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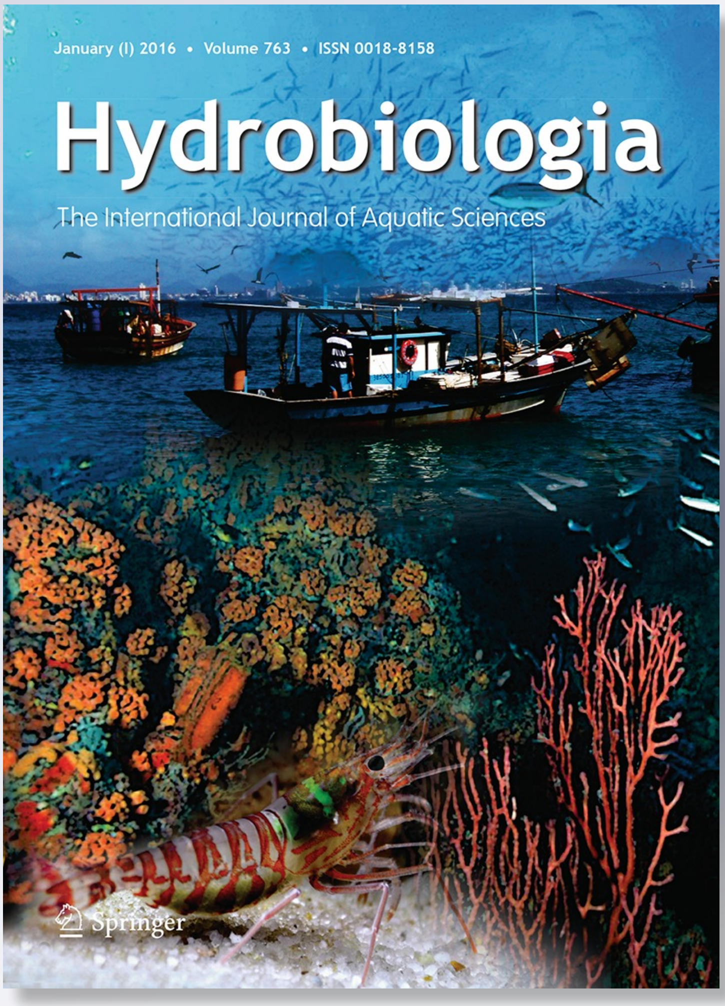

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PRIMARY RESEARCH PAPER

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Abstract Predatory control of community structure, through consumption of herbivores and subsequent positive effects on the biomass or productivity of primary producers is common in marine ecosystems. We designed an experiment to analyse the effect of large-sized predators on the development of the macrofouling assemblage of a harbour. Predation was manipulated by randomly assigning artificial substrata to three treatments: (1) exclosure cages preventing access of large predators, (2) cage controls, i.e. cages with lateral walls but without roofs, allowing predators free access, (3) uncovered panels. Substrata were submersed horizontally and upper surfaces sampled at quarterly intervals over a 1-year period. No differences in species richness were observed among treatments but diversity was lower within exclosure cages than on cage controls/uncovered panels. In sessile assemblages, structure differed between treatments: cage controls/uncovered panels were dominated by algae and associated mesoherbivores, which were scarce/absent within cages. Exposure to predators also affected the structure of mobile assemblages. The sea urchin *Pseudechinus magellanicus* (Philippi) occurred within exclosure cages but was never found on exposed panels. We conclude that large predators exert a significant effect on assemblage structure and diversity, indirectly promoting the development of filamentous algae and mesoherbivores by controlling the abundance of browsers.

Keywords Macrofouling · Harbour · Predator exclusion experiment · Patagonia · Argentina

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Introduction

The top-down control of community structure by predators (Frank et al., 2005) has been described in many ecosystems where predation on herbivore affects biomass or productivity of primary producers (Newcombe & Taylor, 2010). Examples of this process are widespread in the ecological literature. For instance, Ling et al. (2009) have shown that overfishing of a large predatory lobster may reduce the resilience of kelp beds against the threat of a sea urchin, and thus increase the risk of catastrophic shift to sea urchin barrens. Experimental manipulation of predator densities using enclosure or exclosure cages may lead to cascading changes throughout the community, thus revealing interactions and processes operating among different component species (Hall et al., 1990).

