Marine ecosystem engineering by the alien ascidian *Pyura praeputialis* on a mid-intertidal rocky shore

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ABSTRACT: Engineer species transform ecosystems due to their own growth, constitute an integral part of altered environments, and provide new habitats for other species, thus affecting biodiversity and the ecosystem. On rocky shores inside Antofagasta Bay (Northern Chile), the alien ascidian *Pyura praeputialis*, an engineer species, creates broad belts and dense 3-dimensional matrices that modify the intertidal habitat structure. In all, 116 species of macro-invertebrates and algae inhabit this habitat, compared with the 66 species inhabiting adjacent intertidal rocky shores which lack *P. praeputialis*. Of the 145 species recorded at the seascape scale (encompassing both mid-intertidal habitat), 55% were found exclusively in intertidal *P. praeputialis* matrices. Along the coastal gradient, patterns in β-diversity emerge due to the addition of a new set of species to the community inhabiting the *P. praeputialis* matrices and, to a lesser extent, from spatial turnover. We found differences in the shape of the species frequency distribution between the communities inhabiting the engineered and non-engineered mid-intertidal habitats. However, within the same habitat type, there was no difference in the species frequency distribution between functional groups. Occurrence of macro-algae was not affected by habitat type, but occurence of macro-invertebrates increased significantly in *P. praeputialis* matrices. *P. praeputialis* increases species richness at local and seascape scales by providing a novel mid-intertidal habitat which is used by mobile and vagile macro-invertebrates that otherwise would remain excluded from this intertidal level.

KEY WORDS: *Pyura praeputialis* matrices · Ecosystem engineer · Intertidal seascapes · α- and β-diversity · Species frequency distribution · Northern Chile

INTRODUCTION

Ecosystem engineer species (Jones et al. 1994, 1997) create, modify and/or increase habitat heterogeneity (e.g. in the sea: corals, macro-algae, mussels, ascidians), and may be part of biological mechanisms maintaining high species richness at local, seascape (Roff et al. 2003), and regional scales (Tokeshi & Romero 1995, Crooks 1998, Crooks & Khim 1999, Cerda & Castilla 2001, Thiel & Ullrich 2002). According to Jones et al. (1994), the largest effects of engineering may be attributable to species with large per capita impacts, which live in high densities, generate structures that persist for long periods and modulate the distribution and use of resources. However, to predict the effect of an ecosystem engineer species on ecological diversity, it is necessary to under-stand how the species pool responds to these changes (Wright et al. 2002). Several authors have predicted that ecosystem engineers increase species richness by altering habit complexity and providing new habitat (Jones et al. 1994, 1997, Alper 1998, Coleman & Williams 2002, Reichmann & Seabloom 2002, Wright et al. 2002).

Engineered habitats have different community compositions compared to non-engineered ones. This can lead to increased species richness at the landscape scale (i.e. involving multiple patch types), when species are present that are restricted to engineered habitats at least during some stages of their life cycle (Wright et al. 2002). Further, engineer species also create resources that are not otherwise available, and species that utilise them are subsequently present (Gutierrez et al. 2003). This suggests that although sites from engineered and

non-engineered habitats may have similar local or α-diversity patterns. β-diversity, along a geographical gradient (i.e. the spatial turnover in species composition), may show high values when sites from distinctive habitats are compared. However, spatial patterns in β-diversity may also arise from spatial trends in α-diversity (Harrison et al. 1992). Therefore, to understand the increase in species diversity promoted by ecosystem engineers, it is necessary to distinguish between real spatial turnover in species composition between engineered and non-engineered habitats and spatial differentiation between communities which are generated by the addition or loss of species from the regional pool. So far there are no studies addressing changes in marine diversity along geographical gradients with regards to engineering processes. If the consequences of engineering are observed at the landscape (or seascape) scale, with some species present exclusively in the modified habitat and others solely in the non-modified habitat (Wright et al. 2002), then the differences must be also reflected in changes in the species frequency distribution between habitats. Metapopulation models have addressed regional frequency distributions with few common and many rare species (Brown 1984), or a bimodal shape (Hanski 1982). For instance, Collins & Glenn (1997) demonstrated that such patterns depend on the aerial extent of the study (i.e. distance scaling; see van Rensburg et al. 2000 for changes in species frequency distribution between patch types). This may also apply to patterns in species frequency distribution when comparing engineered and non-engineered habitats (hereafter referred to as habitat scaling). Since there are species that inhabit only non-engineered or engineered habitats (Wright et al. 2002), it is expected that at the landscape scale the species frequency distribution does not present common species (i.e. species occurring in all plots across the landscape). The engineering effect on biodiversity would not necessarily be identical for all species in the landscape pool, where some species would benefit from the new habitat availability, while others would be excluded (Wright et al. 2002). Therefore, spatial patterns in species diversity and frequency distribution may change when applied to different taxa (i.e. organismal scaling, Collins & Glenn 1997). In the context of ecosystem engineering, the segregation of species into functional groups (e.g. for rocky intertidal habitats: macro-invertebrates, sessile, mobile, macro-algae) may reveal which species set is most affected, in terms of spatial distribution, by the availability of the engineered habitat, and may also provide information regarding the mechanisms by which a engineer species generates an increase in species richness at the landscape scale.

The barrel-shaped ascidian *Pyura praeputialis* generates extensive aggregations of individuals in the mid-intertidal zone of rocky shores. In Chile, *P. praeputialis* is considered a recent invader (Castilla et al. 2002) and is exclusively present along approximately 60 to 70 km of coastline inside Antofagasta Bay. It shows a notable disjoint geographical distribution (Castilla & Guiñez 2000), with the nearest neighbours present along the southern shores of Australia (Kott 1985, Fairweather 1991, Dalby 1997, Castilla et al. 2002, Monteiro et al. 2002). *P. praeputialis* aggregations attain 3-dimensional (3D) pseudo-colonality (Paine & Suchanek 1983, Guiñez & Castilla 2001) that show wide, almost continuous intertidal belts and high percentage cover (ca. 1800 ind. m^{-2}, Castilla et al. 2000). Cerda & Castilla (2001) reported that the macro-invertebrate diversity of species (96 taxa) inhabiting the *P. praeputialis* matrices is one of the highest values reported for the mid-intertidal zone in this geographical area. Nevertheless, the study did not incorporate mid-intertidal macro-algae, which are known to be important components of species diversity in northern Chile (Camus & Lagos 1996).

The objectives of this paper are to: (1) report on the diversity of macro-algae and macro-invertebrates inhabiting *Pyura praeputialis* matrices, (2) test whether the novel mid-intertidal habitat provided by this alien ascidian promotes an increase in the species richness at the seascape scale (i.e. encompassing both habitat types: rocky shores with and without *P. praeputialis* matrices), (3) explore α- and β-diversity patterns to evaluate whether the increase in species richness is due to the addition or spatial turnover of species, (4) test whether species frequency distribution differs between the 2 contrasting mid-intertidal habitats and between functional groups. Thus, our main underlying hypothesis is that matrices of *P. praeputialis* create new mid-intertidal habitats, otherwise unavailable in the region, which significantly increase species richness at the seascape scale and thereby modify biodiversity and the structure of intertidal communities in northern Chile.

