Effects of sympatric predatory crabs *Romaleon polyodon* and *Cancer plebejus* (Decapoda, Brachyura, Cancridae) on sublittoral macrobenthic communities

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ABSTRACT

Although large crabs are recognized as important sediment disturbers influencing the structure of benthic communities, the role of dominant predatory crabs in soft-bottom habitats along the Humboldt Current Ecosystem, remains largely unknown. A field study was conducted, hypothesizing that the digging activity of these predators disturbs the habitat thereby leading to a reduction in individual abundance, biomass and species richness; these changes result in a modified structure of macrobenthic communities. A directed sampling (crab pits vs. reference areas) showed significant reductions in total abundances in pits compared to reference areas, but no differences were observed in taxonomic richness or benthic biomass. Short-term cage experiment showed significant decreases in total abundance and biomass of macroinvertebrates in predator inclusion treatments compared to exclusions and controls. In consequence, our results confirmed that burrowing activities and the generation of small disturbed sediment patches influence the community structure. These results highlight the importance of large cancrid crabs in soft-bottom habitats, where their modification of the physical configuration of the sediment affects community structure over small spatial scales. Crabs are thus an important source of spatial heterogeneity of the sea-floor landscape. This ecological role must be considered in management strategies of the extensive artisanal fishery for these crabs, as current evidence is showing increasing populations of intermediate predators (like cancrid crabs) in many benthic habitats in response to the depletion of top predators.

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1. Introduction

Benthic predators, such as large crustacean species, are very important creators of small patches of disturbed sediment as they stir up the bottom during feeding and burrowing activities (Hall et al., 1991, 1993; Thrush, 1986). A single predator can create small patches which are recolonized via immigration of post-larval and adult colonizers (Pacheco et al., 2012; VanBlaricom, 1982), while large-scale disturbances (e.g., hypoxia, ice scour, storms) generate large disturbed areas where biota recovery is mediated primarily via larval settlement (Lenihan and Micheli, 2001). Therefore, disturbed patches are predicted to differ in terms of macrobenthic community structure depending on predator abundance and the intensity and frequency of their disturbing activities. Predators may influence the structure of their habitat community by (1) physically modifying the habitat (bioturbation), (2) consuming either a selected prey or a wide spectrum of them, (3) triggering escape responses of their prey, and (4) provoking immigration into the disturbed patch by opportunistic species. Even though these effects may be intuitively recognized,

reviews documenting disturbance and recolonization processes suggest that these different types of biological effects are not always easy to detect (Ólafsson et al., 1994; Thrush, 1999). Studies about the role of predators influencing benthic community structure, particularly those using exclusion/inclusion cage experiments have also suggested that (1) predation is not generally an important process directly structuring soft-sediment communities, and/or (2) complex interactions are common in these systems (e.g., confounding natural seasonal variations of predator densities and their disturbing activities), which may preclude the detection of significant predator effects (Ólafsson et al., 1994; Thrush, 1999). This type of variability found in predation studies makes the role of predators in structuring benthic communities an important topic of research.

Predators such as large crabs of the Cancridae family are important megafaunal components of sedimentary ecosystems. Crabs influence the structure of macrobenthic communities by digging pits when foraging for food, or when burying for resting in the sediment (Hall et al., 1991; Thrush, 1986). Macrobenthic communities in pits created by crabs usually have low species richness but variable species abundances, with some taxa showing drastic reductions and others no changes or even higher densities in pits compared to undisturbed sediments (Hall et al., 1991, 1993). As crabs are constantly digging the sea

floor they are important sources of habitat heterogeneity thereby influencing the patchy distribution of soft-bottom communities.

There is an increasing interest in understanding the effects of large predatory crabs in benthic ecosystems because fisheries are intensively removing predators from upper (e.g., Baum and Worm, 2009; Boudreau and Worm, 2012; Heithaus et al., 2008; Smith et al., 2011) and intermediate (Eriksson et al., 2011) trophic levels. The effects of the removals are reflected in drastic cascade changes in the trophic structure and unpredictable fluctuations in community structure (Eriksson et al., 2011). In some ecosystems the reduction of top predators have promoted the release of intermediate predators (e.g., crabs) that have led to the development of fisheries on them (Quijón and Snelgrove, 2005a,b), while in other ecosystems such as in the Humboldt Current Ecosystem (HCE), where fishery pressures occurs at nearly all trophic levels, the consequences of removal of predators have been poorly documented (e.g., Moreno, 2001; Ory et al., 2012).

In soft-bottom sublittoral habitats along the coast of Peru and Chile (HCE) the hairy crab *Romaleon polyodon* (synonymous of *Cancer setosus* Molina, 1782 and *Cancer polyodon* Poeppig, 1836), and the queen crab *Cancer plebejus* (synonymous of *Cancer coronatus* Molina, 1782) (see Ng et al., 2008; Schram and Ng, 2012; Schweitzer and Feldmann, 2000, for an update on the systematics and nomenclature of the decapod family Cancridae) are conspicuous megafaunal components of the sea floor (Gutiérrez and Zúñiga, 1976; Muñoz et al., 2006; Wolff and Soto, 1992). Spatial overlap exists between large-sized adults of both species but different population dynamics likely allow the co-existence in sandy and muddy sediments in relatively high abundances (Jesse and Stotz, 2002). *R. polyodon* is a nocturnal predator (Wolff and Cerda, 1992) feeding on a wide variety of prey organisms (Cerda and Wolff, 1993), although selective consumption occurs depending on prey availability and habitat characteristics (León and Stotz, 2004). No information about the feeding ecology of *C. plebejus* is available. Although these species conspicuously disturb the sea floor (see Fig. 1), the impacts of these predatory species on the structure of soft-bottom communities are not well known (but see Ortiz, 2008 for effects on some megafaunal components). This is surprising, taking into account the vast literature about the role of large crustaceans (and other bottom predators) shaping the diversity and structure of communities through feeding, disturbance and bioturbation in sedimentary habitats elsewhere (e.g., Boudreau and Worm, 2012; Como et al., 2004; Gee et al., 1985; Hall et al., 1991, 1993; Quijón and Snelgrove, 2005a,b; Reise, 1977, 1978; Thrush, 1986, 1999). In addition, *R. polyodon* and *C. plebejus* together with other large Cancridae and Xanthidae are heavily exploited by artisanal fisheries. In Chile from 1991 to 2007 the landings of *R. polyodon* averaged more than 500 t with a maximum of 1320 t in 1994 and a minimum of less than 100 t in 2003, while an average of 120 t with a maximum of more than 400 t in 1995 and a minimum of less than 10 t in 2003 have been reported for *C. plebejus* (Aedo et al., 2009).

