

# Grazing effects of the sea urchin *Tetrapygus niger* and the snail *Tegula atra* on a rocky shore of central Peru

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*Here we describe habitat use and the grazing effects of the sea urchin Tetrapygus niger and the gastropod Tegula atra in the low intertidal zone of a rocky shore in central Peru (Ancón bay: 11°46'S 77°12'W), where these two species were documented as coexisting with no evidence of habitat segregation between them. Gut content and isotopic analyses revealed differences between their diets: T. atra consumes mainly microalgae while Tetrapygus niger consumed also benthic macroalgae. Individual grazing effects were evaluated with inclusion/exclusion experiments. Tetrapygus niger prevented the colonization of the substrate by sessile organisms, including the dominant mussel Semimytilus alcosus, while Tegula atra reduced the abundance of microalgae and green ephemeral macroalgae during early succession, but these effects were overwhelmed by the rapid increase in cover of S. alcosus. We suggest that Tetrapygus niger plays a key role in this low intertidal community. Through directly limiting mussels to monopolize the substratum, T. niger can reduce the diversity of mussel associated species; conversely, through controlling primary space holders, T. niger can also benefit other grazers that live on bare substrate by maintaining a suitable area for feeding or living.*

**Keywords:** grazing effects, Peru, rocky shore, *Tegula atra*, *Tetrapygus niger*

Submitted 3 August 2012; accepted 20 June 2013; first published online 7 August 2013

## INTRODUCTION

Understanding how interactions among organisms affect the patterns observed in a community is key to comprehend its dynamics and functioning (Raffaelli & Hawkins, 1996; Bertness *et al.*, 2001). For example, in many rocky intertidal habitats, the high diversity of sessile organisms is allowed by the pressure exerted by starfish on competitively superior prey species that would otherwise monopolize the space (e.g. Paine, 1974). In analogous way, subtidal barren areas with low diversity of sessile organisms and dominated by encrusting corallines can be maintained by sea urchins that graze all foliose macroalgae (Lawrence, 1975; Vance, 1979). These examples refer to keystone, single consumer species that can strongly impact prey abundance, controlling most community patterns and processes (Power *et al.*, 1996; Duffy, 2002). However, most systems are inhabited by more than one consumer species that can interact with each other, resulting in varying effects in the structure of the community (e.g. Duffy, 2002).

As already noted, the maintenance of barren areas has been generally attributed to intense grazing by sea urchins (e.g. Lawrence, 1975; Vance, 1979). However, the consequences

of the individual foraging activities of the interacting species that inhabit the barren area may vary due to differences in their temporal and spatial patterns of distribution, feeding preferences and behaviour (Branch & Branch, 1980; Schmitt, 1996; Bulleri *et al.*, 1999). In general, coexisting gastropod grazers have subtle effects on the crustose barrens when compared with sea urchins, since the former cannot deal with the growth of large foliose macroalgae (Moreno & Sutherland, 1982; Fletcher, 1987). In addition, gastropods may require the presence of sea urchins to impede large macroalgae from swamping the areas of crustose corallines creating unsuitable conditions (Underwood & Jernakoff, 1981; Fletcher, 1987).

In moderately protected rocky shores of central Peru (~11°S), the sea urchin *Tetrapygus niger* (Molina, 1782) and the gastropod *Tegula atra* (Lesson, 1830) are the most abundant grazers of the low intertidal zone (Paredes, 1974), where the substrate is covered mainly by crustose corallines. In the south-eastern Pacific, most research on the effect of these grazers on macroalgal assemblages have been conducted in shallow subtidal areas south of 18°S in Chile. For example, in northern and central Chile, *Tetrapygus niger* and *T. tridentata* maintain extensive barren grounds in the shallow subtidal zone by impeding the settling of macroalgal propagules (Vásquez, 1993, 2001). In the boundary between the intertidal and subtidal zones of central Chile, field experiments showed that *T. niger* can impair the colonization of the substrate by foliose macroalgae after the removal of the canopy forming,

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competitively dominant kelp *Lessonia nigrescens* (Ojeda & Santelices, 1984). In southern Chile, *Tegula atra* can remove ephemeral algae in shallow subtidal areas where sea urchins are not present, although this effect is temporary since the perennial kelp *Macrocystis pyrifera* cannot be controlled by *T. atra* and overgrow algae (Moreno & Sutherland, 1982). Thus, it seems that *Tetrapygyus niger* is important in limiting the development of macroalgae in the low intertidal and shallow subtidal zones, while *Tegula atra* would have minor effects. However, no work has been conducted to explore and compare their effects when they coexist. Therefore, the main objective of this work was to evaluate and compare the grazing effects of *Tetrapygyus niger* and *Tegula atra* in the low rocky intertidal zone of central Peru. In addition, we also analysed their distribution patterns and diet in order to account for differences in the use of habitat and prey resources.

