# Predicting rates of consumer-mediated nutrient cycling by a diverse herbivore assemblage

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**Abstract**

Herbivores mediate the abundances of primary producers both from the top-down, by consuming them, and from the bottom-up, by recycling nutrients. Whereas the top-down effects of herbivores on algae in marine ecosystems are well-documented, less is known about their roles as mediators of local-scale nutrient availability. We conducted a series of surveys and measurements of tide pools and the grazers in those pools between October of 2016 and June of 2017 at an intertidal site on the coast of Southern California, USA (33° 35' 16.3" N, 117° 52' 1.5" W). We surveyed grazer abundances in the field, measured biomass of representatives from four different grazer groups (littorine snails, limpets, chitons, and turban snails), measured ammonium excretion rates, and quantified ammonium accumulation rates in tide pools at our study site. We found that different grazer groups were characterized by different per-biomass ammonium excretion rates. Some grazer groups – turban snails and chitons – contributed more ammonium than predicted by their biomass, whereas other grazer groups – littorine snails and limpets – contributed less ammonium than predicted by biomass. Because of these differences between grazer groups, ammonium accumulation rates in tide pools at our study site were effectively predicted based on the ammonium excretion rates of the different grazer groups. However, ammonium accumulation rates were not related to total herbivore biomass. Our results highlight the importance of grazer identity – and particularly the role of species such as turban snails that contribute disproportionately to nutrient recycling – in understanding the contributions of grazers as mediators of bottom-up processes in marine systems.

Key words: ammonium; bottom-up; diversity; grazer; herbivore; nitrogen; rocky intertidal

## Introduction

Despite decades of work documenting the roles of marine herbivores in mediating the diversity and abundance of primary producers (e.g., Kitching and Ebling 1961; Lubchenco 1978; Nielsen 2001; Williams et al. 2013), previous work in benthic marine systems has often ignored the fact that herbivores not only consume algae, they also affect nutrient availability. Herbivores therefore affect primary producers not only from the top-down, via consumption, but also from the bottom-up, by excreting inorganic nutrients as waste products. For example, marine invertebrate herbivores excrete ammonium (Carpenter 1986; Taylor and Rees 1998; Bracken et al. 2014), thereby enhancing nutrient availability, algal growth (Bracken et al. 2014) and productivity (Carpenter 1986). Nitrogen is an important limiting nutrient in coastal marine systems (Ryther and Dunstan 1971; Corwith and Wheeler 2002), so predicting rates of consumer-mediated nitrogen recycling is essential to understanding nutrient availability and limitation in marine ecosystems.

However, most marine systems are characterized by diverse consumer assemblages, which makes predictions of those consumers' roles as mediators of nutrient availability potentially difficult (Burkepile et al. 2013; Layman et al. 2013). For example, Taylor and Rees (1998) found that ammonium excretion rates of a diverse assemblage of mobile epifauna in seaweed beds are nonlinearly related to invertebrate body mass, suggesting that mass- or taxon-specific ammonium excretion rates are necessary in order to predict the contribution of a diverse invertebrate assemblage to nutrient availability. Furthermore, McIntyre et al. (2008) quantified ammonium excretion rates of 47 co-occurring species of freshwater fish and found that even after accounting for body mass, there were significant differences between species' ammonium excretion rates.

We took a similar approach to understanding the role of herbivores as mediators of local-scale nutrient availability in a rocky intertidal ecosystem. Recent work has highlighted the importance of local-scale consumer-mediated nutrient loading in mediating the diversity (e.g., Bracken and Nielsen 2004) and growth (e.g., Bracken 2004; Pfister 2007; Aquilino et al. 2009) of algae on rocky shores, but much of that work has focused either on a single consumer species (e.g., the snail *Littorina littorea*; Bracken et al. 2014) or on consumers that do not actually eat the algae that benefit from the nutrients that they excrete (e.g., the mussel *Mytilus californianus*; Bracken 2004; Bracken and Nielsen 2004; Pfister 2007; Aquilino et al. 2009). Given the high diversity of herbivores in many rocky shore systems (Nielsen 2001; O'Connor et al. 2015), there is a clear need to evaluate the collective role of these consumers as not only top-down consumers of algae but also as bottom-up facilitators.

We addressed this knowledge gap by using a combination of field surveys, measurements of biomass and ammonium excretion of different herbivore species, and measurements of ammonium accumulation rates in tide pools to evaluate the role of a diverse herbivore assemblage in mediating nutrient availability on a Southern California rocky shore. Local-scale nutrient inputs are likely to be especially important in this system, as ambient inorganic nitrogen concentrations in the adjacent nearshore ocean are generally low ($< 5$ μmol $L^{-1}$) and have been declining for the past several years (Martiny et al. 2016). Based on previous work, we hypothesized that different grazer groups would be characterized by different ammonium excretion rates. We therefore predicted that the rate of ammonium accumulation in the field would be better predicted based on the ammonium excretion rates of the component species and not by the total biomass of herbivores in the tide pools.

## Materials and Methods

*Study location and species*

Surveys, field measurements, and collections were conducted in a set of natural tide pools in a rocky reef at Corona del Mar State Beach on the coast of Southern California, USA (33° 35' 16.3" N, 117° 52' 1.5" W). All research was conducted between October of 2016 and June of 2017 under California Department of Fish and Wildlife Scientific Collecting Permit SCP-13405. The rocky substratum at the site is composed of sedimentary Monterey formation intertidal reefs. Volumes of the tide pools in this study averaged X ± SE = 22.6 ± 3.6 L, $n$ = 18, and bottom surface areas averaged 0.46 ± 0.05 $m^2$.