MATERIALS AND METHODS

The study was performed on 7 sites along approximately 200 km of coastline (Fig. 1). All study sites were mid-intertidal rocky platforms that received direct wave exposure, had slopes <20°, and similar substrate heterogeneity (as described in Castilla 1981). Inside Antofagasta Bay we sampled mid-intertidal *Pyura praeputialis* matrices (i.e. belts of *P. praeputialis* matrix habitats: hereafter *Pp*MH) at 3 sites: Curva Lenguado, El Way and El Eden. North and south of the bay we sampled the mid-intertidal rocky habitat at 4 sites where *P. praeputialis* was absent (i.e. *P. praeputialis*-less substrate habitat: hereafter *Pp*-LSH): Caleta El Cobre and Jorguillo Point, both to the south of Antofa-

gasta Bay, and Lagarto Point and La Lobería Point, both to the north of the bay (Fig. 1).

Sampling of *Pp*MH diversity. The optimum plot size for sampling macro-invertebrates in the *Pyura praeputialis* matrices was estimated as a 35×35 cm (0.1225 m^2) quadrant, with 4 replicates per site (Cerda & Castilla 2001). To sample the *P. praeputialis* matrices we used the following procedure: (1) a $35 \times 35 \times 35$ cm iron cube was randomly placed on top of the *Pyura* matrix, at the height of the mid-intertidal fringe (100% cover in all cases) approximately 1 m above the lower intertidal limit of *P. praeputialis* belt (Castilla 1998, Cerda & Castilla 2001), (2) the cube was hammered into the *Pyura* matrix until reaching the underlying rock, (3) individual *P. praeputialis* were carefully removed using iron chisels, (4) all macro-invertebrates and macro-algae (larger than 5 mm) found inside the *P. praeputialis* clumps were collected, (5) the removed *P. praeputialis* clumps were stored in plastic bags, transported to the laboratory and kept at $-18°$C, (6) each clump was separated into *P. praeputialis* individuals, and invertebrates and algae found in or on the tunicate where collected, (7) residual material (i.e. sand, gravel, and broken shells) generated during the sorting was separated out using 500 μm plastic sieves, and remaining invertebrates were collected. All individuals collected were identified to the lowest taxonomic level (Cerda & Castilla 2001).

Sampling of *Pp*-LSH diversity. We sampled mid-intertidal communities on rocky platforms, where the condition of rocky shore lack *Pyura praeputialis* and the mussel *Perumytilus purpuratus* (which is the dominant intertidal species of central Chile, Broitman et al. 2001). In general, the mid-intertidal zone of northern Chile is dominated by 3 sessile species: the barnacles *Jehlius cirratus* and *Notochthamalus scabrosus* and the macro-alga *Ulva* sp. (Camus & Lagos 1996). At each study site, we used 6 randomly placed 50×50 cm (0.25 m^2) sample quadrants following this sampling scheme: (1) plots were randomly placed at the mid-intertidal fringe, approximately 1 m above the upper limit of the *Lessonia nigrescens* kelp belt, (2) macro-invertebrates and macro-algae were removed by hand, using knives and iron chisels, and stored, analysed and taxonomically identified as indicated above.

Data analysis. We constructed a database combining our data for macro-algae and macro-invertebrates, for both mid-intertidal habitat types, with data from Cerda & Castilla (2001) for macro-invertebrates inhabiting the *Pp*MH. Data were pooled from the 2 study programs, presenting differences in the number and size of quadrats used; therefore, standardisation by area was carried out (Gotelli & Colwell 2001). To estimate the degree of overlap in species composition between the 2 habitat types we used non-metric multidimensional scaling ordination (NMS, McCune & Meffort 1999)
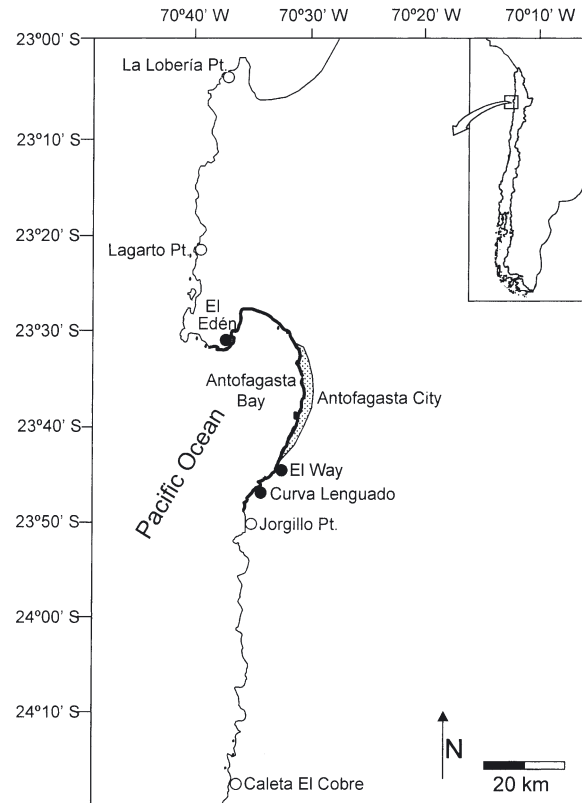

Fig. 1. Study region on the northern Chilean coast. *Pyura praeputialis* only inhabit the rocky intertidal and shallow subtidal areas (bold line) along the coast of Antofagasta Bay (●: study sites). Adjacent sites are located in areas with extended rocky shores (○: *Pyura praeputialis*-less substrate habitat [*Pp*-LSH] study sites)

based on species presence–absence data at the plot level. We also explored differences in levels of similarity in species composition within and between habitat types, calculating the Morisita-Horn similarity index for all pair-wise comparisons of plots[1]. Testing for differences in species composition was done using 1-way ANOVA with 3 levels of comparison: *Pp*-LSH vs *Pp*-LSH, *Pp*MH vs *Pp*MH, and *Pp*MH vs *Pp*-LSH. The proportional data of similarity indices were square-root transformed to meet ANOVA assumptions (SAS Institute 1996). Species richness in *Pp*MH and *Pp*-LSH was estimated by pooling all plots from each habitat type (12 and 24 plots respectively). At the seascape scale, species richness was estimated by pooling data from all plots (n = 36). Estimates of species richness were rarefied to correct for differences in area and sample size, as suggested by Gotelli & Colwell (2001), by using 100 runs of the Coleman rarefaction estimate[1]. In all cases,

