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Habitat structure is more important than nutrient supply in modifying mussel bed assemblage in an upwelling area of the Peruvian coast

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Abstract Upwelling intensity modifies coastal primary production and influences individual traits of habitat-forming species. Along the Peruvian coast, beds of the mytilid *Perumytilus purpuratus* provide structurally complex habitats that harbour many organisms. We predict that in the nutrient-rich system of Central Peru, the modification of structural complexity would have stronger effects on the *Perumytilus* community than nutrient addition. We experimentally examined the effects of nutrient addition on the *Perumytilus*-dominated assemblage and we evaluated the potential effect of varying shell size on the *Perumytilus*-dominated assemblage. Nutrient addition to the mussel bed with slow-release fertilizers caused no changes in the total macro- and microalgal biomass and did not affect abundances or composition of the assemblage. To explore the effect of structural complexity on the *Perumytilus* assemblage, we manipulated mussel size with experimental bags containing small and large individuals. Predators, grazers and mobile organisms were more abundant among smaller mussels, with smaller gap volume, whereas the barnacle *Jehlius cirratus* was more abundant on larger mussels. In conclusion, point-source nutrient addition to the mussel bed did not enhance primary production. However, the modification of structural characteristics related to mussel size induced changes in the faunal assemblage. Thus, it seems that in this nutrient-rich system, nutrient enhancement would not significantly affect *Perumytilus* and its assemblage, whereas structural habitat seems to play an important role in shaping this community.

Keywords Bottom-up · Community structure · Peru · *Perumytilus purpuratus* · Rocky intertidal

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Introduction

Nutrient enrichment of surface waters as a result of the upwelling of deeper oceanic water has been well documented for several shores around the world (e.g. Bosman et al. 1987). On rocky shores, this nutrient enhancement may produce variation at lower trophic levels (bottom–up effect, Menge 1992) by (1) influencing the growth of sessile filter-feeders, which depends on the input of plankton and particulate matter or (2) modifying directly algal productivity (Wieters 2005). Several studies from coastal upwelling areas (Bustamante 1995; Menge et al. 1997, 1999) support the predictions of the bottom–up theory that high offshore production (e.g. high phytoplankton concentration) increases onshore production by enhancing food supply to filter-feeders, leading to improved survival, increased reproductive output and higher growth rates (Blanchette et al. 2007).

In benthic systems, biogenic habitats are often generated by dominant competitors, that is, species that monopolize the primary substratum, and establish a secondary

substratum for smaller organisms (e.g. Bruno et al. 2003). Along the Chilean coast, Wieters (2005) has demonstrated how coastal upwelling may influence the individual traits of such facilitators, modifying the environment and determining thus important consequences for community regulation. In intertidal rocky shores, mytilids create a 3-dimensional structure that consists of three major components: the mussel matrix, an assemblage of associated organisms and accumulated detritus (Suchanek 1985). These structures facilitate colonization by certain organisms (Suchanek 1978, 1985), which would either decrease in density or altogether disappear if mytilids did not exist on the rocky substratum (Tokeshi and Romero 2000). Ecosystem engineering (i.e. the creation, modification and maintenance of habitats by organisms, Jones et al. 1994) by mussels modifies their local environment (e.g. McKindsey and Bourget 2001) by mitigating desiccation stress (Helmuth 1998), buffering hydrodynamic forces (Bertness et al. 2006; O'Donnell 2008), providing refugia against predators (Borthagaray and Carranza 2007) and providing energy for the associated community (Norling and Kautsky 2007). Furthermore, by modifying heterogeneity and structural complexity (i.e. variation in habitat structure attributable to the absolute abundance of individual structural components, Beck 2000), shell size seems to play an important role influencing community structure of the assemblage associated with mussel beds (Tsuchiya and Nishihira 1986). For instance, larger shells usually support more individuals of a given fouling species and a greater richness of fouling species than smaller ones (see Gutiérrez et al. 2003).

The mytilid *Perumytilus purpuratus* (Lamarck, 1819; hereafter *Perumytilus*) inhabits the mid intertidal rocky shores in the south-eastern Pacific from Ecuador (2°00′ S 77°30′ W), down the west coast of South America to Cape Horn, and in the South Atlantic as far north as La Lobería, Argentina (41°8′ S 63°10′ W, Prado and Castilla 2006). The matrices that form *Perumytilus* harbour a great number of invertebrates and macroalgae (Alvarado and Castilla 1996; Prado and Castilla 2006). Previous studies suggest that on rocky shores, *Perumytilus* matrices primarily provide structural protection to the associated community, mainly composed of suspension-feeding organisms (Thiel and Ullrich 2002), while they trap sediment, affecting the composition of faunal assemblages and reducing evenness as sediment retention increases (Prado and Castilla 2006). Thus, *Perumytilus* can be considered a bioengineer playing a key role in structuring communities and determining local biodiversity on rocky shores of the south-eastern Pacific.