Predation may have important effects on the community structure of epibenthic assemblages on hard substrata. Brown & Swearingen (1998) showed that barnacle density on open or partially caged substrata was lower than on caged substrata, supporting the hypothesis that predators were effective at regulating barnacle abundance. Small predators of early ontogenetic life stages of epibenthic organisms may have long-lasting effects on the composition of marine epifaunal communities (Osman et al., 1992; Osman & Whitlatch, 1995, 2004). Other studies found, however, that predation had little impact on the recruitment success of taxa and did not alter community structure (Sams & Keough, 2007). Timing of predation may also be important when analysing the effect of predators on a marine encrusting assemblage, as mortality during post-settlement stages may be compensated by high recruitment rates. Predation may be an important process for determining the identity of species without changing the total number of co-occurring taxa (Vieira et al., 2012).

Foraging by fish is regarded as one of the key ecological processes shaping the structure of benthic assemblages (reviewed in Choat, 1982), although predation by fish may not always explain the observed abundances of prey (Connell, 2001). The effect of large consumers may be direct, by strongly reducing invertebrate prey abundances (e.g. Anderson & Connell, 1999), or may alter the overall community composition by indirect effects, such as modifying the abundance of smaller meso-predators (Lavender et al., 2014).

Fouling assemblages of hard substrata are composed of different guilds interacting among each other, such as primary producers, herbivores and predators. Browsing by molluscan consumers, i.e. chitons and limpets, is known to cause a substantial impact on the composition of fouling assemblages by increasing the amount of free space (Nydam & Stachowicz, 2007). For example, limpets transplanted onto steel panels successfully controlled the fouling organisms and brought down barnacle density in the Mediterranean Sea (Safriel & Erez, 1987). Similarly, sea urchins have been used to control fouling during suspended culture of bivalves (Lodeiros & García, 2004), and significantly reduced the weight of fouling on scallop shells and cultivation nets, suggesting that biological control could be an efficient method of addressing this problem in scallop cultivation (Ross et al., 2004).

The Atlantic shores of Patagonia have been historically regarded as a remote and pristine coastal region, as they are sparsely populated, with relatively few industrialised areas and with a high abundance of charismatic fauna and flora (Bortolus & Schwindt, 2007). A comprehensive survey of the exotic marine species in the SW Atlantic, however, revealed that it is populated by a variety of non-indigenous and cryptogenic species, some of which have already had a significant ecological impact (Orensanz et al., 2002). Harbours often act as a source of invasive species (Hutchings & Glasby, 2004; Bishop & Hutchings, 2011) that later may find their way towards the surrounding natural environment. Therefore, it is critical to understand the ecological processes regulating the biodiversity and structure of their encrusting assemblages. Surveys of the fouling communities of Patagonian harbours have been rarely undertaken, and the available information on the biota encrusting hard substrata is thus scarce (but see Bastida, 1973; Rico & López Gappa, 2006; Rico et al., 2010, 2012; Tatián et al., 2010). Therefore, the aim of this study has been to test whether the exclusion of large predators produced significant changes in structure, species richness and diversity of macrofouling assemblages developed on experimental substrata submersed in a Patagonian harbour.

Materials and methods

Study area

Comodoro Rivadavia harbour (Argentina, SW Atlantic) lies in San Jorge Gulf (45°51′35″S, 67°27′23″W, see Fig. 1 in Rico & López Gappa, 2006). Its physical environment was described in a previous study (Rico et al., 2010). Briefly, the range of sea surface temperatures is about 15°C, with a maximum around 19°C in February (summer) and a minimum of 4°C in August (winter). Tidal amplitudes during spring and neap tides are 6.2 and 4.3 m, respectively. Salinity shows minor variations around 33.4–33.7 psu, due to the absence of freshwater courses and the scarcity of precipitation in the area (Paruelo et al., 1998; Bertness et al., 2006). Oceanographic surveys of San Jorge Gulf confirm this pattern for the coastal zone, where the extreme values recorded for 1999 and 2000 ranged between 33.1 and 33.8 psu (Fernández et al., 2005).