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[1]Colwell RK (1997) EstimateS: statistical estimation of species richness and shared species from samples, Version 5. Available at www.viceroy.eeb.uconn.edu/estimates

the estimated species richness reached an asymptotic value indicating an adequate sample size. The size of the effect of *Pp*MH on species richness (ΔS) in the mid-intertidal zone was assessed by estimating the difference in species richness between both habitat types. This was accomplished by computing the 2 observed distributions for species richness (S), with mean S_2 for *Pp*-LSH and S_1 for *Pp*MH. This was calculated as: $\Delta S = S_1 - S_2$. To avoid non-independence of pair-wise differences between S_1 and S_2 we approximated the distribution of ΔS through simulations in a Bayesian framework (see Albert 1996). Using a uniform non-informative prior distribution, we simulated 5000 random values from each normal distribution using the Coleman estimated species richness and its standard deviation (Colwell 1997). The difference between S_2 and S_1 was computed for each pair of simulated values, and the 95% Student's *t*-test confidence interval for the posterior simulated distribution of ΔS was estimated. These analyses provided us with an error measure in the estimation (e.g. Wright et al. 2002). We computed ΔS using the Coleman estimated species richness at the asymptotic value and the estimate corrected for the sampled area (Gotelli & Colwell 2001, Wright et al. 2002). Given that the *Pp*MH plots were smaller than the *Pp*-LSH plots, we selected a corrected area of 1.4 m^2 to compare the estimated species richness between the contrasting habitats (11 plots from *Pp*MH and 6 plots from *Pp*-LSH).

To explore how the presence of mid-intertidal *Pyura praeputialis* matrices modifies the spatial geographic diversity pattern along the studied rocky shores, we grouped the species into 4 functional groups: macro-algae, sessile macro-invertebrates, mobile macro-invertebrates, and vagile macro-invertebrates. For each functional group, and for the entire set of taxa, we calculated the α- and β-diversity along the geographical gradient. To examine the spatial turnover in species composition between adjacent sites, we used Whittaker's (1972) measure of β-diversity, $\beta\text{-}1 = (S/m) - 1$; where S is the combined number of species in the paired, adjacent sites, and m is the average richness for the 2 sites. This measurement ranges from zero (complete similarity) to 1 (complete dissimilarity). However, to distinguish between the true spatial turnover from the spatial trends in the α-diversity patterns induced by simple losses or additions of new species, we used the β-2-diversity index $= (S/\alpha_{max}) - 1/(n-1)$; where α_{max} refers to the maximum value of α-diversity of all n sites (Harrison et al. (1992). The spatial patterns of α-, β-1- and β-2-diversity, calculated for the entire set of taxa, were correlated with the corresponding diversity index, but calculated separately for each functional group. The analysis provided an approximation for which functional groups were more important in the generation of the geographical pattern of differentiation in species composition.

To assess whether the frequency distributions of species inhabiting *Pp*MH was different from those in *Pp*-LSH, we calculated the proportion of plots (P) occupied by each species i, as $P_i = p/n$; where p is the number of plots occupied by the species and n is the total number of plots. The analysis was done at the scale of plots since there was evidence of changes in species diversity at the level of individual *Pyura praeputialis* (Monteiro et al. 2002) and not at the scale of the sites (Cerda & Castilla 2001). We explored the effect of habitat scaling (see Collins & Glenn 1997) by plotting the species frequency distribution of the mid-intertidal community for each habitat type and at the seascape scale. We also explored the effect of organismal scaling (Collins & Glenn 1997) by plotting the species frequency distribution for 2 functional groups (macro-invertebrates and macro-algae) within the 3 habitat categories. To understand whether *Pp*MH, in addition to causing changes in the shape of the species frequency distribution, also promoted an increase or decrease in species occurrence, we estimate the effect of *Pp*MH as the difference, $\Delta P_{it} = P_{i\,Pp\text{MH}} - P_{i\,Pp\text{-LSH}}$. We plotted the frequency distribution of ΔP to obtain the shape and direction of the effect, using the entire taxa data set, and segregated the data into macro-invertebrate and macro-algae functional groups. Difference in organismal, habitat scaling and in the shape of ΔP between functional groups was tested using a Kolmogorov-Smirnov 2-sample test, whereas the direction of the effect of ΔP was tested using a 1-sample Wilcoxon signed-rank test (Sokal & Rohlf 1991).

RESULTS

Effects on mid-intertidal species richness

Community compositions of the mid-intertidal *Pp*MH and the corresponding rocky mid-intertidal habitat (*Pp*-LSH) were different (Table 1). Of the

Table 1. Species richness for macro-algae and macro-invertebrates (separated by functional groups) inhabiting the mid-intertidal of the *Pyura praeputialis* matrix habitats (*Pp*MH), *Pyura*-less substrate habitat (*Pp*-LSH) and species common to both mid-intertidal habitats (last column) in the rocky shore of the study zone

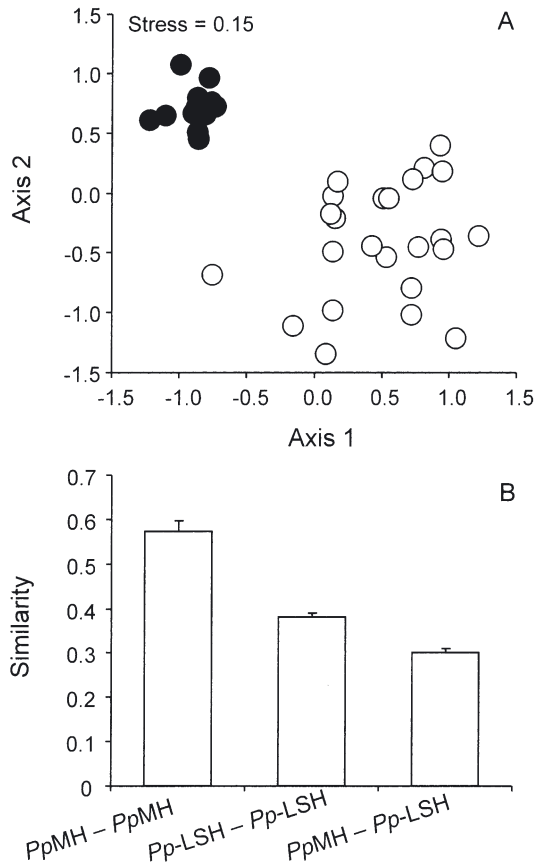| Functional group	*Pp*MH	*Pp*-LSH	Common
Algae			
Sessile	7	12	13
Invertebrates			
Mobile	56	9	17
Sessile	9	7	7
Vagile	7	1	0
Total	79	29	37

Fig. 2. (A) Ordination of community composition between intertidal habitats. Ordination of plots based on species presence using non-metric multi-dimensional scaling. ●: *Pyura praeputialis* matrix habitats (*Pp*MH); ○: rocky platforms or *P. praeputialis*-less substrate habitat (*Pp*-LSH). (B) Similarity (mean ± 1 SE of Morisita-Horn similarity index for pairwise comparison) of community composition within (*Pp*MH or *Pp*-LSH) and between (*Pp*MH and *Pp*-LSH) mid-intertidal habitat types

79 species recorded exclusively in the *Pp*MH, 91% corresponded to macro-invertebrates and 9% to macro-algae species. In the *Pp*-LSH there was a total of 29 intertidal species, of which 59% were macro-invertebrates and 41% macro-algae species. Thirty-seven species were common to both mid-intertidal habitats (Table 1). The difference in community composition was evident using NMS, which showed a strong segregation between *Pp*MH and *Pp*-LSH plots (Fig. 2A). Furthermore, there was a significant difference in the similarity of plots within and between habitat types (ANOVA, $F_{2, 969}$ = 72.76, p = 0.0001) (Fig. 2B). A comparison of the community composition within *Pp*MH was highly similar, in contrast to the comparison within *Pp*-LSH plots. The between-habitat comparison, *Pp*MH vs *Pp*-LSH, showed a lower level of similarity (Fig. 2B).