Despite the importance of biogenic habitats in structuring intertidal assemblages, it is not clear yet how their positive effects are related to other structuring processes in benthic communities (e.g. disturbance, predation, competition, primary production; Valdivia and Thiel 2006). Open, upwelling-dominated coastlines are thought to be less susceptible to the effects of additional nitrogen because of the large amount of nitrogen supplied by coastal upwelling (see Nielsen 2003). Moreover, previous studies have reported weaker responses to nutrient addition of primary and secondary producers as background nutrient increases (e.g. Posey et al. 2006; Teichberg et al. 2008), while along the Peruvian coast, upwelled nutrients may overwhelm the effects of anthropogenic inputs on the structure of intertidal communities (Firstater et al. 2010). On the other hand, since on rocky shores *Perumytilus* mainly provides structurally complex habitats, changes in structural complexity would affect the associated community regardless of the system productivity. Thus, we predict that in a nutrient-rich system, nutrient enhancement would have a minor effect on the assemblage associated with *Perumytilus*, whereas modification of mussel shell size would have larger effects on the *Perumytilus* assemblage. In this study, we experimentally examined in a nutrient-rich system, the effects of nutrient addition on the *Perumytilus* assemblage and we evaluated the potential effect of varying shell size on the *Perumytilus* assemblage.

Materials and methods

Study site

The study was performed on the rocky shore areas located south of Ancón Bay (11°46′ S, 77°11′ W; Fig. 1), on the Peruvian central coast. This area, subjected to a semidiurnal tidal cycle with an average amplitude of 0.54 m (Dirección de Hidrografía y Navegación 2006), is part of the Peruvian coastal upwelling ecosystem and is located within a main upwelling centre, receiving waters with high nutrient concentrations, low oxygen content and experiencing frequent phytoplanktonic blooms (Tarazona et al. 2003). In Ancón Bay, *Perumytilus* is commonly found in rock crevices of the upper-mid intertidal zone, forming dense beds in the mid zone, with an associated community that comprises up to 87 species (Paredes and Tarazona 1980).

Effects of nutrient supply on the assemblage of *Perumytilus* beds and microphytobenthic Chl-*a*

The responses to nutrient addition of the mussel-associated community and the microphytobenthic Chl-*a* on mussel shells were examined in a short-term field experiment in which nutrient level was manipulated. The experiment was
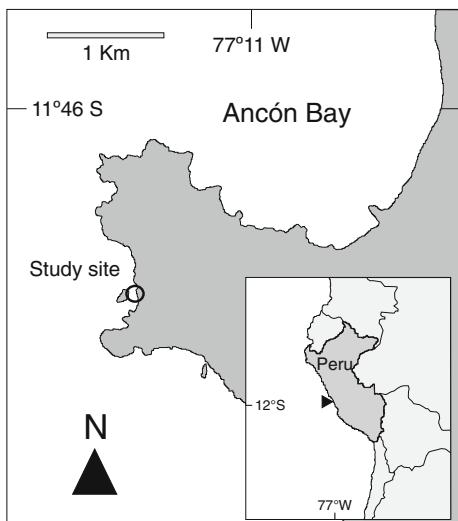
Fig. 1 Map of the area of Ancón Bay, indicating the study site (*open circle*)

conducted between April and June 2008. This timescale was considered appropriate since previous studies on the effects of nutrients on macroalgae, periphyton and mussel communities have detected significant responses after 2 months or less of continuous nutrient enrichment (e.g. Worm and Sommer 2000; Hillebrand and Kahlert 2001; Valdivia and Thiel 2006). Twenty plots (ten replicates per treatment: nutrient addition and control) were distributed in the mid intertidal zone, over a mussel bed of approximately 200 m^2. Each plot consisted of a 10 × 10 cm area fully covered with mussels. Two small areas at the upper and lower edge of each plot (parallel to shoreline) were cleared from mussels in order to introduce fertilizer bags. The fertilizer bags (20 × 3 cm nylon bags with 1-mm mesh size) contained 60 g slow-release fertilizer (Multicote, Schultz Company, USA) with nitrogen (18%), phosphate (6%) and potassium (12%). This amount of fertilizer has been demonstrated to enhance nutrient availability over a wide range of nutrient background concentrations (Worm et al. 2000). The bags in experimental controls were filled with inert stones (for details, see Valdivia and Thiel 2006), and all bags were fixed to the rock with stainless screws. Unfortunately, due to methodological constraints in obtaining a reliable measure of nutrients from the plots, we could not directly assess the nutrient release in the mussel bed. However, slow-release fertilizer pellets increase nutrients in sediments and water column, remaining largely unaffected by wave exposure (see Worm et al. 2000 for review of enrichment methods).