These tide pools were very high on the shore; tidal elevations, determined using a self-leveling laser level (CST/berger, Watseka, Illinois, USA), averaged X ± SE = 1.58 ± 0.04 m above the local tidal datum at mean lower-low water. Based on predicted tide heights at the entrance to Newport Bay (Flater 1998), 1.1 km from our study site, these tide pools were only submerged for 5.8% of the time over the year immediately preceding our measurements. In the absence of waves, based on these predictions, tide pools were submerged only during the highest tides of each month, and they were often isolated for several days at a time during neap tides. The median isolation time for these pools in the absence of wave splash was 23.0 h, but waves reduced the typical duration of pool emersion (M. Bracken, *personal observation*). Thus, given a wave swell height of 0.5 m, which is not unusual at our study location (O'Reilly et al. 2016), tide pools would be either washed over or covered for 32.6% of the time, with a median isolation time of 8.3 h.

Despite their elevation on the shore, these pools were characterized by a diverse invertebrate assemblage primarily composed of herbivorous gastropods. These included littorine

snails (*Littorina scutulata* [Gould 1849] and *Littorina plena* [Gould 1849]), limpets (*Lottia limatula* [Carpenter 1864], *L. scabra* [Gould 1846], and *L. strigatella* [Carpenter 1864]), chitons (*Cyanoplax hartwegii* [Carpenter 1855] and *Nuttalina californica* [Reeve 1847]), and turban snails (*Tegula funebralis* [A. Adams 1854] and *T. gallina* [Forbes 1850]). Collectively, these grazing mollusks represented the vast majority of invertebrates in the tide pools, though pools also contained occasional mussels (e.g., *Brachidontes adamsianus* [Dunker 1856] and *Mytilus californianus* [Conrad 1837]), hermit crabs (e.g., *Pagurus samuelis* [Stimpson 1857]), and sea anemones (*Anthopleura* spp.). None of these invertebrates were abundant enough, relative to the grazers, to appreciably modify nutrient availability. Other, smaller invertebrates, such as copepods and amphiphods, were rare to absent in the pools. Macroalgae were also virtually absent from the tide pools, and the grazers primarily consumed periphyton.

*Grazer abundances and attributes*

We surveyed grazer abundances in 18 tide pools by spreading a flexible mesh net across the bottom of each pool (Foulweather Trawl Supply, Newport, Oregon, USA; Bracken and Nielsen 2004). The net was composed of 10 cm × 10 cm squares and facilitated both counting of grazers and measurement of tide pool surface area. Grazer abundances were divided by the volume of each tide pool (i.e., ind $L^{-1}$), as we were interested in the potential for grazers to mediate the concentration (μmol $L^{-1}$) of ammonium in the pools.

We collected 10 representative individuals each of *Littorina scutulata*/*plena* (these species are not differentiable in the field)*, Lottia limatula, Lottia scabra, Lottia strigatella, Cyanoplax hartwegii*, *Nuttalina californica*, *Tegula funebralis,* and *Tegula gallina* from the tide pools. Samples were representative of the size range of each taxon present in the tide pools. We

129 dried individuals to constant mass at 60 °C, weighed them, combusted them for 4 h in a muffle
130 furnace at 450 °C, and weighed them again to calculate mean ash-free dry mass values for each
131 species. These were then averaged to calculate mean values (mg $ind^{-1}$) for each grazer group:
132 littorine snails, limpets, chitons, and turban snails.

133 Ammonium excretion rates of members of each grazer group were evaluated in
134 microcosms containing 200 mL of saltwater (salinity of 35; Instant Ocean® Sea Salt, Blacksburg,
135 Virginia, USA). Each microcosm contained a travertine tile that approximated the sedimentary
136 Monterey formation rocks at our study site. Water in the microcosms was not stirred or aerated
137 in order to simulate a still-water tide pool environment. Temperatures were maintained at 20 °C
138 to ensure constant conditions across experimental trials that were representative of field
139 conditions. Grazers were collected from the field immediately prior to experimental
140 measurements of ammonium accumulation. We made sure that the individuals collected were
141 representative of the size range present in the tide pools. A consistent biomass of grazers (X ± SE
142 = 0.91 ± 0.01 g) was added to each microcosm at the beginning of each experimental trial.
143 Because members of the different grazer groups were characterized by different individual
144 masses (Table 1), maintaining a constant mass across grazer groups necessitated different

Table 1. Biomass (ash-free dry mass) and ammonium ($NH_4^+$) excretion rates of tide pool herbivores. Values are X ± SE.

| | Biomass | $NH_4^+$ excretion | |
|---|---|---|---|
| Grazer group | (mg $ind^{-1}$) | (μmol $h^{-1}$ $ind^{-1}$) | (μmol $h^{-1}$ $g^{-1}$) |
| Littorine snails | 6.8 ± 0.5 | 0.021 ± 0.004 | 3.1 ± 0.6 |
| Limpets | 20.6 ± 1.8 | 0.046 ± 0.015 | 2.2 ± 0.7 |
| Chitons | 58.3 ± 11.1 | 0.357 ± 0.359 | 6.1 ± 1.0 |
| Turban snails | 183.8 ± 11.6 | 1.751 ± 0.353 | 9.5 ± 1.9 |

numbers of individuals for each group in each microcosm: 135 littorine snails, 45 limpets, 15 chitons, or 5 turban snails. During trials, microcosms were covered with flexible windowscreen mesh secured by a rubber band to prevent escapes and limit external sources of potential ammonium contamination.

Microcosm trials were run for ~19 h, which was between the median isolation time of field tide pools in the absence of wave splash (23.0 h) and after accounting for a 0.5 m swell height (8.3 h). Initial water samples ($n$ = 2) were taken from each microcosm prior to adding the grazers, and a second set of samples was taken at the end of the trial. The ammonium concentration in the water samples was analyzed using the phenolhypochlorite method (Solórzano 1969) on a UV-1800 benchtop spectrophotometer (Shimadzu, Carlsbad, California, USA). Ammonium accumulation rates were calculated on both a per-individual ($\mu mol\ h^{-1}\ ind^{-1}$) and per-biomass ($\mu mol\ h^{-1}\ g^{-1}$) basis based on the change in ammonium concentrations over time. Ammonium accumulation rates were measured in $n$ = 8 microcosms for each grazer group, split into two trials of $n$ = 4 replicate microcosms each. Changes in ammonium concentrations in an equivalent number of control microcosms without grazers were minimal and were accounted for when calculating ammonium accumulation rates. Initial ammonium concentrations averaged $X \pm SE = 0.9 \pm 0.2\ \mu mol\ L^{-1}$.

