



The role of *Argopecten purpuratus* shells structuring the soft bottom community in shallow waters of southern Peru



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ABSTRACT

Accumulation of *Argopecten purpuratus* shells often occurs after El Niño events in shallow waters of Independencia Bay (14°17'S–76°10'W; Pisco, Peru). Here we experimentally investigate the effects of their shell accumulation on macrobenthos assemblages in soft bottom, shallow areas of the bay. A field experiment (from May 2006 to May 2007), including four treatments with different coverage levels of empty shells of *A. purpuratus*, were randomly arranged in: (1) areas devoid of shells (“Empty” treatment: experimental control), (2) 50% of the plot area covered with shells haphazardly distributed over the bottom (“medium” treatment), (3) 100% of the plot area covered with shells, forming a 10 cm valve layer (“full” treatment) and (4) “natural control”. We found a total of 124 taxa throughout the experiment. Polychaetes, crustaceans and mollusks were the most abundant groups in “natural controls”, dominated by the gastropod *Nassarius gayi* and the polychaetes *Prionospio peruana*, *Platynereis bicanaliculata* and *Mediomastus branchiferus*. The abundance of individuals (N) and the species richness (S) were higher in the “medium” treatment, but only in one month under positive sea bottom thermal anomalies. Similarity analysis (Bray–Curtis) showed that “natural control”, “empty” and “full” treatments were more similar among them than the “medium” treatment. Multidimensional analysis showed no clear species association among treatments and a higher grouping among the samplings of Jun-06, Aug-06 and Nov-06. Our results also showed that the commercial crab *Romaleon polyodon* and the polyplacophora *Tonicia elegans* were positively affected by shell accumulations (“medium” treatment), while the limpet *Fissurella crassa* was negatively affected. Our study shows that directly by changing habitat structure or indirectly by changing sediment characteristics, the addition of scallop shells to the soft bottom can modify the macrobenthic assemblage; however, the seasonal oceanographic variability (e.g. upwelling, El Niño) could have stronger effects controlling this system than the presence of the shells itself.

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1. Introduction

One of the forces controlling the structure of communities is the creation or modification of habitats by other organisms, a process known as ecosystem engineering (sensu Jones et al., 1994). For example, valve production can modify the complexity and heterogeneity of the habitat, changing the availability of resources to other organisms (e.g. Guay and Himmelman, 2004; Gutiérrez et al., 2003). Shells of bivalves can alter

the supply of settling substrate for hard bottom epibenthic organisms, refuge against predators or stressing abiotic factors, and particle and solute transportation by changing the flux and water infiltration, ultimately modifying the survival and distribution of many species (Gutiérrez et al., 2003; Stewart et al., 1998; Wright and Jones, 2006). Thus, shell availability in soft bottom areas where their presence is uncommon could extensively modify the community structure.

The Peruvian scallop *Argopecten purpuratus* is distributed from northern Peru (Paita, 5°S, 81°W) to central Chile (Tongoy, 37°S, 71°W; Marinovich, 1973) and is one of the major commercial resources in shallow waters of Peru (Argüelles and Castillo, 2001). In Peru, the Independencia Bay (14°17'S–76°10'W) sustains one of the most important scallop fisheries, and is also one of the most productive areas of benthic invertebrates in the region (Mendo and Wolff, 2003; Tarazona et al., 2007; Wolff et al., 2007). This area is influenced by the upwelling system of the Humboldt Current, which is also affected by the El Niño Southern Oscillation cycle (ENSO; Arntz, 1990; Tarazona et al., 2003).

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Important natural stock fluctuations of *A. purpuratus* are a common phenomenon positively correlated with the El Niño (EN) events (warm phase of ENSO). During strong EN events, such as those occurring in 1983–1984 and 1997–1998 with the occurrence of higher than average sea surface temperatures during summer, the habitat conditions for the Peruvian scallops improve (Mendo and Wolff, 2003; Arntz et al., 1985; Wolff et al., 2007), generating an increase in population size, production and larval supply (Mendo et al., 1987; Tarazona et al., 2007; Wolff and Mendo, 2000). Shell beds of dead animals and new habitats are colonized by scallops during these periods, followed by an important mortality after the EN events (Wolff and Mendo, 2000), with the consequent new shell accumulation on the sea bottom. Therefore, by providing a new, potentially structurally complex habitat, *A. purpuratus* could be acting as an ecosystem engineer, modifying the local benthic community. If so, shell accumulation could also be used as a tool to improve recruitment of other commercially important species (e.g. crabs, limpets and snails; Aguilar et al., 2002). In this regard, the objective of this work is to evaluate the effect of the accumulation of *A. purpuratus* shells on the total abundance of individuals, species richness and diversity of the macrobenthic assemblage and on the settlement of commercially important species.

2. Materials and methods

2.1. Study area and sampling of macrobenthic assemblage

To evaluate the specific composition and relative abundance of the subtidal macrobenthic organisms, bimonthly samplings were conducted from May 2006 to May 2007 in the soft bottom (~12 m depth) of Independencia Bay (La Vieja island, 14°17'14.38" S–76°10'40.48" W, Fig. 1), by scuba diving. The sea bottom temperature (SBT) was registered at 22 m depth with a CTD brand Sea Bird at a close fixed station (less than 100 m from the sampling sites) from three years starting on January 2006. The sea bottom thermal anomalies relative to the neutral phase of the ENSO were determined for

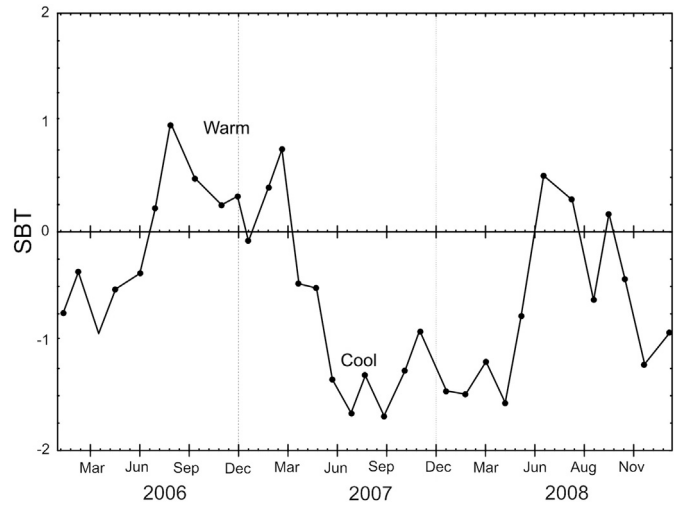


Fig. 2. Sea bottom temperature (SBT) anomalies in Independencia Bay at 20 m depth. 'Cool' and 'Warm' refer to negative and positive thermal anomalies, respectively, relative to the neutral phase (zero in y axis) of the ENSO.

this period. The 150 km² bay is affected by one of the strongest upwelling centers of Peru (Punta San Juan, south of the bay; Graco et al., 2013; Zuta and Guillén, 1970) and is part of the Peruvian coastal (or Humboldt) upwelling system (Tarazona et al., 2003). Coastal waters in the bay are relatively cold during the neutral phase of ENSO and La Niña conditions, fluctuating between 13 °C in winter and 23 °C in summer (Arntz et al., 1991; Belapatiño Candela, 2007), mostly as a result of sub-surface Equatorial waters (Morón et al., 1988; Quispe et al., 2010). During EN conditions, the temperature of coastal water elevates as a result of the incursion of Subtropical surface waters (Morón et al., 1988; Quispe et al., 2010). Salinity only decreases significantly during EN when oceanic waters approach the coast (Tarazona et al., 1985).



Fig. 1. Map indicating the study area in La Vieja island, Independencia Bay, Peru.

Table 1

Classification according to feeding habits (grazers, suspension-feeders, deposit-feeders, and predators/scavengers) and mobility (sessile and mobile) of all species found.