At the end of the experiment, the mussels and the associated organisms were removed from the plots by scraping, taking care to collect all mobile fauna, and stored frozen in plastic bags. Samples were then sieved through a 1-mm mesh, and all organisms were identified to the lowest

possible taxonomic level (usually genus or species). The invertebrates were counted, and dry mass of algae was determined by drying at 80°C to constant weight. Algal species were grouped into functional groups (foliose, corticated and thinly corticated) following Steneck and Dethier (1994). Faunal organisms were also classified according to their feeding habits (grazers, suspension-feeders, deposit-feeders and predators/scavengers) and mobility (sessile and mobile). This was done on the basis of morphological characteristics of specimens and available literature (see Valdivia and Thiel 2006).

Univariate and multivariate statistical analyses were performed to test the effects of nutrient addition on mussel assemblage. Separate *t*-tests were performed to analyse differences in mussel densities, total algal biomass, algal functional groups, total abundance of invertebrates, feeding guilds and mobility groups. Homogeneity of variances could not be achieved by any transformation for deposit-feeder data; therefore, raw data were analysed with the more conservative value of $\alpha = 0.01$ (see Connell and Glasby 1999). Two separate sets of multivariate analyses were performed, one for macrofauna with abundance data and the other for algae with biomass data. Based on Bray-Curtis similarity matrices on fourth root-transformed data (Clarke and Warwick 2001), two one-way analyses of similarities (ANOSIMs) were performed (Clarke 1993). In addition, the percentage contributions of each taxon to patterns of dissimilarity between treatments were calculated (Clarke 1993), and taxa contributing to at least 10% of the dissimilarity were considered important differentiators (Bulleri 2005). The abundances of these taxa were then analysed by means of separate *t*-tests (Zar 1999).

Chl-*a* content, an indicator of total microalgal load, that provides an important food resource for grazers on exposed rocky shores (Thompson et al. 2004; Armitage et al. 2006), was measured on the mussel shells following an adaptation of the method proposed by Thompson et al. (1999). For this, two mussels (~25-mm shell length) were selected from each sample, cleaned from all visible macroalgae, dissected and soft tissue carefully removed from their valves. One empty valve from each individual was then placed in a single container with 100% ethanol. After 7 h of pigment extraction, Chl-*a* biomass was determined with a spectrophotometer. After extraction, digital pictures of the shells were taken and their 2-dimensional surface areas were measured with image analyser software (ImageJ 1.4). Averaged content of Chl-*a* was then expressed as µg cm^{-2}. Differences in Chl-*a* biomass between treatments were evaluated with a *t*-test.

Effects of mussel size on the assemblage

To test the effect of *Perumytilus* size on the community structure, a transplant experiment with small (shell length

6–17 mm) and large (shell length > 30 mm) mussels was performed in May 2007. These size ranges were chosen to represent the natural size variability in the study area determined on the basis of the size frequency distribution plot. Mussels were cleaned of epifauna and groups of ∼50 small and ∼6 large mussels, respectively, were placed in net bags (10-mm mesh) occupying a standardized total volume of ∼30 cm^3. Bags were placed in two 6-l buckets filled with seawater for 1 day to stimulate attachment of byssal threads between mussels. Twelve bags of each treatment were then randomly fastened to a patch of bare rock in the mid intertidal zone with stainless screws. After 80 days, in August 2007, all organisms were removed from bags. They were identified to the lowest possible taxonomic level, counted, including epibiont barnacles, and classified as described previously. Macroalgae were not quantified because they settled mainly on net bags. As many mussels disappeared from several bags, analyses were restricted to those with more than 20 small ($n = 7$) and at least 4 large mussels ($n = 7$).