In this study, we conducted a field sampling and an exclusion/ inclusion experiment aiming to determine the immediate effects of abundant crab predators (*R. polyodon* and *C. plebejus*) on the soft-bottom macrobenthic community structure. We predicted that patches disturbed by large crab predators will differ from areas not disturbed by these species, because the reduction in species abundance and species richness in disturbed patches leads to a changed community structure.

2. Materials and methods

2.1. Study area

This study was conducted from late July to early September 2011 (during austral winter) at a sublittoral site on the coast of Antofagasta in northern Chile. This region is characterized by strong upwelling, where cold waters with high nutrient and low oxygen contents rise to
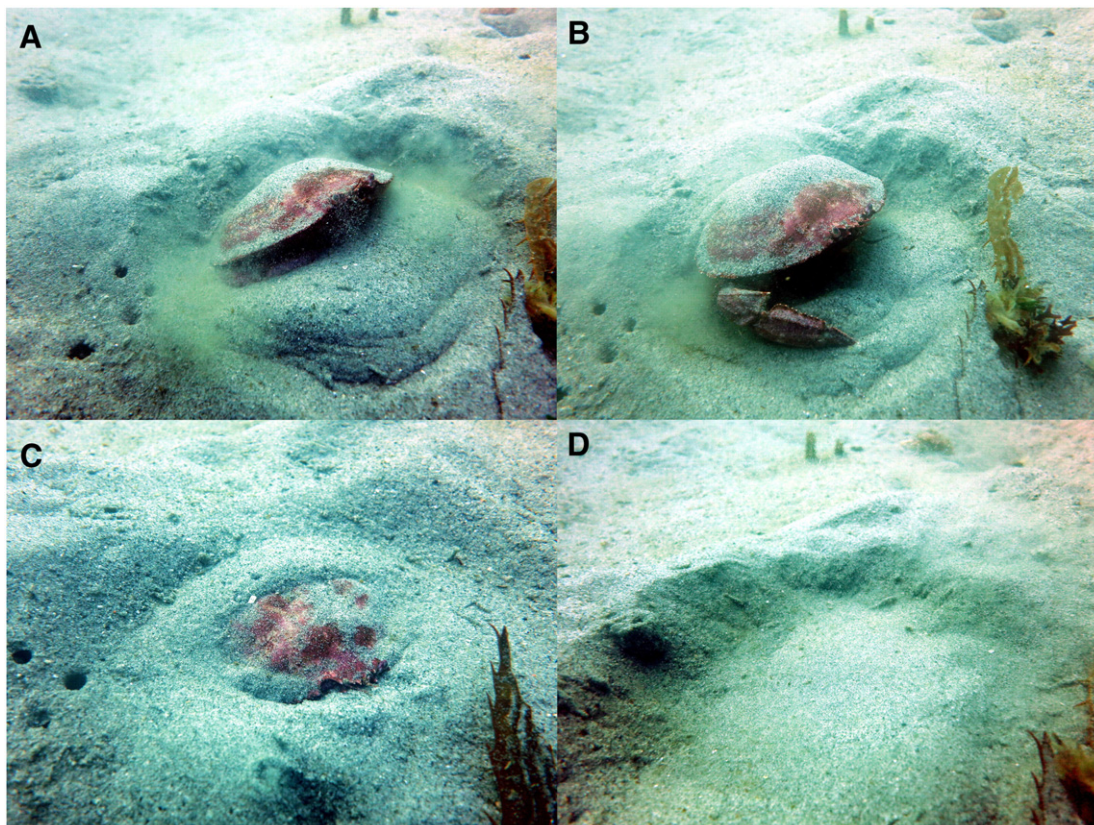

Fig. 1. *Cancer plebejus* disturbing sediment: A, crab lifting sediment; B, detail of the claw protruding into the sediment; C, buried crab; D, pit left by the crab.

the surface (Pacheco et al., 2011; Piñones et al., 2007). The study site (Bolsico: 23°28′S; 70°36′W) is located in a small cove at the southern part of the Península Mejillones. A previous study (Pacheco et al., 2012) and many hours of diving observation at this site suggested that large *R. polyodon* and *C. plebejus* are the most common predators, occurring sympatrically in sufficiently high abundance to create extensive, disturbed areas. No other bottom predators, such as large flat fish or rays, were observed in sufficient quantities to be considered important sea-floor disturbers. The bottom current velocity 0.5 m above the sediment surface was measured using an acoustic current meter (Falmouth Scientific 2-Dimensional Acoustic Current Meter, model 2D-ACM) placed 50 cm above the bottom and exposed for 4 h (10 am to 2 pm) in early August 2011, during five consecutive days. The field work, including sampling and manipulative inclusion/exclusion experiments were conducted from July 21st until September 5th 2011.

