nutrient	1, 15	0.266	0.614
Caridean shrimp C:P			
Season	1, 14	6.082	**0.027**
Nutrient	1, 14	0.019	0.892
Season * nutrient	1, 14	0.026	0.875
Caridean shrimp N:P			
Season	1, 14	6.149	**0.026**
Nutrient	1, 14	0.044	0.837
Season * nutrient	1, 14	0.013	0.912
Gastropod C:N			
Season	1, 11	0.036	0.853
Nutrient	1, 11	7.429	**0.02**
Season * nutrient	1, 11	0.49	0.498
Gastropod C:P			
Season	1, 10	0.906	0.364
Nutrient	1, 10	4.348	0.064
Season * nutrient	1, 10	0.002	0.968
Gastropod N:P			
Season	1, 10	0.509	0.492
Nutrient	1, 10	3.941	0.075
Season * nutrient	1, 10	0.001	0.977
Gastropod wet weight			
Season	1, 6	16.383	**0.007**
Nutrient	1, 6	38.7	**0.001**
Season * nutrient	1, 6	0.012	0.918
Gastropod lip growth			
Season	1, 6	12.319	**0.013**
Nutrient	1, 6	13.105	**0.011**
Season * nutrient	1, 6	0.015	0.908
Epiphyte C:N			
Season	1, 71	48.625	**≤0.0001**
Nutrient	1, 71	5.557	**0.021**
Season * nutrient	1, 71	0.488	0.487
Epiphyte C:P			
Season	1, 65	22.903	**≤0.0001**
Nutrient	1, 65	30.525	**≤0.0001**
Season * nutrient	1, 65	5.26	**0.025**
Epiphyte N:P			
Season	1, 65	1.994	0.163
Nutrient	1, 65	13.278	**0.001**
Season * nutrient	1, 65	3.026	0.087
Thalassia testudinum C:N			
Season	1, 64	4.905	**0.03**
Nutrient	1, 64	2.513	0.118
Season * nutrient	1, 64	1.398	0.241
Thalassia testudinum C:P			
Season	1, 58	3.696	0.059
Nutrient	1, 58	24.259	**≤0.0001**
Season * nutrient	1, 58	0.715	0.401
Thalassia testudinum N:P			
Season	1, 58	1.294	0.26
Nutrient	1, 58	21.456	**≤0.0001**
Season * nutrient	1, 58	0.255	0.616

Significant *p*-values ($p \leq 0.05$) are in bold print

well as *T. testudinum* and epiphyte stoichiometric data (other than epiphyte C:P) were analyzed using independent *t* tests ($\alpha = 0.05$) with the two populations being ambient and enriched. All statistical analyses were performed using IBM SPSS 20.0.0® 2011.

Results

Nutrient effects on primary producer stoichiometry

Nutrient loading rates during the study ranged from 281 to 949 mmol m^{-2} d^{-1} for nitrogen and 41–141 mmol m^{-2} d^{-1} for phosphorous (Baggett et al. 2010). Epiphyte and *Thalassia testudinum* C:P and N:P values obtained at the end of the study were significantly lower in enriched than in ambient treatments, indicating that elevated nutrient loading occurred and that phosphorous in particular was taken up by epiphytes and seagrass (Tables 3, 4).

Grazer recovery

Grazer recovery was low and varied among experimental trials and treatments (Table 1). Overall percent recoveries were highest in the hermit crab treatments, with an overall average of 65.00 % (±47.26 %) recovered in the ambient treatments and 70.00 % (±47.61 %) recovered in the enriched treatments. Overall, an average of 50.91 % (±35.06 %) was recovered in ambient gastropod treatments and an average of 25.00 % (±27.14 %) was recovered in enriched gastropod treatments. In caridean shrimp treatments, average overall recovery was 35.43 %

Table 3 Average epiphyte C:P values by season

	Ambient	SE	Enriched	SE
Fall	434.347	40.271	289.683	43.779
Spring	926.055	61.913	357.682	64.935