## MATERIALS AND METHODS

### Study site

The study was conducted from October 2005 to December 2007 in the low intertidal zone of a moderately protected rocky shore south of the Ancón bay (central Peru, 11°46'S, 77°12'W). The site is located on the eastern side of an island located ~70 m from the coast, and despite the fact that it is sheltered from severe wave action, currents can be intense and waves can reach up to 2 m high on stormy days. Tides are semidiurnal with a maximum range from -0.17 to 1.21 m with respect to Chart Datum (Dirección de Hidrografía y Navegación—Perú, 2006). The low intertidal zone is delimited by the upper limit of distribution of the barnacle *Megabalanus psittacus* and the lower limit of spring low tides (i.e. the infralittoral fringe; *sensu* Paredes, 1974). At the study site, the substrate is mostly occupied by encrusting coralline algae (probably *Mesophyllum* sp. and other calcareous crusts; Meneses, 1993), while other sessile invertebrates and algae are scarce (F. Hidalgo, personal observation).

### Organism cover in the low intertidal zone

General descriptive data of organisms' cover in the study area were obtained by sampling the low intertidal zone with randomly placed quadrats (0.25 × 0.25 m; N = 30) in October 2005 and May 2007. Samplings were conducted during low tide and the cover of sessile organisms was estimated by the point intercept method (81 points).

### Distribution patterns of *Tetrapygyus niger* and *Tegula atra*

We used two procedures to evaluate the distribution patterns of *Tetrapygyus niger* and *Tegula atra* in the low intertidal zone. The first one was conducted by recording the number of individuals present in permanent 50 × 50 cm quadrats during low tide. Quadrats were marked with epoxy putty approximately in the centre of eight bedrock areas, ~2 m<sup>2</sup> each, separated from each other by cracks or pools. Four of these areas had an average slope <30% and were referred to as 'horizontal' surfaces, the other four had an average slope >60% and

were referred to as 'vertical' surfaces. These contrasting slope surfaces were selected to account for possible interspecific differences in microhabitat distribution that may result from the interaction among competition, food preferences or different vulnerability to predation or wave dislodgement (e.g. Hahn & Denny, 1989; Bulleri *et al.*, 1999; Rochette & Grand, 2004; Cobb & Lawrence, 2005; Espinosa *et al.*, 2006). To account for between-days variations in the abundance of *T. atra* and *Tetrapygyus niger*, counts were repeated seven times at intervals of 5–7 days. The number of individuals of each species was log-transformed to meet parametric assumptions and was compared among days of sampling and surface inclinations with two-way ANOVAs (Zar, 1999). Here and thereafter, when interactions between factors were found, the multiple comparisons Tukey HSD test was used to identify how factors interacted (Zar, 1999).

The second sampling procedure accounted for differences in the abundance of *T. niger* and *Tegula atra* in the low intertidal zone in relation to the tidal cycle. For this, the tidal cycle was divided in to three intervals: 'low tide, from 1 h before to 1 h after low tide (i.e. the low intertidal zone exposed, but washed by waves and splash); 'high tide', from 1 h before to 1 h after high tide (i.e. the low intertidal zone completely underwater); and 'mid tide', from 2 h before to 4 h after both low and high tides (i.e. the low intertidal zone partially submersed during flooding and ebbing, respectively). Samplings were done with quadrats (25 × 25 cm) randomly placed on 'vertical' (slope >60%) and 'horizontal' (slope <30%) rock surfaces. Because counts were always conducted in the low intertidal zone and some areas were not accessible during high and mid tide, a variable number of replicates (30–100) were used depending on the tide interval and substrate slope considered. The size of individuals sampled was also recorded (*T. atra*: shell diameter; *Tetrapygyus niger*: test diameter). Data were compared among surface inclinations and tide intervals with two-way ANOVAs (Zar, 1999). Counts data were log-transformed to meet parametric assumptions (Zar, 1999). To determine the type of distribution of each species at each tide interval and on each surface inclination, we calculated the variance/mean quotient (Margalef, 1974; see Espinosa *et al.* 2006). With the distribution data obtained in the quadrats of 25 × 25 cm during low tide, we evaluated if there was any relationship between the abundance of *T. niger* and *Tegula atra* using a Spearman's rank correlation analysis (Zar, 1999). In addition, the spatial segregation between *T. atra* and *Tetrapygyus niger* within the quadrats was analysed with nearest neighbour contingency tables (Pielou, 1961; see Branch & Branch, 1980), by measuring the distances between each individual and the closest neighbour in each quadrat. Segregation between species was evaluated by comparing the observed and expected distributions with chi-square statistics (Pielou, 1961). To determine the degree of segregation, the coefficient of segregation (S) was calculated (Pielou, 1961).