2.2. R. polyodon and C. plebejus density estimates

To estimate the densities of both species, two scuba divers searched for crabs along transects deployed in a "Y" shape with a 120° angle between all legs. Each leg was 50 m long and 3 m wide, thus covering an area of 100 m². Divers identified and counted crab species by swimming close and in parallel position to each other, maintaining themselves a half meter of distance above the bottom. Each diver visually surveyed a 1 m wide strip to the side of the transect line, and thus both divers covered a width of 2 m along the transect. Totally buried and/or semi-buried crabs were lifted out from the sediment in order to correctly identify the species. Each diver annotated the numbers of individuals for each species on acrylic boards. Four transects were positioned at four locations randomly selected within the study area at a depth of 9 m. The final average density of crabs was expressed as ind. m^{-2}.

2.3. Directed sampling

In the study area the pits left by the crabs either by burrowing or feeding were visually identifiable but it was difficult to determine when the pit was made, thus different colonizers may be using the disturbed patch depending on the time when the pit was created. To avoid this temporal variability, we searched for large-sized crabs (~15 cm width carapace) of both species, once a crab was detected (either burrowed or scavenging) it was carefully lifted from the sediment by a diver taking the animal from the posterior ventral part and depositing it in a plastic bag. The resulting pits left by the crabs (which are similar in shape and depth to those observed in the surrounding sediment) were sampled using a core (10 cm diameter and 15 cm high) that was inserted 10 cm into the sediment. In addition, areas without crabs (i.e., references) were sampled with the same core but avoiding those patches with signs of crab disturbance. A total of ten crab pits and ten reference areas were sampled. The data for both species were pooled because the pits made by large individuals (~15 cm carapace wide) of the two crab species are very similar in elliptical area (~1200 cm²) and depth (~5 cm, based on the measurement of 10 pits of each species). Besides, both species are morphologically similar, particularly in chela size in female and male individuals.

Sediment samples were deposited in labeled plastic bags. On board, the sediment sample containing macrobenthic organisms was fixed with a 10% formalin solution stained with Rose Bengal. Thereafter, the crabs were sacrificed by introducing the formalin solution into the stomach using a syringe. In the laboratory, sediment samples were washed and sieved through a 0.5 mm mesh with a 0.3 mm mesh underneath, in order to retain very small organisms. Biomass (dry mass in grams) of the different taxa was obtained after oven drying for two days at 60 °C, then organisms were weighed with a digital scale (0.001 g precision).

2.4. Stomach content analysis

In the laboratory crabs were sexed and measured (i.e., carapace length and width) with a digital caliper of 0.01 mm precision. The wet mass of crabs was measured with an analytical scale (0.01 g precision). Animals were dissected and entire stomachs extracted. The weight of the stomach content was estimated as the difference between the empty and full stomach weight. The content was identified to the lowest taxonomic level possible, counted as item and weighed (wet weight in g).

2.5. Cage exclusion/inclusion experiment

To describe the isolated effect of the crabs on the structure of the macrobenthic communities, a cage exclusion/inclusion experiment was conducted. The literature suggests that predicted effects such as increases in abundance of macrobenthos in plots where predators were excluded with cages, often cannot unequivocally be attributed to the absence of predators and it could also be due to an artifact effect. For example, cages reduce flow, especially in shallow areas with strong currents, creating conditions that enhance sedimentation of organically richer particles, thus providing comparatively more food to benthic organisms (see review in Ólafsson et al., 1994). In addition, flow reduction inside the cages may favor larval settlement. Thus, in order to minimize the risk of potential cage artifacts, we have followed the recommendations by Ólafsson et al. (1994): (1) cage experiments must be conducted in very low current locations (e.g., deep or sublittoral areas), (2) predator inclusion treatments could be used for isolating the effect of the predator, (3) predator densities inside inclusion treatments should not exceed the density observed in the natural environment, and (4) the experiment should be done at short temporal intervals, thus avoiding the variability induced by cage artifacts occurring during long-term exposure. Therefore, a short-term experiment was conducted in a low flow site including the following treatments: exclusion cage (a metallic cube of 1 m side, 1 m² area and 50 cm high covered with a 0.5 cm black mesh), inclusion cage (three large crab individuals, ~15 cm carapace width, two *C. plebejus* and one *R. polyodon* inside the cage according to the observed *in situ* aggregations, see Results section), partial cage (half covered cage at the side and top), control (the cage with no mesh covering) and reference which were samples from the natural surrounding areas (Fig. 2).

The experiment was run for four days and then sediment samples were collected from the center of each experimental plot using the same core as in the directed sampling evaluation. Three replicates per treatment were used and the whole experimental setup was repeated three consecutive times, adding up to a total of 9 replicates per treatment. Cages were moved to undisturbed sediments for each of the consecutive runs. Each inclusion cage received three new crabs of the same size during each repetition. In addition, the crabs used in the inclusion experiment were collected for further stomach content analysis.