Assessing changes in ammonium concentrations using only two points assumes a linear relationship between ammonium accumulation and time. To verify this assumption, we conducted a second set of trials where we collected water samples over time (0.00, 0.25, 0.50, 1.00, 2.00, 4.00, 6.00, and 22.75 h) instead of only at the beginning and end of trials. We conducted these trials for littorine snails and turban snails because they are the most abundant grazer groups in the tide pools, collectively composing > 90% of grazer biomass in the field. We

compared linear and saturating (Michaelis-Menten) fits to the relationship between ammonium concentration (μmol $L^{-1}$) and time (h) using the corrected Akaike Information Criterion ($AIC_c$; Burnham and Anderson 2002) and found that a linear relationship always provided a better fit to the data.

*Relative contributions to ammonium accumulation and biomass*

Relative contributions of different grazer groups to ammonium accumulation rates and biomass were calculated based on the per-individual rates of ammonium excretion (μmol $h^{-1}$ $ind^{-1}$, Table 1), the average biomass of each individual (mg $ind^{-1}$, Table 1), and the total number of individuals of each grazer group in each of tide pools ($n$ = 18) at Corona del Mar State Beach. We estimated the total ammonium accumulation rate in each tide pool by multiplying the abundance of each grazer in that pool by the measured ammonium excretion rate for that grazer group. These values were then summed across the four grazer groups. The relative contribution of each grazer group to the total ammonium accumulation rate was then calculated as a percentage of the total. Similarly, we estimated the total biomass of grazers in each tide pool by multiplying the average biomass of the members of each grazer group by the number of individuals of that grazer group quantified in our field surveys. The relative contribution of each grazer group to total biomass was then calculated as a percentage of that total. We calculated the difference between each grazer group's contribution to excretion and its contribution to biomass by subtracting, for each tide pool, the percentage contribution to biomass from the contribution to excretion.

*Predicting the contribution of a diverse grazer assemblage to ammonium accumulation*

We quantified ammonium accumulation rates in tide pools ($n$ = 5) at Corona del Mar State Beach over a single day-time low tide. We deliberately chose a subset of pools that were fully submerged during high tide and then isolated by the receding tide in the morning. Waves were relatively large that day, so pools were only completely isolated from the ocean for ~6 h before they were splashed again by the combination of waves and the incoming tide. We collected water samples from each pool every hour while the pools were isolated and used the slope of the relationship between ammonium concentration (μmol $L^{-1}$) and time (h) to calculate the observed rate of ammonium accumulation (μmol $L^{-1}$ $h^{-1}$). We also counted and identified all grazers in those pools on that day.

We compared ammonium accumulation rates measured in the field with predictions based on (1) the total estimated biomass of grazers in each pool or (2) the ammonium accumulation rate in the pool predicted based on the measured ammonium excretion rates of each grazer group. Total estimated biomass was calculated by multiplying the average biomass of the members of each grazer group (Table 1) by the number of individuals of that grazer group quantified in our field surveys on that day. The predicted ammonium accumulation rate was estimated by multiplying the average ammonium excretion rate of the members of each grazer group (μmol $h^{-1}$ $ind^{-1}$, Table 1) by the number of individuals of that grazer group quantified in our field surveys.

*Statistical analyses*

Data were primarily analyzed using general linear models (PROC GLM) and t tests in SAS v. 9.4 (SAS Institute 2012), including regression and ANOVA, after verifying that the data met the assumptions of normality and homogeneity of variances. Analyses included evaluations

of mean individual mass as a function of grazer group (littorine snails, limpets, chitons, and turban snails) and ammonium excretion rates (both per-individual and per-biomass) as a function of trial (as a blocking factor) and grazer group. Relative contributions of each grazer group to biomass versus ammonium accumulation were assessed for each grazer group by subtracting, for each tide pool, the calculated % contribution to biomass from the % contribution to excretion. Averages for the $n$ = 18 tide pools were then compared to zero using one-sample t tests. The metabolic scaling relationship between biomass (mg $ind^{-1}$) and ammonium excretion rate (μmol $h^{-1}$ $ind^{-1}$) was evaluated by taking the logarithm ($log_{10}$) of the mean biomass and excretion rate of each herbivore group, then quantifying the relationship between them using a general linear model (i.e., $\log_{10}[excretion] = a \cdot \log_{10}[biomass] + b$; Glazier 2005). Of particular interest was the slope of this relationship ($a$), which corresponds to the scaling exponent. Observed rates of ammonium accumulation in the field were evaluated as either a function of (1) predicted ammonium accumulation rates based on measured excretion rates of the different grazer groups or (2) estimated total grazer biomass. These relationships were evaluated using general linear models.

## Results

*Grazer abundances and attributes*

Littorine snails were by far the most numerically abundant grazers in tide pools at Corona del Mar State Beach (Fig. 1A); the number of *Littorina scutulata*/*plena* individuals per volume was two orders of magnitude higher than the number of any other grazer group, and they were the most abundant grazer in 17 of the 18 tide pools. However, littorines were also the smallest of the grazers, with average masses 1-2 orders of magnitude lower than the other grazer groups