### Diet analysis

Gut content analyses were conducted to assess the diet of *Tegula atra* and *Tetrapygyus niger*. To analyse gut content, 30 average-size individuals of each species were collected in the low intertidal zone and fixed in the field with 10% formaldehyde diluted in seawater. In the laboratory, guts were dissected and food items consumed were identified under a

dissection microscope. Dietary composition was assessed by mean occurrence percentage (%O) of each prey taxon (Hyslop, 1980). As a complement of gut content analyses, isotopic analyses of each consumer were conducted. Stable isotopic signatures reflect long-term (weeks–years) diet composition (Hobson, 1999), whereas stomach contents analysis indicates intake over the previous few hours. For the analysis, 20 individuals of either *Tetrapygyus niger* and *Tegula atra* were collected in the low intertidal zone and kept alive until processing within 12 h after collection. Each sample (*T. niger*, N = 4; *T. atra*, N = 5) was a pool of muscle tissue of 4–5 individuals. Muscle was extracted from the Aristotle's lantern in *Tetrapygyus niger* and from the foot in *Tegula atra*. Samples were then dried at 60°C for 48 h, milled to a fine powder and packed into tin capsules for isotope analysis. All samples were analysed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  at the Stable Isotope Facility of the University of California (Davis), using a PDZ Europa ANCA-GLS elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer. Differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between *Tetrapygyus niger* and *Tegula atra* were compared with *t*-tests (Zar, 1999).

### Grazing effects

The grazing effects of *Tetrapygyus niger* and *Tegula atra* were evaluated using caging field experiments. Experiments were conducted from November 2005 to March 2006, and repeated from April to October 2006. During the first period, the experimental design encompassed five treatments (N = eight replicates per treatment), in order to analyse overall and individual effects: (1) inclusions of *T. atra*; (2) inclusions of *Tetrapygyus niger*; (3) exclusion cages without herbivores to control for grazing effects; (4) control cages to controlling caging artefacts; and (5) total controls. Cages (length  $\times$  width  $\times$  height = 20  $\times$  20  $\times$  5 cm) were built with stainless steel wire mesh (mesh size = 5 mm) and were fixed to the substratum with a central bolt; control cages were of the same size but with two opposite sides open to allow access to grazers; and total controls were areas (20  $\times$  20 cm) marked in the substratum with epoxy putty in the corners. In the inclusions, we used two individuals of the average field sizes per cage (sea urchins, 20 mm in test diameter; snails, 18 mm in shell diameter) to match average natural densities. Cages were inspected regularly to maintain experimental levels of grazers in the respective treatments. No animals were found dead or missing in the inclusions throughout the experiment. In the first experimental period, we measured the percentage cover of the main sessile organisms with the point intercept method (100 points) at the end of the experimental period (i.e. after 4 months). One-way ANOVAs (Zar, 1999) were then used to compare the cover of sessile organisms among treatments. During the second experimental period we also evaluated grazing effects at early successional stages by measuring the percentage cover of sessile organisms at days 10, 20, 35, 80 and 180 since the start of the experiment. Given that no cage artefacts were observed during the first experimental period, and that the cover within inclusions of *T. niger* resemble that of the controls (see Results), control cages and total controls were not used in the second period. Repeated measures ANOVAs (Crowder & Hand, 1990) were then used to compare the cover of sessile organisms among treatments (i.e. inclusions of *Tegula atra*, inclusions of *Tetrapygyus niger* and exclusions) and dates. Percentage

cover data were square root transformed to meet parametric assumptions (Zar, 1999).

## RESULTS

### Organisms cover in the low intertidal zone

The encrusting coralline algae occupied >80% of the substrate in the low intertidal zone, while the percentage cover of other sessile organisms was <5%, the barnacle *Megabalanus psittacus* and the anemone *Phymactis clematis* being the most common (Figure 1).