Taxa	Feeding	Mobility	Reference	
Anthozoa	<i>Actinaria</i> sp.	Predator	Sessile Tarazona et al. (1996)	
Platyhelminthes	<i>Polycladida</i> sp.	Predator	Mobile Tarazona et al. (1996)	
Polychaeta	<i>Aphelochaeta</i> sp.	Deposit feeder	Mobile Fauchald and Jumars (1979)	
	<i>Prionospio peruana</i>	Deposit feeder	Mobile Fauchald and Jumars (1979)	
	<i>Caulleriella magnaoculata</i>	Deposit feeder	Mobile Fauchald and Jumars (1979)	
	<i>Chaetopterus</i> sp.	Suspension feeder	Sessile Fauchald and Jumars (1979); Tarazona et al. (1996)	
	<i>Chone</i> sp.	Suspension feeder	Sessile Fauchald and Jumars (1979); Tarazona et al. (1996)	
	<i>Diopatra chilensis</i>	Predator	Mobile Tarazona et al. (1996)	
	<i>Dodecaceria</i> sp.	Deposit feeder	Mobile Fauchald and Jumars (1979)	
	<i>Eumida</i> sp.	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Flabelligerina</i> sp.	Deposit feeder	Mobile Fauchald and Jumars (1979)	
	<i>Glycera</i> sp.	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Goniada</i> sp.	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Grubeopolynoe</i> sp.	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Harmothoe</i> sp.	Predator	Mobile Tarazona et al. (1996)	
	<i>Heteromastus</i> sp.	Deposit feeder	Mobile Günther (1996)	
	<i>Leitoscoloplos</i> sp.	Deposit feeder	Mobile Tarazona et al. (1996)	
	<i>Lepidonotus</i> sp.	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Lumbrineris tetraura</i>	Predator, (deposit feeder)	Mobile Fauchald and Jumars (1979); Carrasco and Oyarzún (1988); Tarazona et al. (1996)	
	<i>Maldane</i> sp.	Deposit feeder	Mobile Fauchald and Jumars (1979)	
	<i>Mediomastus branchiferus</i>	Deposit feeder	Mobile Tarazona et al. (1996)	
	<i>Neanthes</i> sp.	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Nephtys impressa</i>	Predator	Mobile Tarazona et al. (1996)	
	<i>Nereis callaona</i>	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Odontosyllis lineata</i>	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Onuphis</i> sp.	Predator	Mobile Tarazona et al. (1996)	
	<i>Ophiodromus</i> sp.	Predator	Mobile Tarazona et al. (1996)	
	<i>Opistosyllis</i> sp.	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Owenia collaris</i>	Suspension feeder	Sessile Tarazona et al. (1996)	
	<i>Owenia</i> sp.	Suspension feeder	Sessile Tarazona et al. (1996)	
	<i>Paleonotus</i> sp.	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Pectinaria</i> sp.	Deposit feeder	Mobile Tarazona et al. (1996)	
	<i>Phragmatopoma virgini</i>	Suspension feeder	Sessile Tokeshi and Romero (1995)	
	<i>Phyllochaetopterus</i> sp.	Suspension feeder	Sessile Fauchald and Jumars (1979)	
	<i>Platynereis bicaniculata</i>	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Polycirrus</i> sp.	Suspension feeder	Sessile Fauchald and Jumars (1979)	
	<i>Polydora aggregata</i>	Deposit feeder	Mobile Tarazona et al. (1996)	
	<i>Polynoe</i> sp.	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Potamilla</i> sp.	Suspension feeder	Sessile Fauchald and Jumars (1979)	
	<i>Questa</i> sp.	Deposit feeder	Mobile	
	<i>Schistomeringos</i> sp.	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Steggoa negra</i>	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Sthenelais</i> sp.	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Syllis</i> sp.	Predator	Mobile Fauchald and Jumars (1979)	
	<i>Thelepus</i> sp.	Deposit feeder	Mobile Fauchald and Jumars (1979)	
	<i>Syllis</i> sp. 2	Predator	Mobile Fauchald and Jumars (1979)	
	Unidentified Alciopidae	Predator	Mobile Fauchald and Jumars (1979)	
	Unidentified Capitellidae	Deposit feeder	Mobile Fauchald and Jumars (1979); Tarazona et al. (1996)	
	Unidentified Dorvilleidae	Deposit feeder	Mobile Fauchald and Jumars (1979)	
	Unidentified Hesionidae	Deposit feeder, predator	Mobile Fauchald and Jumars (1979); Shaffer (1979)	
	Unidentified Neridae	Predator	Mobile Fauchald and Jumars (1979)	
	Unidentified Orbiniidae	Deposit feeder	Mobile Tarazona et al. (1996)	
Unidentified Phyllodocidae	Predator	Mobile Fauchald and Jumars (1979)		
Unidentified Sabellidae	Suspension feeder	Sessile Fauchald and Jumars (1979)		
Unidentified Serpulidae	Suspension feeder	Sessile Fauchald and Jumars (1979)		
Unidentified Syllidae	Predator	Mobile Fauchald and Jumars (1979)		
Unidentified Terebellidae	Suspension feeder	Sessile Fauchald and Jumars (1979)		
Oligochaeta	Unidentified Oligochaeta	Deposit feeder	Mobile Valdivia and Thiel (2006)	
Gastropoda	<i>Bursa ventricosa</i>	Predator	Mobile Taylor et al. (2008)	
	<i>Crepidula</i> sp.	Suspension feeder	Sessile Valdivia and Thiel (2006)	
	<i>Crepidatella</i> sp.	Grazer	Mobile Taylor et al. (2008)	
	<i>Crucibullum</i> sp.	Grazer	Mobile Taylor et al. (2008)	
	<i>Fissurella crassa</i>	Grazer	Mobile Santelices et al. (1986)	
	<i>Fissurella peruviana</i>	Grazer	Mobile Laudien et al. (2007)	
	<i>Mitrella</i> sp.	Grazer	Mobile Taylor et al. (2008)	
	<i>Nassarius dentifer</i>	Predator	Mobile Taylor et al. (2008); Tarazona et al. (1996)	
	<i>Nassarius gayi</i>	Predator	Mobile Taylor et al. (2008); Tarazona et al. (1996)	
	<i>Phydiana inca</i>	Suspension feeder	Sessile	
	<i>Prisogaster niger</i>	Grazer	Mobile Vásquez and Vega (2004)	
	<i>Tegula euryomphalus</i>	Grazer	Mobile Taylor et al. (2008)	
	<i>Thaisella chocolata</i>	Predator	Mobile Taylor et al. (2008)	
	<i>Trophon</i> sp.	Predator	Mobile Taylor et al. (2008)	
	Bivalvia	<i>Argopecten purpuratus</i>	Suspension feeder	Sessile Laudien et al. (2007)
		<i>Entodesma delicatum</i>	Suspension feeder	Sessile
		<i>Nucula</i> sp.	Suspension feeder	Sessile Laudien et al. (2007)

Table 1 (continued)

Taxa	Feeding	Mobility	Reference
	<i>Oorbitella</i> sp.	Suspension feeder	Sessile
	<i>Pitar</i> sp.	Suspension feeder	Sessile
	<i>Semele solida</i>	Suspension feeder	Sessile
	<i>Semimytilus algosus</i>	Suspension feeder	Sessile
Polyplacophora	<i>Tonica elegans</i>	Grazer	Mobile
Brachiopoda	<i>Disciniscia lamellosa</i>	Suspension feeder	Sessile
Decapoda	<i>Alpheus inca</i>	Predator, deposit feeder	Mobile
	<i>Romaleon polyodon</i>	Predator	Mobile
	<i>Cycloanthops sexdecimdentatus</i>	Deposit feeder	Mobile
	<i>Coenobita</i> sp.	Predator	Mobile
	<i>Collodes</i> sp.	Predator	Mobile
	<i>Emerita analoga</i>	Suspension feeder	Mobile
	<i>Eurypanopeus transversus</i>	Deposit feeder	Mobile
	<i>Pagurus villosus</i>	Predator, detritivore	Mobile
	<i>Petrolisthes desmarestii</i>	Suspension feeder	Mobile
	<i>Pilumnoides perlatus</i>	Deposit feeder	Mobile
	<i>Pinnixa</i> sp.	Suspension feeder	Mobile, commensal
	<i>Pinnotheres</i> sp.	Suspension feeder	Mobile, commensal
	<i>Talipeus</i> sp.	Grazer	Mobile
	Unidentified Caridea	Predator	Mobile
	Unidentified megalopa	Predator	Mobile
	Unidentified xanthidae		Mobile
Amphipoda	<i>Oediceroides</i> sp.	Grazer, deposit feeder	Mobile
	Unidentified Caprellidae	Grazer	Mobile
	Unidentified Corophiidae	Grazer	Mobile
	Unidentified Gammaridae 1	Grazer	Mobile
	Unidentified Gammaridae 2	Grazer	Mobile
Isopoda	Unidentified Isopoda		Mobile
Cumacea	Unidentified Cumacea	Suspension feeder, deposit feeder	Mobile
Leptostraca	<i>Nebalia</i> sp.	Predator	Mobile
Ostracoda	Unidentified Ostracoda	Suspension feeder	Mobile
Cirripedia	<i>Balanus laevis</i>	Suspension feeder	Sessile
	<i>Verruca</i> sp.	Suspension feeder	Sessile
Echinodermata	Unidentified Ophiuroidea	Deposit feeder	Mobile
Chordata	Unidentified Gobiidae	Predator	Mobile

Ten core samples of 10 cm in diameter and 25 cm depth were taken at each sampling date. Samples were sieved through a 500 μ m mesh, and retained organisms were fixed in 10% formalin until processed. All individuals were identified to the lowest possible taxonomic level (usually genus or species) and counted. These samples were used as “natural controls” for the shell addition experiment (see Section 2.2).

2.2. Effects of shell bed on macrobenthic assemblage composition

To assess the effect of the accumulation of *A. purpuratus* shells on the benthic assemblage we performed an experiment manipulating shell densities in the bottom. Shells used in the experiment were empty valves discarded from industrial processing, left exposed to the air for one year and then cleaned to remove all organisms adhered on them. The mean scallop shell length used was 65 ± 3 mm. The experiment was carried out from May 2006 to May 2007 at a depth of 12 m. For this, 30 experimental plots (using a metal frame of 50 cm \times 50 cm

area and 20 cm height, screened with a 10 mm mesh at the lateral sides and open on the top) were installed on the bottom separated by more than 5 m from each other. Plots were randomly assigned to the following treatments (ten replicates per treatment): (1) areas without shells (“empty” treatment: experimental control), (2) 50% of the plot area covered with shells haphazardly distributed on the bottom (“medium” treatment) and (3) 100% of the plot area covered with shells forming a 10 cm valve layer (“full” treatment). Additionally, ten un-manipulated areas, marked with stakes in the bottom, were used as “natural control” (see Section 2.1). Total experimental area occupied ~ 1 ha. Shell densities were periodically maintained in the respective treatments by removing or adding shells by hand through scuba diving. Samplings were started after one month (in June 2006) in order to reduce the disturbance effects of the initial shell manipulation and to give time to macrofauna to colonize and/or immigrate to the experimental plots. Plots, including the “natural control”, were re-sampled every other month. At each plot, a core sample (10 cm diameter,

Table 2

Percentage of the total abundance and number of individuals, in brackets, found for the more representative taxonomic groups in each treatment considering all sampling times.

Taxa	Treatments				Mean \pm SD abundance by taxa
	Full	Medium	Empty	Control	
Polychaetes	50.9 (1922)	38.1 (2741)	44.8 (1750)	49.8 (2123)	45.9 \pm 5.84
Crustaceans	22.4 (847)	44.5 (3205)	22.7 (887)	20.8 (888)	27.6 \pm 11.30
Mollusks	16.9 (637)	12.2 (880)	23.3 (908)	19.1 (813)	17.88 \pm 4.62
Echinoderms	4.4 (167)	2.6 (189)	4.6 (178)	5.1 (219)	4.18 \pm 1.09
Others	5.3 (201)	2.5 (183)	4.7 (183)	5.2 (220)	4.43 \pm 1.31

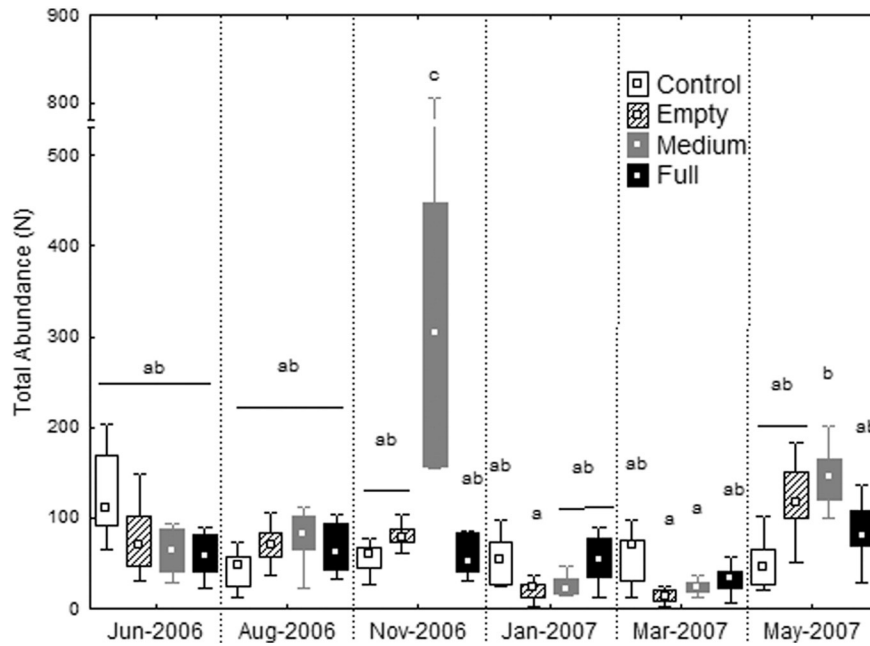


Fig. 3. The total abundance (N) of macrofaunal assemblages among “natural control”, “empty”, “medium” and “full” treatments, and throughout the year. Different letters denote significant differences in ascendant order.