2.6. Statistical analysis

Number of taxa, total abundance and dry biomass were used as univariate response variables and community structure (based on distance matrices calculated from the abundance) was used as multivariable data for comparisons. In the directed sampling, univariate data were analyzed using one-way ANOVA using "crab presence" (crab pits vs. references) as fixed factor. Data were log-transformed when normality was not achieved. To explore dissimilarities/similarities between community structures (based on the Bray–Curtis distance matrix using taxa abundance and biomass), Canonical Ordination Plots (COP) were constructed. To test for significant effects in the multivariable data set, PERMANOVA was performed considering "crab presence" as fixed factor.
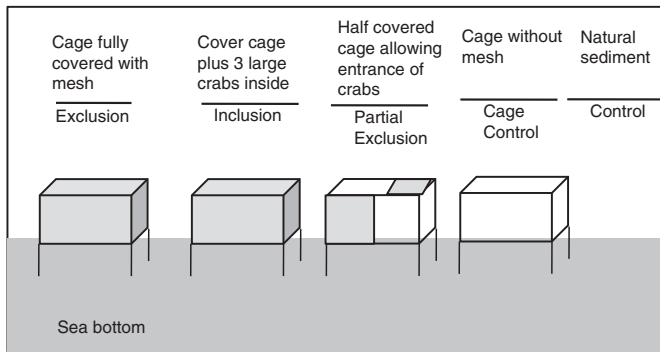
Fig. 2. Experimental treatments used during the cage experiment in the sublittoral zone of Bolsico.

For the cage experiment, we used the same uni- and multivariate response variables, but for the statistical analysis the cage treatment (inclusion, exclusion, partial exclusion, control and reference) and time (i.e., three times when the experiment was repeated) were considered fixed factors for a two-way ANOVA. The a posteriori Tukey test was used to detect the treatments accounting for the significance. Since we used only three replicates for each treatment, Monte Carlo P-values were calculated to assess the significance of PERMANOVA results. ANOVA was conducted using the JMP statistical software. COP and PERMANOVA were run in PRIMER with PERMANOVAβ3 software (Anderson et al., 2008). No statistical analysis was conducted for the gut content since the obtained data were insufficient for meaningful statistics.

Table 1
Mean ± standard deviation (n = 10) of the abundance [number of individuals / (core 0.0078 m^2)] of macroinvertebrates found during the directed sampling.

Phyllum	Taxa	Crab pit	Free crab
Mollusca	*Mysella* sp.	15.9 ± 17.5	12 ± 12.6
	Linucula pisum	5.5 ± 4.7	9 ± 6.7
	Tagelus dombeii	0.9 ± 0.9	0.6 ± 1.4
	Semele sp.	2.9 ± 3.7	4.2 ± 3.5
	Nassarius gayi	0.1 ± 0.3	0.8 ± 1
Crustacea	*Eudevenopus gracilipes*	9.1 ± 5.6	30.1 ± 21.1
	Aora typica	0.2 ± 0.6	0.1 ± 0.4
	Microphoxus sp.	21 ± 11.9	30 ± 14.4
	Sarsiellidae	11.4 ± 18.0	–
	Cylindroleberididae 1	1.1 ± 2.8	2.5 ± 1.7
	Cylindroleberididae 2	1.5 ± 2.1	–
	Liljeborgiidae	2.5 ± 3.4	1.6 ± 1.6
	Heterophoxus sp.	1.2 ± 1.4	0.7 ± 0.7
	Decapoda post-larvae	–	0.2 ± 0.7
	Caridea ind.	0.5 ± 1.6	–
	Diastylis planifrons	0.5 ± 0.8	0.7 ± 1
	Callianassa sp.	–	0.2 ± 0.5
	Stomatopoda ind.	–	0.1 ± 0.4
	Pinnixa valdiviensis	–	0.1 ± 0.4
Polychaeta	Polynoidae	1.5 ± 1.3	1.5 ± 1.3
	Capitellidae	1.7 ± 1.8	0.6 ± 0.9
	Phyllodocidae	0.2 ± 0.6	–
	Nereidae	0.3 ± 0.7	0.1 ± 4
	Gliceridae	0.1 ± 0.3	0.1 ± 4
	Cirratulidae	3 ± 4.2	1.2 ± 1.6
	Spiophanes bombyx	8 ± 12.2	2.2 ± 4.5
	Maldanidae	–	0.3 ± 0.7
	Oweniidae	–	0.3 ± 1.1
	Spionidae	0.4 ± 1.3	8.3 ± 12
	Nephtyidae	0.2 ± 0.6	–
	Hesionidae	0.1 ± 0.3	–
	Polychaeta ind.	–	0.1 ± 0.4
Nematoda	Nematod ind.	0.7 ± 1.5	1.5 ± 3.2
Nemertea	Nemertine ind.	0.7 ± 1.6	1.1 ± 1.5
Chordata	*Branchiostoma elongatum*	–	0.1 ± 0.4

3. Results

3.1. Densities of R. polyodon and C. plebejus

The maximum number of *R. polyodon* found on a transect was 14 and the minimum was four with an average of 0.08 ind. m^{-2}. The highest number of *C. plebejus* was 36 and the lowest value was 18 in one transect, with an average of 0.27 ind. m^{-2}. Crabs were often observed in aggregations of three to seven individuals close to each other in some segments of the transects.