### Distribution patterns of *Tetrapygyus niger* and *Tegula atra*

Samplings in permanent 50  $\times$  50 cm quadrats during low tide showed that both *Tegula atra* and *Tetrapygyus niger* were more abundant on vertical than horizontal rock surfaces (*T. atra*:  $F_{6, 42} = 4.27$ ,  $P = 0.045$ ; *T. niger*:  $F_{6, 42} = 8.23$ ,  $P = 0.006$ ; Figure 2), and that their abundance varied along the days of sampling (*T. atra*:  $F_{6, 42} = 5.12$ ,  $P = 0.0005$ ; *T. niger*:  $F_{6, 42} = 3.38$ ,  $P = 0.008$ ; Figure 2). The samplings with 25  $\times$  25 cm quadrats revealed that the higher abundance on vertical surfaces was consistent throughout the tidal cycle for *T. atra* ( $F_{1, 404} = 9.72$ ,  $P = 0.002$ ; Figure 3), which was also more abundant during high and mid tide than at low tide ( $F_{2, 404} = 8.70$ ,  $P < 0.001$ ; Tukey HSD test,  $P < 0.001$  for each contrast; Figure 3). In contrast, this sampling showed no statistical differences in the abundance of *T. niger* between surface inclinations ( $F_{1, 404} = 0.03$ ,  $P = 0.87$ ; Figure 3) or among tide intervals ( $F_{2, 404} = 2.20$ ,  $P = 0.11$ ; Figure 3). Sizes of *T. niger* individuals were not different between surface inclinations or tide intervals (mean, SD = 19.74, 5.86 cm; two-way ANOVA; surface:  $F_{1, 411} = 0.48$ ,  $P = 0.49$ ; tide:  $F_{2, 411} = 2.21$ ,  $P = 0.11$ ). For *T. atra*, slightly larger individuals were present at high (mean, SD = 17.11, 4.14 cm) and mid tide (mean, SD = 16.81, 4.03 cm) than at

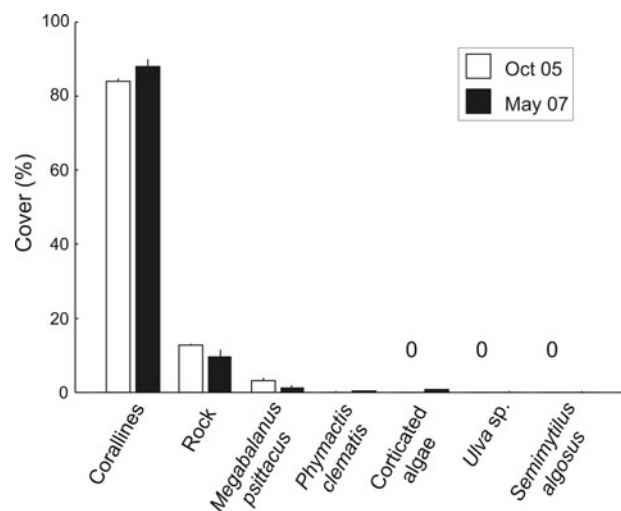


Fig. 1. Percentage cover (mean  $\pm$  SE) of sessile organisms and bare rock in the low intertidal zone. No corticated algae, *Ulva* sp. and *Semimytilus algosus* were found in the sampling of October 2005, indicated by a zero.

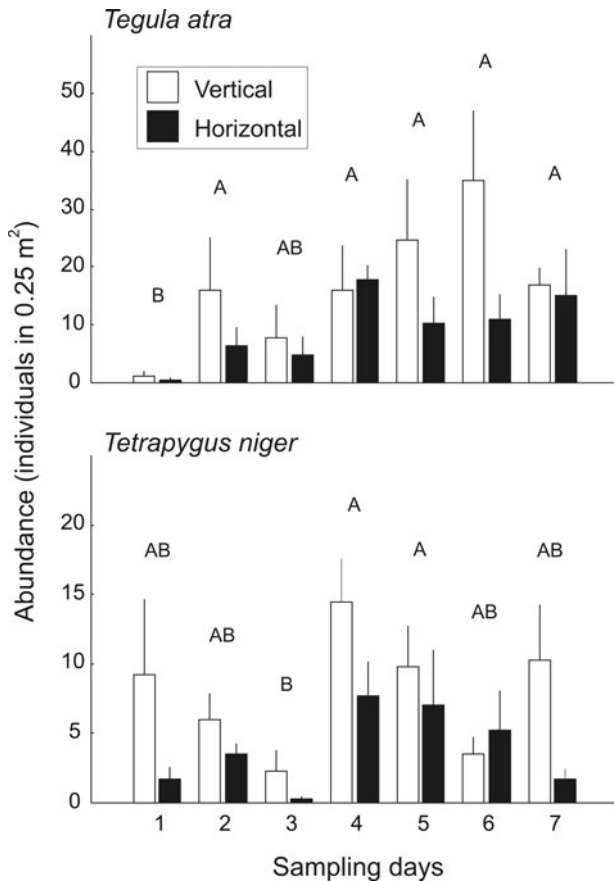


Fig. 2. Abundance (mean + SE) of *Tegula atra* and *Tetrapygyus niger* in the permanent marked plots of 50 × 50 cm on vertical and horizontal rock surfaces at different days of sampling. Different upper case letters indicate differences in the abundance of each species among days of sampling. Individuals were always more abundant on vertical surfaces (for the sake of clarity, this is not presented with letters).

low tide (mean, SD = 15.91, 4.56 cm), without differences between vertical (mean, SD = 16.62, 4.26 cm) and horizontal surfaces (mean, SD = 16.61, 4.31 cm; two-way ANOVA; surface:  $F_{1, 558} = 0.001$ ,  $P = 0.97$ ; tide:  $F_{2, 558} = 3.17$ ,  $P = 0.04$ ). In all cases, both species showed an aggregated pattern of distribution (variance/mean quotient ranging from 2.04 to 17.10,  $P < 0.05$  in all cases; according to the scattergraph of Margalef (1974)).