Differences in species composition translated into differences in species richness (Fig. 3A). Asymptotic Coleman species richness estimates (mean ± 1 SD) for each habitat type were: 65.5 ± 0.68 for *Pp*-LSH, and 116.4 ± 1.2 for *Pp*MH (Fig. 3A). At the seascape scale, the species richness estimated by random sampling of plots from both habitat types was higher than that estimated for each habitat individually (S = 144.5 ± 0.69). At the asymptote of the Coleman estimate, the effect size of the *Pp*MH on species richness with respect to richness in the *Pp*-LSH, was positive and significant, with ΔS = 50.91 species ± 0.042 SD (Student's *t*-test, p < 0.0001) (Fig. 3B). Nevertheless, the Coleman estimates corrected for area showed that the difference in species richness in both habitat types rose to ΔS = 62.8 spe-
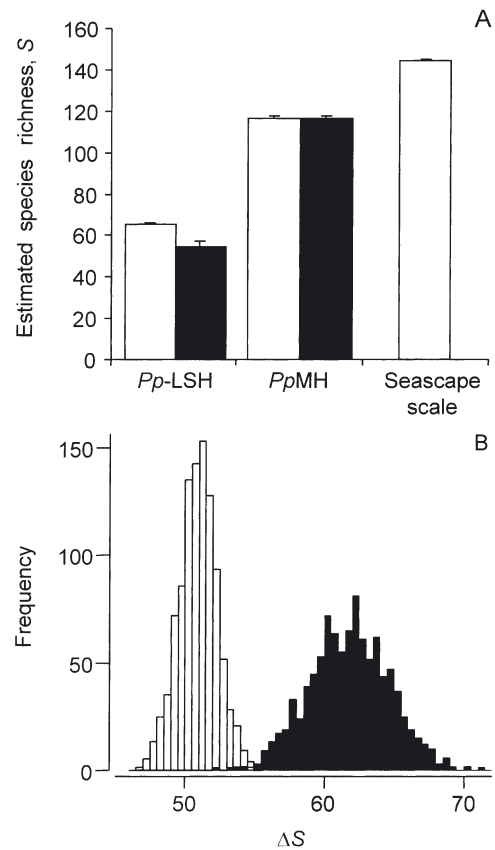

Fig. 3. *Pyura praeputialis.* (A) Asymptotic estimated species richness (S; ±1 SD) of hypothetical intertidal seascapes composed only by rock substrata (*P. praeputialis*-less substrate habitat, *Pp*-LSH), only by *P. praeputialis* matrix habitats (*Pp*MH), and the combination of both habitats types (seascape scale). Black bars represent the Coleman rarefaction estimate of species richness in an equal sized area of 1.4 m² in both habitat types. (B) Histogram for simulated values of ΔS, the averaged effect size of *P. praeputialis* on mid-intertidal species richness. ΔS was calculated as the difference between both habitat types in the Coleman estimate of species richness at the asymptotic value (white bars) and corrected for an equal sized area (black bars)

cies ± 0.092 SD (Student's *t*-test, p < 0.0001) (Fig. 3B). These patterns caused increased richness at the seascape scale, which exhibited 28.06 species ± 0.04 SD more than the richness estimated in the *Pp*MH. Of the 145 species recorded at the seascape scale, 55% were found exclusively in *Pp*MH plots, whereas 25% of the species shared both habitat types, and only 20% were found exclusively in *Pp*-LSH (Table 1).

Effects on spatial turnover in species composition

The geographical patterns along the studied rocky shores showed that for the entire taxa set, α-diversity increased in the sites with *Pp*MH and decreased in *Pp*-LSH sites (Fig. 4A). In addition, high differences in community composition, or β-1-diversity, were found in the pair-wise comparison between different habitat types (Fig. 4A). These spatial patterns, for total mid-intertidal species, corresponded well with those of α- and β-1-diversity for total macro-invertebrate species (Fig.4B), but less so with the spatial

pattern for total macro-algae (Fig. 4C, see Table 2 for *r*-Pearson correlation and p-values). In general, the relationship of α- and β-1-diversity patterns among the entire taxa set and the functional groups was positive and significant for all invertebrates and mobile invertebrates (Fig. 4A,D, Table 2). However, the β-2 estimate did not translate into high values of community differentiation for the pair-wise comparison between different habitat types (× in Fig. 4). In addition, the relationship of β-2-diversity patterns among the entire taxa set and the functional groups was non-significant in all cases (Table 2). Along-shore spatial patterns in β-1 support that differences in community composition between habitat is influenced by invertebrates (in general) and mobile invertebrates (in particular), after removing the spatial trends in α-diversity (i.e. the increase in richness in *Pp*MH sites); the β-2 estimates do not show a clear spatial turnover. Thus, spatial differentiation among habitat types emerge from the addition of species, mainly mobile invertebrates and, to a lesser extent, to spatial turnover in species composition.
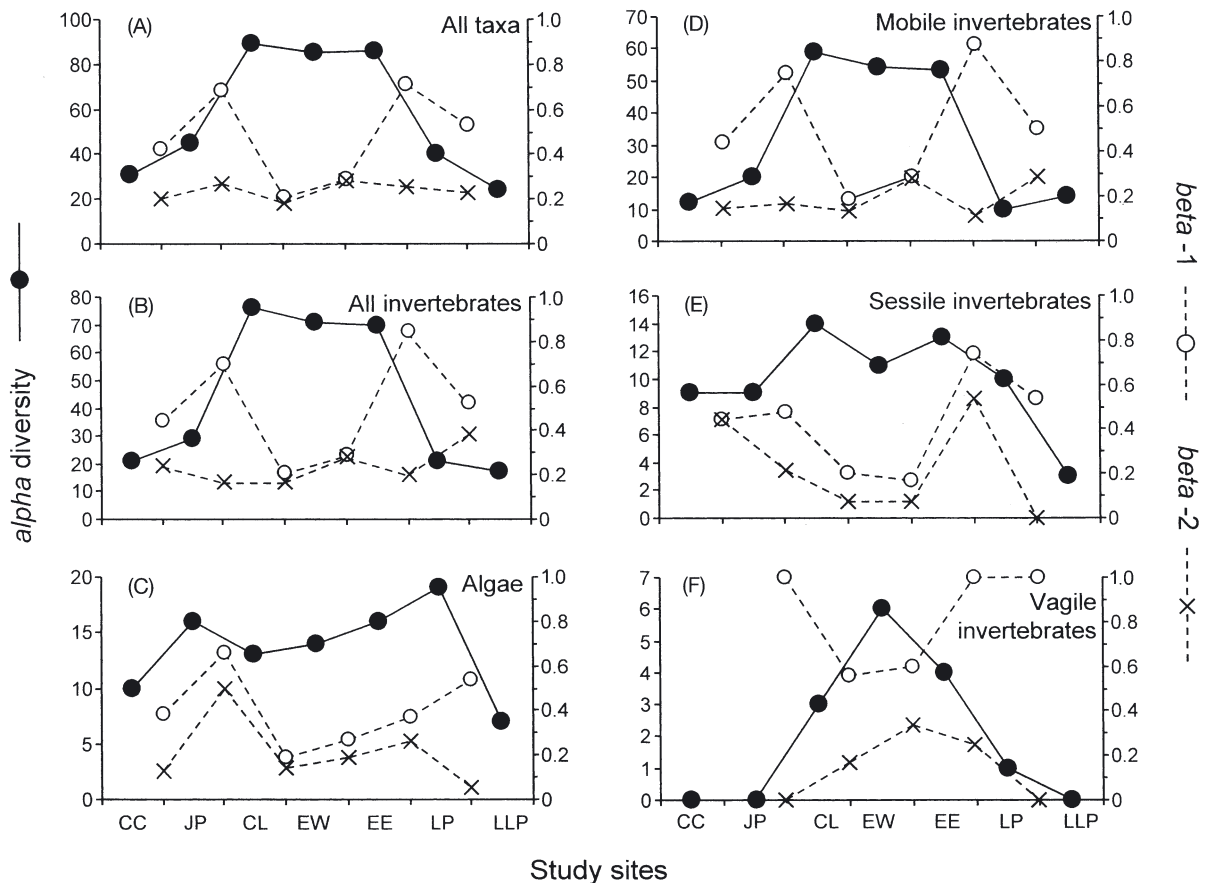