Knowledge of the biota inhabiting Comodoro Rivadavia harbour is fragmentary and scattered in the literature. The intertidal assemblages are dominated by filamentous algae and the non-indigenous barnacle *Balanus glandula* Darwin, while the subtidal is characterised by the presence of spirorbid polychaetes and the herbivorous keyhole limpet *Fissurella radiosa* Lesson (Rico & López Gappa, 2006). Decapod crustaceans are common in the shallow subtidal of San Jorge Gulf. The spider crab *Eurypodius latreillii* Guérin and other brachyurans such as *Peltarion spinosulum* (White) and *Halicarcinus planatus* (Fabricius) are frequent in the benthos. The squat lobster *Munida gregaria* (Fabricius) (=*M. subrugosa* Dana) is particularly abundant in coastal waters, being a key species in the trophic web of San Jorge Gulf (Vinuesa, 2005). Subtidal herbivores are mainly represented by gastropods and sea urchins, such as *Tegula patagonica* (d'Orbigny) and *Pseudechinus magellanicus* (Philippi), respectively (Penchaszadeh et al., 2004; Teso et al., 2009). Several demersal fishes are common predators of benthic organisms. The Patagonian redfish (*Sebastes oculatus* Valenciennes), a nocturnal ambush predator, is one of the most common species in the Comodoro Rivadavia coastal area (Galván et al., 2009a, b).

Experimental design and sampling

Artificial substrata were submersed in the harbour 4 m below mean low water and were never exposed to air during low tides. They consisted of forty-eight 20 cm × 20 cm × 0.4 cm (400 cm^2) low-density polyethylene panels screwed to four 1.6 m × 1 m horizontal supporting structures of galvanised iron resting on natural rock or concrete blocks approximately 10 cm above the bottom. All four structures were deployed contiguously in a site protected from wave action by the breakwater (see Fig. 1 in Rico & López Gappa, 2006). Panels were roughened to encourage settlement/recruitment and to prevent the detachment of sessile organisms. Following Underwood & Anderson (1994), substrata were submersed simultaneously, but samples were taken independently with regard to time, i.e. each panel was not censused more than once.

Panels were randomly assigned to 3 treatments: (1) exclosure cages (E), where they were completely covered by plastic cages of 2 × 2 cm mesh size. This size was chosen so as to exclude large benthic/demersal predators although simultaneously avoiding undesired effects that could bias the interpretation of results (Como et al., 2006). The height of the cage was 7.5 cm, and both the sides and the roof were held away from the panel. As the mesh was 1.8 mm thick, the percentage of shadow cast by the mesh was very low, not exceeding 10% of the surface. (2) Cage controls (C), where they were surrounded by partial cages that covered the vertical walls but not the roof, allowing predators free access to the panel surfaces, in order to assess any possible artefacts caused by the experimental methodology (Steele, 1996). (3) No cages, where the panels were uncovered (U). The latter had been part of the experimental surfaces analysed in a previous study (see Rico et al., 2012).

Artificial substrata were submersed in summer (January 5, 2004) and were collected at quarterly intervals by randomly extracting 4 replicated panels (one from each supporting structure) at 3, 6, 9, and 12 months after starting the experiment. Only the upper surfaces were analysed. Therefore, a total of 48 sampling units were examined (3 treatments × 4 submersion lengths × 4 replicates). During the collection of samples, each panel was placed in seawater within a zip-locked plastic bag to prevent the loss of organisms. Samples were then fixed in a solution of 4% formaldehyde in seawater and later preserved in 70% ethanol. The condition of the exclosure cages and cage controls was inspected at quarterly intervals by SCUBA divers, but no damages were found, mainly due to the protected location chosen for this study.

To avoid any border effect, only the central 10 × 10 cm (100 cm^2) was analysed. Sessile organisms were identified to the lowest taxonomic level possible without disturbing their spatial distribution. Specimens occurring outside the central 100 cm^2 were collected for taxonomic purposes. Coverage of each taxon was quantified by superposing a transparent plastic sheet with a grid of 100 evenly spaced points. The same grid point was counted twice whenever we detected a species covering another species. Thus, the total cover values may be higher than 100 due to overlapping of organisms. Samples of biofilm scraped off from the substratum and examined under microscope were found to be dominated by diatoms.

The abundance of mobile organisms associated with each treatment and submersion length was also recorded.