25 cm depth) was collected from the central area, avoiding repeat the same area between successive samplings. Organisms settled on the shells were removed by scraping the shell and included in the analysis. Samples were processed as described in Section 2.1.

Each sample was evaluated for the same attributes of community characteristics, including total individual abundance (N), species richness (S), and diversity (both the Shannon–Wiener diversity index—using \ln ; H' —and the Simpson index— λ —were used). Repeated measures two-way ANOVAs were used to evaluate differences in the

values among treatments and sampling dates. As the assumption of sphericity was violated, a Huynh–Feldt correction was done (Zar, 1999).

To compare species assemblages among treatments and sampling dates, we performed both multivariate and univariate analyses. Bray–Curtis similarity matrices, using fourth root-transformed data, were calculated and non-metric Multidimensional Scaling (nMDS) ordinations were used to provide visual representations of sample similarities (Clarke, 2001). We used the permutational multivariate analysis of variance (repeated measures PERMANOVA) to test for differences

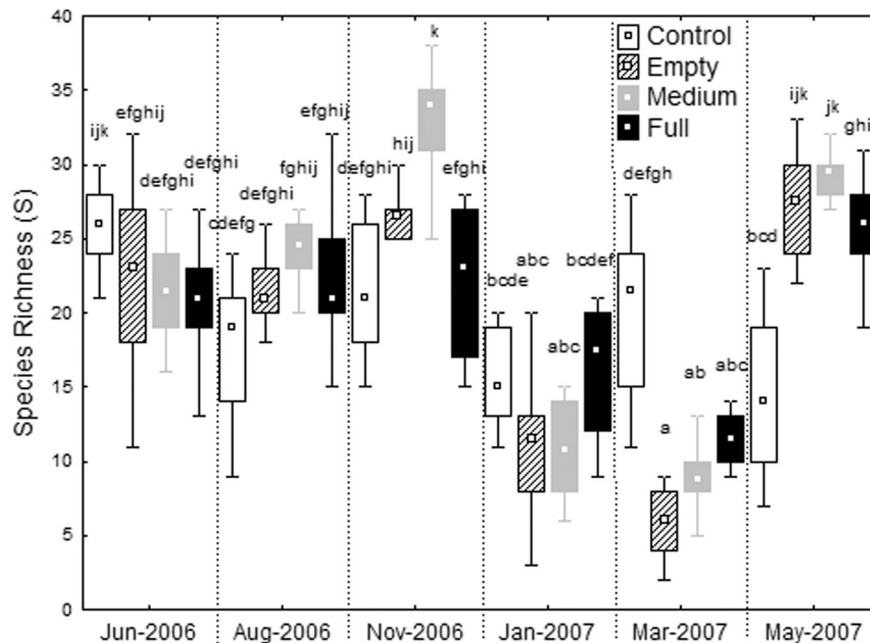


Fig. 4. Species richness (S) of macrofaunal assemblages among “natural control”, “empty”, “medium” and “full” treatments, and throughout the year. Different letters denote significant differences in ascendant order.

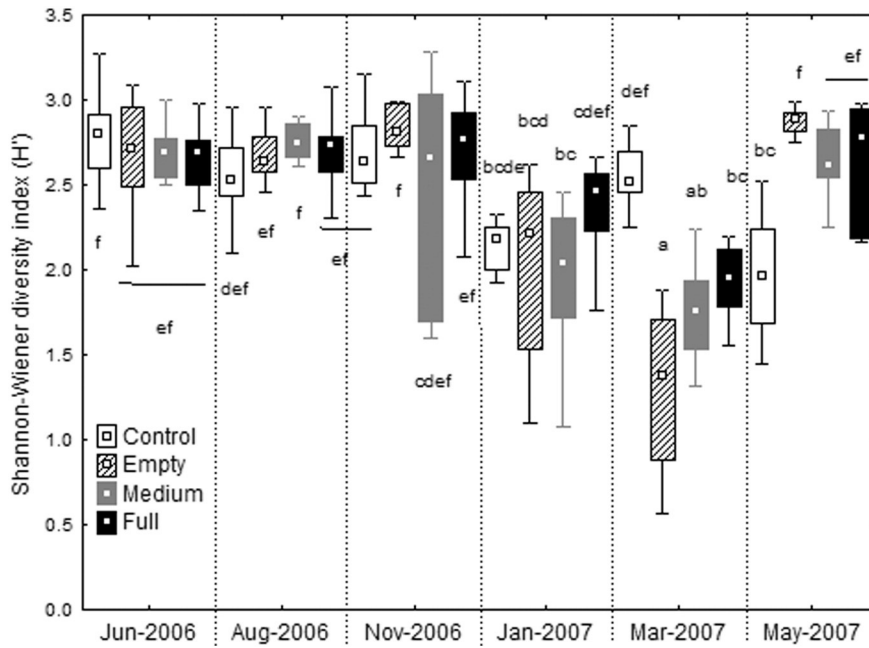


Fig. 5. The Shannon–Wiener diversity index (H') of macrofaunal assemblages among “natural control”, “empty”, “medium” and “full” treatments, and throughout the year. Different letters denote significant differences in ascendant order.

among treatments and sampling dates (PRIMER 6 software; Clarke and Gorley, 2006). All permutation tests relied on 999 permutations of residuals under a reduced model to obtain p-values. This permutation method is the more appropriate because it provides the best statistical power and the most accurate Type I error (Anderson et al., 2008). Since assumptions of homogeneity of dispersions (by PERMDISP) between dates were not found (see Results), we only analyzed the difference among treatments for each date with one-way PERMANOVA. When significant at the 0.05 level, the treatments were compared through a posteriori pair-wise comparisons using 999 random permutations to obtain p-values. The percentage contribution of each

taxon to patterns of dissimilarity among treatments and sampling dates were calculated (SIMPER, Clarke, 1993). This method compares average abundances and examines the contribution of each species to similarities within a given group, or dissimilarities between groups (Clarke, 2001); the taxa contributing to at least 5% of dissimilarity were identified, and those contributing to more than 10% were considered important differentiators (Bulleri, 2005). The null hypothesis of no difference in the abundance of these taxa was then analyzed by Kruskal–Wallis non-parametric analyses among treatments and sampling dates because assumptions for parametric tests were not met (Zar, 1999).

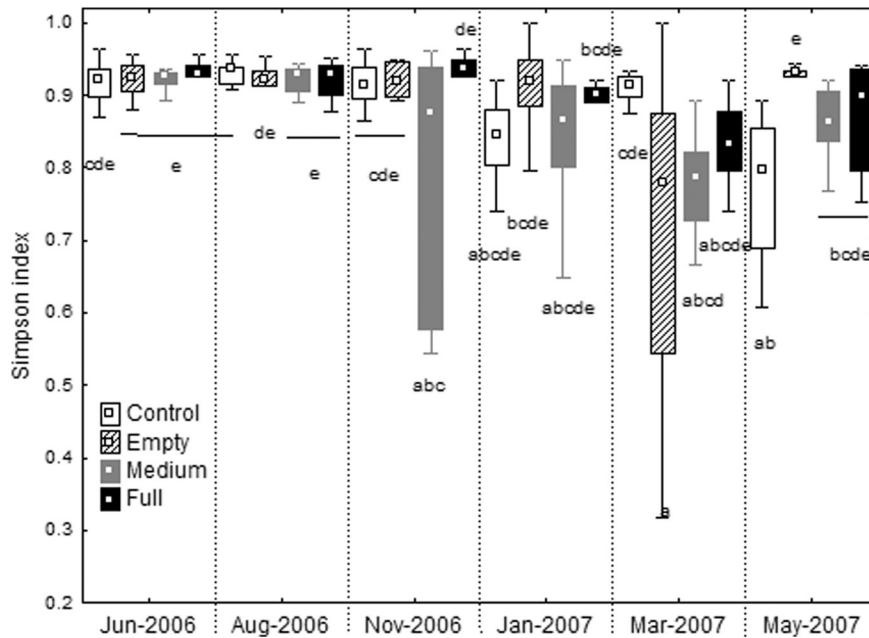


Fig. 6. Simpson index of macrofaunal assemblages among “natural control”, “empty”, “medium” and “full” treatments, and throughout the year. Different letters denote significant differences in ascendant order.

Table 3

Summary of the PERMANOVA main tests to assess differences in the structure of the whole assemblage between treatments (natural control, empty, medium, and full) among sampling dates.

Source of variation	df	SS	MS	Pseudo-F	p-Value	Perms
JUN-06						
Treatment	3	6478.8	2159.6	2.203	0.001	998
Residuals	36	35,290	980.28			
Total	39	41,769				
AUG-06						
Treatment	3	6136.6	2045.5	1.8454	0.001	997
Residuals	36	39,905	1108.5			
Total	39	46,042				
NOV-06						
Treatment	3	11,098	3699.4	4.4379	0.001	998
Residuals	36	30,009	833.58			
Total	39	41,107				
JAN-07						
Treatment	3	15,002	5000.6	2.965	0.001	997
Residuals	35	59,029	1686.5			
Total	38	74,031				
MAR-07						
Treatment	3	20,508	6835.9	3.7014	0.001	997
Residuals	34	62,793	1846.9			
Total	37	83,301				
MAY-07						
Treatment	3	11,555	3851.8	4.4782	0.001	998
Residuals	36	30,964	860.12			
Total	39	42,520				

2.3. Commercial species

Commercial important species were identified (following Aguilar et al., 2002, see Section 3.3) in the different treatments throughout the year and the null hypothesis of no difference in the abundance among treatments and dates were evaluated by repeated measures two-way ANOVA (Zar, 1999).

2.4. Functional groups

Additionally, organisms were also classified according to their feeding habit (grazers, suspension-feeders, deposit-feeders, and predators/scavengers) and mobility (sessile or mobile) in order to analyze possible changes in the relations among functional groups in the community among treatments. Organisms were classified based on their morphological characteristics and the available literature (see Valdivia and Thiel, 2006). Separated Kruskal–Wallis tests, followed by non-parametric Tukey-type tests (Zar, 1999), were performed to evaluate the null hypothesis of no difference in the abundance of feeding guilds among treatments and across the year, given that parametric assumptions were not met.