3.2. Crab pits versus reference sediments

A total of 35 macrobenthic taxa were recorded from pits disturbed by *R. polyodon* and *C. plebejus* and from reference sediments. The most abundant taxa in this sampling included the amphipods *Eudevenopus gracilipes* and *Microphoxus* sp., the bivalves *Mysella* sp. and *Pisum* sp., ostracods of the family Sarsiellidae, and polychaetes *Spiophanes bombyx* in addition to unidentified cirratulids (Table 1). Overall species abundance was lower in crab pits compared to undisturbed areas, but a few species were more abundant in pits, e.g., the bivalve *Mysella* sp., ostracods of the family Sarsiellidae and spionid polychaetes *S. bombyx* (Table 1). The ANOVA indicated no significant differences in taxon richness and dry biomass between crab pits and reference areas (both cases $p > 0.05$) (Fig. 3). The total
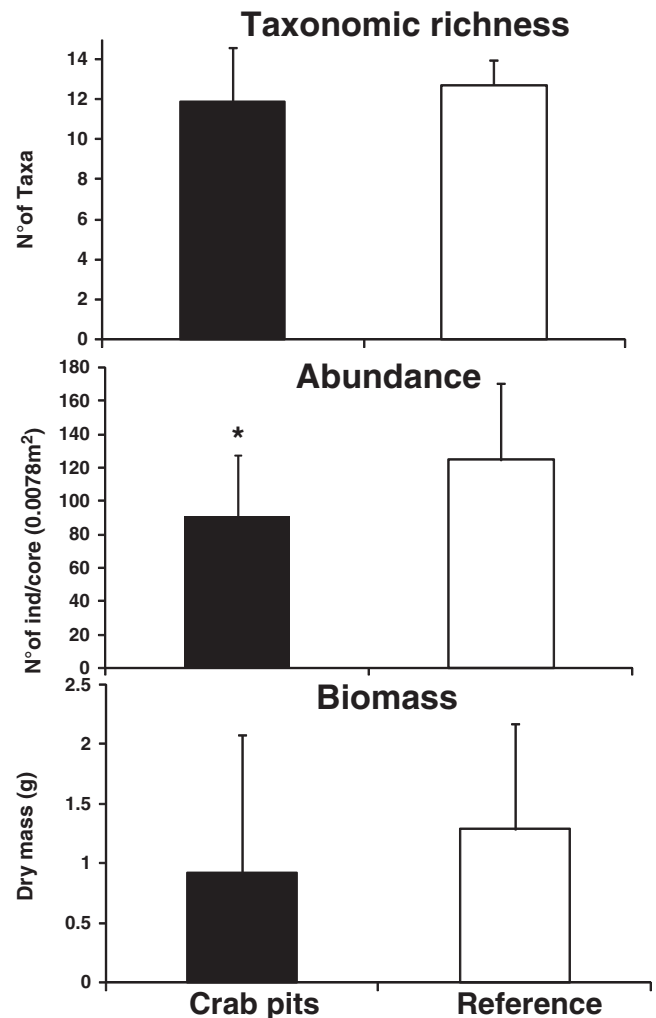

Fig. 3. Mean and standard deviation (+SD; n = 10) of the univariate community parameters estimated after the directed sampling. Significant different treatments are denoted with "*".

abundance of macrobenthos was higher in the reference areas than in the crab pits (one-way ANOVA, $F_{1, 19} = 3.29$, $p < 0.05$). In terms of community structure the canonical ordination plot clearly shows dissimilarities between the pits and reference areas (Fig. 4). One-way PERMANOVA detected significant effects in community structure between crab pits and crab-free reference areas (Pseudo-$F_{1, 19} = 2.2$, $p < 0.05$).

3.3. Stomach contents

From the ten crabs collected during the directed sampling only three animals had some stomach content, consisting in shell fragments of the razor clam *Tagelus dombeii* and remains of small, unidentified crustaceans. The average wet weight of the content was 0.06 ± 0.04 g. Similarly, of the total 27 crabs used in the inclusion treatment, 10 animals showed signs of feeding. These stomachs also contained fragments of *T. dombeii* and fragments of small cancrid crabs together with remains of other, unidentified crustaceans. The average wet weight of the content was 0.49 ± 0.41 g.

3.4. Cage experiment

The results of the cage experiment indicated a reduction in the number of taxa, total abundance and biomass of the macrobenthic community in the inclusion treatment (Fig. 5). Similar to the directed sampling result, there was a trend for less taxa in inclusions than in exclusions and the rest of the treatments but no significant effects were detected ($p > 0.05$). Overall, species specific abundances were lower in inclusion cages but several taxa reached higher abundances (Table 2). Total abundance reduction was significant ($F_{4, 14} = 3.1$, $p < 0.05$) in the treatment factor but not for time and the interaction factor ($p > 0.05$). The Tukey test confirmed that the differences in total abundance were due to the higher abundances in the exclusion and partial exclusion treatment. Total abundance in inclusion, control and reference samples remained at the same levels. In addition, the reduction in biomass was significant ($F_{4, 14} = 4.2$, $p < 0.05$) in the treatment factor but not for time and the interaction factor ($p > 0.05$). The Tukey test revealed that the biomass in the inclusion cage was significantly lower than the biomass in the rest of the treatments.
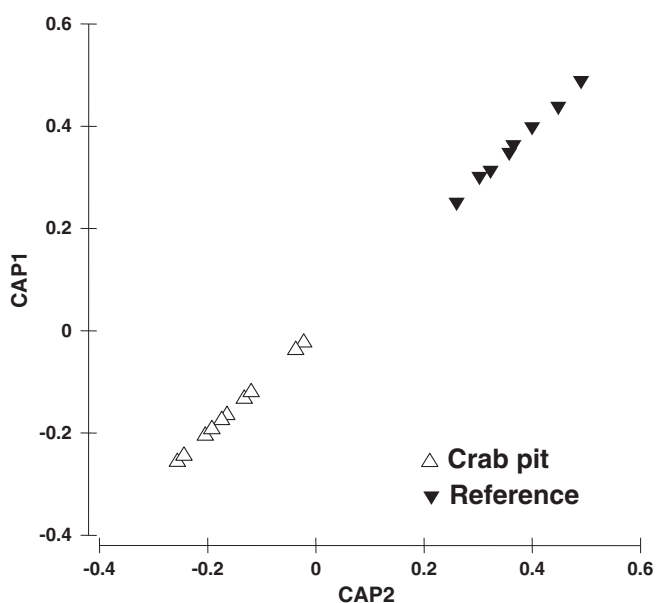