Data analysis

The DIVERSE routine of the PRIMER package was used to calculate the richness and the Shannon–Wiener diversity index (natural logarithms) of the sessile organisms in each sample (Clarke & Warwick, 2001). Changes in species richness and the diversity index among different treatments and lengths of succession were analysed with two-way ANOVAs, with treatment (3 levels: E, C and U) and length of succession (4 levels: 3, 6, 9 and 12 months) as fixed factors. Homogeneity of variances of significant factors was verified with the Bartlett test. A posteriori comparisons for all possible pairwise combinations of treatments or submersion lengths were performed with the Tukey HSD test (Zar, 2010). In multiple pairwise comparisons, the family-wise Type I error rate was controlled by applying the Dunn–Sidak procedure (Quinn & Keough, 2002). The nominal significance level of these tests ($\alpha = 0.05$) was thus adjusted to $\alpha' = 0.017$ for treatment comparisons. All the univariate tests were done using the statistical programming language R (R Development Core Team, 2011).

Coverage data of sessile organisms were square root transformed before multivariate analyses to downweight the influence of dominant taxa. A triangular similarity matrix was obtained by applying the Bray-Curtis index. Similarities among samples belonging to different treatments were graphically displayed with non-Metric Multidimensional Scaling (nMDS) (Clarke & Warwick, 2001). Lists of species discriminating between pairs of treatments were obtained with the SIMPER routine of the PRIMER package (Clarke & Warwick, 2001). The abundance of mobile species was also square root transformed before multivariate analysis. The null hypotheses of no differences in assemblage structure of sessile biota or mobile fauna among treatments or submersion lengths were tested using PERMANOVA (Anderson, 2005).

As the temporal changes observed in this fouling assemblage were already analysed in a previous article dealing with succession (Rico et al., 2012), this factor will not be discussed in detail during the present study.

Results

Sessile biota

The fouling assemblage was mainly composed of filamentous algae such as *Polysiphonia* aff. *abscissa* J.D. Hooker & Harvey and *Ulva* spp. (formerly *Enteromorpha* spp., see Hayden et al., 2003), while ascidians, bryozoans and spirorbid polychaetes (*Romanchella scoresbyi* (Harris)) were very scarce and barnacles were absent (Fig. 1, Online Resource 1, see also Rico et al., 2012).

Sessile assemblages held in average 5.4 species, regardless of predation regime (two-way ANOVA, $F_{2,\ 36} = 0.681$, $P = 0.513$) or submersion length ($F_{3,\ 36} = 0.327$, $P = 0.806$; interaction: $F_{6,\ 36} = 0.521$, $P = 0.788$) (Fig. 2). However, the high coverage of biofilm (Online Resource 1) resulted in a lower diversity in surfaces protected against predators (E) than in cage controls (C) and uncovered panels (U) ($F_{2, 36} = 7.942$, $P = 0.001$; Tukey HSD, E vs. U: $P = 0.013$, E vs. C: $P = 0.002$, U vs. C: $P = 0.725$), regardless of submersion lengths ($F_{3,\ 36} = 0.289$, $P = 0.833$; interaction: $F_{6,\ 36} = 1.014$, $P = 0.432$) (Fig. 2).

Exposure to predators and length of succession affected the sessile assemblage structure (PERMANOVA, treatments: $F_{2,\ 36} = 9.533$, $P = 0.001$, submersion lengths: $F_{3,\ 36} = 4.067$, $P = 0.001$). The exclusion effect was found to be consistent across submersion lengths (interaction: $F_{6,\ 36} = 1.032$, $P = 0.414$). Coverage values of algae were consistently higher on U/C than within E. Tubicolous polychaetes tended to have higher coverage within E than on U/C. On the other hand, ascidians and bryozoans/hydrozoans were unaffected by predation (Fig. 1). Hence, differences in assemblage structure between E and U/C were highly significant (PERMANOVA, pairwise contrasts, E vs. U: $t = 3.584$, $P = 0.001$, E vs. C: $t = 2.907$, $P = 0.001$). This can be seen in the nMDS ordination, where the samples corresponding to E tend to cluster towards the right and lower sides of the plot (Fig. 3). The species that most contributed to significant differences in community structure between U/C and E were