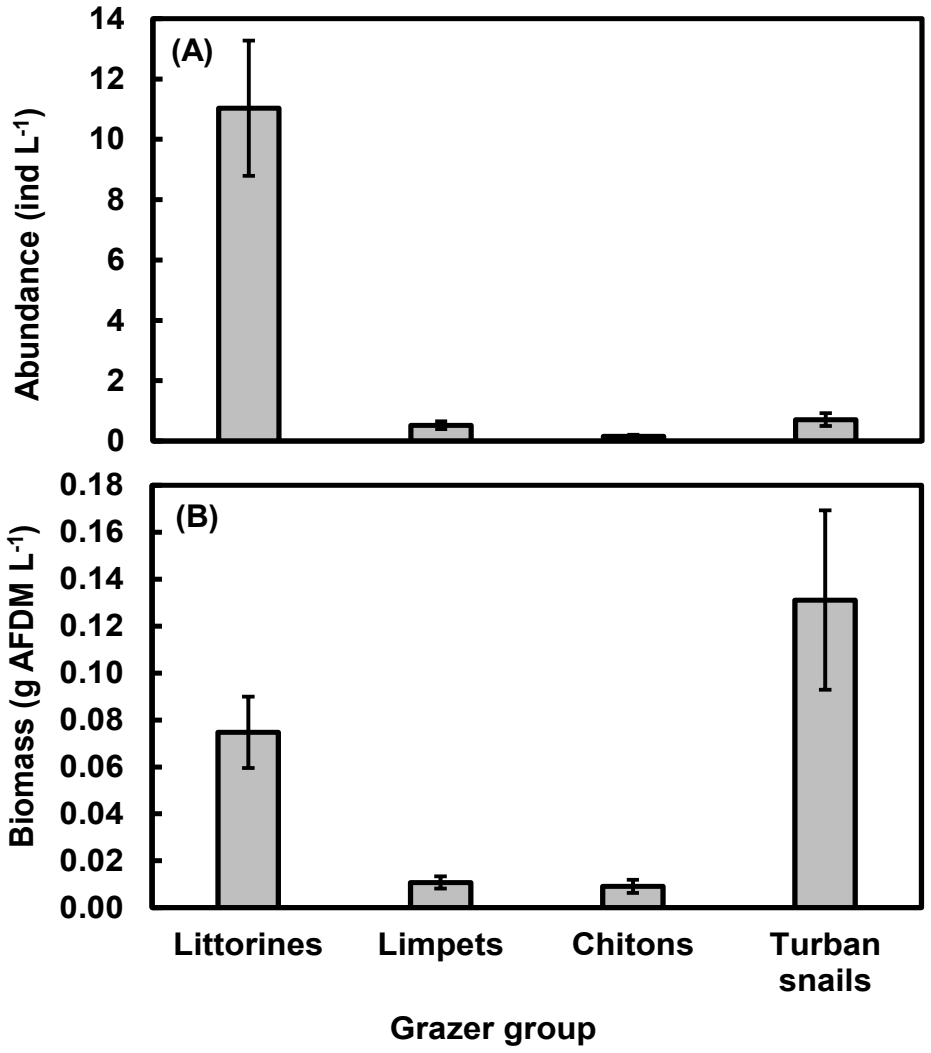


Figure 1. Abundance and biomass estimates of tide pool herbivores. (A) Littorine snails (*Littorina scutulata/plena)* were by far the most numerically abundant herbivores in the tide pools (ind $L^{-1}$). (B) Turban snails (*Tegula* spp.) were the herbivores with the highest total biomass in the tide pools (g ash-free dry mass [AFDM] $L^{-1}$), followed by littorine snails, limpets (*Lottia* spp.), and chitons (*Nuttalina fluxa* and *Cyanoplax hartwegii*). Note that counts of different herbivore species in tide pools were non-independent of each other, so statistical comparisons were not made for abundance or biomass. In both panels, values are X ± SE.

237 (Table 1). Grazer groups, thus, differed substantially in mass (ANOVA, $F$ (3,56) = 149.97, $P <$

238 0.001). Turban snails were the heaviest grazers, followed by chitons, limpets, and littorines,

239 though littorine and limpet masses were statistically indistinguishable (Tukey test, $P > 0.05$).

240 Thus, despite their relatively low abundances, the majority of the biomass in tide pools was

241 composed of turban snails, followed by littorines, limpets, and chitons (Fig. 1B).

242 The different grazer groups also differed substantially with respect to their ammonium
243 excretion rates on both a per-individual basis (ANOVA, $F$ (3,27) = 21.3, $P < 0.001$; Table 1) and
244 a per-biomass basis (ANOVA, $F$ (3,27) = 7.6, $P < 0.001$; Table 1, Fig. 2). Turban snails excreted
245 the most ammonium, both per-individual and per-biomass, excreting at rates 3-4 times higher
246 than those of littorine snails and limpets (Table 1).
247
248 *Relative contributions to ammonium accumulation and biomass*
249 Relative contributions of different grazer groups to ammonium accumulation rates and
250 biomass were expressed as average percentage contributions of each group to the total biomass
251 and the total ammonium accumulation in the tide pools. Turban snails made the greatest
252 contribution to total ammonium excretion rates, followed by littorine snails, chitons, and limpets
253 (Fig. 3A). In contrast, littorines made the greatest contribution to biomass, followed by turban
254 snails, limpets, and chitons (Fig. 3A).

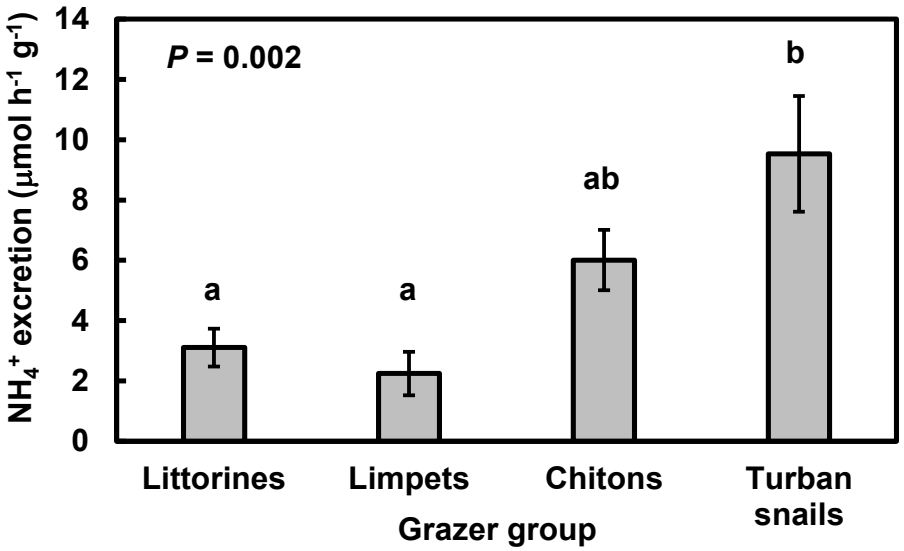


Figure 2. Ammonium ($NH_4^+$) excretion rates of tide pool herbivores. Per-biomass ammonium excretion rates (µmol $h^{-1}$ $g^{-1}$) differed substantially between different herbivore groups ($P$ = 0.002). Letters indicate statistically significant differences ($P < 0.05$) after Tukey correction for multiple comparisons. Values are X ± SE.