Fig. 4. Canonical ordination plot calculated from Bray–Curtis dissimilarity/similarity measures with square root transformed data of community' structure from crab pits and reference areas.
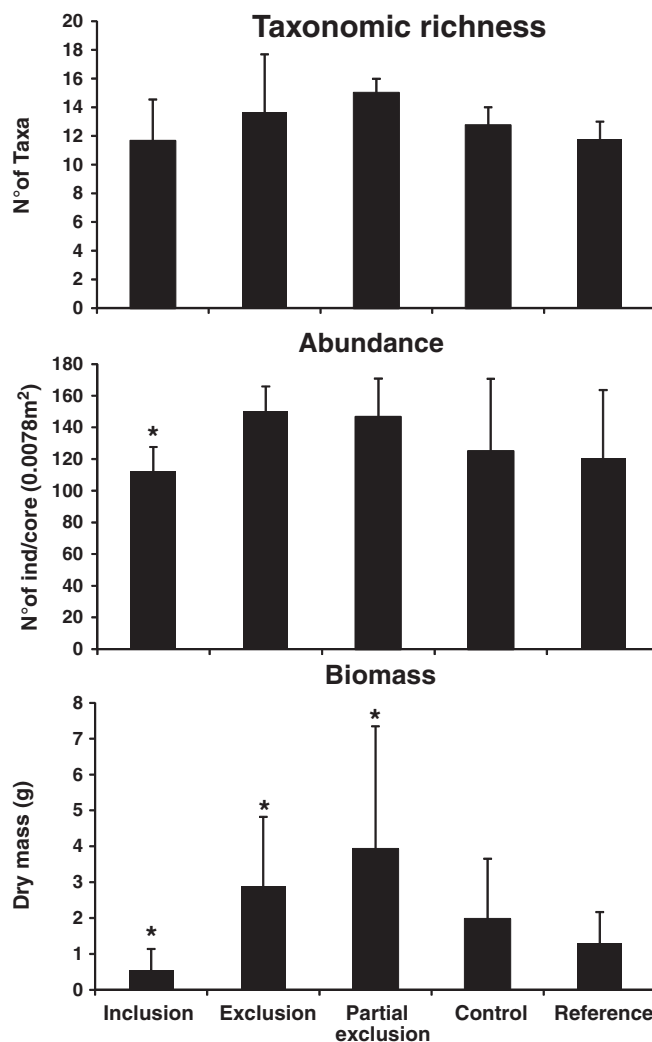

Fig. 5. Mean and standard deviation ($+$SD; n = 9) of the univariate community parameters estimated after the cage inclusion/exclusion experiment. Significant different treatments are denoted with "*".

In terms of structure, the canonical ordination plot shows that the community structure of the inclusion treatment had the strongest dissimilarity compared to the exclusion, partial exclusion, control and reference communities (Fig. 6). In line with this pattern of dissimilarity, the two-way PERMANOVA detected significant effects for treatment (Pseudo-$F_{4, 44} = 1.6$, $p < 0.05$), time (Pseudo-$F_{2, 44} = 6.7$, $p < 0.05$) and the interaction factor (Pseudo-$F_{8, 44} = 1.7$, $p < 0.05$). Accordingly, pair-wise comparisons confirmed that the differences were caused by the inclusion (t = 1.52, $p < 0.05$) and exclusion (t = 1.33, $p < 0.05$) on each sampling day.

4. Discussion

The results of this study suggest that disturbance produced by large *R. polyodon* and *C. plebejus* influence macrobenthic communities by diminishing the abundances of macrobenthic organisms and thus modifying community structure as shown in other studies for large crabs and shrimps (e.g., Beseres and Feller, 2007; Hall et al., 1991; Micheli, 1997). Substratum modification by the mechanical action of removing sediment during digging for resting or foraging appears to be an important process influencing community structure (Auster and Crockett, 1984; Auster et al., 1991; Hall et al., 1991, 1993). It is recognized that pit-digging is a conspicuous behavior of cancrid crabs regardless of their success in capturing prey. In fact, a great percentage of pits created

Table 2
Mean ± standard deviation (n = 9) of the abundance [number of individuals / (core 0.0078 m^2)] of macroinvertebrates found during the cage experiment. Partial exclusion (part. ex.), indeterminate (ind.).