Table 4 Results of independent *t* tests

	Ambient mean	Std. error	Enriched mean	Std. error	*df*	*p*
Seagass stoichiometry						
Epiphyte C:N	21.24	1.07	18.92	0.77	1, 73	0.09
Epiphyte N:P	28.39	2.92	17.3	1.88	1, 67	**0.002**
Thalassia testudinum C:N	18.56	0.22	18.07	0.35	1, 66	0.23
Thalassia testudinum C:P	1119.76	43.32	813.31	43.44	1, 60	**≤0.001**
Thalassia testudinum N:P	59.98	2.05	45.58	2.09	1, 60	**≤0.001**
Grazer growth						
Gastropod wet weight gain (g)	0.27	0.06	0.63	0.08	1, 8	**0.01**
Gastropod lip growth (mm)	6.36	0.95	10.19	1.47	1, 8	0.06
Caridean shrimp individual dry weight (g)	1.7×10^{-3}	9.5×10^{-5}	2.0×10^{-3}	8.0×10^{-5}	1, 6	0.06
Caridean shrimp carapace length (mm)	1.96	0.08	1.92	0.12	1, 6	0.8
Hermit crab carapace length (mm)	4.78	0.91	5.06	0.25	1, 4	0.78
Hermit crab dry weight (g)	0.03	0.01	0.03	0.002	1, 4	0.84
Grazer fecundity						
Hermit crab egg diameter (mm)	0.54	0.02	0.5	0.05	1, 3	0.67
Hermit crab clutch weight (g)	2.6×10^{-5}	1.4×10^{-5}	1.8×10^{-5}	4.0×10^{-6}	1, 3	0.7
Grazer stoichiometry						
Gastropod C:N	4.8	0.12	5.4	0.13	1, 13	**0.01**
Gastropod C:P	166.11	32.33	77.6	12.97	1, 12	**0.03**
Gastropod N:P	35.69	7.55	14.68	2.61	1, 12	**0.03**
Caridean shrimp C:N	4.96	0.05	4.81	0.05	1, 17	**0.05**
Caridean shrimp C:P	148.07	25.78	155.2	27.23	1, 16	0.85
Caridean shrimp N:P	30.07	5.42	32.33	5.87	1, 16	0.78
Hermit crab C:N	7.24	0.53	7.46	0.26	1, 8	0.72
Hermit crab C:P	93.84	7.08	90.91	7.93	1, 8	0.8
Hermit crab N:P	13.03	0.77	12.3	1.13	1, 8	0.61

Significant *p* values ($p \leq 0.05$) are in bold print

(±17.21) in ambient treatments and 25.86 % (±20.29 %) in enriched treatments. The number of grazers recovered corresponded to final densities that were greater than reported natural densities for the caridean shrimp and hermit crabs, and close to or within the range of natural densities reported for the gastropods (Table 1).

Grazer growth and fecundity

Nutrient enrichment had a significant positive effect on the growth of the gastropod, with in-shell wet weight gain being significantly greater in enriched than in ambient treatments (independent *t* test, $t_8 = -3.621$, $p = 0.01$) (Fig. 2). No significant effects of nutrient enrichment on the growth of caridean shrimp or hermit crabs were present (Table 4).

Hermit crabs, which were only used in fall 2004, were the only experimental grazer for which gravid individuals or egg masses were observed at the termination of the experiments. There were no significant differences in hermit crab egg diameter or clutch weight between nutrient treatments (Table 4).

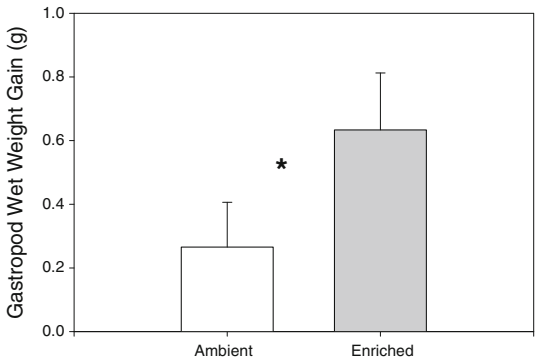

Fig. 2 Effects of nutrients on gastropod wet weight gain (mean ± SD). *Asterisk* denotes a significant difference between the two treatments ($p \leq 0.05$)

Grazer C:N:P

Nutrient enrichment did not have any significant effects on hermit crab stoichiometry but did significantly affect gastropod and caridean shrimp stoichiometry.