3. Results

3.1. Sea bottom thermal anomalies and macrobenthic community assemblage

The sea bottom thermal anomalies relative to the neutral phase of ENSO showed positive values from Jul-06 to the beginning of Dec-06, with a neutral value at the end of Dec-06, and negative anomalies starting in Mar-07 up to May-07 (Fig. 2).

The macrobenthic assemblage was represented by 124 taxa (Table 1). Polychaetes, crustaceans and mollusks were the most abundant groups representing 49.8%, 20.8% and 19.1% of the total, respectively (“natural control”, Table 2). The less represented groups were echinoderms, nemerteans, phoronids, brachiopods, actinias, oligochaetes and fishes. The total number of individuals analyzed in natural

control plots was 4263. The most abundant species were the gastropod *Nassarius gayi* (12% of the total) and the polychaetes *Prionospio peruana* (8.7%), followed by *Platynereis bicanaliculata* (4.5%) and *Mediomastus branchiferus* (4.3%).

3.2. Effects of shell bed on macrobenthic assemblage composition

The experiment manipulating scallop shell densities over the bottom showed that the total abundance of individuals (N), pooled throughout all sampling dates, was twice higher in the “medium treatment” than in the others (Table 2). Furthermore, the dominant groups also changed in “medium treatments” respect to the others, being there dominated by crustaceans (44.5%), followed by polychaetes (38.1%) and mollusks (12.2%); additionally, the presence of echinoderms was reduced (2.6%). No differences were observed among “natural control”, “full” and “empty” treatments (Table 2). The abundance (N) across the year differed between months and treatments (Interaction $F_{(15, 216)} = 10.38$, $p < 0.001$, Fig. 3), with higher values in “medium” treatment in Nov-06 and minimum values in “empty” treatment in Jan-07 and in “empty” and “medium” treatments in Mar-07 (Tukey HSD test, $p < 0.05$).

Along the whole study we identified 96 species (S) in “natural control”, 90 in “full” treatment and 88 in “medium” and “empty” treatments. These values differed between months and treatments (Interaction $F_{(15, 216)} = 12.99$, $p < 0.0001$; Fig. 4), with minimum values in Jan-07 and Mar-07 in “empty” and “medium” treatments respect to the others. The maximum mean values were found in “medium treatments” in Nov-06, and in “empty”, “medium” and “full” treatments in

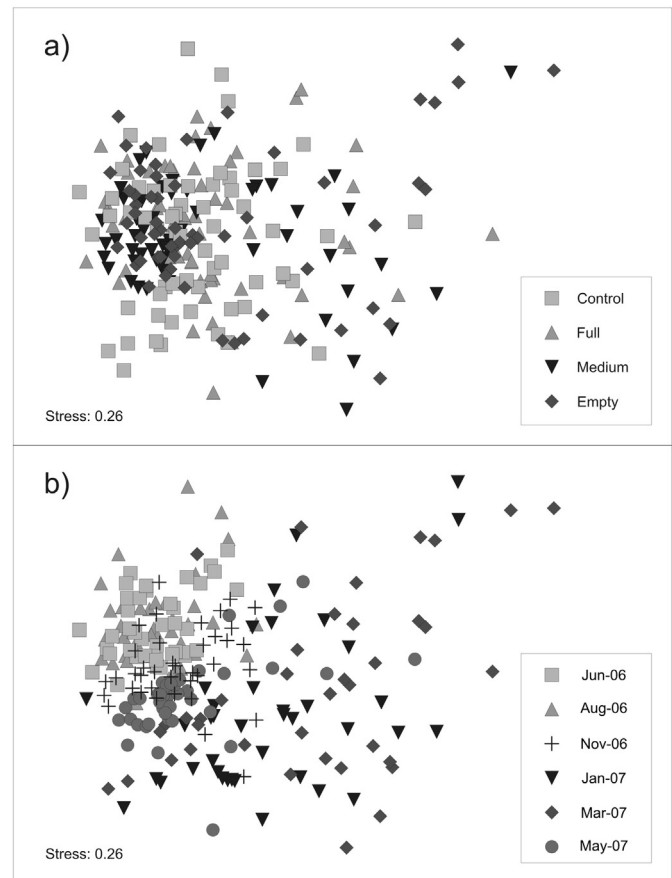


Fig. 7. Non-metric Multidimensional Scaling (nMDS) plots of data comparing (a) macrofaunal abundance among “natural control”, “empty”, “medium” and “full” treatments, and (b) throughout the year.

Table 4

SIMPER results showing the benthic species that contributed most to the dissimilarity between “natural” control (NAT), “empty” (EMP), “medium” (MED) and “Full” treatments pooled data for the whole year.

	% dissimilarity					
	NAT–EMP	NAT–MED	NAT–FULL	EMP–FULL	EMP–MED	MED–FULL
Infaunal species						
<i>Prionospio peruana</i>	6.41	8.34	6.61	–	5.51	6.14
<i>Mediomastus</i> sp.	5.38	6.99	6.51	6.86	5.89	7.82
<i>Platynereis bicaniculata</i>	6.38	–	5.31	–	–	–
Epifaunal species						
<i>Nassarius gayi</i>	11.60	8.61	9.40	12.15	11.40	8.37
Caprellidae	–	9.62	–	–	8.63	8.60
Cumulative contribution of dissimilarity	29.77	33.56	27.83	19.01	31.44	30.93
Average dissimilarity	65.33	67.44	64.97	62.82	60.16	62.32

May-07 in relation to the “natural control”, except for the first sampling date (Jun-06) where no difference were found with “natural control”.

The Shannon–Wiener diversity index (H') varied from 0.57 to 3.29 (high diversity with values higher than 3). The observed differences were in general related with sampling dates, with minimum values in Jan-07 in all treatments and in Mar-07 in “empty”, “medium” and “full” treatments (Interaction “treatment” \times “sampling date” $F_{(15, 216)} = 8.31, p < 0.001$; Tukey HSD test, $p < 0.05$; Fig. 5).

The Simpson index (λ) also differed among months and treatments ($F_{(15, 216)} = 4.49, p < 0.001$), with a minimum value of 0.32 and the maximum close to 1 (higher values, less diversity). The differences observed were in general related with sampling dates with minimum values in Mar-07 in “empty” treatment in relation to the “natural control” (Tukey HSD test, $p < 0.05$; see Fig. 6).

Regarding the abundance data, the assumptions of homogeneity of dispersions (by PERMDISP) showed no differences between treatments ($F_{(3, 233)} = 1.25; p$ (perm) = 0.41) but there are differences between dates ($F_{(5, 231)} = 30.93; p$ (perm) = 0.001). Thus, we only analyzed the difference between treatments for each date (see Section 2.2.). The structure of the assemblage showed a significant treatments effect in all sampling dates (PERMANOVA; Table 3). The nMSD ordinations showed a higher grouping among Jun-06, Aug-06 and Nov-06 (see Fig. 7a, 7b). A posteriori test showed that almost all treatments in all sampling dates were different among them (all $ps < 0.05$, pairwise tests) with the exception of “full” vs. “empty” in Jun-06, “full” vs. “natural control” and “medium” in Aug-06, “empty” vs. “natural control” in Nov-06, and “empty” vs. “medium” in Jan-07 and Mar-07.

SIMPER analysis showed that the taxa accounting for the 5% of dissimilarity among treatments were the polychaetes *P. peruana*, *Mediomastus* sp. and *Platynereis bicaniculata* among the infaunal organisms, and the gastropod *N. gayi* and the Amphipoda Caprellidae among the epifaunal organisms (Table 4). These dissimilarities were due to increased abundances of all the species involved in “medium” treatment respect to “natural control”, “empty” and “full” treatments; an increase in *Mediomastus* sp. and a decrease of the other species in “full” treatment respect to the “natural control” and “empty” treatment, and an increase in *N. gayi* and *Mediomastus* sp. in “empty” treatment respect to “natural control”. In addition, taxa accounting for 5% of dissimilarity among sampling dates were the polychaetes *P. peruana*, *Caulleriella oculata*, *Glycera* sp., *Mediomastus* sp., *Nereis callaona*, and *P. bicaniculata* among the infaunal species; and among the epifaunal species, the phoronid *Phoronis* sp., the gastropod *N. gayi*, and the Caprellidae and Corophiidae amphipods, the decapod *Pinnixa* sp. and an Ophiuridae (Table 5). These dissimilarities were given by an increase in abundance of *N. gayi* and Caprellidae in Nov-06, *N. gayi* in Jan-07, *P. peruana* in May-07 and *Phoronis* sp. in Jun-06 respect to all other sampling dates. The low cumulative contribution to dissimilarity of each pairwise test (Tables 4 and 5) represented by the above species indicates that other benthic species also contributed to the dissimilarities among treatments and sampling dates, but this was less than 5%.

The abundance of *N. gayi* was higher in Nov-06 ($H_{5, 237} = 20.46, p < 0.05$, Fig. 8) with respect to other months and in the “medium” treatment than in the others ($H_{3, 237} = 7.65, p = 0.049$). The Caprellidae showed higher abundance in Nov-06 ($H_{5, 237} = 49.91, p < 0.05$, Fig. 8) with respect to other months and higher abundance in “medium” and “natural control” treatment than in the others ($H_{3, 237} = 6.55, p < 0.05$). The phoronid *Phoronis* sp. showed the higher abundance in Jun-06 following by Aug-06 and Nov-06 showing a decrease across the year ($H_{5, 237} = 135.91, p < 0.05$, Fig. 8); no difference was found between treatments ($H_{3, 237} = 1.64, p > 0.05$). *P. peruana* showed a decrease of the abundance from Jun-06 to Mar-07 with a posterior maximum in May-07 ($H_{5, 237} = 111.55, p < 0.05$, Fig. 8); the “natural control” treatment showed higher abundance than “empty” treatment ($H_{3, 237} = 11.46, p < 0.05$).

3.3. Commercial species

The commercial species identified throughout the experiment were the crabs *Romaleon polyodon* and *Emerita analoga*; the gastropods *Fissurella crassa*, *Bursa ventricosa*, *Crepidula* sp., *Crepidatella* sp., *Fissurella peruviana* and *Thaisella chocolata*; the polyplacophora *Tonicia elegans*; and the bivalves *A. purpuratus* and *Semele* sp. (see Table 1). Only *R. polyodon*, *F. crassa* and *T. elegans* were found in high enough number to be analyzed statistically. The abundance of the crab *R. polyodon* was higher in Nov-06 at “medium” than at “empty” and “full” treatments, presented inter-medium values in the “natural control”, and showed lower abundance in the rest of the months and treatments (Interaction “treatment” \times “sampling date”; $F_{(15, 213)} = 2.12, p < 0.05$). The abundance of the gastropod *F. crassa* was higher in “empty” treatment in May-07; presented inter-medium values in “natural control” in Jun-06, in “empty” treatment in Aug-06 and in “medium” treatment in May-07; and showed lower values in the rest of the months (Interaction “treatment” \times “sampling date”; $F_{(15, 213)} = 2.13, p < 0.05$). The abundance of the polyplacophora *T. elegans* was lower in “full” treatment in all months analyzed and in “empty” treatments in Aug-06, Jan-07 and Mar-07; showed inter-medium values in “medium” treatment in Nov-06 and Mar-07 and in “natural control” in Aug-06 and May-07; and showed higher values in “natural control” in the rest of the months, in “medium” treatment in Jun-06 and May-07, and in “empty” treatment in Nov-06 and May-07 (Interaction “treatment” \times “sampling date”; $F_{(15, 213)} = 2.48, p < 0.05$).