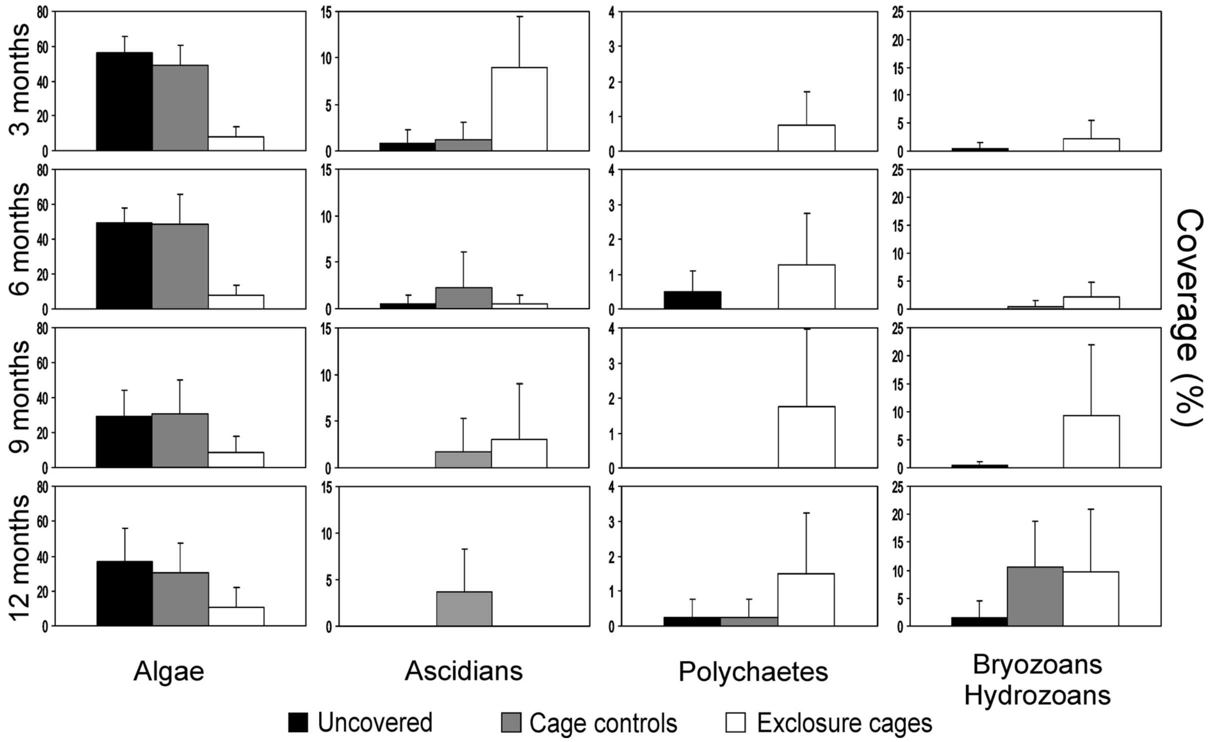

Fig. 1 Coverage (%) of algae, ascidians, polychaetes and bryozoans/hydrozoans for different treatments and submersion lengths. *Vertical lines* represent SDs