The amount of interstitial space (i.e. the available space among mussels, see Bartholomew et al. 2000) and total sample volume was estimated. Retrieved mussels (4–6 large and 24–64 small mussels, see "Results") were cleaned and placed in jars (120 mm height × 60 mm diameter), crowded as they occur in natural beds. Inside the jars, large mussels were mono or two layered, whereas small mussels were four to seven layered. Then, jars were filled with water until all mussels were covered. Gap volume within mussels was then estimated as the total volume of water added. Finally, individual shell areas were estimated based on calculation for the area of an ellipse (with shell length and width as major and minor axes, respectively). Differences in total sample volume, gap volume and total shell area between small and large mussels were examined with t-tests. Homoscedasticity could not be achieved for total sample volume and shell area data. For these variables, raw data were therefore analysed with $\alpha = 0.01$ (see above).

Two sets of analyses on abundance data, one standardized per cm^2 of the total sample shell area and another standardized per cm^3 of gap volume, were used to explore the differences in species composition between mussel sizes. Multivariate analyses were performed as described previously and the abundances of the most important differentiators (species that contribute at least 10% of the dissimilarity) were analysed by means of separate t-tests. Additionally, the differences in total abundance, feeding guilds and mobility groups of invertebrates were examined with separate t-tests. Abundance data of *Semimytilus algosus* (Gould, 1850), *Jehlius cirratus* (Darwin, 1854), grazers, suspension-feeders, mobile and sessile organisms, and total abundance were transformed to $X^{0.25}$ to meet

t-test assumptions. Univariate analysis on deposit-feeders data was not performed because these were only found in one sample of each treatment.

The use of replicate experimental sites, taking into account the spatial variability in the responses of organisms (Chapman 2000), would have ensured the generality of our results; however, constraints of feasibility and appropriate access to similar areas prevented us from using replicate sites. Consequently, our inferences are restricted to the studied area.

Results

Effects of nutrient supply on the assemblage of *Perumytilus* beds and microphytobenthic Chl-*a*

Twenty-six taxa were found in the *Perumytilus* bed (Table 1). Mussel density (mean = 89.3 individuals per 100 cm^2, SD = 32.4) was not different between nutrient addition and control plots ($t = -1.18$, $df = 17$, $P = 0.25$). There were no differences in total algal biomass, total abundance of invertebrates and abundances of the feeding groups between treatments (Table 2; Figs. 2, 3).

Analysis of similarities for algae and invertebrates did not reveal differences in the species composition between treatments (ANOSIM global $R = -0.03$ and -0.02 for algae and invertebrates, respectively, $P = 0.6$ for both). Finally, there were no differences in Chl-*a* biomass on mussel surface between nutrient addition (mean = 0.39 μg cm^{-2}, SD = 0.28) and controls (mean = 0.23 μg cm^{-2}, SD = 0.18; $t = -1.46$, $df = 17$, $P = 0.16$).

Effects of mussel size on the assemblage

Total sample volume did not differ between treatments ($t = -0.3$, $df = 12$, $P = 0.77$), ranging from 17.3 to 25.9 cm^3 for large mussels (4–6 retrieved mussels) and from 11.3 to 34.5 cm^3 for small mussels (24–64 retrieved mussels). Gaps within large mussels were more than threefold larger than within small mussels ($t = -8.54$, $df = 12$, $P < 0.001$). However, there were no differences between total shell areas ($t = -0.1$, $df = 12$, $P = 0.92$).

A total of 14 invertebrates species were found in transplants (Table 1). The analysis of similarity (ANOSIM) revealed significant differences between mussel size treatments when comparing structure of faunal assemblages per cm^2 of total shell area ($R = 0.196$, $P = 0.01$); moreover, these differences increased when comparing structure per cm^3 of gap ($R = 0.348$, $P = 0.001$).

The barnacle *Jehlius cirratus*, *Semimytilus algosus* recruits and the sessile polychaete *Phragmatopoma moerchi* (Kinberg, 1867) contributed most to the differences

Table 1 Invertebrates associated with *Perumytilus purpuratus* during nutrient addition and transplant experiments