3.4. Functional groups

Almost all groups were more abundant in Nov-06 than in all other months (Fig. 9). The deposit feeders showed higher abundance in the “medium” treatment in Nov-06 and May-07 than in others treatments ($H_{3, 40} = 25.88$ and $H = 18.86; p < 0.05$ respectively). In Jan-07, “full” treatment showed a higher abundance than “empty” treatment ($H_{3, 39} = 9.69, p = 0.021$), and in Mar-07 “medium” and “empty”

treatments showed lower abundances than “natural control” ($H_{3,38} = 24.24$, $p < 0.001$). The grazers showed higher abundance in the “medium” than the other treatments in Nov-06 ($H_{3,40} = 23.40$, $p < 0.001$) and in “natural control” than in “medium” and “empty” treatments in Jan-07 and Mar-07, respectively ($p < 0.05$); in May-07 the “natural control” showed the lowest value ($H_{3,40} = 15.08$, $p < 0.05$). The abundance of predators was higher in “medium” than in “full” treatment and “natural control” in Nov-06, and higher than in “empty” treatment in May-07, with no difference in the other months.

Suspension-feeders represented the functional group with the highest overall abundance, and also showed greater abundance in “medium” than in “full” treatment and “natural control” in Nov-06 and May-07 ($H_{3,40} = 29.86$ and $H = 25.05$ respectively; $p < 0.05$), and in “natural control” and “full” treatment than in “empty” treatment in Jan-07 and Mar-07 ($p < 0.05$). The scavengers only showed differences in Nov-06 with higher abundance in “medium” treatment than in “natural control” and “full” treatment ($H_{3,40} = 13.45$, $p < 0.05$), and in May-07 with lower abundance in “natural control” than in “empty” treatment ($H_{3,40} = 9.02$, $p < 0.05$). The omnivorous showed the same pattern with higher abundance in “medium” than other treatments in Nov-06 ($H_{3,40} = 21.25$, $p < 0.05$) and in “medium” and “empty” treatments than “natural control” in May-07 ($H_{3,40} = 19.96$, $p < 0.05$); in Mar-07, higher abundance was observed in “natural control” than in “empty” treatment ($H_{3,38} = 15.36$, $p < 0.05$). These three later functional groups showed higher abundance in “natural controls” than in the other treatments at the beginning of the experimental period (Jun-06; $p < 0.05$).

4. Discussion

Our results show great temporal variability both in the composition of the soft bottom macrobenthic assemblage as well as in the effects of the accumulation of *A. purpuratus* shells on it. Additionally, commercially important species such as the crab *R. polyodon* and the polychaeta *T. elegans* were positively affected by shell accumulation, and the limpet *F. crassa* was negatively affected.

The macrozoobenthic assemblage of Independencia Bay was characterized by its variability along time, being dominated by polychaetes (such as *P. peruana*), and followed by mollusks (such as *N. gayi*) and the phoronid *Phoronis* sp. We found a maximum of 124 species, which is higher than a previous study in the area reporting 91 species, also with polychaetes as the most abundant group for similar depth (Tarazona et al., 1991). The influence of upwelling waters with high nutrient supply (during non-EN years, average primary production in the area is around $1 \text{ kg C m}^{-2} \text{ y}^{-1}$, the highest in the global ocean; Tarazona et al., 2003) can determine the presence of a high number of individuals and higher species richness (Lanari and Coutinho, 2014), but low diversity index (Arntz et al., 1991; Tarazona et al., 1991, 2003; Taylor et al., 2008), as found in our study (see Arntz et al., 1991). The decrease in the Shannon–Wiener and Simpson indexes in the last part of this study could be related with the increase in the upwelling intensity in winter by the influence of strong winds (Tarazona et al., 2003; Taylor et al., 2008). Several studies in the same area showed that seasonal variation of plankton biomass and primary productivity are decoupled with the variation in the upwelling intensity (Tarazona et al., 2003). However, under strong EN conditions, diversity increases by the incorporation of non-native species when warm waters reach the coast (Arntz et al., 1985; Tarazona et al., 1988b, 1998, 2003; Taylor et al., 2008); thus, the positive thermal anomalies in the sea bottom observed from Jul-06 to the beginning of Dec-06, with a neutral value at the end of Dec-06, and negative anomalies starting in Mar-07 up to May-07 could explain the variability in the temporal pattern found in diversity; additionally, the abundance of the small gastropod *N. gayi*, which is an opportunistic species linked to EN and post-EN events (Tarazona et al., 1988a, 1996), increased in the positive thermal anomalies period and was favored with the accumulation of shells (see below). The negative peaks in sea bottom temperature (SBT) coincide with a decrease in S–W and

Simpson diversity indexes and the generally high variability in all data analyzed. This is probably a response to an increased mortality of native and non-native benthic invertebrates incorporated in the community when warm waters, but not completely developed EN event, reach the coast in the first period of this study (our data and Hidalgo et al., 2011). Therefore, both upwelling and EN could be influencing the structure of this assemblage at the end of the study period, the upwelling by increasing productivity and thus favoring some dominant species (Lanari and Coutinho, 2014), and EN by affecting the mortality rate of other species through thermal stress (Sorte et al., 2011; Thatje et al., 2008)..

Independencia Bay is an area influenced by strong winds and currents, upwelling cycles (Quispe et al., 2010; Tarazona et al., 1991; Taylor et al., 2008) and also by the addition of organic matter and shells of the scallop *A. purpuratus*, which increases its population size during EN events (Mendo et al., 1987; Tarazona et al., 2007; Taylor et al., 2008; Wolff and Mendo, 2000). Thus, the area is controlled mainly by physical forces (Tarazona et al., 1991). The experimental addition of scallop shells to the soft bottom resulted in an increase in the total abundance (N), and species richness (S) of the macrobenthos in Nov-06. Similar responses occurred with the addition of Iceland scallop *Chlamys islandica* shells to sandy and rocky bottoms in the Gulf of St. Lawrence, Canada ($50^{\circ}12'N$, $63^{\circ}30'W$; Guay and Himmelman, 2004); with the addition of barnacle shells to benthic communities in Florida, USA ($27.97^{\circ}N$, $82.53^{\circ}W$; Bros, 1987); and with the addition of empty native (*Anodonta anatina*, *Unio tumidus*) and invasive (*Corbicula fluminea*, *Sinanodonta woodiana*) bivalve shells to the Danube at Göd river, Hungary (1669 km river, $47^{\circ}40'N$, $19^{\circ}07'E$; Bódis et al., 2014), all of which increased the abundance, species richness and diversity of benthic invertebrates. Shells and shell aggregations introduce complexity and heterogeneity into benthic environments (Bódis et al., 2014; Gutiérrez et al., 2003), control the availability of settling substrata for fouling organisms (Albrecht and Reise, 1994; Buschbaum, 2000) and refuges from predators (Brock, 1979; Gotceitas and Colgan, 1989; Guay and Himmelman, 2004), and the transport of particles and solutes in the benthic environment (see Gutiérrez et al., 2003). Habitat heterogeneity can increase diversity (Chapman and Underwood, 1994; Menge et al., 1985) as a result of new settlement and/or immigration of motile species (Bros, 1987; Guay and Himmelman, 2004). The modified habitat could thus affect the population dynamics of some species and community level processes (e.g. Gutiérrez and Iribarne, 1999; Lenihan et al., 2001), finally influencing the assemblage composition as observed in the present study. Although data on the abiotic conditions in the experimental plots were not available, several works evidence the effects of bivalve shells on the alteration of the community structure (Gutiérrez and Iribarne, 1999; Gutiérrez et al., 2003; Guay and Himmelman, 2004; Sousa et al., 2009; Bódis et al., 2014), supporting our results.

The degree of shell aggregation could determine the magnitude of the effects on the community (Gutiérrez et al., 2003). As showed in our field experiment, the individual abundance and species richness increase when shells cover half of the bottom surface (“medium” treatment) in Nov-06, while 10 cm of shell layer on the bottom (“full” treatment) showed negative or not effect on the assemblage. Similar results were found with the addition of Iceland scallop (*C. islandica*) shells to sandy bottoms of the Gulf of St. Lawrence, showing that species diversity rapidly increased with shell abundance and leveled off when shells covered half of the bottom, whereas species richness leveled off when shells almost completely covered the bottom (Guay and Himmelman, 2004). The degree in which shells are aggregated influences both the provision of refuges by shell cavities and interstices (Bódis et al., 2014; Firstater et al., 2011), the surfaces available for colonization (by surface superposition; Guay and Himmelman, 2004) and the characteristics of hydraulic flow over the bed, altering sedimentation rates (Eckman and Nowell, 1984; Nowell, and Jumars, 1984; Gutiérrez et al., 2003). Thus, the accumulation of high shell densities can differently affect the

Table 5

SIMPER results showing the benthic species that contributed most to the dissimilarity between sampling dates.

	% dissimilarity							
	Jun06–Aug06	Aug06–Jan07	Jun06–Jan07	Aug06–Mar07	Jan07–Mar07	Jun06–Mar07	Aug06–May07	Jan07–May07
Infaunal species								
<i>Prionospio peruana</i>	–	–	–	–	–	–	20.96	22.53
<i>Mediomastus</i> sp.	6.92	9.04	5.39	8.39	7.97	–	5.73	6.99
<i>Platynereis bicaniculata</i>	–	–	–	5.92	8.49	–	–	–
<i>Nereis callaona</i>	5.80	7.92	–	8.11	–	–	–	–
<i>Caulerrella oculata</i>	5.10	6.41	–	6.70	–	–	–	–
<i>Glycera</i> sp.	5.40	5.85	6.20	6.33	–	6.81	–	–
Epifaunal species								
<i>Nassarius gayi</i>	7.41	10.45	7.91	8.35	16.05	8.06	5.66	7.32
Caprellidae	–	–	–	–	–	–	–	–
Corophiidae	–	–	–	–	–	–	–	5.19
<i>Phoronis</i> sp.	8.56	–	9.67	–	–	9.93	–	–
<i>Pinnixa</i> sp.	–	–	–	–	–	–	–	–
Ophiurida	6.55	5.44	7.80	5.33	–	7.84	–	–
Cumulative contribution of dissimilarity	45.74	45.11	36.97	49.14	32.51	32.64	32.35	42.04
Average dissimilarity	62.73	72.25	74.63	76.07	68.85	76.93	67.97	74.19

community, as happened in the present study. However, several theories have predicted the effect of disturbance (Connell, 1978) and productivity (Grime, 1973) and a combination of both (i.e. dynamic equilibrium model; Huston, 1979) on communities. For instance, the dynamic equilibrium model assumes that the diversity represents a balance between growth rates (productivity/organic enrichment) and disturbance, with maximum diversity observed when the assemblage receives intermediate levels of both productivity and disturbance. In our study, shells covering half of the bottom surface (“medium” treatment) could represent an intermediate level of disturbance, being thus supported by the intermediate disturbance hypotheses (Connell, 1978), although the several criticisms, misinterpretation and misrepresentations on this hypotheses (see Fox, 2013; Sheil and Burslem, 2013) suggest that it should not be considered without additional information.