Fig. 4. α-, β-1- and β-2-diversity patterns for (A) the all taxa set and (B–F) functional groups across the geographical gradient. β-measures were calculated between pairwise adjacent sites. Sites are aligned from south to north (see Fig. 1). Abreviations: CC = Caleta El Cobre, Jp = Jorgillo Point, CL = Curva Lenguado, EW = El Way, EE = El Eden, LP = Lagarto Point, LLP = La Loberia Point

Table 2. Correlation in α-, β-1- and β-2-diversity among all taxa (see Fig. 4A) with the corresponding measure for each functional group (Fig. 4B–F). Correlation based on n = 7 sites for α-diversity and n = 6 pairwise comparison of adjacent sites for β-indices. Significance was evaluated using a Bonferroni correction: ***p < 0.001; **p < 0.01; ns: correlation was not significant

Functional group	α *r*-Pearson	β-1 *r*-Pearson	β-2 *r*-Pearson
Invertebrates	0.99***	0.98***	0.06 ns
Algae	0.35 ns	0.77 ns	0.59 ns
All taxa with:			
mobile invertebrates	0.98***	0.98***	0.34 ns
sessile invertebrates	0.84 ns	0.90 ns	0.06 ns
vagile invertebrates	0.89**	0.60 ns	0.37 ns

Effects on species frequency distribution

At the seascape scale, the species frequency distribution showed an inverse relationship between the pro-portion of plots occupied and the number of species, with a mode (48 species) at a the lower proportion and, as predicted, a total absence of species at the highest proportion of plot occupied (zero species with a pro-portion of plot occupied of 1, Fig. 5A). When species frequency distributions were separated by habitat type (habitat scaling), the distribution in *Pp*MH appeared to be multi-modal, with 3 modes, at low, mid- and high occurrence (18, 15 and 20 spp. respectively) (Fig. 5B). For species inhabiting *Pp*-LSH, the species frequency distribution also showed an inverse relationship, with modes at low and intermediate proportions of plot occupied (Fig. 5C). Significant statistical differences in species frequency distribution (p < 0.05) emerged when comparisons were done among habitat types (i.e. habitat scaling), but non-significant differences were founded in frequency distribution among functional groups within the same habitat type (i.e. organismal scaling, p > 0.05) (see Fig. 5). In the *Pp*MH a total of 109 species exhibited an increasing, and 36 a decreas-ing, trend in the plot occurrence ΔP (Fig. 6A). This dis-
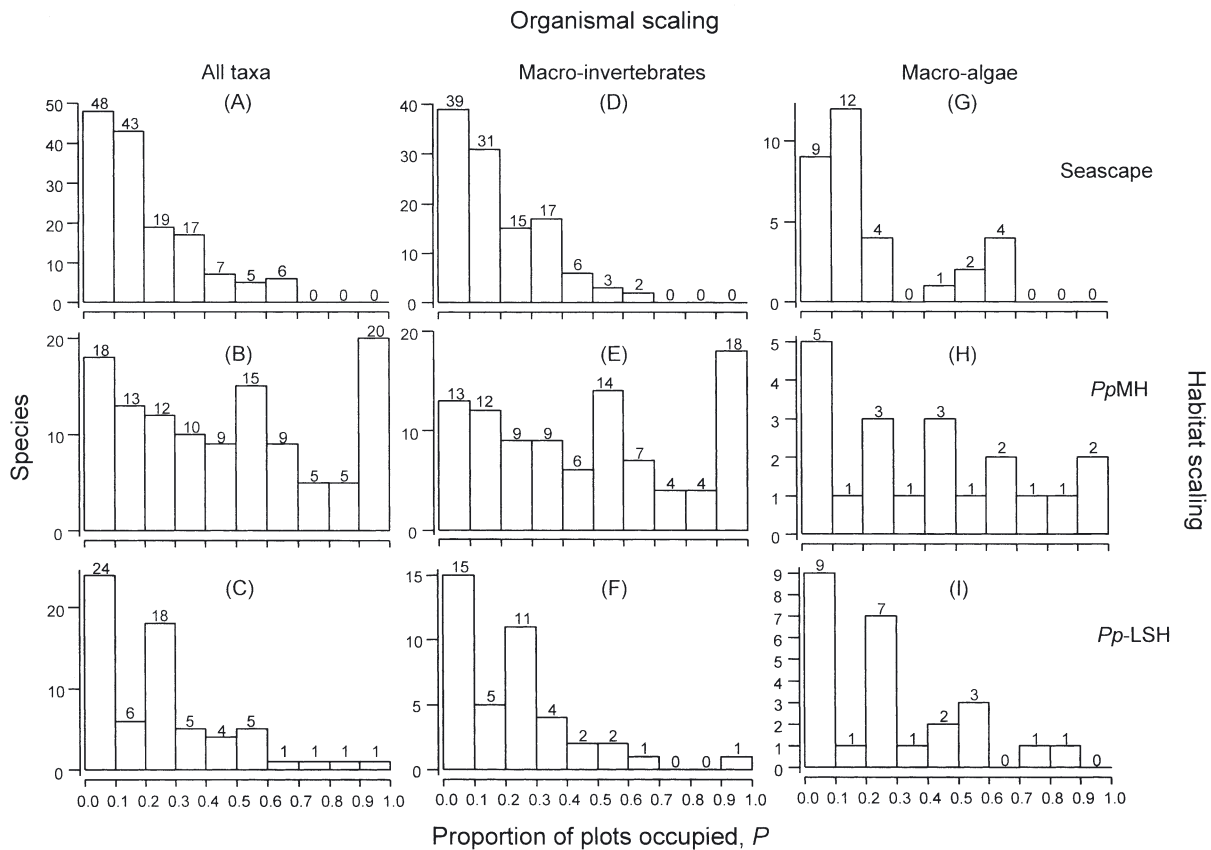