Taxa		Feeding guild	Mobility	Experiment
CNIDARIA	*Phymactis clematis*	SF	S	T, N
PLATYHELMINTHES	Polycladida indet.	P	M	T
NEMERTEA	Nemertea indet.	P	M	T, N
	Aquilaspio spp.	DF	M	T
	Halosydna spp.	P	M	N
ANNELIDA	*Phragmatopoma moerchi*	SF	S	T, N
	Pseudonereis gallapagensis	P	M	T, N
	Scoletoma tetraura	P	M	N
	Steggoa negra	P	M	N
	Syllis spp.	P	M	N
MOLLUSCA				
Bivalvia	*Rochefortia* spp.	SF	S	N
	Semimytilus algosus (<5 mm)	SF	S	T, N
Gastropoda	*Crepipatella dilatata*	SF	M	N
	Fissurella spp.	G	M	N
	Nassarius dentifer	P	M	N
	Scurria spp.	G	M	N
	Siphonaria lessoni	G	M	T, N
Polyplacophora	*Chiton* spp.	G	M	N
	Acanthopleura spp.	G	M	N
BRACHIPODA	*Discinisca lamellosa*	SF	S	N
ARTHROPODA				
Cirripedia	*Jehlius cirratus*	SF	S	T, N
	Balanus laevis	SF	S	T
Decapoda	*Acanthocyclus gayi*	P	M	N
	Petrolisthes spp.	SF	M	N
	Decapoda indet.			N
Peracarida	*Dynamenella* spp.	G	M	T, N
	Gammaridae indet.	G	M	T, N
Others	Megalopa larvae	P	M	T, N
ECHINODERMATA				
Ophiuroidea	*Ophiactis kroyeri*	DF	M	T, N

Feeding guild (*G* grazers, *DF* deposit-feeders, *SF* suspension-feeders, *P* predators/scavengers); mobility (*S* sessile, *M* mobile); and experiment (*T* transplant experiment, *N* nutrient addition experiment)

between treatments, accounting for 23.3, 14.8 and 11.6% of the dissimilarity by cm^2 of total shell area, and 17.6, 17.8 and 10% by cm^3 of gap, respectively. The polychaete *Pseudonereis gallapagensis* (Kinberg, 1866) was also an important differentiator when analysing gaps (10.7% of the dissimilarity).

When analysing abundances per cm^2 of total shell area, density of *Jehlius cirratus* was higher on large mussels, but no further difference was detected by univariate tests (Table 3; Fig. 4). When considering abundances per cm^3 of gap, *Pseudonereis gallapagensis* was the only species with higher abundance in samples with small mussels. With respect to functional groups, predators, grazers and mobile organisms were also more abundant among small mussels. On the other hand, the abundances of *Semimytilus algosus* recruits, *Jehlius cirratus*, suspension-feeders, sessile and

total abundance did not vary between treatments (Table 3; Fig. 4).

Discussion

Effects of nutrient supply on the assemblage of *Perumytilus* beds and microphytobenthic Chl-*a*

The extent to which the ecosystem engineering effects of habitat-forming organisms may depend on environmental conditions remains largely unexplored (Wright and Jones 2006; Menge et al. 2008). The results of our experimental nutrient addition to the *Perumytilus* bed agree with previous studies, finding no response of microalgal biomass and only weak response of the macrofaunal abundance to local

Table 2 Results of *t*-tests on algal total biomass, invertebrates' total abundance and functional groups of *Perumytilus purpuratus* assemblage in mussel bed fertilization experiment

	t-Value	*P*
Algae		
Total biomass	0.57	0.57
Foliose	0.22	0.82
Corticated	−0.51	0.6
Thinly corticated	0.8	0.43
Invertebrates		
Total abundance	0.06	0.95
Grazers	0.46	0.64
Suspension-feeders	−0.29	0.77
Deposit-feeders	0.74	0.47
Predators	0.22	0.83
Mobile	0.67	0.5
Sessile	−0.28	0.77

For all tests, $df = 17$
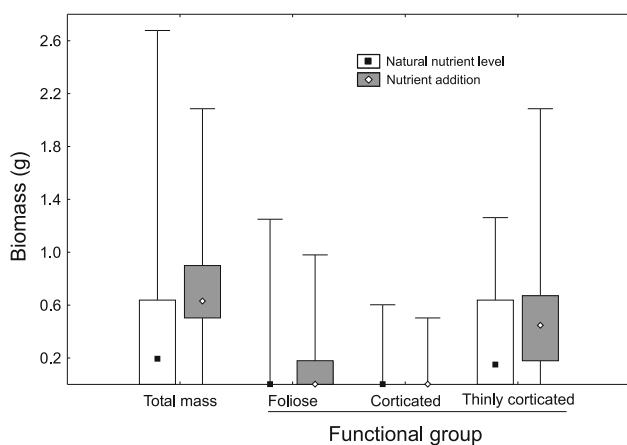
Fig. 2 Effect of nutrient addition on total biomass of different algal functional groups of *Perumytilus purpuratus* bed assemblages (median; box, 25th to 75th percentiles; whiskers, 5th to 95th percentiles)

nutrient enrichment in areas with high levels of background nutrients (Posey et al. 2006; Valdivia and Thiel 2006). It is likely that local nutrient enrichment alone may be insufficient in stimulating structural changes in exposed rocky shore communities (Bokn et al. 2003; Thompson et al. 2004).