The abundance of *Tegula atra* and *Tetrapygyus niger* was positively correlated on horizontal surfaces ( $r = 0.44$ ,  $P = 0.02$ ), but no relationship was observed on vertical surfaces ( $r = 0.17$ ,  $P = 0.42$ ). However, nearest neighbour analysis showed that the two species were positively segregated within the sampling units (i.e. 25 × 25 cm) on both surface inclinations (horizontal:  $\chi^2 = 67.33$ ,  $P < 0.0001$ ,  $S = 0.429$ ; vertical:  $\chi^2 = 91.62$ ,  $P < 0.0001$ ,  $S = 0.450$ ), with interspecific nearest neighbours occurring less often than expected under conditions of random occupancy.

## Diet analysis

Both gut content and isotopic analyses revealed striking differences between the diet of *Tetrapygyus niger* and *Tegula atra*. Gut content analysis showed that all *Tetrapygyus niger* stomachs contained microalgae, and most had also

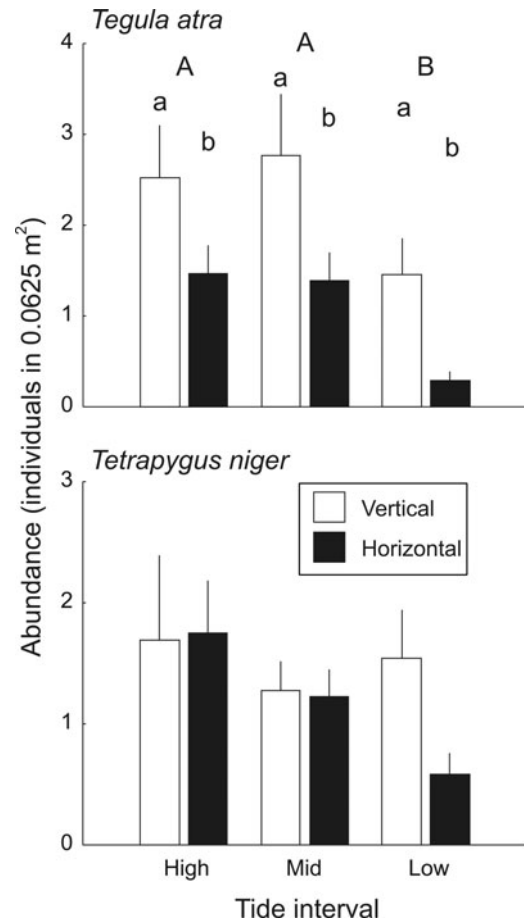


Fig. 3. Abundance (mean + SE) of *Tegula atra* and *Tetrapygyus niger* during high, mid and low tide on vertical and horizontal rock surfaces. Different lower case and upper case letters indicate differences in the abundance of each species between surface inclinations and among tide intervals, respectively.

macroalgae (mainly *Gelidium* spp., *Ulva* spp. and red filamentous macroalgae). Conversely, while most *Tegula atra* stomachs had microalgae, just a small proportion contained macroalgal remains. Mussel recruits were also found in stomachs of both *Tetrapygyus niger* (53.33%) and *Tegula atra* (6.67%, Table 1). In *Tetrapygyus niger*, shell fragments and crustaceans remains were also present in a large proportion of the stomachs analysed; one crab carapace was also found in a *Tegula atra* stomach (Table 1). Isotopic signature of N ( $\delta^{15}\text{N}\text{‰}$ ) was higher in *Tetrapygyus niger* (mean, SD = 13.85, 0.36) than in *Tegula atra* (mean, SD = 13.05, 0.19;  $t = 4.29$ ,  $df = 7$ ,  $P = 0.003$ ) and the isotopic signature of C ( $\delta^{13}\text{C}\text{‰}$ ) was smaller in *Tetrapygyus niger* (mean, SD = -16.10, 0.19) than in *Tegula atra* (mean, SD = -15.25, 0.13;  $t = -7.88$ ,  $df = 7$ ,  $P = 0.0001$ ).