The impact of adding shells on the community may differ according to the invertebrate species involved and respond to the habitat characteristics where initially lived, their trophic position in the food web, and their ability to adapt to the new habitat (Bódis et al., 2014). The natural community in the area was dominated by polychaetes; however, the addition of scallop shells covering half of the bottom surface (“medium” treatment) increased the abundance of epifaunal species such as the gastropod *N. gayi* and amphipod Caprellidae, being important differentiators in this assemblage. This difference could be due to the increase of hard substrate for new settlement and/or due to increased refuge; thus, they may have moved into shell plots to feed or to avoid predators (Tallmark, 1980), given that algal debris often accumulate on shell patches on sandy bottoms. Similar results were found with the addition of empty native and invasive bivalve shells to the Danube River (Bódis et al., 2014). However, the important species differentiators (more than 10% dissimilarity) among “full”, “empty” and “natural control” treatments were *N. gayi* and the increase or decrease of different polychaete species; this is probably a consequence of sediment accumulation in interstices among shells in the “full” treatment (Tsuchiya and Nishihira, 1986), favoring habitat conditions for the polychaetes (i.e. *Mediomastus* sp.), as happen in the natural assemblages.

Two of the commercial species identified in our experiments were positively affected in treatments with shells covering half of the bottom surface, and one negative affected; however, they did not contribute to explain differences among treatments in the assemblage composition. The crab *R. polyodon* showed an increment in abundance in the “medium” treatment, specifically in Nov-06 when the number of individuals of all species were increased too. This mobile predator crab (Taylor et al., 2008) possibly moves into this area because of an increase in

the abundance of their prey. The addition of oyster shells to a muddy bottom in Grays Harbor Estuary, WA, USA (47°N, 124°W) increased the mortality of the infaunal bivalve *Macoma balthica* due to increased predation by the Dungeness crabs *Cancer magister* (Iribarne et al., 1995). However, we did not find a decrease of other functional groups in this month (Nov). The suspension feeders, scavengers and omnivores decreased in all treatments except in the ambient sediment (“natural control”) at the start of the experiment time is possibly related with the initial impact of adding empty shell and plots to the soft bottom before the succession process starts. Then, the decrease in the abundance of all the functional groups in the following month after Nov-06 was possibly related to a seasonal effect on the community rather than a top-down control. However, under normal upwelling periods, a top-down process was suggested as the principal force structuring the community in a trophic model for Independencia Bay system (Taylor et al., 2008). The limpet *F. crassa* was negatively affected by the presence of scallop shells (“medium” and “full” treatments). For this grazer that normally lives with their ventral foot firmly attached to hard rock surfaces and mainly in intertidal habitats (Oliva and Castilla, 1986; Paredes, 1986), the addition of shells might limit their movement and even create barriers. A similar explanation may apply to the polyplacophora *T. elegans*, which is associated to rocky shores (Paredes et al., 1999) in intertidal and subtidal areas and showed a higher abundance in “medium” treatments and was negatively affected in “full” treatments.

In conclusion, our data show that the addition of scallop shells to the sea bottom increases the total abundance and species richness of most epibenthic and infaunal invertebrate species only under positive thermal anomalies in the sea bottom relative to the neutral phase of the ENSO. Although the process involved in this pattern cannot be definitely determined, there is no doubt that these are directly (by changing the habitat structure) or indirectly (by changing the sediment characteristics) mediated by the scallop shells modifying the assemblage composition under these conditions. However, in areas where upwelling influence and ENSO cycles are common, the seasonality can have stronger effects than the presence of the shells itself and thus, the shells of scallops do not seem to be a useful tool for restoring macrobenthic communities in these systems.

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% dissimilarity						
Jun06–May07	Mar07–May07	Aug06–Nov06	Jan07–Nov06	Jun06–Nov06	Mar07–Nov06	May07–Nov06
17.25	22.35	–	–	–	–	16.59
–	6.49	5.48	5.85	–	–	–
–	7.23	–	–	–	5.13	–
–	–	–	–	–	–	–
–	–	–	–	–	–	–
–	6.15	9.45	11.48	8.71	11.17	7.57
–	–	11.64	12.36	11.44	9.70	10.26
–	5.66	–	–	–	–	–
7.12	–	–	–	6.75	–	–
–	–	5.85	6.61	5.05	6.91	–
5.35	–	–	–	5.57	–	–
29.72	47.88	32.42	36.31	37.51	32.91	34.43
71.04	77.36	66.63	73.60	68.19	76.88	67.38

suggestions that largely improved the manuscript. This study was conducted and financed in the framework of the EU-project “Climate variability and El Niño Southern Oscillation: Implications for natural resources and management, CENSOR” (contract 511071).

This paper is in memory of Prof. Dr. Juan Tarazona, friend, acknowledged scientist and co-author of this work who passed away few months ago. We want to express our gratitude to Dr. Juan Tarazona for his help and hospitality while doing research in Peru.

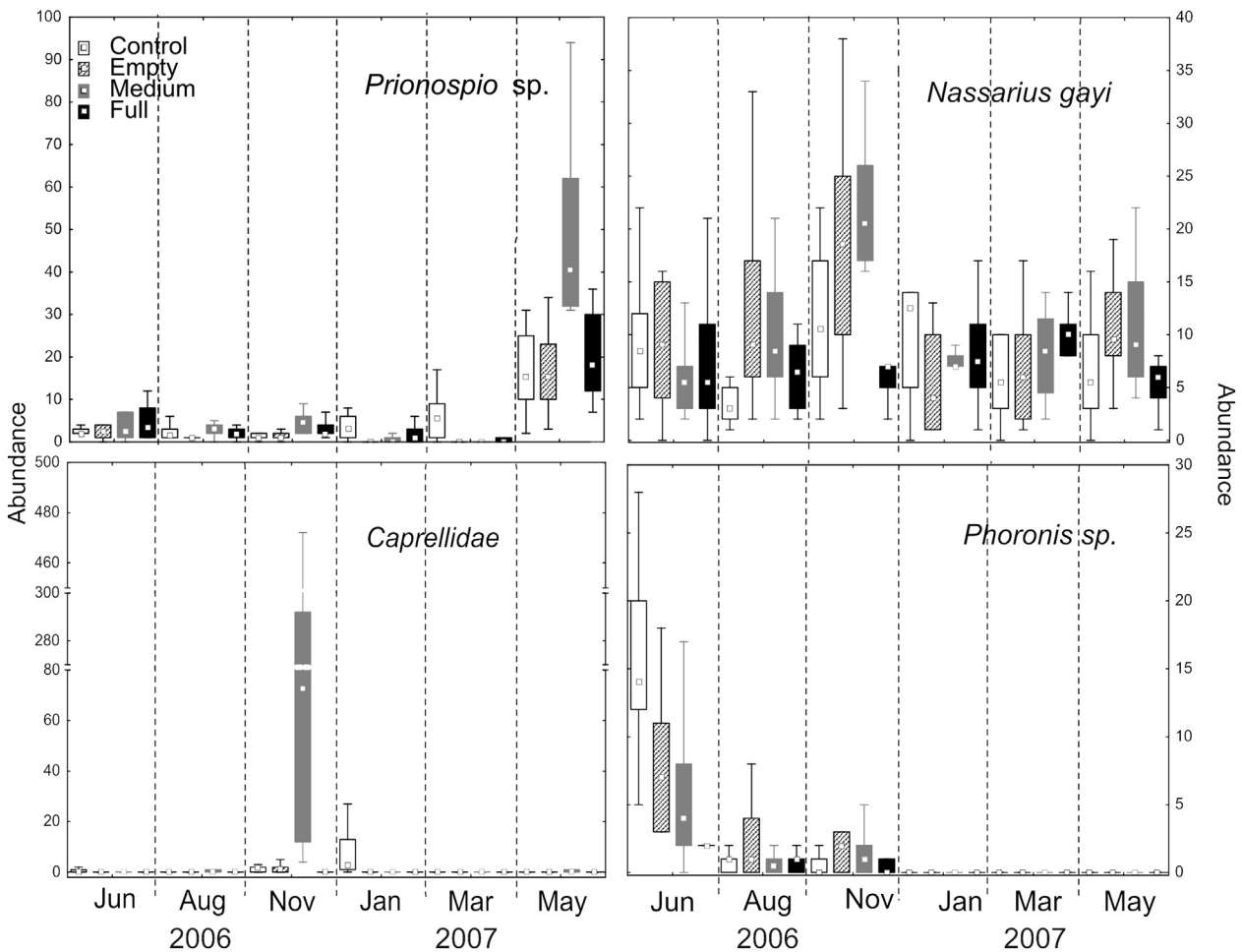


Fig. 8. Median abundance of the most important differentiators of the macrofauna at Independencia Bay among “natural control”, “empty”, “medium” and “full” treatments and throughout the year. Here and thereafter, the boxes are constructed with 25th to 75th percentiles; whiskers, 5th to 95th percentiles.