Nutrient addition did not result in increased microphytobenthos on the surface of *Perumytilus* shells, which may be due to several reasons. Nitrogen availability and herbivores have strong and antagonistic effects on microalgal biomass, species composition and diversity (Hillebrand et al. 2000). Since grazers could freely enter our fertilized plots, it is possible that their effect might have prevented

biofilm growth. Since nutrient addition increases food quality and thereby attract grazers (Worm and Sommer 2000), a higher abundance of grazers would be expected in enriched plots; however, abundances were similar between treatments. This could be due to the high mobility of grazers that allow them to quickly move within the mussel bed (Valdivia and Thiel 2006). Moreover, a meta-analysis on experiments with periphyton (Hillebrand 2002) has shown that even in high-productivity areas, grazing pressure increases with increasing nitrogen availability. Thus, enrichment would lead to increased microalgal biomass (bottom–up effect), but grazers would also remove more biomass in enriched nutrient plots (top–down effect, Sommer 1999; Hillebrand et al. 2000). The exclusion of grazers combined with our nutrient enrichment treatment would have provided a valuable insight into the relative strength of bottom–up and top–down control on biofilm; however, the use of cumbersome devices to manipulate mobile grazers in the mussel bed would have probably distorted natural conditions as well (see Parker et al. 1993).

Regarding the associated fauna, the abundance of single species or feeding groups remained unaffected by nutrient addition. Up to 92 associated species were registered in the *Perumytilus* beds of the Peruvian and Chilean shores (Paredes and Tarazona 1980, Prado and Castilla 2006). In this study, the number of taxa reported (26) is thought to be underestimated since some groups, such as the polychaete *Syllis* or the limpet *Scurria*, may contain at least 3 and 4 species, respectively, which could not be distinguished (see Tokeshi and Romero 1995). Nevertheless, the results of our analyses are still valid for interpretation since they were based on the abundances of feeding groups. Invertebrate assemblages associated with *Perumytilus* beds were dominated by sessile suspension-feeders (barnacles and anemones), followed by grazers (chitons and limpets) and other groups. Thus, as suggested for assemblages of mussel beds from the Chilean shore (Thiel and Ullrich 2002), most organisms obtain their feeding resources from the water column rather than from materials deposited on or by the mussels, using mussel shells as structural support.

Effects of mussel size on the assemblage

There were no changes in the species composition related to mussel size. However, differences in densities of single species and feeding groups were observed when analysing densities both per area and interstitial volume of small and large mussels. All species that differed between mussel sizes were sessile. The barnacle *Jehlius cirratus* was more abundant per unit area among large mussels, and the tube-building polychaete *Phragmatopoma moerchi* was restricted to large mussels, although the total shell surface areas

Fig. 3 Effect of nutrient addition on total abundance, faunal feeding guilds and mobility groups of *Perumytilus purpuratus* bed assemblages (median; *box*, 25th to 75th percentiles; *whiskers*, 5th to 95th percentiles)
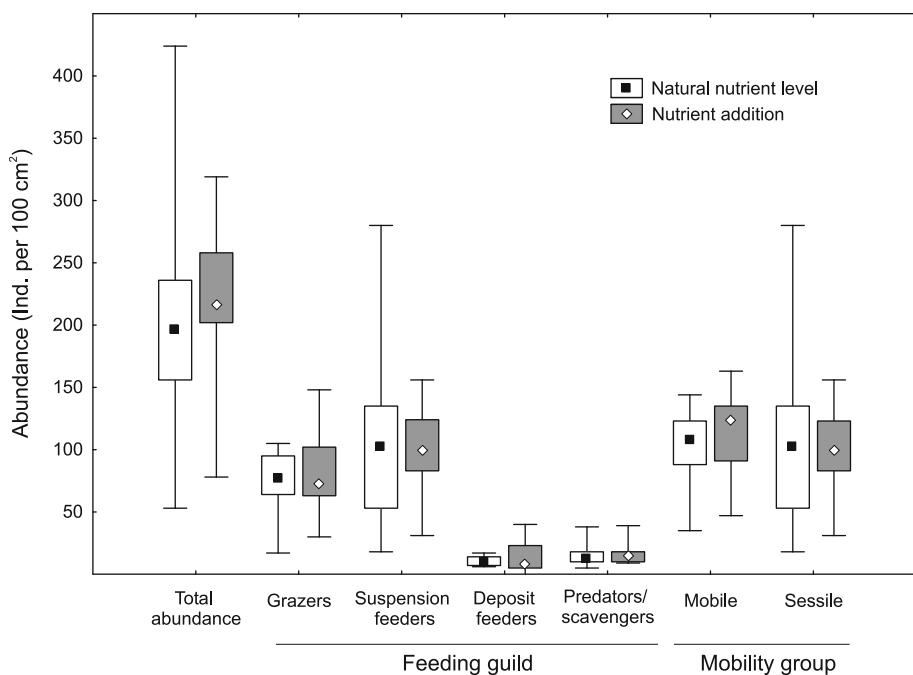