## Grazing effects

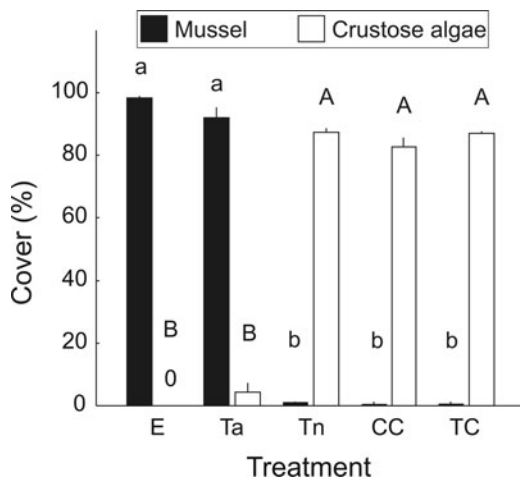
The experiment to evaluate grazing effects showed that *Tetrapygyus niger* was able to keep the crustose surface free of other sessile organisms, while *Tegula atra* could not impede the colonization of the substrate by the mussel *Semimytilus algosus*. At the end of the first experimental period, the crustose coralline surface remained uncovered by other sessile organisms in the inclusions of *Tetrapygyus niger*

**Table 1.** Occurrence percentage (%O) of alimentary items in *Tetrapygyus niger* and *Tegula atra* stomachs. %O is the number of stomachs containing that alimentary item divided by the total number of stomachs containing food × 100.

Alimentary item	%O	
	<i>Tetrapygyus niger</i>	<i>Tegula atra</i>
Microalgae <sup>a</sup>	100	80
Macroalgae		
<i>Ulva</i> spp.	76.67	
<i>Porphyra</i> sp.	10	
<i>Gelidium</i> spp.	76.67	
<i>Polysiphonia</i> spp.	13.33	
<i>Ceramium</i> spp.	6.67	
Non identified red filamentous	96.67	6.67
<i>Dyctiota kunthii</i>	43.33	
Calcareous crustose macroalgae	90	20
<i>Chondacanthus chamissoi</i>	23.33	
Mytilids		
Recruits	53.33	6.67
Shell fragments	20	
Byssal threads	6.67	
Chiton shell fragments	3.33	
Crustaceans		
No identified rests	40	
Amphipods	3.33	
Decapods	6.67	3.33
Non-identified chitinous fragments	3.33	

<sup>a</sup>, including diatoms and macroalgae sporelings.

and in controls (both control cages and total controls), while it was completely covered by *S. algaosus* in the inclusions of *Tegula atra* and in the exclusions (one-way ANOVAs; for *Semimytilus algaosus*:  $F_{4, 25} = 749.73, P < 0.001$ ; for crustose corallines:  $F_{4, 25} = 183.08, P < 0.001$ ; Figure 4).



**Fig. 4.** Percentage cover (mean + SE) of the mussel *Semimytilus algaosus* and calcareous crustose macroalgae within inclusions of *Tegula atra* (Ta), inclusions of *Tetrapygyus niger* (Tn), exclusions (E), control cages (CC) and total controls (TC) at the end of the first experimental period. Lower case and upper case letters indicate differences in cover of mussel and crustose algae, respectively, among treatments.

The samplings during the second experimental period revealed an increased cover of microalgae and *Ulva* spp. in the exclusions at day 20 since experiment starting (repeated measures ANOVA, date × treatment interaction; microalgae:  $F_{8, 60} = 2.25, P < 0.05$ ; *Ulva* spp.:  $F_{8, 60} = 2.49, P < 0.05$ , Figure 5), while the cover of the sessile polychaete *Phragmatopoma moerchi* was higher in the inclusions of *T. atra* than in the other treatments at days 20 and 35 (repeated measures ANOVA, date × treatment interaction,  $F_{6, 45} = 3.26, P < 0.01$ , Figure 5). After day 35 since experiment starting, the cover of microalgae, *Ulva* spp. and *P. moerchi* in the exclusions and inclusions of *T. atra* was swamped by the increasing cover of *S. algaosus*, which reached ~100% cover in these treatments at day 80, remaining ~0% in the inclusions of *Tetrapygyus niger* (repeated measures ANOVA, date × treatment interaction:  $F_{8, 60} = 7.26, P < 0.0001$ ; Figure 5). The cover of crustose corallines decreased through time in the exclusions and inclusions of *Tegula atra*, remaining ~80–90% in the inclusions of *Tetrapygyus niger* (repeated measures ANOVA, date × treatment interaction,  $F_{8, 60} = 10.66, P < 0.001$ , Figure 5).

DISCUSSION

*Tetrapygyus niger* and *Tegula atra* are the most abundant grazers in the low intertidal zone of protected rocky coasts of central Peru, and our results showed that at these areas *Tetrapygyus niger* prevents the fast colonization of the crustose surface by the mussel *Semimytilus algaosus*, while *Tegula atra* is unable to do so, according with most previous works reporting strong effects of sea urchins and more subtle effects of gastropod grazers in barren grounds (e.g. Fletcher, 1987).