255 Two grazer groups, turban snails (one-sample t test, $t17 = 5.2$, $P < 0.001$) and chitons
256 (one-sample t test, $t17 = 3.0$, $P = 0.008$), were predicted – based on laboratory excretion
257 measurements and abundances in tide pools – to make greater contributions to ammonium

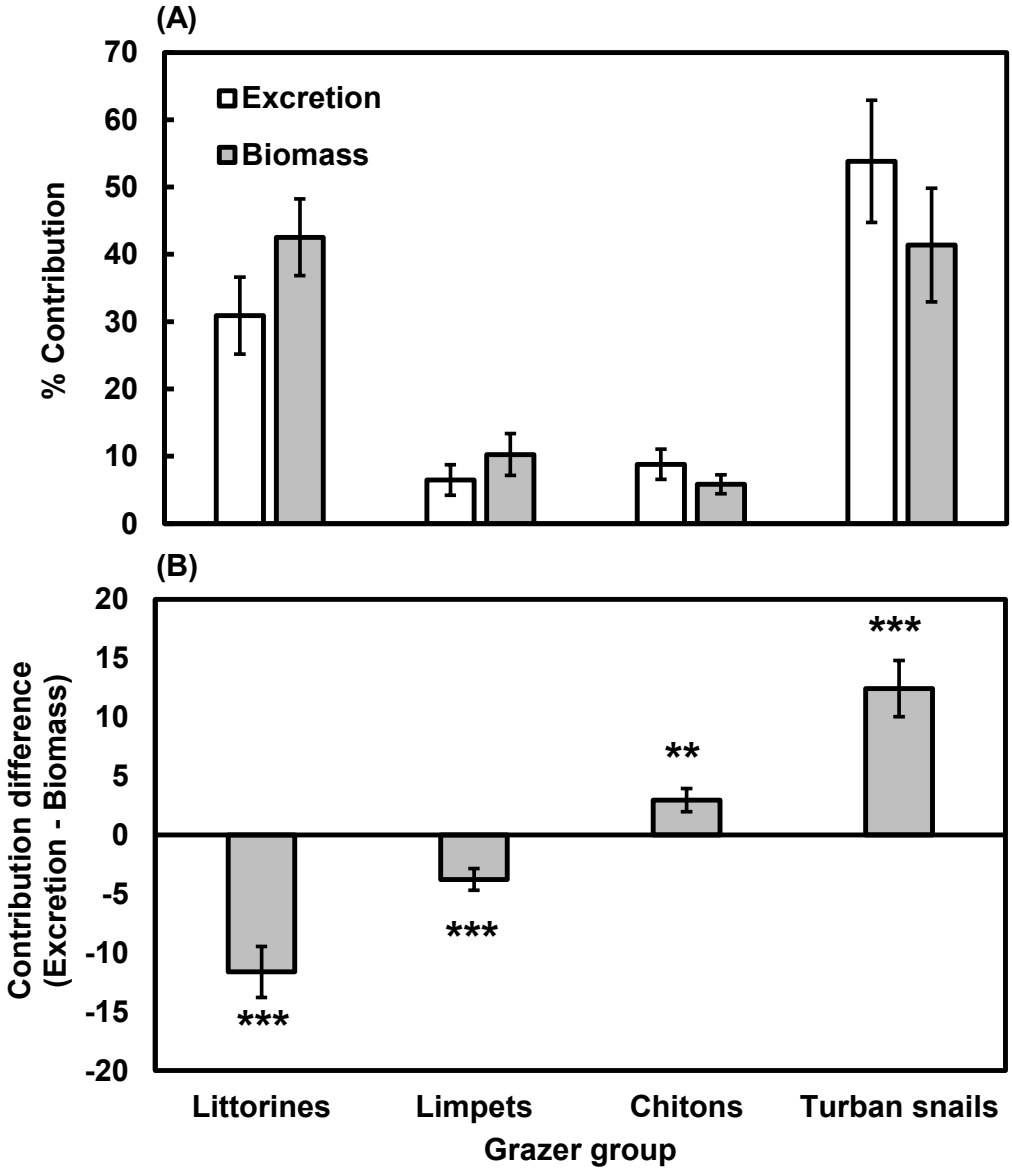


Figure 3. Estimated contributions of different herbivores to ammonium excretion rates and total herbivore biomass. (A) Percent contributions of each grazer group to the estimated total excretion rate and biomass in 18 tide pools on a California rocky shore. (B) Differences (excretion *minus* biomass) between grazer group contributions to excretion and biomass. A positive value (> 0) indicates that a group's predicted contribution to excretion exceeds its contribution to biomass, whereas a negative value (< 0) indicates that a group's predicted contribution to excretion is less than its contribution to biomass. Asterisks indicate statistically significant differences from zero: $P < 0.001$ (***) and $P < 0.01$ (**). In both panels, values are X ± SE.

258 accumulation rates in tide pools than predicted based on their biomass (Fig. 3B). In contrast, the
259 other two groups, littorines (one-sample t test, $t17 = 5.4$, $P < 0.001$) and limpets (one-sample t
260 test, $t17 = 4.1$, $P < 0.001$), were predicted to make lesser contributions to ammonium
261 accumulation than predicted based on biomass (Fig. 3B).