Fig. 5. Effects of habitat type (*Pp*MH = *Pyura praeputialis* matrix habitats; *Pp*-LSH = *P. praeputialis*-less substrate habitat, or rocky platforms; seascape scale = pooled habitats) and functional group (algae, invertebrates and all taxa set) on species frequency distribution. Numbers above each bar indicate the number of species. Habitat scaling corresponds to comparison of species frequency distribution the vertical axis (Kolmogorov-Smirnov test, p < 0.05 in all cases). Organismal scaling corresponds to comparison on the horizontal axis (Kolmogorov-Smirnov test, p > 0.05 in all cases)

tribution of ΔP was positive, with a median $\Delta P = 0.271$ (Wilcoxon signed-rank test, p < 0.0001). A similar pattern was found for the macro-invertebrate functional groups (Fig. 6B; ΔP median = 0.333, p < 0.0001). Here, 94 species increased their plot occurrence in *Pp*MH, and 19 species decreased in occurrence. However, for the macro-algal species (Fig. 6C), the opposite pattern was observed: median $\Delta P = -0.062$ (Wilcoxon signed-rank test, p < 0.427). The frequency distribution

of ΔP for macro-algae was significantly different from that of macro-invertebrates and for all taxa combined (Kolmogorov-Smirnov 2-sample test, p < 0.01).

DISCUSSION

Exposed intertidal rocky shores are species-rich environments, showing zonation patterns, and containing numerous invertebrate and algal taxa, where primary substrate is usually scarce (Castilla 1981, Paine & Levin 1981). In many cases, the maintenance of species diversity in these habitats has been considered the result of biotic and abiotic mechanisms, operating mainly on dominant competitors for primary substrate (Connell 1961, Paine 1966, Dayton 1971). Nevertheless, as far as species diversity goes, less importance has been given to species that generate secondary substrates (i.e. allogenic engineers, Jones et al. 1994; but see Suchanek 1986, Lohse 1993, Seed 1996, Crooks 2002, Gutierrez et al. 2003), and thereby add to habitat complexity. In this vein, the 60 to 70 km of modified mid-intertidal rocky shore inside Antofagasta Bay, Chile, represents a unique ecological situation, due to the prevalence of extensive matrices of the dominant tunicate *Pyura praeputialis* (Castilla 1998, Castilla et al. 2000, Guiñez & Castilla 2001). This alien ecosystem engineer, has recently (i.e. during the last century/ies?) invaded the Bay of Antofagasta (Castilla et al. 2002), and harbors at least 96 species of macro-invertebrates (Cerda & Castilla 2001) and 20 species of macro-algae (this paper). Cerda & Castilla (2001) reported that these species utilize the interstices, cavities and secondary substratum of the *P. praeputialis* matrices (also see Monteiro et al. 2002). Nevertheless, this set of species is also present in the regional pool, but restricted to lower intertidal environments (under boulders, in cavities, crevices, inside holdfasts of macroalgae (Vásquez & Santelices 1984), or in the subtidal zone. Thus, the large increase in species richness in matrices of *P. praeputialis* results from the creation of novel habitats in the mid-intertidal zone, and to the presence of a large number of species able to exploit the new habitat resource. This allows for an extension of the species vertical distribution and biodiversification of the mid-intertidal at the seascape scale.

The results demonstrate the important increase in the mid-intertidal rocky shore species richness at sites with *Pyura praeputialis* matrices (total richness = 116 species), in contrast to sites where *P. praeputialis* was naturally absent (total richness = 66 species) (see Table 1). Thus, at the seascape scale, encompassing both mid-intertidal habitat types, the richness was 145 species (Table 1). Monteiro et al.
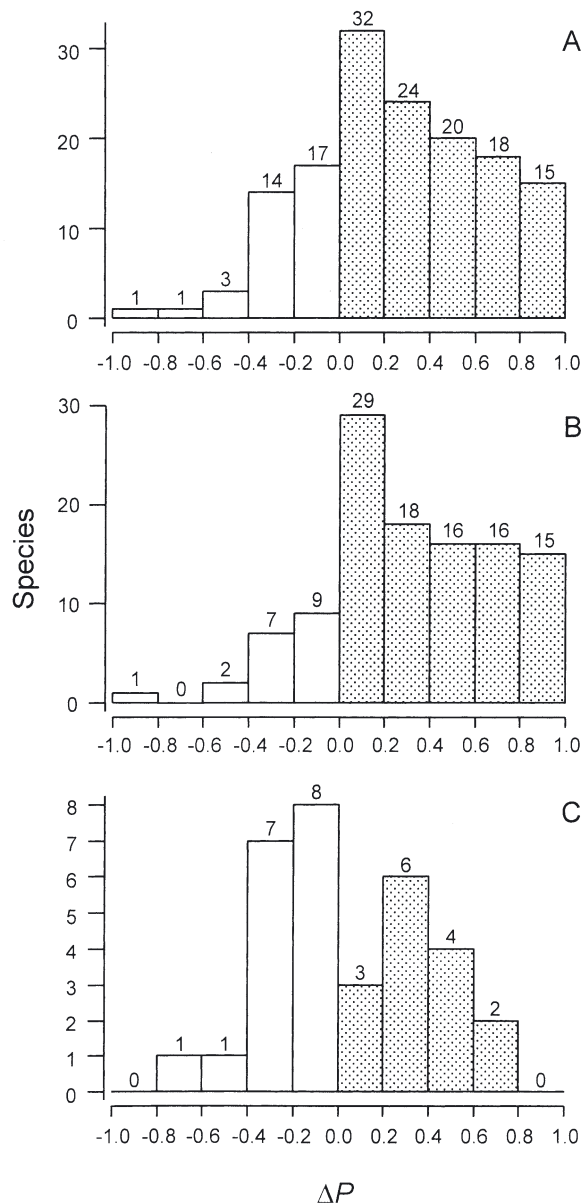