Table 3 Results of *t*-tests on most important differentiators and functional groups in mussel transplant experiment

	By cm^2 of total shell area *t*-Value	By cm^3 of gap *t*-Value
Differentiators		
Jehlius cirratus	−3.12**	−1.75
Semimytilus algosus	1.17	2.02
Pseudonereis gallapagensis	–	2.77**
Functional groups		
Grazers	−0.15	3.74**
Predators/scavengers	0.53	2.7**
Suspension-feeders	−1.58	0.58
Mobile	−0.09	4.13**
Sessile	−1.58	0.57
Total abundance	−1.38	2.1

** Indicate significant difference ($P < 0.05$). For all tests, $df = 12$

of small and large mussels were similar. The microtopography and chemical properties of the shell surface are important factors controlling the settlement of epibionts on mytilids (Bers et al. 2010); however, it is possible that larvae that actively explore the substratum before settling, such as barnacle cyprids, selected the larger and continuous surface of large mussels reducing, thus, the risk of overgrowing the substratum organisms (i.e. the mussel) and inducing further the settling of conspecifics (Thompson et al. 1998; Wahl 2009).

Differences in the structure of the associated community increased when analysing abundances per unit volume of interstitial space. At this level, *Jehlius cirratus*, *Semimytilus algosus* recruits and *Phragmatopoma moerchi* were also identified as differentiators between differently sized mussels. Moreover, the polychaete *Pseudonereis gallapagensis*, a large free-ranging predator, contributed to distinguish between treatments and was more abundant among small mussels. Even though there was more interstitial space among large mussels, more grazers, predators and mobile organisms per unit volume were also found in small mussel gaps. The internal structure of mussel interstitial space, filled with sediment, byssal threads and shell fragment favours occupancy by a variety of small animals through creation of several microhabitats (Tsuchiya and Nishihira 1985, 1986). Our measures of interstitial volume did not take into account these components; however, we can speculate about an enhancement of habitat complexity within small mussels compared with larger ones. Habitat complexity can have strong effects on the local distributions of some intertidal organisms (Beck 2000). In transplants, smaller and denser mussels constituted a more complex matrix, which could provide a more suitable environment, reducing desiccation and improving protection for mobile fauna that can actively select their habitat (Tsuchiya and Nishihira 1986).

In our transplant experiment, the total sample volumes were similar; thus, differences in mussel size entailed differences in density. An increase in almost threefold shell length represented a reduction of about 8.5-fold in the number of mussels per unit volume. Similar relationships between size and density have been observed when sampling natural patches per unit area (Tsuchiya and Nishihira