262 We evaluated the relationship between individual grazers' excretion rates (μmol $h^{-1}$ $ind^{-1}$)
263 and biomasses (mg $ind^{-1}$) on a log-log plot (Fig. 4). This transformation linearized the curvilinear
264 relationship between the variables and provided insights into the nature of the scaling
265 relationship. Excretion increased with biomass ($r2 = 0.97$) with a scaling exponent (the slope of
266 the relationship) of 1.40.

267

268 *Predicting the contribution of a diverse grazer assemblage to ammonium accumulation*

269 We quantified rates of ammonium accumulation over time in $n = 5$ tide pools at Corona
270 del Mar State Beach (Fig. 5). Ammonium accumulated at a rate of X ± SE = 0.16 ± 0.06 μmol

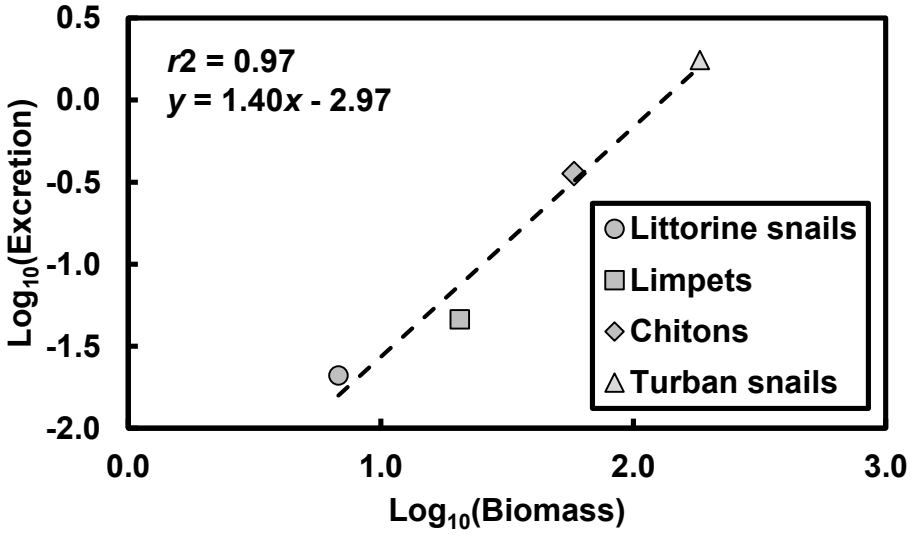


Figure 4. Log-log plot of biomass vs. excretion rates of individual herbivores. Excretion rates (originally measured in μmol $h^{-1}$ $ind^{-1}$) were linearly related to biomass (originally measured in mg ash-free dry mass $ind^{-1}$) when both variables are plotted on logarithmic scales. The slope of this relationship (1.40) represents the scaling relationship in the power curve.

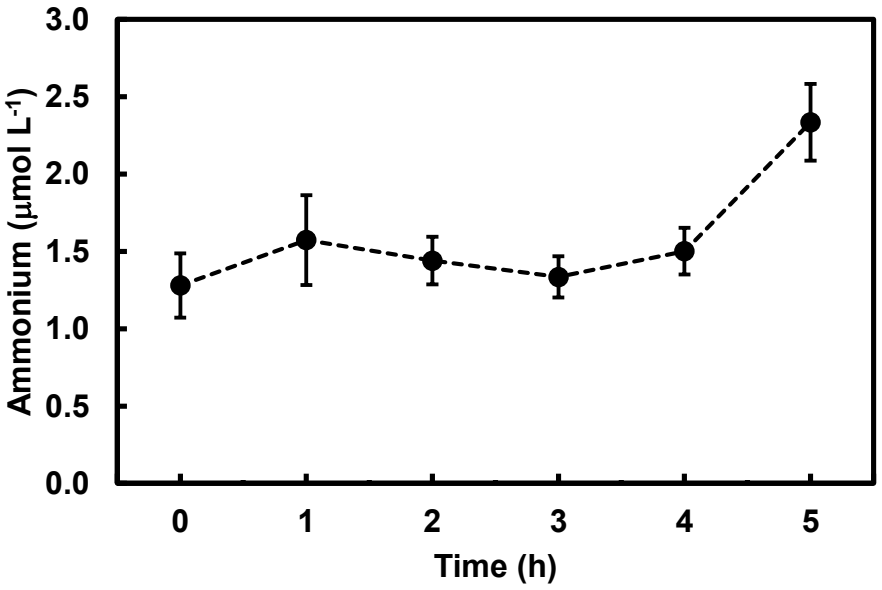


Figure 5. Ammonium concentrations in tide pools. Ammonium (μmol $L^{-1}$) accumulated in pools after they were isolated by the receding tide. Values are X ± SE of samples taken from $n = 5$ tide pools at Corona del Mar State Beach.

271 $L^{-1}$ $h^{-1}$ (one-sample t test, $t4 = 14.6$, $P < 0.001$). Five hours after pools were isolated, average
272 ammonium concentrations in the pools were higher than the concentration in the adjacent ocean
273 (one-sample t test, $t4 = 5.4$, $P = 0.006$). The rate of ammonium accumulation in those tide pools
274 was predicted more effectively by incorporating the excretion rates of the different grazer groups
275 (Fig. 6A; Linear regression, $r2 = 0.81$, $F1,3 = 13.1$, $P = 0.036$) than by the total estimated
276 biomass of the grazers present in the tide pools (Fig. 6B; Linear regression, $r2 = 0.42$, $F1,3 = 2.2$,
277 $P = 0.236$). Note, however, that even when rates of ammonium accumulation were linearly
278 related to rates predicted based on ammonium excretion by the component species (i.e., Fig. 6A),
279 accumulation rates were substantially lower than predicted based on excretion rates. If
280 ammonium accumulation rates matched predicted rates, they would fall on the dashed line in Fig.
281 6A. Instead, measured accumulation rates were < 30% of predicted rates.

282 In these tide pools, littorines composed X ± SE = 68 ± 14% of the biomass but
283 contributed only 55 ± 19% of the ammonium accumulation. In contrast, turban snails composed
284 only 31 ± 14% of the biomass but contributed 45 ± 19% of the ammonium.