Phyllum	Taxa	Inclusion	Exclusion	Part. ex.	Control	Reference
Mollusca	*Mysella* sp.	23 ± 9.4	19 ± 5.3	24.9 ± 7.7	27.1 ± 17.9	10 ± 10.3
	Linucula pisum	5.2 ± 3.5	6.7 ± 5.4	4.7 ± 3.9	5.3 ± 3.2	8 ± 4.2
	Tagelus dombeii	0.4 ± 0.7	0.2 ± 0.7	0.2 ± 0.4	0.7 ± 0.8	0.6 ± 1.4
	Semele sp.	2 ± 2.1	3.3 ± 1.7	3.7 ± 1.6	3.1 ± 2.3	3.3 ± 1.3
	Mytilidae	–	0.2 ± 0.4	0.1 ± 0.3	–	–
	Nassarius gayi	–	0.3 ± 1	0.2 ± 0.7	0.2 ± 0.4	0.8 ± 1
Crustacea	*Eudevenopus gracilipes*	13 ± 14.3	18.6 ± 28.4	19.3 ± 22.4	21.3 ± 23.9	25.1 ± 14.1
	Aora typica	1.6 ± 2.4	0.8 ± 1	0.2 ± 0.7	0.2 ± 0.4	0.1 ± 0.4
	Microphoxus sp.	24.7 ± 17.3	24.8 ± 6.2	24.7 ± 13.5	30.5 ± 12.3	26 ± 12.2
	Sarsiellidae	18.7 ± 14.4	47.6 ± 19.6	47.2 ± 26.3	44 ± 34.9	–
	Cylindroleberididae 1	1.3 ± 1.9	2 ± 1.6	2.2 ± 1.7	2.7 ± 2.1	1.5 ± 1.2
	Cylindroleberididae 2	1 ± 1.4	2 ± 1.2	2.1 ± 3.1	1.1 ± 1.1	–
	Liljeborgiidae	1.3 ± 2.2	1.1 ± 1.4	1.9 ± 3.2	1.2 ± 1.5	1.6 ± 1.6
	Heterophoxus sp.	0.9 ± 1.4	0.6 ± 0.7	1.6 ± 1.2	1 ± 1.6	0.7 ± 0.7
	Decapoda post-larvae	0.1 ± 0.3	0.6 ± 1.3	–	–	0.2 ± 0.7
	Caridea ind.	–	–	–	–	1.5 ± 1.2
	Diastylis planifrons	0.4 ± 0.9	0.1 ± 0.3	0.3 ± 0.5	0.5 ± 0.8	0.5 ± 0.8
	Callianassa sp.	–	0.1 ± 0.3	0.2 ± 0.4	0.2 ± 0.6	0.2 ± 0.6
	Stomatopoda ind.	0.2 ± 0.4	–	0.1 ± 0.3	–	–
	Cancer coronatus juvenile	0.1 ± 0.3	0.1 ± 0.3	–	–	–
	Amphipod ind.	0.1 ± 0.3	–	0.1 ± 0.3	–	–
Polychaeta	Polynoidae	1.4 ± 1.7	1.8 ± 1.9	1.4 ± 1.4	2 ± 1.3	1.8 ± 1.2
	Capitellidae	2.6 ± 4.1	1.7 ± 2	2.8 ± 2.7	2.5 ± 3	0.6 ± 0.9
	Nereidae	–	1.1 ± 1.5	1.2 ± 2.5	0.1 ± 0.3	
	Gliceridae	–	–	–	–	0.1 ± 4
	Cirratulidae	5.6 ± 5.2	5.1 ± 7	2.7 ± 5	5.2 ± 10	1.4 ± 1.8
	Spiophanes bombyx	0.9 ± 1.8	0.4 ± 0.9	0.2 ± 0.7	–	2.4 ± 4.7
	Maldanidae	–	–	–	0.3 ± 0.7	0.3 ± 1.1
	Oweniidae	–	–	0.2 ± 0.4	0.5 ± 1.1	0.4 ± 0.7
	Spionidae	1.9 ± 2.7	3.3 ± 4.9	2.2 ± 2.3	3.2 ± 1.8	4.2 ± 2.5
	Ophelidae	0.2 ± 0.4	–	0.2 ± 0.4	0.1 ± 0.3	0.4 ± 0.7
	Arenicola sp.	–	–	0.4 ± 1.3	–	–
	Polychaeta ind.	–	0.1 ± 0.3	–	–	–
Nematoda	Nematod ind.	–	–	0.1 ± 0.3	0.3 ± 0.9	1.2 ± 3.2
Nemertea	Nemertine ind.	0.2 ± 0.7	0.7 ± 0.5	1 ± 1.4	0.9 ± 1.4	2.1 ± 1.5
Chordata	*Branchiostoma elongatum*	–	–	–	0.1 ± 0.3	0.1 ± 0.4
Echiura	Echiurid ind.	–	–	0.1 ± 0.3	–	–
Sipuncula	Sipunculid ind.	–	0.1 ± 0.3	–	–	–

by crabs in a given sedimentary area are thought to be the result of unsuccessful foraging attempts (Hall et al., 1991; Smith et al., 1999; Thrush, 1986). We found the majority of the crabs having either no or very little stomach contents, thus supporting this notion. In addition, we focused the combined effect of the two species on large sizes that might prefer to consume medium/large-sized preys (León and Stotz,
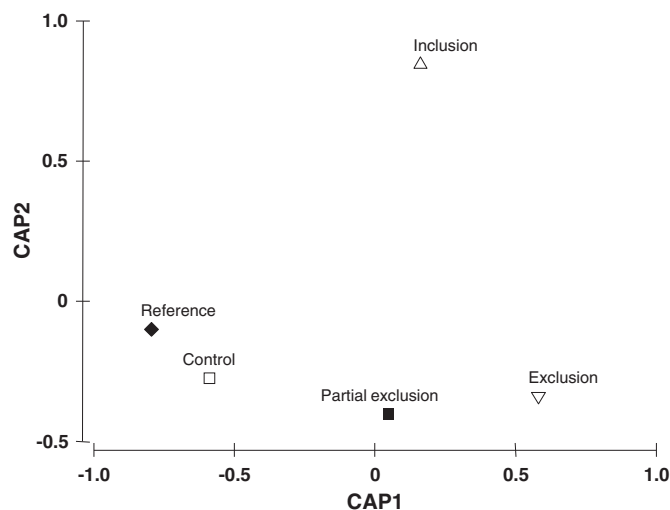

Fig. 6. Canonical ordination plot calculated from Bray–Curtis dissimilarity/similarity measures with square root transformed data of the average (centroids) of the cage experiment treatments.

2004) as manipulating very small individuals could be difficult for large crabs (e.g., Mascaró and Seed, 2001a,b). During the course of our study, the razor clam *T. dombeii* was the most recognizable prey item in the stomachs of the predators, but clams in the area are mostly small juveniles (Pacheco et al., 2012). Regardless of the foraging success, the accumulated pits dug by crabs (and other digging predators) are an important source of seafloor heterogeneity.