Fig. 4 Effect of *Perumytilus purpuratus* size on total abundance, feeding guilds and mobility groups of associated fauna, standardized by **a** cm^2 of total shell area and **b** cm^3 of gap (median; *box*, 25th to 75th percentiles; *whiskers*, 5th to 95th percentiles). *Letters* denote significant differences ($\alpha < 0.05$)
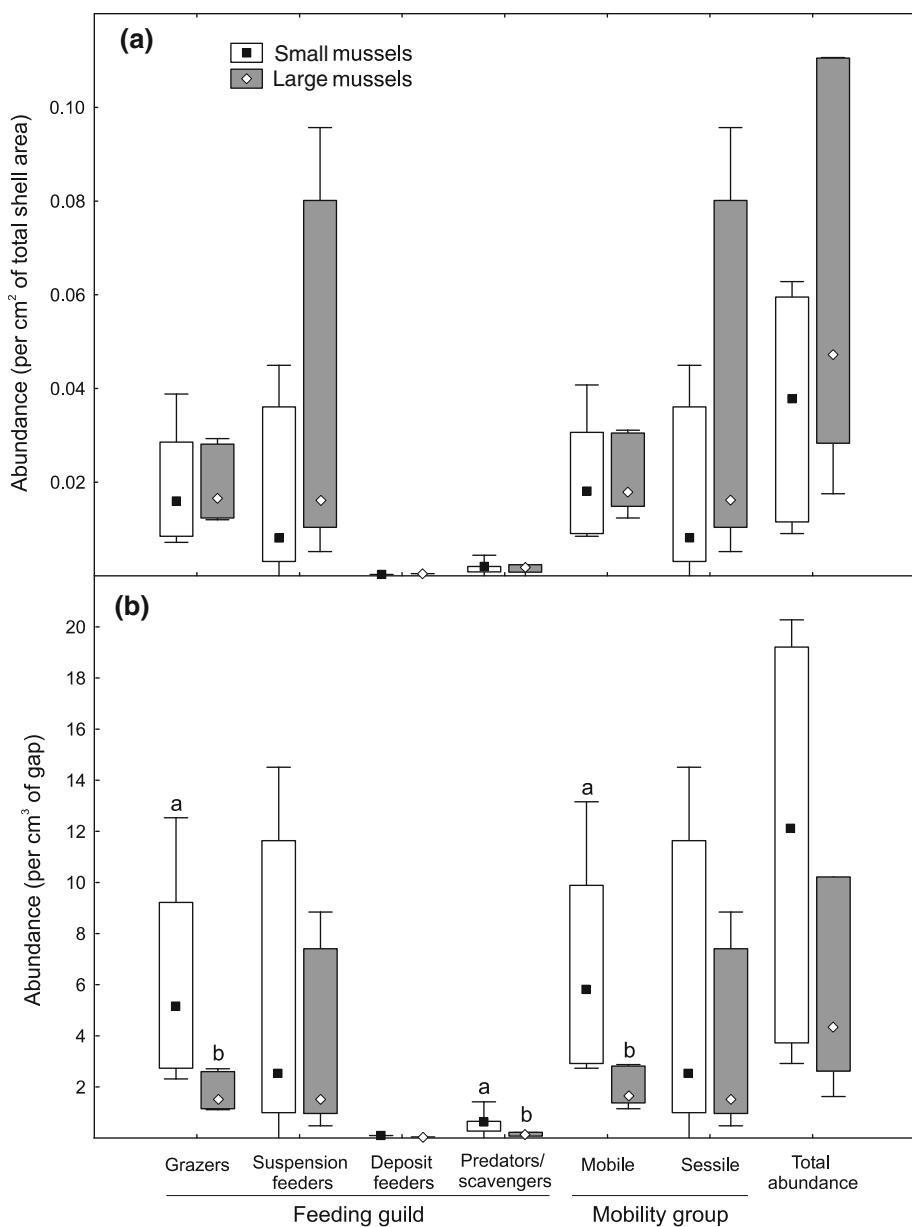
1986). Therefore, it is not surprising to find variation in macroinvertebrate densities that are often positively related to mussel densities (e.g. Vaughn and Spooner 2006). Moreover, since interactions at the population level, playing an important role in the space regulation in the *Perumytilus* bed, are highly density dependent (e.g. self-thinning, Guiñez and Castilla 1999), an additional transplant experiment varying mussel size and keeping density constant would have allowed us to decouple both structural elements, adding some valuable insight into mechanisms underlying space occupancy.

Coastal upwelling, by altering the primary production over the large scale, may control trait-dependent habitat modification and regulate the relative importance of facilitation in marine rocky intertidal communities (Wieters

2005). In Ancón Bay, local nutrient addition did not result in the enhancement of primary production or changes in the community structure of the *Perumytilus* bed, but differences in mussel size led to variation in habitat structure which was reflected in the lower densities of many associated organisms among larger mussels. Present results suggest that in upwelling areas, where nutrient would not be a limiting factor, local nutrient enhancement would not significantly affect *Perumytilus* and its assemblage, whereas biologically generated structural habitat seems to play an important role in shaping this community. However, since this study was conducted at a single site, further experiments spanning larger spatial scales are necessary to determine the generality of these findings within nutrient-rich areas, while consumer manipulation would also

elucidate the role of grazing in controlling primary production.

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