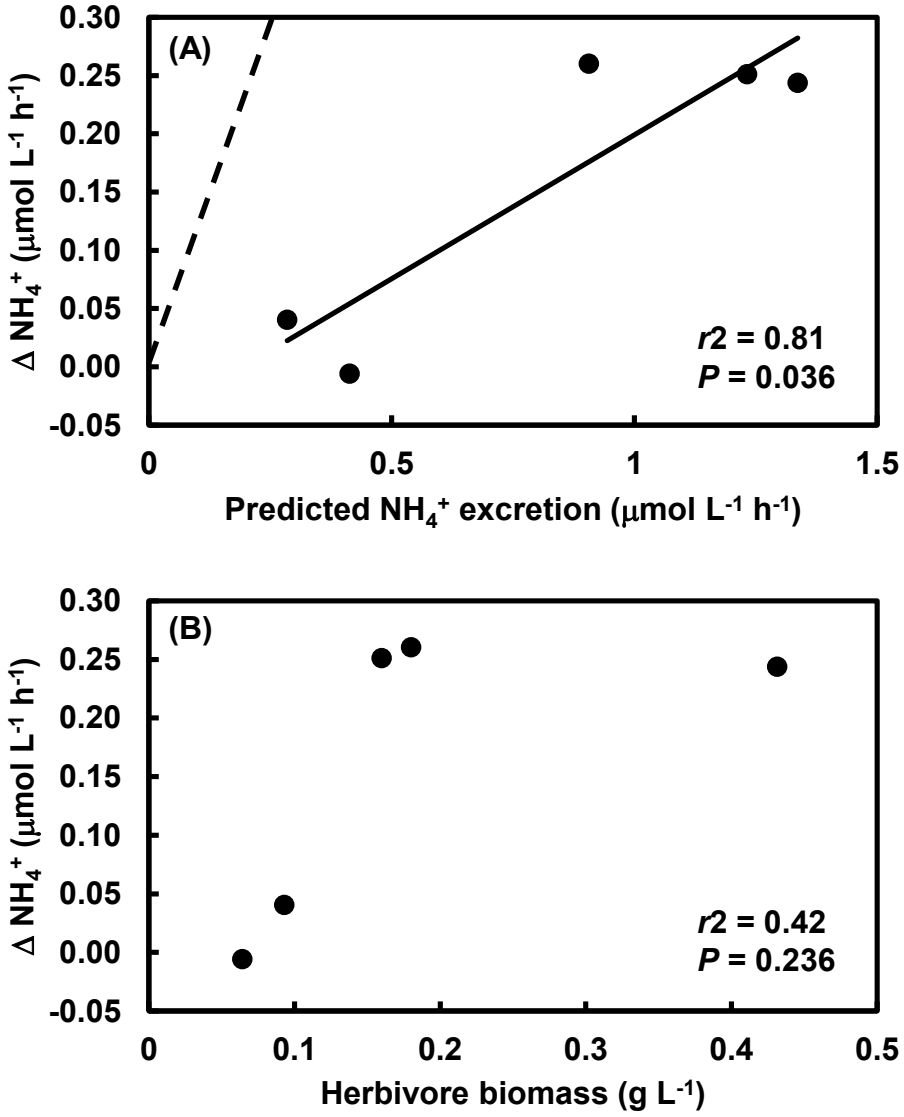


Figure 6. Measured rates of ammonium ($NH_4^+$) accumulation as functions of predicted ammonium excretion rates and estimated total herbivore biomass. (A) Rates of $NH_4^+$ accumulation (μmol $L^{-1}$ $h^{-1}$) in $n$ = 5 tide pools were strongly correlated to excretion rates estimated using measured rates of the grazer groups in each tide pool ($r2$ = 0.81, $P$ = 0.036). The dashed line indicates the rate of ammonium accumulation predicted by laboratory excretion rates. (B) Measured $NH_4^+$ accumulation rates were not correlated to estimates of total herbivore biomass in the pools ($r2$ = 0.42, $P$ = 0.236).

285

286 **Discussion**

287 Different grazer groups were characterized by different per-biomass ammonium
288 excretion rates. Some groups (i.e., turban snails, chitons) contributed more to ammonium
289 accumulation than predicted based on biomass, whereas others (i.e., littorine snails, limpets)
290 contributed less to ammonium excretion than predicted by their biomass. These differences are
291 supported by the scaling relationship between ammonium excretion ($\log_{10}$[excretion]) and
292 biomass ($\log_{10}$[biomass]). The scaling exponent of 1.40 is higher than the typical value of ~0.75
293 (i.e., the ¾ power law; Glazier 2005). In general, mass-specific metabolic rates tend to decline as
294 individual body mass increases (i.e., scaling exponents < 1). However, values > 1 are not
295 uncommon, and scaling exponents > 2 have been reported for invertebrates (Glazier 2005).
296 These "positively allometric" relationships occur when larger organisms have higher mass-
297 specific metabolic rates. This is the pattern we observed here, where the largest grazers (*Tegula*
298 spp.) were also characterized by the highest excretion rates. One grazer group, the limpets,
299 deviated from the regression line on the log-log plot, with lower values than the other three
300 groups. This reflects limpets' lower contribution to ammonium accumulation rates – relative to
301 the other grazer groups – than expected based on biomass. Note also that our comparisons were
302 made across species, whereas most comparisons are based on scaling relationships calculated
303 within species (Glazier 2005). For example, Carey et al. (2013) suggested that differences in the
304 scaling exponents of six chiton species were related to differences in activity, metabolism, and
305 habitat. Temperature can also modify scaling exponents (Glazier 2005), though our
306 measurements of excretion were all measured at a constant, field-relevant temperature.

Measured rates of ammonium accumulation in tide pools on the shore were therefore better predicted based on the ammonium excretion rates of the component grazer groups than by their estimated total biomass. These results support our hypothesis that different grazer groups would be characterized by different ammonium excretion rates (e.g., Bray et al. 1988) and align well with previous findings, especially from freshwater systems, that taxon-specific ammonium excretion rates are necessary in order to predict spatial variation in nutrient cycling (McIntyre et al. 2008).