We could not rule out the possibility of a stronger predator effect over the macrobenthic community during night hours, as *R. polyodon* has been suggested to be mainly a nocturnal predator (Wolff and Cerda, 1992). Wolff and Cerda (1992) showed that *R. polyodon* reaches peaks in stomach fullness at night between 19:00 and 03:00. Our sampling was conducted at day hours (between 10:00 and 11:00) when gastric evacuation had occurred, and thus we may have overlooked some prey organisms that could have been consumed at night and were fully digested by then. In order to better evaluate the importance of direct prey consumption by these predatory crabs, nocturnal experiments and surveys are strongly recommended.

The majority of studies dealing with the effects of predators in benthic communities have focused on the variation of species abundances to describe changes in community structure (e.g., Barros, 2005; Beseres and Feller, 2007; Como et al., 2004; Fernandes et al., 1999; Frid, 1989; Hall et al., 1991; Pillay et al., 2007a), and little attention has been given to the changes in biomass of the invertebrate community (e.g., Posey et al., 2006). In this study, biomass was the response variable that showed a remarkable reduction in the inclusion treatment of the cage experiment, and a decreasing (albeit non-significant) trend in crab pits during the directed sampling. The interpretation of those observed changes may reflect tradeoffs

between biomass and numerical responses. During the directed sampling, the little variation in biomass suggests that crabs excavated the pits mainly for resting during day hours and not necessarily for feeding. In these resting pits, large invertebrates were present and likely there were no attempts to consume them. Large-sized crabs tend to feed on intermediate/large prey organisms (Mascaró and Seed, 2001a,b; Smith et al., 1999) even if that requires more time and energy by digging deeper in the sediment (e.g., Smith et al., 1999).

On the other hand, during the cage experiment crabs were in the inclusion cages for three nights and most likely they fed during that time. Consequently, they have removed larger prey organisms, which are supported by the significant reduction in macrofauna biomass in the crab inclusions. Abundances were similar in all treatments and this was likely due to small invertebrates not detected or captured by crabs or larger animals that could actively escape from these predators. This conclusion is supported by our results of colonization experiments in defaunated sediment in which small invertebrates dominated during early stages of succession (Pacheco et al., 2012).

The creation of small patches of disturbed sediment is an important process for the functioning of benthic ecosystems (Boudreau and Worm, 2012; Reise, 2002; Thistle, 1981). Disturbed sediments are quickly colonized by opportunistic species that require disturbance for survival and these also facilitate colonization of subsequent immigrants (Frid, 1989; Pacheco et al., 2010; Pillay et al., 2007b; VanBlaricom, 1982). In addition, disturbance by reworking the sediment is important for several biogeochemical processes such as the exchange of nutrients across the sediment–water interface and the oxygenation of the upper sediment layers. Large infaunal species (e.g., bivalves, polychaetes, sea urchins) have been suggested to be very important bioturbators playing a critical role in such processes (Lohrer et al., 2004; Reise, 2002). Adult individuals of R. polyodon and C. plebejus are mainly epifaunal but according to our results and observations they also might be considered important bioturbators since they rework the sediment. Ortiz (2008) also observed these crab species showing a "sediment mining" behavior when searching for prey, creating disturbed patches that were up to 20 cm deep.

It is worth noting the ecological role of these species in benthic habitats as they are subject of intensive artisanal fishery along their distributional range (i.e., sublittoral soft-bottom areas in the Humboldt Current ecosystem along the coast of Chile and Peru) (Aedo et al., 2009). Furthermore, the removal or alterations of top fish predators altered coastal food webs, causing important changes in benthic communities. An illustrative example is the case of the collapse of cod (Gadus morhua) fishery in eastern Canada. Apparently, with the absence of this demersal fish predator in the ecosystem, several prey species including large decapod crabs have increased in abundance, leading to the development of an alternative fishery (Quijón and Snelgrove, 2005a,b). Not only crabs, also clawed lobsters (Homarus spp.) and pandalid shrimps increased in abundance as a consequence of reduction in abundance of large fish predators (Estes et al., 2013; Steneck, 2012). Field and laboratory experiments have demonstrated that predation by these crab species constitutes a significant structuring force of benthic communities, influencing species composition, abundance and in some cases diversity (Quijón and Snelgrove, 2005a,b). In line with those results, our study suggests that fishery for cancrid crabs might have an indirect effect on macrofauna, since these crustaceans influence the abundance and structure of benthic communities. On the other hand, even without fisheries, the effects of cancrid species are complex, propagating too many components of the benthic ecosystem (i.e., mega- and macro-fauna). For example, in an area where crabs are not caught (i.e., Puerto Aldea, Tongoy bay, northern-central Chile), Cancer porteri is a dominant component of the shallow soft-bottom community but undergoes a seasonal migration too deeper waters during summer when R. polyodon increases in abundance and dominates the assemblage of large predatory crabs (Jesse and Stotz, 2002).

The seasonal reduction in the abundance of C. porteri triggered positive responses in the abundances of R. polyodon, the predatory starfish Meyenaster gelatinosus and the infaunal assemblage but negative responses in C. plebejus, the starfish Luidia magallanica, and the scallop Argopecten purpuratus (Ortiz, 2008). The aforementioned examples together with our results highlight the importance of the effects and complex interactions between mega- and macro-faunal components of the benthic habitats that must be considered in the fishery management plans of cancrid crabs.

In conclusion, the community structure of the soft-bottom macrobenthos evaluated here is influenced by the disturbing activities of predatory crabs. Since these species are under fishery pressure, future studies should reveal whether the extraction generates propagating effects on benthic communities.

Acknowledgments

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