Fig. 6. Effect of *Pyura praeputialis* matrices on the proportion of plots occupied by intertidal species, ΔP, including (A) all taxa and separating for (B) macro-invertebrates and (C) macro-algae functional groups. Stippled bars: positive effect; white bars: negative effect

(2002) reported 64 taxa inhabiting mid-intertidal *P. stolonifera* (= *P. praeputialis*) clumped matrices in Australia, whereas on individual *P. stolonifera* 84 taxa were found. These differences, with respect to our findings, may correspond to geographically specific historical and evolutionary processes affecting intertidal biota differently in Australia and Chile (Paine & Suchanek 1983, Castilla & Guiñez 2000, Castilla et al. 2002). The results also suggest the significance (and generality) of the *P. praeputialis* matrices enhancing intertidal species richness (but see Monteiro et al. 2002). For instance, the trends in increased species richness in the engineered mid-intertidal habitat at Antofagasta corresponds well with the effect of landscape modifications caused by the allogenic engineer, the beaver *Castor canadiense*, in riparian ecosystems (Wright et al. 2002). However, for *C. canadiense*, researchers have attributed the observed increase in vascular plant diversity, in engineered habitats, to the increase in beaver disturbance regime, through the elimination of competitively dominant plants (see Hacker & Gaines 1997 for positive interactions in plant communities; Coleman & Williams 2002 for marine systems).

Our study demonstrated that matrices of *Pyura praeputialis* showed an increase in species richness at the local scale (α-diversity, Fig. 4). Therefore, the increase in species richness at the seascape scale does not only imply a spatial turnover in species composition between habitat types, but also reflects a significant addition of new species to the mid-intertidal rocky community that otherwise would remain excluded from this intertidal level. Cerda & Castilla (2001) reported that macro-invertebrate diversity did not show differences between sites inside Antofagasta Bay, suggesting that the effect of *P. praeputialis* matrices on the increase of species richness was similar along the coast of the bay. This conclusion is supported by the NMS ordination analysis (Fig. 2), where we found high similarity and increased aggregation of species inhabiting *P. praeputialis* matrices. The results show that several species may be excluded from the mid-intertidal seascape level in the absence of the *Pp*MH. Wright et al. (2002) reached a similar conclusion regarding the allogenic engineer *Castor canadiense*.

The species frequency distribution changed between habitats types, thereby suggesting that *Pyura praeputialis* matrices play an important role in the underlying processes determining the species abundance of mid-intertidal seascapes. The results also suggest that models describing species frequency distributions (e.g. Hanski 1982, Brown 1984) do not apply to all habitats, particularly not to engineered ones. In general, the importance of habitat scaling in species frequency distributions has not been included in the context of regional or landscape patterns of diversity induced by ecosystem engineers. Nevertheless, this has been suggested as an important factor that complicates the fitting of empirical patterns to the species distributions predicted by some models (Collins & Glenn 1997). Our results suggest that habitat scaling has a strong effect on the pattern of distribution of rocky shore mid-intertidal species in northern Chile. Monteiro et al. (2002) reported that assemblages associated with *Pyura stolonifera* in Australia can also be segregated according to habitat type (clumped matrices versus sparse individuals), adding to the generality of changes in species distribution with respect to habitat scaling in the *P. praeputialis* matrices. Numerous studies have shown that different intertidal bio-habitats are associated with different community structures (e.g. Suchanek 1986, Lohse 1993, Tokeshi & Romero 1995, Thompson et al. 1996, Crooks 1998, 2002, Crooks & Khim 1999, Thiel & Ulrich 2002, Wright et al. 2002, Gutierrez et al. 2003). One of the main distinctive patterns reported in our study is the unimodal distribution of species, showing a lack of common species at the seascape scale (Fig. 5A). This distribution has been proposed by Brown (1984) to address patterns of species abundance at very large geographic areas (>10^3 km, Collins & Glenn 1991). So far, the pattern may be considered a direct result from differences in community composition between habitat types, or the fact that engineered habitats are inhabited by species excluded from other habitats (Wright et al. 2002). Further, this result may also indicate the ineffectiveness of the sampling techniques for the studied community (Collins & Glenn 1997).

In spite of the fact that in the *Pp*MH macro-invertebrates showed higher values for occurrence than macro-algae (Fig. 6), in the analysis of these rocky shore mid-intertidal communities, organismal scaling did not emerge (Fig. 5). This suggests that the patterns in abundance and occurrence of different functional groups respond in a similar way to the habitat effect. Collins & Glenn (1997) suggested that animals might perceive their environments as heterogeneous or homogeneous based on the relationship of dispersal and body size to their environment. In our case, differences in life history traits of the main functional groups did not translate into different patterns of species distribution. This similitude, in spite of differences in composition and richness, suggests a re-organization of the rocky shore mid-intertidal community in both habitat types (Marquet et al. 1990).

The α- and β-diversity patterns found for this set of intertidal species suggests that the addition of species has a larger role in determining species composition than spatial turnover. The barnacle *Notochthamalus*

scabrosus, one of the dominant species of the mid-intertidal rocky shores (Camus & Lagos 1996), become excluded inside the *P. praeputialis* matrices, while *Jehlius cirratus* and *Ulva* spp. occur at low densities (Cerda & Castilla 2001). This suggests that sessile species, irrespective of their functional group may be negatively affected by the dominance of *P. praeputialis*. However, when comparing between habitat types, the macroalgae and sessile invertebrate groups had a similar number of species in each habitat type, whereas a high number of mobile and vagile invertebrate species inhabit almost exclusively the *Pp*MH (see Table 1). These results suggest that the sessile species may be more important in determining the spatial differentiation of the mid-intertidal communities between contrasting habitat types, while mobile and vagile macro-invertebrates may be responsible for the increase in species richness inside the *P. praeputialis* matrices.

The macro-invertebrate species reported for mid-intertidal matrices of *Pyura praeputialis* in Antofagasta, tend to be restricted to lower intertidal levels in sites where this tunicate is not present, and show cryptic behaviour (Castilla 1981, Vásquez & Santelices, 1984, Monteiro et al. 2002). Therefore, their presence in the mid-intertidal rocky shore habitats inside Antofagasta Bay necessarily requires the presence of *P. praeputialis* matrices. This suggests that the recent invasion of the alien *P. praeputialis* into Antofagasta Bay (Castilla et al. 2002) has modified, at both the local and seascape scales, mid-intertidal species richness. These results are consistent with studies suggesting that alien ecosystem engineer species which increase habitat heterogeneity also modify the distribution of the resident biota, and increase species richness (e.g. *Musculista senhousia*, see Crooks 1998, 2002, Crooks & Khim 1999). However, our conclusions are restricted to the intertidal horizontal line studied, because species added to the *Pyura* habitat stemmed from nearby deeper habitats (Cerda & Castilla 2001). This implies that the expansion of subtidal species into the intertidal may be accompanied by a vertical decrease in β-diversity.