However, observed rates of ammonium accumulation were < 30% of predicted rates. This discrepancy between observed and predicted rates of ammonium accumulation may be explained by uptake of ammonium by periphyton in the tide pools. Despite the apparent lack of primary producers in these tide pools – there are few to no macroalgae in them – the pools are highly productive; rates of net primary production (mg $O_2$ $L^{-1}$ $h^{-1}$) are equivalent to those that we have measured in macroalgae-dominated pools (M. Bracken and G. Bernatchez, *unpublished data*). The periphyton in the pools are likely taking up substantial quantities of excreted ammonium, as has been observed in other intertidal systems (Longphuirt et al. 2009). We have observed appreciable differences between ammonium fluxes in the dark (accumulation) and light (uptake) in these tide pools, further supporting the role of periphyton in mediating ammonium availability (M. Bracken and G. Bernatchez, *unpublished data*). Subsequent work could include experimental ammonium additions to tide pools with and without grazers to evaluate whether uptake by periphyton can account for the difference between observed and predicted rates of ammonium accumulation.

What mechanisms could potentially underlie the observed differences between species with respect to ammonium excretion rates? One possibility is dietary specificity. However, little

330 is known about the diets of these co-occurring herbivores. All of the grazer groups consume
331 diatoms (Castenholz 1961; Best 1964; Nicotri 1977; LaScala-Gruenewald et al. 2016), but the
332 identities of the resources available (likely a diverse mixture of benthic microalgae,
333 cyanobacteria, and macroalgal sporelings [LaScala-Gruenewald et al. 2016]) remain unknown at
334 our study site. Furthermore, there is little evidence for resource partitioning among co-occurring
335 molluscan grazers (Nicotri 1977; Hawkins et al. 1989; LaScala-Gruenewald et al. 2016). Thus,
336 underlying mechanisms for differences in per-biomass nutrient recycling rates, which include not
337 only diet but also organismal physiology, remain unknown.

338 Regardless of the underlying mechanism, it is clear that some species contribute more
339 than others to ammonium accumulation rates in tide pools, and the loss of these species may
340 have disproportionate effects on nutrient availability. McIntyre et al. (2007) describe how
341 consumer extinctions can influence nutrient cycling and highlight the fact that the loss of certain
342 vulnerable species (e.g., those targeted by humans) may have particularly large effects on
343 nutrient availability. Populations of large, conspicuous gastropods such as turban snails have
344 declined in Southern California due to human impacts (Murray et al. 1999). We demonstrated
345 that turban snails contributed substantially more ammonium than predicted based on their
346 biomass. Thus, whereas turban snails represented less than a third of the total herbivore biomass
347 in the tide pools where we measured ammonium accumulation rates, they contributed nearly half
348 of the ammonium.

349 More generally, we found that different functional groups of grazers differ with respect to
350 their effects on an important biogeochemical processes. Understanding the roles of species in
351 ecosystems (Lawton 1994) is essential for predicting rates of nutrient cycling and other
352 biogeochemical rates (Naeem 2002). Intertidal grazers play an essential role in marine

353 ecosystems by converting organic nitrogen in the algae that they eat into inorganic nitrogen that
354 can be readily taken up and assimilated by primary producers (Giannotti and McGlathery 2001;
355 Bracken et al. 2014). And – given differences between grazer species in their ammonium
356 excretion rates – a diverse grazer assemblage (e.g., one that contains groups such as turban snails
357 and chitons characterized by higher rates of per-biomass nitrogen excretion) may be more
358 effective at recycling nutrients.

359 Our study also adds another dimension to the body of research that links trophic
360 complexity, biodiversity, and ecosystem functioning. Many studies in marine systems have
361 demonstrated that more diverse grazer assemblages are more effective at controlling algal
362 biomass (Duffy et al. 2003, 2015; Matthiessen et al. 2007; Eklöf et al. 2012). If those grazers
363 also contribute nutrients – and especially if grazer diversity affects not only top-down control but
364 bottom-up facilitation by grazers – then a mechanistic understanding of the effects of grazer
365 diversity on primary producers requires partitioning grazers' consumptive and facilitative effects
366 (Bracken et al. 2014).

367 One important caveat regarding our work is that our measurements and surveys were
368 conducted in tide pools, which are isolated at low tide, allowing ammonium to accumulate
369 (Bracken and Nielsen 2004). Tide pools are functionally field mesocosms – they contain most
370 species present on local rocky shores and are amenable to measuring nutrient excretion and
371 uptake rates and conducting experimental manipulations (Nielsen 2001; Bracken and Nielsen
372 2004; Pfister 2007) – but they are also hydrodynamically different from wave-swept shores and
373 nearshore systems, where excreted nitrogen is likely to be advected away. Macroalgae were also
374 virtually absent from these tide pools due to a combination of grazing activity and environmental
375 stress. The microalgal biofilms in the pools likely assimilated much of the ammonium from the

water column – observed rates of ammonium accumulation were < 30% of the predicted rates – but the simplicity of the system probably enhanced our ability to link observed and predicted rates of ammonium accumulation. However, consumer-mediated nutrient inputs are important even in subtidal and wave-exposed intertidal habitats (Taylor and Rees 1998; Aquilino et al. 2009), suggesting that our findings are relevant to a broader suite of marine systems.

In conclusion, we have shown that grazers are important local-scale contributors of nitrogen to intertidal habitats. Thus, in addition to their traditional top-down role, grazers play potentially important roles in nutrient cycling. Because different groups in diverse grazer assemblages are characterized by different rates of per-biomass ammonium excretion, predicting rates of grazer-mediated ammonium accumulation requires measurement of the ammonium excretion rates of each grazer group. However, once these data are incorporated, ammonium accumulation rates in the field can be effectively predicted. Understanding the roles of consumers in ecosystems – including not only consumption but also facilitation – is essential for understanding marine biodiversity and ecosystem functioning.

**Compliance with Ethical Standards**

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