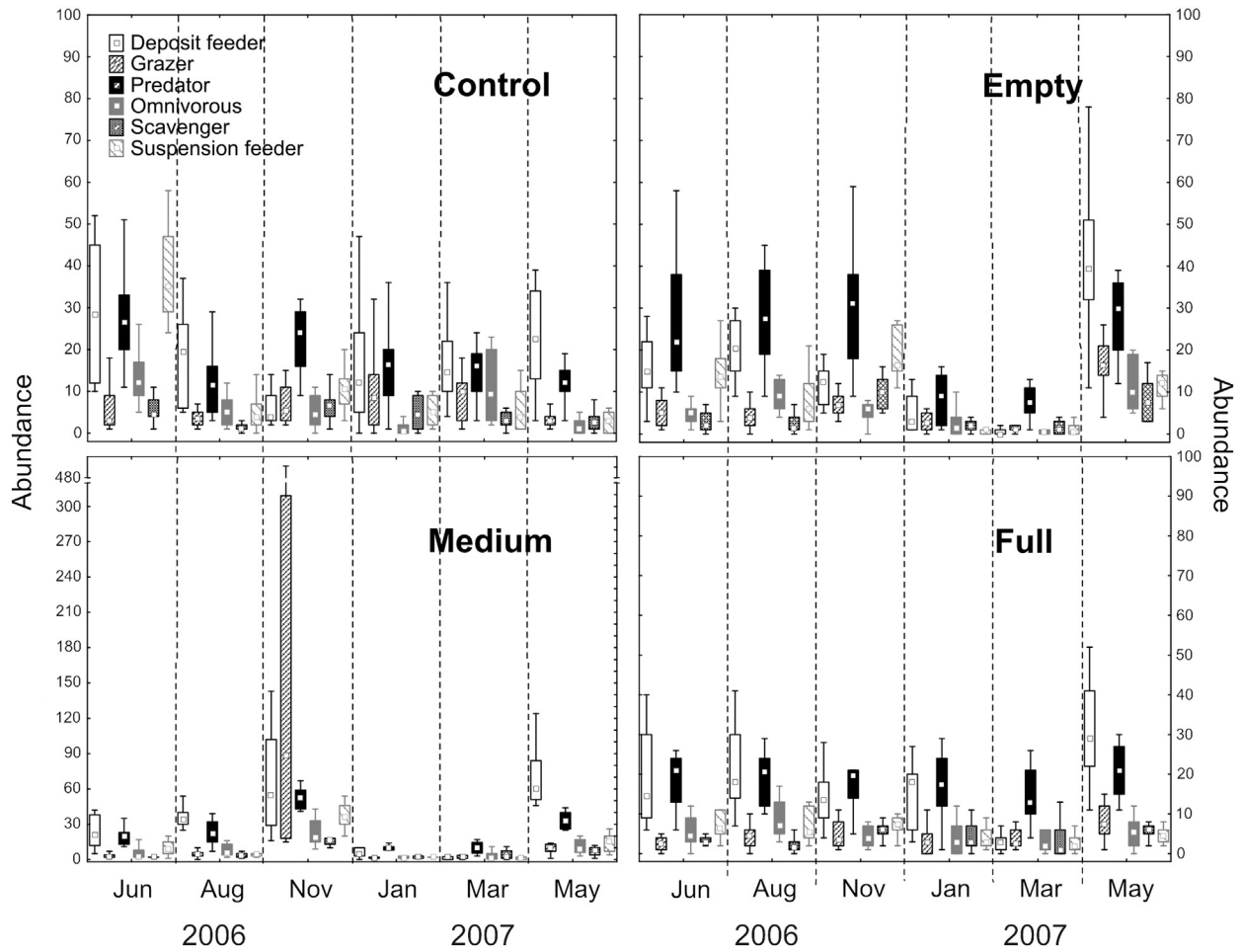


Fig. 9. Median abundance of the functional groups of the macrofauna among “natural control”, “empty”, “medium” and “full” treatments and throughout the year at Independencia Bay.

References

Aguilar, S., Roque, C., Yamashiro, C., Mariátegui, L., 2002. Effects of El Niño 1997–1998 on Commercial Marine Invertebrates of the Peruvian. *Coast. Inv. Mar.* 30 (1, Supl. Symp), 129–130.

Albrecht, A., Reise, K., 1994. Effects of *Fucus vesiculosus* covering intertidal mussel beds in the Wadden Sea. *Helgoländer Meeresun.* 48, 243–256.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA + for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK 214 pp.

Argüelles, J., Castillo, G., 2001. Talla, densidad y distribución de *Argopecten purpuratus* entre enero y septiembre de 1998 en la Bahía de San Lorenzo–Callao–Perú. In: El Niño en América Latina: impactos biológicos y sociales, edited by: Tarazona, J., Arntz, W.E., Castillo de Maruenda, E., CONCYTEC, Lima, 163–167.

Arntz, W.E., Tarazona, J., 1990. Effects of El Niño 1982–83 on benthos, fish and fisheries off the south American Pacific coast. In: *Global Ecological Consequences of the 1982–83 El Niño—Southern Oscillation*. Elsevier Oceanography Series 52, pp. 323–360.

Arntz, W.E., Flores, L.A., Maldonado, M., Carvajal, G., 1985. Cambios de los factores ambientales, macrobentos y bacterias filamentosas en la zona de mínimo oxígeno frente al Perú durante “El Niño” 1982–1983. In: Arntz, W.E., Landa, A., Tarazona, J. (Eds.), *El Niño. Su impacto en la fauna marina*. Bol. Inst. Mar., pp. 65–77 (vol. Extraord.), Perú–Callao.

Arntz, W.E., Tarazona, J., Gallardo, V.A., Flores, L.A., Salzwedel, H., 1991. Benthos communities in oxygen deficient shelf and upper slope areas of the Peruvian and Chilean Pacific coast, and changes caused by El Niño. In: *modern shelf anoxia*. Geol. Soc. Lond., Spec. Publ. 58, 131–154. <http://dx.doi.org/10.1144/GSL.SP.1991.058.01.10>.

Belapatiño Candela, A.O., 2007. Variabilidad del asentamiento larval de mitílidos en Bahía Independencia, Pisco–Perú, durante el periodo 1996–2003. Bachelor Thesis. Universidad Nacional Mayor de San Marcos. Lima, Peru 65 pp.

Bódis, E., Tóth, B., Szekeres, J., Borza, P., Sousa, R., 2014. Empty native and invasive bivalve shells as benthic habitat modifiers in a large river. *Limnologia* 49, 1–9.

Brock, R.E., 1979. An experimental study on the effects of grazing by parrot fishes and role of refuges in benthic community structure. *Mar. Biol.* 51, 381–388.

Bros, W.E., 1987. Effects of removing or adding structure (barnacle shells) on recruitment to a fouling community in Tampa bay. *J. Exp. Mar. Biol. Ecol.* 105, 275–296.

Bulleri, F., 2005. Role of recruitment in causing differences between intertidal assemblages on seawalls and rocky shores. *Mar. Ecol. Prog. Ser.* 287, 53–65.

Buschbaum, C., 2000. Direct and indirect effects of *Littorina littorea* (L.) on barnacles growing on mussel beds in the Wadden Sea. : *Island, Ocean and Deep-Sea Biology*. Springer Netherlands, pp. 119–128.

Carrasco, F.D., Oyarzún, O., 1988. Diet of the polychaete *Lumbrineris tetraura* (Schmarda) (Lumbrineridae) in a polluted soft-bottom environment. *Bull. Mar. Sci.* 42 (3), 358–365.

Chapman, M.G., Underwood, A.J., 1994. Dispersal of the intertidal snail, *Nodilittorina pyramidalis*, in response to the topographic complexity of the substratum. *J. Exp. Mar. Biol. Ecol.* 179 (2), 145–169.

Chícharo, M.A., Leitão, T., Range, P., Gutierrez, C., Morales, J., Morais, P., Chícharo, L., 2009. Alien species in the Guadiana estuary (SE-Portugal/SW-Spain): *Blackfordia virginica* (Cnidaria, Hydrozoa) and *Palaemon macrodactylus* (Crustacea, Decapoda): potential impacts and mitigation measures. *Aquat. Invasions* 4, 501–506.

Clarke, K.R., 1993. Non-parametric multivariate analysis of changes in community structures. *Aust. J. Ecol.* 18, 117–143.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth, UK 190 pp.

Clarke, K.R., Warwick, R.M., 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. PRIMER-E, Plymouth.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1309.

Eckman, J.E., Nowell, A.R.M., 1984. Boundary skin friction and sediment transport about an animal-tube mimic. *Sedimentology* 31, 851–862.

Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Annu. Rev.* 17, 193–284.

Firstater, F.N., Hidalgo, F.J., Lomovasky, B.J., Ramos, E., Gamero, P., Iribarne, O.O., 2011. Habitat structure is more important than nutrient supply in modifying mussel bed assemblage in an upwelling area of the Peruvian coast. *Helgol. Mar. Res.* 65 (2), 187–196.

Fox, J.W., 2013. The intermediate disturbance hypothesis is broadly defined, substantive issues are key: a reply to Sheil and Burslem. *Trends Ecol. Evol.* 28, 572–573.

Gotceitas, V., Colgan, P., 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. *Oecologia* 80, 158–166.

Graco, M., Ledesma, J., Flores, G., Girón, M., 2013. Nutrientes, oxígeno y procesos biogeoquímicos en el sistema de surgencias de la corriente de Humboldt frente a Perú. *Rev. Peru. Biol.* 14 (1), 117–128. <http://dx.doi.org/10.15381/rpb.v14i1.2165>.