It has been suggested that *Pyura praeputialis* is an ecosystem engineer presenting diverse ecological characteristics that effect macro-invertebrates. These include: (1) interference, by providing nursery areas for juveniles which offer protection against predation (for gastropods and decapods, including species which are exploited by intertidal food-gathers; Varas 1996, Fairweather 1991), (2) increasing the chance of survival, by reducing the risk of desiccation for species without external protection (i.e. Polychaeta, Nemertea; Cerda & Castilla 2001), (3) positive interactions among species, since more diverse communities may have enhanced ecosystem functions (Chapin et al. 1998, Stachowicz 2001), (4) coexistence mediated by spatial and temporal variation in recruitment (Chesson 1986), given that the disturbance regime and patch dynamics of *P. praeputialis* in Antofagasta may promote the coexistence of fugitive species, both inside and on top of the ascidian matrices (Alvarado et al. 2001, Monteiro et al. 2002). Future experimental work should address such issues to understand how the species diversity patterns described here and the role of the *P. praeputialis* matrices are linked by the mechanisms above.

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Appendix 1. List of macroinvertebrate and macroalgae species. Mobile: able to change spatial location; sessile: attached to primary or secondary substrata; vagile: low mobility, but not attached. Habitat type: (1) inhabits only *Pyura praeputialis* matrices; (2) only rocky substrata; (3) inhabits both

Taxonomic group	Species	Habitat type
INVERTEBRATES		
Mobile		
Nemertea: Anopla	*Lineus atrocaeruleus*	1
	Unidentified Nemertea A	1
	Unidentified Nemertea B	1
	Unidentified Nemertea C	2
Mollusca		
Polyplacophora	*Acanthopleura echinata*	1
	Acanthopleura nigra	1
	Chaetopleura peruviana	1
	Enoplochiton niger	2
	Chiton granosus	3
Gastropoda	*Caecum chilense*	1
	Calyptraea trochiformis	3
	Scurria scurra	1
	Scurria zebrina	1
	Concholepas concholepas	1
	Crepidula dilatata	1
	Eatoniella latina	1
	Fissurella cumingi	1
	Fissurella limbata	1
	Fissurella maxima	1
	Liotia cancellata	1
	Mitrella unifasciata	1
	Prisogaster niger	1
	Tegula atra	1
	Thais haemostoma	1
	Trimusculus peruvianus	1
	Collisela orbignyi	2
	Collisela plana	2
	Nodilittorina araucana	2
	Nodilittorina peruviana	2
	Scurria böhmita	2
	Scurria viridula	2
	Scurria parasitica	3
	Scurria variabilis	3
	Scurria ceciliana	3
	Fissurella crassa	3
	Scurria araucana	3
	Siphonaria lessoni	3
Annelida: Polychaeta	*Cirratulus* sp.	1
	Cirrifornia sp.	1
	Dalhousiella sp.	1
	Halosydna sp.	1
	Hemipodus sp.	1
	Hydroides chilensis	1
	Lumbrineris sp.	1
	Marphysa sp.	1
	Naineris sp.	1
	Nereis callaona	1
	Perinereis falklandica	1
	Pherusa sp.	1
	Unidentified Syllidae A	1
	Typosyllis magdalena	1
	Typosyllis sp.	1
	Pseudonereis gallapagensis	3
	Nereis grubei	3
Arthropoda: Crustacea		
Decapoda	*Betaeus emarginatus*	1
	Acanthonyx petiveri	1
	Pilumnoides perlatus	1
	Gaudichaudia gaudichaudi	1
	Pagurus edwarsii	1
	Pagurus villosus	1
	Paraxanthus barbiger	1
	Petrolisthes granulosus	1
	Petrolisthes violaceus	1
	Pisoides edwarsi	1
	Synalpheus spinifrons	1
	Acanthocyclus gayi	3
	Allopetrolisthes angulosus	3
Amphipoda	*Hyale rubra*	1
	Elasmopus chilensis	1
	Jassa sp.	1
	Aora typica	1
	Hyale media	3
	Hyale grandicormis	3
Isopoda	*Jaeropsis* sp.	1
	Dynamenella sp.	3
Tanaidacea	Unidentified Tanaidacea A	1

Taxonomic group	Species	Habitat type
Echinodermata		
Asteroidea	*Patiria chilensis*	1
	Stichaster striatus	2
	Heliasther helianthus	3
Echinoidea	*Tetrapygus niger*	3
Holothuroidea	*Patallus mollis*	1
Ophiuroieda	*Ophiactis kroyeri*	1
Sessile		
Porifera	Unidentified Porifera A	1
	Unidentified Porifera B	2
Cnidaria: Anthozoa	*Anthothoe chilensis*	1
	Unidentified Anthozoa	3
	Phymactis clematis	3
Bryozoa: Gymnolaemata	*Beania magellanica*	1
	Bugula flabellata	3
Mollusca: Bivalvia	*Chama pellucyda*	1
	Brachidontes granulata	3
	Perumytilus purpuratus	3
	Semimytilus algosus	3
Annelida: Polychaeta	Unidentified Spirorbidae A	1
	Phragmatopoma moerchi	1
Arthropoda		
Crustacea: Cirripedia	*Verruca laevigata*	1
	Austramegabalanus psittacus	2
	Balanus flosculus	2
	Balanus laevis	1
	Jehlius cirratus	2
	Notochthamalus scabrosus	2
Insecta	Unidentified Chironomidae (larvae)	3
Chordata: Ascidiacea	*Molgula ficus*	1
	Unidentified colonial ascidian	2
	Pyura chilensis	2
Vagile		
Mollusca		
Gastropoda	*Iselica chilensis*	1
Bivalvia	*Carditella tegulata*	1
	Entodesma cuneata	1
	Lasaea petitiana	1
	Mysella sp.	1
	Nucula interflucta	1
	Protothaca thaca	1
	Nucula pisum	2
ALGAE		
Chlorophyta	*Bryopsis peruviana*	1
	Chaetomorpha linum	1
	Enteromorpha compressa	1
	Cladophora sp.	2
	Ulva sp.	2
	Chaetomorpha aerea	3
	Ulva rigida	3
Rhodophyta	*Ceramiun rubrum*	1
	Gymnogongrus furcellatus	2
	Hypnea spicifera	2
	Rhodhymenia skottsbergii	2
	Rhodoglossum denticulatum	2
	Centroceras clauvulatum	3
	Chondrus canaliculatus	3
	Corallina oficinallis	3
	Gelidium chilensis	3
	Hildenbrandia lecanellieri	3
	Lithothamnion sp.	3
	Polysiphonia sp.	3
	Porphyra columbina	3
Phaeophyta	*Colpomenia phaeodactyla*	1
	Dyctiota dichotoma	1
	Petalonia fascia	1
	Glossophora kunthii	2
	Giffordia mitchelliae	2
	Ralfsia pacifica	2
	Lessonia nigrescens	2
	Endarachne binghamiae	3
	Colpomenia sinuosa	3
	Halopteris hordacea	3
Cyanophyta	*Nostoc* sp.	2
	Lyngbia confervoides	2