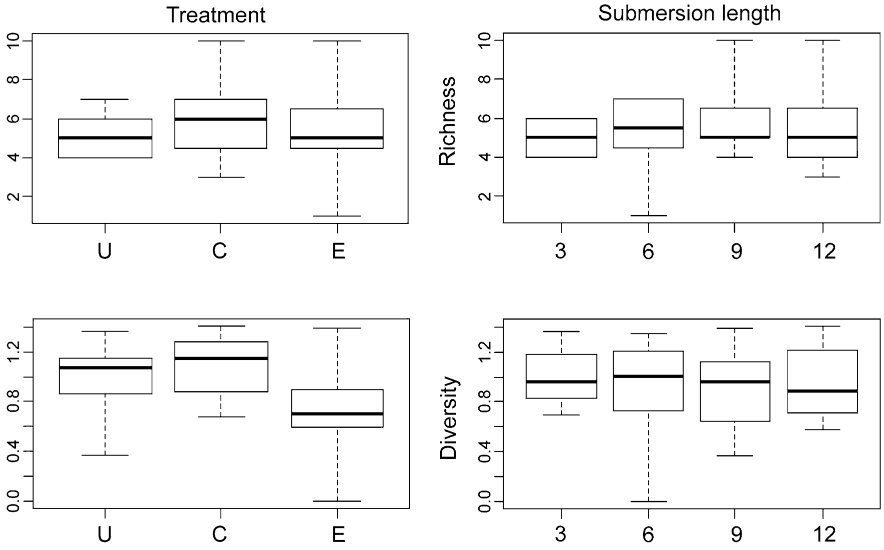

Fig. 2 Species richness and diversity (Shannon–Wiener index) for different treatments (*U* uncovered, *C* cage controls, *E* exclosure cages) and submersion lengths (months). *Box plots* indicate the median, first and third quartiles and range of each distribution

filamentous algae (SIMPER routine, Table 1). While assemblages exposed to large predators (U/C) were dominated by filamentous algae as *Polysiphonia* aff. *abscissa*, *Ulva* spp. and *Ectocarpus* sp., assemblages protected against predators (E) were mostly occupied by a layer of biofilm (Table 1). Uncovered panels did not

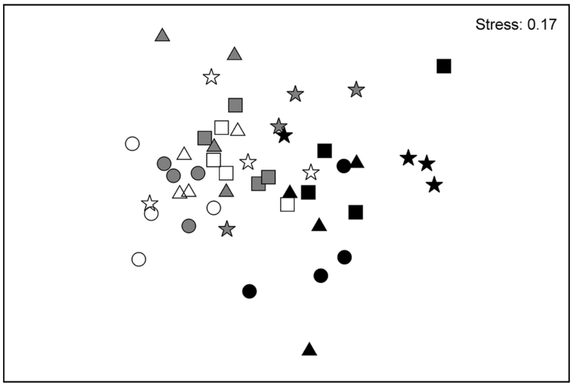

Fig. 3 nMDS ordinations of fouling assemblages. *Black* exclosure cages. *Grey* cage controls, *Empty* uncovered panels. *Symbols* indicate submersion lengths: 3 months (*circles*), 6 months (*triangles*), 9 months (*squares*) and 12 months (*stars*)

differ from cage controls (PERMANOVA, pairwise contrast, U vs. C: $t = 1.176$, $P = 0.232$) (Fig. 3).

Mobile fauna

Exposure to predators and length of succession also affected the structure of the mobile assemblage (PERMANOVA, treatments: $F_{2,\ 36} = 2.033$, $P = 0.011$, submersion lengths: $F_{3,\ 36} = 3.219$, $P < 0.001$). The exclusion effect was also consistent across submersion lengths (interaction: $F_{6,\ 36} = 1.232$, $P = 0.143$). Mesoherbivores (amphipods and isopods) were found exclusively on U/C but not within E at a given submersion length (Table 2). The small crab *H. planatus* was also found on these surfaces. They were associated with the presence of turfs formed by the filamentous seaweeds *Polysiphonia* aff. *abscissa* and *Ulva* spp. On the contrary, relatively large and voracious herbivores, such as the gastropods *T. patagonica* and *Fissurellidea patagonica* (Strebel), and the sea urchin *P. magellanicus*, were present on surfaces protected from large predators, but not on exposed panels (Table 2). Consequently, differences in assemblage structure were significant between U and E (PERMANOVA, pairwise contrast, $t = 1.526$, $P = 0.013$), but not between U and C ($t = 0.744$, $P = 0.831$). The probability associated with the pairwise contrast between C and E was low but did not reach statistical significance ($t = 1.457$, $P = 0.030$).

Discussion

Large predators exerted a significant effect on the fouling assemblage of Comodoro Rivadavia harbour, indirectly promoting the development of a filamentous algal turf and its associated fauna of small mesoherbivores by limiting the abundance of benthic browsers. Large-sized browsers such as the sea urchin *P. magellanicus* were probably directly responsible for the disappearance of the algal turf on surfaces protected from predators. It is not clear whether sea urchins and herbivorous gastropods recruited within the cages or migrated and found refuge there when they were small-sized juveniles, but they were not eliminated by predators within the exclosure cages.