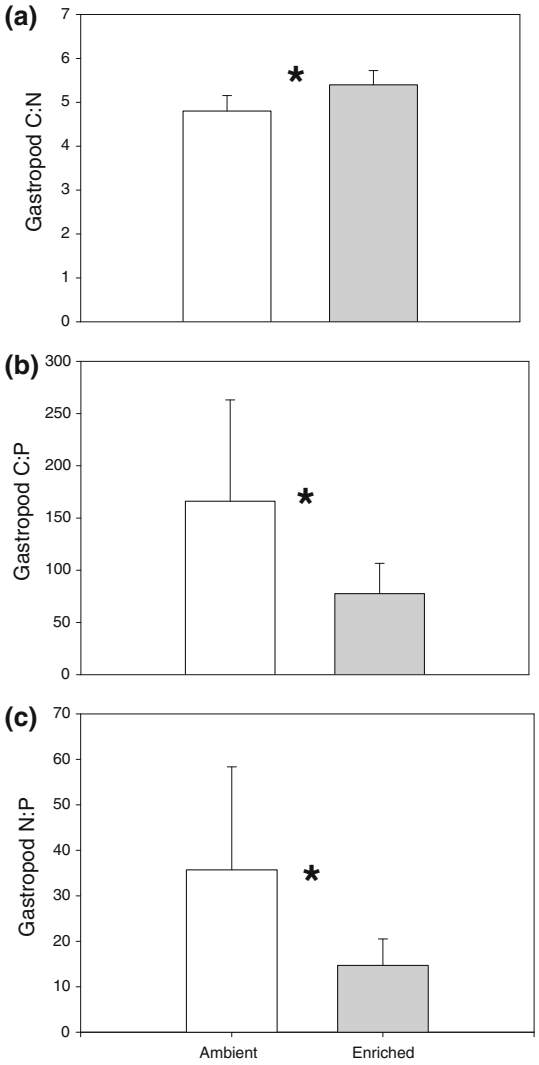

Fig. 3 Effects of nutrients on caridean shrimp C:N (mean ± SD). *Asterisk* denotes significant differences between the two treatments ($p \leq 0.05$)

Gastropod C:P (independent t test, $t_{12} = 2.541$, $p = 0.03$) and N:P (independent t test, $t_{12} = 2.629$, $p = 0.03$) were significantly lower in enriched than in ambient treatments; however, gastropod C:N was significantly higher in enriched treatments (independent t test, $t_{13} = -3.307$, $p = 0.01$) (Fig. 3; Table 4). Caridean shrimp C:N was significantly lower in enriched treatments (independent t test, $t_{17} = 2.101$, $p = 0.05$) (Fig. 4; Table 4), but there were no significant effects of nutrient enrichment on caridean shrimp C:P and N:P. It is important to note, however, that although the difference between caridean shrimp C:N in enriched and ambient treatments was statistically significant, the actual difference between the average C:N values was quite small (approximately 3 %), and thus, this result is not likely to be biologically relevant.

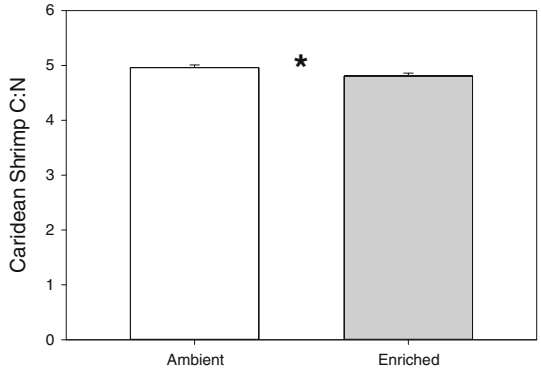

Fig. 4 Effects of nutrients on gastropod C:N (**a**), C:P (**b**), and N:P (**c**) (mean ± SD). *Asterisk* denotes significant differences between the two treatments ($p \leq 0.05$)