*Semimytilus algaosus* is the dominant space holder at mid intertidal areas of central Peru (Paredes, 1974; Tokeshi & Romero, 1995). This is a fast recruiting, fast growing mussel whose abundance is controlled by predation of the starfish *Heliaster helianthus*, though it has little effect on mussels' colonization of bare rock during succession, probably because grazers negatively affect recruitment due to bulldozing or crushing the young settlers (Hidalgo et al., 2011). In the low intertidal, *S. algaosus* was never found directly on the primary substratum, but on refuges such as fronds of macroalgae growing as epiphyte of the barnacle *Megalalanus psittacus* (F. Hidalgo, personal observation), probably because there they escape grazing. Previous studies in Chile showed that grazing by *Tetrapygyus niger* can be intense, generating halos in beds of intertidal pool benthic algae (Contreras & Castilla, 1987) and impeding the colonization of the substrate by foliose and corticated macroalgae in the intertidal–subtidal boundary (Ojeda & Santelices, 1984). Our comparison of the effects of the most abundant grazers indicates that unlike what occurs in Chile regarding the interaction between sea urchins and algae (e.g. Ojeda & Santelices, 1984; Vásquez, 1993, 2001), *S. algaosus* in Peru has the potential to fast colonize the substrata in the low intertidal zone and overgrowth macroalgae when *T. niger* is absent.

Different feeding capabilities of benthic herbivores may play a central role in determining the different patterns of distribution and abundances of their prey resources (see Branch & Branch, 1980; Steneck & Watling, 1982; Schmitt, 1996). In our case, the strong effect of urchins may be related to their coarse-grained method of grazing over the substratum, with

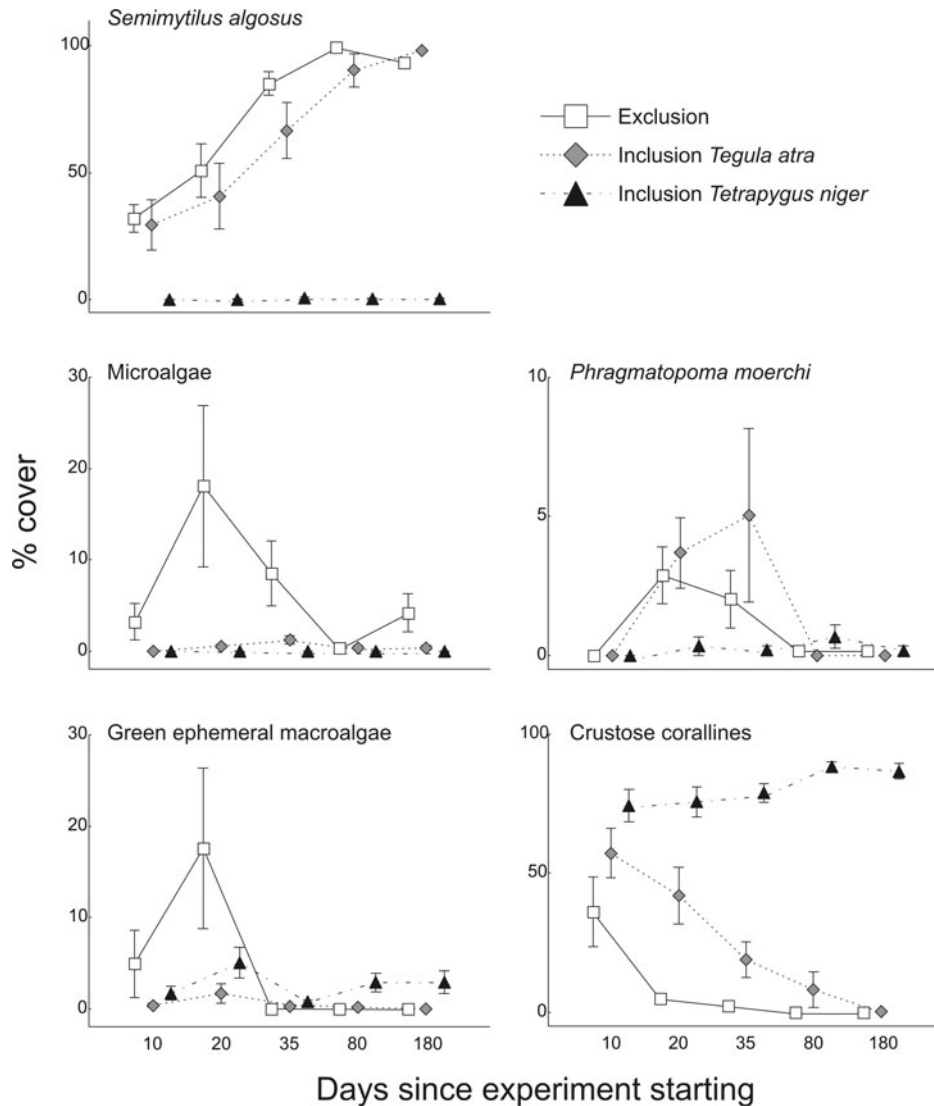


Fig. 5. Percentage cover (mean  $\pm$  SE) of *Semimytilus algalus*, microalgae, green ephemeral macroalgae, the sessile polychaete *Phragmatopoma moerchi*, and crustose coralline within exclusions, inclusions of *Tegula atra* and inclusions of *Tetrabygus niger* at days 10, 20, 35, 80 and 180 after beginning the second experimental period.