Table 1 SIMPER test for significant contrasts between treatments

Species	Average abundance Uncovered	Average abundance Exclosure cages	Average dissimilarity	Contribution %	Cumulative contribution %
Polysiphonia aff. *abscissa*	28.06	3.25	10.92	23.73	23.73
Ulva spp.	6.56	0.63	5.58	12.12	35.86
Biofilm	47.19	67.00	5.49	11.93	47.78
Ectocarpus sp.	6.13	1.19	5.37	11.67	59.45
Species	Average abundance Cage controls	Average abundance Exclosure cages	Average dissimilarity	Contribution %	Cumulative contribution %
Polysiphonia aff. *abscissa*	18.50	3.25	7.74	17.42	17.42
Ulva spp.	13.13	0.63	7.46	16.78	34.20
Ectocarpus sp.	5.00	1.19	4.60	10.35	44.55
Biofilm	50.63	67.00	4.57	10.29	54.84

Species lists were truncated whenever cumulative percentage exceeded 50%

Table 2 Abundance of mobile species (mean ± SD) found exclusively on uncovered panels (U)/cage controls (C) or exclosure cages (E) at a given submersion length

Species	Group	3 months	6 months	9 months	12 months
Mobile species found exclusively on U/C, but not within E at a given submersion length					
Atyloella magellanica (Stebbing)	Amphipoda			2.00 ± 2.56	
Caprella sp.	Amphipoda		0.13 ± 0.35	0.13 ± 0.35	
Corophium sp.	Amphipoda			2.13 ± 2.10	
Gondogeneia cf. *dentata* Alonso	Amphipoda	1.13 ± 1.46			
Gondogeneia sp.	Amphipoda		0.38 ± 1.06	0.63 ± 1.19	
Haplocheira barbimana robusta K.H. Barnard	Amphipoda	0.63 ± 1.19	0.13 ± 0.35	0.88 ± 1.73	
Jassa alonsoae Conlan	Amphipoda			1.13 ± 1.13	
Paradexamine nana Stebbing	Amphipoda		0.13 ± 0.35	0.75 ± 0.89	
Paramoera sp.	Amphipoda	0.50 ± 0.93		1.75 ± 3.41	
Exosphaeroma sp.	Isopoda	1.13 ± 2.23	0.13 ± 0.35		
Eurypodius latreillii Guérin	Decapoda				0.38 ± 0.74
Halicarcinus planatus (Fabricius)	Decapoda	0.13 ± 0.35	0.25 ± 0.71		
Potamilla sp.	Polychaeta		0.13 ± 0.35		
Lasaea sp.	Bivalvia	0.25 ± 0.71	0.50 ± 0.76		
Crepidula sp.	Gastropoda			0.13 ± 0.35	
Nacella deaurata (Gmelin)	Gastropoda				0.50 ± 0.93
Siphonaria lessoni Blainville	Gastropoda	0.25 ± 0.46	0.25 ± 0.46		
Plaxiphora aurata (Spalowsky)	Polyplacophora			0.13 ± 0.35	
Mobile species found exclusively within E, but not on U/C at a given submersion length					
Achelia sp.	Pycnogonida				0.25 ± 0.50
Eurypodius latreillii Guérin	Decapoda			0.25 ± 0.50	
Potamilla sp.	Polychaeta			0.25 ± 0.50	
Crepidula sp.	Gastropoda	0.25 ± 0.50			0.50 ± 0.58
Fissurellidea patagonica (Strebel)	Gastropoda			0.25 ± 0.50	
Tegula patagonica (d'Orbigny)	Gastropoda			1.00 ± 1.41	0.50 ± 0.58
Trophon geversianus (Pallas)	Gastropoda				0.50 ± 0.58
Plaxiphora aurata (Spalowsky)	Polyplacophora				0.25 ± 0.50
Pseudechinus magellanicus (Philippi)	Echinoidea		1.00 ± 1.15	1.00 ± 2.00	1.00 ± 1.41
Helcogrammoides cunninghami (Smitt)	Pisces			0.25 ± 0.50	

Values are expressed as number of individuals per sampling unit

The absence of large browsers on panels exposed to predators made possible the development of an assemblage of filamentous seaweeds. This structurally complex habitat exerted a positive effect (i.e. facilitation, Stachowicz, 2001), providing refuge against demersal predators for a variety of juvenile or small crabs, amphipods and isopods found on the exposed experimental surfaces (Table 2). Filamentous seaweeds belonging to the genera *Polysiphonia*, *Ulva* and *Ectocarpus* may be regarded as autogenic engineers (sensu Jones et al., 1994, 1997), as they give shelter and provide a suitable physical environment for various organisms via their tissues. The association between benthic macroalgae and epiphytal amphipod communities has been the subject of many studies and may be influenced by seaweed complexity (Russo, 1990; Kelaher, 2002), biodiversity (Bates & DeWreede, 2007), and the identity of the host species (Bates, 2009), among other factors.