Discussion

The nutrient loading rates achieved in our study were much greater than N and P loading rates reported for eutrophic estuaries such as Chesapeake Bay (1.9 mmol m^{-2} d^{-1} N, 0.11 mmol m^{-2} d^{-1} P), Delaware Bay (19.2 mmol m^{-2} d^{-1} N, 1.6 mmol m^{-2} d^{-1} P), Narragansett Bay (2.7 mmol m^{-2} d^{-1} N, 0.22 mmol m^{-2} d^{-1} P), and the Thames Estuary (87.7 mmol m^{-2} d^{-1} N, 8.7 mmol m^{-2} d^{-1} P) (values estimated by Heck et al. 2006 from Nixon et al. 1986), and significant nutrient effects on the stoichiometry of the primary producers indicate that the nutrients were successfully incorporated into their tissues. The high level of nutrient enrichment achieved in this experiment had significant effects on gastropod growth and stoichiometry and caridean shrimp stoichiometry, but had no significant effects on the growth of caridean shrimp and the growth and stoichiometry of hermit crabs. This contrasts with other studies of the effects of diet on crustacean growth which found that growth rates of amphipods (Kraufvelin et al. 2006) and isopods (Hemmi and Jormalainen 2002; Cruz-Rivera and Hay 2003) are often greater when fed nutrient-enriched algae.

Our results on the effects of nutrient enrichment on grazer stoichiometry are harder to interpret. While there are several studies that examined the effects of food quality on fresh-water plankton stoichiometry (e.g., Elser et al. 2002; Van Nieuwerburgh et al. 2004; Ferrao-Filho et al. 2007), there are few that examined its effect on the C:N:P ratios of higher order benthic consumers. Existing studies of the effects of food quality on the nutrient stoichiometry of freshwater macroinvertebrates vary in their results. For example, Bowman et al. (2005) found that the C:N:P ratios of benthic mayflies differed little between nutrient-rich and nutrient-poor sites, and Stelzer and Lamberti (2002) found that food quality and quantity had no effect on the C:N:P ratio of their gastropod grazers. Conversely, Liess and

Hillebrand (2006) found that nitrogen enrichment decreased C:P and N:P ratios of gastropod grazers and suggested that the snails they used were potentially N-limited and possibly grew faster in N-enriched conditions.

Studies on the effects of nutrient enrichment on grazer fecundity and egg characteristics have also produced mixed results. For example, Færøvig and Hessen (2003) found that the C, N, and P content as well as egg mass in *Daphnia magna* and a freshwater crayfish did not differ between reproducing females fed food of varying quality. Conversely, Hemmi and Jormalainen (2002) found that the eggs of isopods fed nutrient-enriched algae were larger and more numerous than those of isopods in the control treatment. In addition, Kraufvelin et al. (2006) found significantly greater numbers of egg-carrying females in gammarids raised on a diet of enriched periphyton, and Cruz-Rivera and Hay (2003) found that low-quality food reduced fecundity for four out of five amphipods in their study.

There are several possible reasons why we observed relatively few nutrient effects in our experiment, and why those we found were primarily linked to gastropods. One likely explanation is that a larger portion of the gastropod's diet may have consisted of epiphytes than did the diets of caridean shrimp and the hermit crab. Although caridean shrimp and hermit crabs are primarily recognized as epiphyte grazers, they may also feed on detritus. It is possible that the caridean shrimp and hermit crabs spent a substantial amount of time feeding on detritus present in the cylinders rather than on the enriched epiphytes and thus did not receive the maximum effects of nutrient enrichment. Although detached dead blades contain much lower N and P concentrations (between 25 and 90 % of initial content) than those when alive (Romero et al. 2006), it is possible that the caridean shrimp were able to consume enough additional N in the enriched treatments, whether from the detritus directly or from bacteria present on the detritus, to result in a significantly lower C:N.

Another possibility is that the life stage and mortality of the caridean shrimp may also have affected how these grazers responded to nutrient enrichment. *Thor floridanus*, which made up a large proportion of our shrimp numbers, have a life span of about 4–5 months (Bauer and Van Hoy 1996). It is possible that the shrimp had already reached adult size and were near the end of their life when they were added to the cylinders at the beginning of the experiments; thus, their growth was not affected significantly by nutrient enrichment. The observed lack of significant effects on the C:P and N:P ratios of caridean shrimp and hermit crabs may be tied to the lack of growth observed with these organisms. The Growth Rate Hypothesis (GRH) states that when organisms are experiencing rapid rates of growth, C:P and N:P ratios may decrease due to the increased amounts of P-rich RNA in the organism's tissues (see discussion in Sterner and Elser 2002). With the gastropod, we observed significantly greater growth under enriched conditions as well as significantly lower C:P and N:P, a result which is in accordance with the GRH. The lack of significant growth effects coupled with the lack of significantly lower C:P and N:P ratios of the caridean shrimp and hermit crabs is also in accordance with the GRH.