which they can bulldoze the small underlying invertebrates (see Day & Branch, 2002). In contrast, the effects of *Tegula atra* were comparatively negligible, since it just reduced the abundance of microalgae and green ephemeral macroalgae during early succession, being unable to impede the fast colonization of the substrate by *S. algalus*. The presence of *S. algalus* recruits in the gut content of both grazers indicates that they can potentially affect mussels directly by consumption; however, the feeding apparatus of *T. atra* would impede them to ingest mussels once they have attained a size beyond which they can escape grazing by snails (see Wahl & Hoppe, 2002), and this is reflected in the comparatively lower number of *T. atra* stomachs containing mussels. Furthermore, the presence of shell fragments of mussels in the stomachs of *Tetrabygus niger* indicates that urchins can also break the valve of larger individuals with the teeth of the lantern, or passively swallow valve pieces when feeding on macroalgae. It should be noted here that we are assuming that the effects of *T. niger* and *Tegula atra* on community structure act in additive manner, with *T. atra* having negligible

effects. The positive effects of *T. atra* on *Phragmatopoma moerchi* may be related to the selective elimination of microalgae and green macroalgae that may compete with *P. moerchi* settlers for substrate colonization.

The differential use of resources such as habitat and food can allow the coexistence of species sharing the same habitat (e.g. Branch & Branch, 1980; Vásquez *et al.*, 1984; Cobb & Lawrence, 2005). In this regard, we did not find strong evidence of habitat segregation between *Tetrabygus niger* and *Tegula atra* at the temporal and spatial scales investigated here. However, gut content analysis did reveal differences in their diets. Microalgae were the main food item present in *T. atra* stomachs, while most *Tetrabygus niger* stomachs had also filamentous, foliose and corticated macroalgae. The rhipidoglossan radula of *Tegula atra* is mainly adapted to graze filamentous and microscopic algal forms (see Reyes *et al.*, 2001), while the Aristotle's lantern of *Tetrabygus niger* makes it able to consume benthic foliose and corticated macroalgae (see Contreras & Castilla, 1987), supporting our results. While it seems from this analysis that *Tegula atra*

and *Tetrapygyus niger* are functionally redundant in terms of consuming microalgae, both species have different feeding mechanisms and this may affect the mode the food is taken. *Tegula atra* would actually feed on microalgae, while *Tetrapygyus niger* would ingest them accidentally as epiphytes growing on other benthic algae. The differences in the gut contents were also sustained by the carbon and nitrogen isotopes signatures for *T. niger* and *Tegula atra*. The difference in carbon isotope signature (~1‰) might reflect the different energy sources of both consumers, while a similar difference in nitrogen isotope signature (~1‰) is insufficient to separate both species in different trophic positions (consumers from different trophic levels tend to be nitrogen enriched by ~3‰ per trophic level; Lajtha & Michener, 2007).

In summary, we can argue that *Tetrapygyus niger* plays a key role in this low intertidal community. Through directly limiting *S. algosus* to monopolize the substratum, *T. niger* can indirectly reduce the diversity of mussel associated species, including recruits of commercially valuable species such as *Fissurella* spp., which cannot persist outside mussel matrices (Tokeshi & Romero, 1995). Conversely, through controlling primary space holders, sea urchins can also benefit other grazers, including *Tegula atra*, and filter-feeders that live on bare substrate (see Tokeshi & Romero, 1995), by creating a suitable area for feeding or living (e.g. Branch & Branch, 1980; Ayling, 1981; Steneck & Watling, 1982).

## ACKNOWLEDGEMENTS

We want to express our gratitude to the colleagues and friends of the Universidad Nacional Mayor de San Marcos, especially to J. Tarazona, E. Ramos, P. Gallegos and A. Gamarra, for providing us with their laboratory and logistics and field assistance during our work in Peru. We also thank Marina de Guerra del Perú for allowing us access to the study sites, and G. Alvarez and F. Botto for their help with the isotopic analysis. The manuscript has been improved with the comments of one anonymous referee.

## FINANCIAL SUPPORT

This study was conducted and financed in the frame of the EU-project CENSOR (Climate variability and El Niño Southern Oscillation: impacts for natural resources and management, Contract 511071).

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