This study found that changes in species richness among treatments differing in predation pressure were non-significant. A 2-yr exclusion experiment in a community heavily grazed by the sea urchin *Evechinus* resulted in an increase in cover of ephemeral algae and coralline turf algae, but no basic change in species composition (Ayling, 1981). Similarly, Vieira et al. (2012) showed that predation can produce significant changes in community composition, without changing the total number of co-occurring taxa. In our study, the persistence of browsers in exclosure cages and its absence in unprotected surfaces changed the proportion of the fouling taxa, mainly filamentous algae and biofilm, without changing the overall species richness.

At local scales, consumers may prevent the monopolisation of space and hence increase diversity by predating on the dominant competitor (Paine, 1966; Parrish & Saila, 1970; see also Dürr & Wahl, 2004 for a modern example). In the present study, however, the benthic browsers found within cage exclosures brought about the opposite effect, i.e. they were associated with decreased levels of diversity, which was not due to a decrease in species richness, but to an increase in the coverage of biofilm. Although sea urchins, as well as other herbivores, may be able to browse on biofilm, apparently they were not capable to remove it completely from the panel surface.

Our results suggest that *P. magellanicus* is one of the main herbivores responsible for the control of filamentous algal turfs in this fouling assemblage. A comprehensive study encompassing populations occurring along 17° of latitude on the Argentine coast showed that this sea urchin is omnivorous, its diet depending mostly on the biotic community in which they occur (Penchaszadeh et al., 2004).

Three species of fish were frequently observed by SCUBA divers around our experimental devices (G. Durbas, pers. comm.): the Patagonian redfish (*S. oculatus*), the Cunningham's triplefin (*Helcogrammoides cunninghami* (Smitt)) and a thornfish, *Bovichtus argentinus* MacDonagh. *S. oculatus* has been reported as one of the most common fishes in the Comodoro Rivadavia coastal area (Galván et al., 2009b). It is a nocturnal ambush predator that feeds on organisms moving near its refuge (Galván et al., 2009a). In northern Patagonia, it mainly consumes small reef fishes, squat lobsters, mantis shrimps and crabs (Sanchez & Prenski, 1996; Barrientos et al., 2006; Galván et al., 2009a). As sea urchins were never observed among the food items analysed and gastropods were rare in its diet (Barrientos et al., 2006), the available data suggest that the Patagonian redfish probably used our supporting structures as a refuge but was not responsible for the absence of large herbivores on the exposed panels. Egg masses laid by *H. cunninghami* within cages showed that the 2 cm meshes used in our study were no obstacle for this small triplefin. A food web analysis performed in a Chilean intertidal fish assemblage evidenced that this sit-and-wait microcarnivore mainly forages on amphipods and copepods (Muñoz & Ojeda, 1997). The diet of *B. argentinus* is presently unknown. Its feeding habits, however, might be similar to those of *B. chilensis* Regan, a carnivore that forages on shrimps, crabs, amphipods, copepods and isopods in the Chilean intertidal (Muñoz & Ojeda, 1997).

Therefore, the literature on the feeding habits of the fish species seen in the vicinity of our study site does not allow us to reach a sound conclusion about which predators may be responsible for the effects found in this assemblage. Further studies involving direct observations by divers or feeding trials of animals kept in aquaria will be necessary to elucidate this issue.

Conclusion

Large predators exert a significant effect on the upper surfaces of experimental substrata submersed in a Patagonian harbour, indirectly promoting the development of filamentous algae and their associated mesoherbivores by controlling the abundance of benthic browsers. This study provides evidence on the critical role played by large-sized predators in determining the structure of an epifaunal harbour assemblage and highlights the advantages of incorporating an experimental approach to fouling studies.

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