A final possibility is that compensatory feeding by the hermit crabs and caridean shrimp occurred during the experimental trials. A previous study by Cruz-Rivera and Hay (2000) demonstrated that some species of marine amphipods exhibit compensatory feeding when offered low-quality foods and that, depending on the species, compensatory feeding may be adequate enough to allow them to achieve fitness equal to that of organisms fed a high-quality diet. It is possible that caridean shrimp and hermit crabs present in unenriched treatments, through compensatory feeding, were able to attain growth equal to that of their counterparts in the nutrient-enriched treatments, thus resulting in no significant differences in growth between the two nutrient treatments.

Compensatory feeding by gastropods may have resulted in the odd result of their significantly lower C:N in ambient rather than in enriched treatments. As previously mentioned, no significant nutrient * season interactions were found with any grazer growth or stoichiometry parameters, even though experiments were performed in different seasons and different study sites, which may suggest that the nutrient regimes between the two sites were similar in their P-limitation. A study on compensatory feeding by freshwater snails by Fink and von Elhert (2006) suggested that compensating for low P-availability is more difficult than compensating for low N- and P-availability and that when only P-availability is low, excess N is ingested by the organisms through their efforts to compensate for low P-availability. It is possible that the P-limitation at our study sites led to compensatory feeding by gastropods in the unenriched treatments, resulting in excess N in their tissues. The excess N would account for the significantly lower C:N in unenriched treatments than found in gastropods in the enriched treatments. This compensatory feeding was not enough, however, for the gastropods in unenriched treatments to attain equal growth to those in the enriched treatments, as was also the case in Fink and von Elhert (2006).

One must also consider the role intraspecific competition may have played in our results. Although our recovery of grazers was quite low, our recovered individuals still resulted in final densities that were much greater than in natural densities for caridean shrimp and hermit crabs (Table 1). Densities of recovered gastropods were either within (enriched treatments) or close to (ambient treatments) the range of natural densities. While grazer

mortality during the experiments is a factor in grazer recovery, the actual final densities of grazers present at the end of the experiments may have been somewhat higher than recovered densities since the recovery process itself was not 100 % efficient. Gastropod grazers residing on cylinder walls, rather than seagrass blades, at the time of collection may have been missed by the suction sampler. In addition, collecting suction samples on a shell hash substrate can be damaged to delicate organisms collected within the sampling, and as such, it was not uncommon to find headless caridean shrimp during sample processing. Because these headless shrimp could not be definitively identified as caridean shrimp, we only included fully intact caridean shrimp in our analyses and thus likely underestimated the actual amount of caridean shrimp present at the end of the experiments. If we were to assume though that grazer recovery is approximately equal to grazer survivorship, it is interesting to note that the majority of nutrient effects occurred in gastropod treatments, where recovered densities were within or close to natural densities. Perhaps densities in the gastropod treatments were low enough so that competition for food resources did not exist, and the gastropods were able to achieve greater growth on the higher quality food present within the enriched treatments. In the caridean shrimp and hermit crab treatments, where average recovered densities ranged from two to four times greater than natural densities, intraspecific competition may have resulted in decreased food resources which may have, in turn, negatively impacted grazer growth in both the ambient and enriched treatments.

In summary, our study demonstrates that nutrient effects on the stoichiometry of primary producers can positively affect the growth of marine invertebrate epiphyte grazers and may also alter the stoichiometry of the grazers. However, these effects were species-specific and may be dependent upon the life stage, specific diets, compensatory feeding habits of the grazers, and/or intraspecific competition. These effects may, in turn, alter community structure by affecting the fitness and/or fecundity of some grazers but not others, thus leading to shifts in the relative abundance of grazer species. Changes in the relative abundances of invertebrate epiphyte grazers, as well as other primary consumers, may, in turn, affect higher trophic levels. Since eutrophication is increasing in both marine and freshwater habitats, further research is necessary to understand the effects of nutrient enrichment on consumers and why there is such variation in the responses of different taxa and between freshwater and marine environments.

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