- Grime, J.P., 1973. Control of species density in herbaceous vegetation. *J. Environ. Manag.* 1, 151–167.
- Guay, M., Himmelman, J.H., 2004. Would adding scallop shells (*Chlamys islandica*) to the sea bottom enhance recruitment of commercial species? *J. Exp. Mar. Biol.* 312, 299–317.
- Günther, C.-P., 1996. Development of small mytilus beds and its effects on macrofaunal intertidal macrofauna. *Mar. Ecol. Prog. Ser.* 130, 117–130.
- Gutiérrez, J.C., Iribarne, O.O., 1999. Role of Holocene beds of stout razor clams in structuring present benthic communities. *Mar. Ecol. Prog. Ser.* 185, 213–228.
- Gutiérrez, J.C., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos* 101, 79–90.
- Hidalgo, F.J., Firstater, F.N., Lomovasky, B.J., Iribarne, O.O., 2011. Effects of a predatory starfish on substrate colonization by a dominant mussel. *Mar. Ecol. Prog. Ser.* 432, 103–114.
- Huston, M.A., 1979. A general hypothesis of species diversity. *Am. Nat.* 113, 81–101.
- Iribarne, O., Armstrong, D., Fernández, M., 1995. Environmental impact of intertidal juvenile Dungeness crab habitat enhancement: effects on bivalves and crab foraging rate. *J. Exp. Mar. Biol. Ecol.* 192 (2), 173–194.
- Jofré Madariaga, D., Ortiz, M., Thiel, M., 2013. Demography and feeding behavior of the kelp crab *Talipeus marginatus* in subtidal habitats dominated by the kelps *Macrocystis pyrifera* or *Lessonia trabeculata*. *Invertebr. Biol.* 132, 133–144.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Kruczynski, W.L., 1975. A radioactive tracer study of food uptake by *Pinnotheres maculatus* in molluscan hosts. *Biol. Bull.* 148, 60–67.
- Lanari, M.D.O., Coutinho, R., 2014. Reciprocal causality between marine macroalgal diversity and productivity in an upwelling area. *Oikos* 123 (5), 630–640.
- Laudien, J., Rojo, M.E., Oliva, M.E., Arntz, W.E., Thatje, S., 2007. Sublittoral soft bottom communities and diversity of Mejillones Bay in northern Chile (Humboldt current upwelling system). *Helgol. Mar. Res.* 61, 103–116.
- Lee, C.N., Morton, B., 2005. Demography of *Nebalia* sp. (Crustacea: Leptostraca) determined by carrion bait trapping in Lobster Bay, Cape d'Aguiar Marine Reserve, Hong Kong. *Mar. Biol.* 148, 149–157.
- Lenihan, H.S., Peterson, C.H., Byers, J.E., Grabowski, J.H., Thayer, G.W., Colby, D.R., 2001. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. *Ecol. Appl.* 11 (3), 764–782.
- Lomovasky, B.J., Firstater, F.N., Salazar, A.G., Mendo, J., Iribarne, O.O., 2011. Macro benthic community assemblage before and after the 2007 tsunami and earthquake at Paracas Bay. *J. Sea Res.* 65, 205–212.
- Marincovich, L., 1973. Intertidal mollusks of Iquique, Chile. National History Museum of Los Angeles County, Scientific Bulletin 16 (1–49 pp.).
- Mendo, J., Wolff, M., 2003. El impacto de El Niño sobre la producción de concha de abanico (*Argopecten purpuratus*) en Bahía Independencia, Pisco. *Perú. Ecol. Aplic.* 2, 51–57.
- Mendo, J., Valdivieso, V., Yamashiro, C., 1987. Cambios en la densidad, número y biomasa de la población de concha de abanico (*Argopecten purpuratus*) en la Bahía Independencia (Pisco, Perú) durante 1984–87. *II COLACMAR*, Lima, Perú.
- Menge, B.A., Lubchenco, J., Ashkenas, L.R., 1985. Diversity, heterogeneity and consumer pressure in a tropical rocky intertidal community. *Oecologia* 65 (3), 394–405.
- Morón, O., Lostanau, N., Escudero, L., 1988. Parámetros oceanográficos en Bahía Independencia, Perú, entre mayo de 1985 y julio de 1987. *Bol. Inst. Mar Perú, Callao Vol. Extraordinario* 25–34.
- Nowell, A.R.M., Jumars, P.A., 1984. Flow environments of aquatic benthos. *Annu. Rev. Ecol. Syst.* 15, 303–328.
- O'Connor, N.E., Bruno, J.F., 2007. Predatory fish loss affects the structure and functioning of a model marine food web. *Oikos* 116, 2027–2038.
- Oliva, D., Castilla, J.C., 1986. The effect of human exclusion on the population structure of key hole limpets *Fissurella crassa* and *F. limbata* on the Coast of Central Chile. *Mar. Ecol. Prog. Ser.* 34, 201–217.
- Pardo, L.M., Palma, A.T., Prieto, C., Sepulveda, P., Valdivia, I., Ojeda, F.P., 2007. Processes regulating early post-settlement habitat use in a subtidal assemblage of brachyuran decapods. *J. Exp. Mar. Biol. Ecol.* 344, 10–22.
- Paredes, C.Q., 1986. La familia Fissurellidae (gastropoda, Archaeogastropoda) en el Perú. *Revista de Ciencias de UNMSM* 74 (1), 75–86.
- Paredes, C.Q., Huamán, P., Cardoso, F., Vivar, R., Vera, V., 1999. Estado actual del conocimiento de los moluscos acuáticos en el Perú. *Rev. Peru. Biol.* 6 (1).
- Pillay, D., Branch, G.M., Forbes, A.T., 2007. Effects of *Callinassa kraussi* on microbial biofilms and recruitment of macrofauna: a novel hypothesis for adult–juvenile interactions. *Mar. Ecol. Prog. Ser.* 347, 1–14.
- Quispe, D., Graco, M., Correa, D., Tam, J., Gutiérrez, D., Morón, O., Flores, G., Yamashiro, C., 2010. Variabilidad espacio-temporal de condiciones hidrofísicas en Bahía Independencia, Pisco-Perú, desde 1955 al 2004. *Ecología Aplicada (Lima)* 9 (1), 9–18.
- Santelices, B., Vasquez, J., Meneses, I., 1986. Patrones de distribución y dietas de un gremio de moluscos herbívoros en hábitats intermareales expuestos de Chile central. *Monografías Biológicas* 4, 147–171.
- Shaffer, P.L., 1979. The feeding biology of *Podarke pugettensis* (Polychaeta: hesionidae). *Biol. Bull.* 156, 343–355.
- Sheil, D., Burslem, D.F.R.P., 2013. Defining and defending Connell's intermediate disturbance hypothesis: a response to Fox. *Trends Ecol. Evol.* 28, 571–572.
- Siegel, P.R., 1984. Food-induced size-specific molt synchrony of the sand crab, *Emerita analoga* (Stimpson). *Biol. Bull.* 167, 579–589.
- Sorte, C.J., Jones, S.J., Miller, L.P., 2011. Geographic variation in temperature tolerance as an indicator of potential population responses to climate change. *J. Exp. Mar. Biol. Ecol.* 400 (1), 209–217.
- Sousa, R., Gutiérrez, J.L., Aldridge, D.C., 2009. Non-indigenous invasive bivalves as ecosystem engineers. *Biol. Invasions* 11, 2367–2385.
- Stewart, T.W., Miner, J.G., Lowe, R.L., 1998. Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell-generated habitat. *J. North Am. Benthol. Soc.* 17, 81–94.
- Tallmark, B., 1980. Population dynamics of *Nassarius reticulatus* (Gastropoda, Prosobranchia) in Gullmar Fjord. *Mar. Ecol. Prog. Ser.* 3, 51–62.
- Tarazona, J., Arntz, W., Cañahuire, E., 1996. Impact of two “El Niño” events of different intensity on the hypoxic soft bottom macrobenthos off the central Peruvian coast. *Mar. Ecol. Prog. Ser.* 17, 425–446.
- Tarazona, J., Arntz, W., Hoyos, L., 1988a. A Repartición de los recursos alimenticios entre tres peces bentofagos frente al Perú antes, durante y después de El Niño 1982–83. In: Salzwedel, H., Landa, A. (Eds.), *In: Recursos y Dinámica del Ecosistema de Afloramiento Peruano*, pp. 107–114.
- Tarazona, J., Salzwedel, H., Arntz, W., 1988b. b. Positive effects of “El Niño” on macrozoobenthos inhabiting hypoxic areas of the Peruvian upwelling system. *Oecologia* 76, 184–190.
- Tarazona, J., Espinoza, R., Solís, M., Arntz, W., 2007. Growth and somatic production of the fan scallop (*Argopecten purpuratus*) in Independencia Bay, Pisco (Peru) during El Niño and La Niña events. *Rev. Biol. Mar. Oceanogr.* 42, 275–285.
- Tarazona, J., Gutiérrez, D., Paredes, C., Indacochea, A., 2003. Overview and challenges of marine biodiversity research in Peru. *Gayana* 67, 206–231.
- Tarazona, J., Aguilar, P., Tovar, O., Ortega, H., Lamas, G., 1998. Estado del conocimiento de la diversidad biológica en el Perú: Una sinopsis. In: Halfiter, G. (Ed.), (Comp.), “La Diversidad Biológica de Iberoamérica III” *Acta Zoológica Mexicana, Nueva Serie Volumen Especial*, 231. Instituto de Ecología, A.C., Xalapa, México, pp. 85–102.
- Tarazona, J., Cañahuire, E., Salzwedel, H., Jeri, T., Arntz, W., Cid, L., 1991. Macro zoobenthos in two shallows areas of Peruvian upwelling ecosystem. In: Elliott, M., Ducrot, J.P. (Eds.), “Estuaries and Coasts: Spatial and Temporal Intercomparisons”. *ECSA 19 Symposium*, Amsterdam, pp. 251–258.
- Tarazona, J., Paredes, C., Romero, L., Blascock, V., Guzmán, S., Sánchez, S., 1985. Características de la vida planctónica y colonización de los organismos epilíticos durante el fenómeno “El Niño”. In: Arntz, W., Landa, A., Tarazona, J. (Eds.), “El Niño y su impacto en la fauna marina”. *Bol. Ins. Mar Perú-Callao. Vol. extr.*, pp. 41–50.
- Taylor, M.H., Wolff, M., Mendo, J., Yamashiro, C., 2008. Changes in trophic flow structure of Independence Bay (Peru) over an ENSO cycle. *Prog. Oceanogr.* 79, 336–351.
- Thatje, S., Heilmayer, O., Laudien, J., 2008. Climate variability and El Niño Southern Oscillation: implications for natural coastal resources and management. *Helgol. Mar. Res.* 62 (1), 5–14.
- Thiel, M., Zander, A., Baeza, J.A., 2003. Movements of the symbiotic crab *Liopetrolisthes mitra* between its host sea urchin *Tetrapygus niger*. *Bull. Mar. Sci.* 72, 89–101.
- Tokeshi, M., Romero, L., 1995. Filling a gap: dynamics of space occupancy on a mussel-dominated subtropical rocky shore. *Bol. Inst. Mar Perú*, 119, 167–176.
- Tsuchiya, M., Nishihira, M., 1986. Island of *Mytilus edulis* as a habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization. *Mar. Ecol. Prog. Ser.* 31, 171–178.
- Valdivia, N., Thiel, M., 2006. Effects of point-source nutrient addition and mussel removal on epibiotic assemblages in *Perumytilus purpuratus* beds. *J. Sea Res.* 56, 271–283.
- Vásquez, J., Vega, J.M.A., 2004. Ecosistemas marinos costeros del Parque Nacional Bosque Fray Jorge. In: Squeo, F.A., Gutiérrez, J.R., Hernández, I.R. (Eds.), *Historia Natural del Parque Nacional Bosque Fray Jorge*. Ediciones Universidad de La Serena, La Serena, Chile, pp. 235–252.
- Wolff, M., Mendo, J., 2000. Management of the Peruvian bay scallop (*Argopecten purpuratus*) metapopulation with regard to environmental change. *Aquatic Conserv.: Mar. Freshw. Ecosyst.* 10, 117–126.
- Wolff, M., Taylor, M., Mendo, J., Yamashiro, C., 2007. A catch forecast model for the Peruvian scallop (*Argopecten purpuratus*) based on estimators of spawning stock and settlement rate. *Ecol. Model.* 209, 333–341.
- Wright, J.P., Jones, C.G., 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. *Bioscience* 56 (3), 203–209.
- Zar, J.H., 1999. *Biostatistical Analysis*. 4th edition. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, p. 718.
- Zuta, S., Guillén, O., 1970. Oceanografía de las Aguas Costera del Perú. *Bol. Inst. Mar Perú, Callao* 2, 157–324.