

## Predation and anthropogenic impact on community structure of boulder beaches

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**Summary:** Predator impacts on intertidal community structure have been studied for rocky platforms, but intertidal boulder fields, a habitat with a greater extension and heterogeneity, have not yet been considered. Keeping in mind that disturbances are considered an important force in determining intertidal habitat diversity, the aims of this work were to describe and quantify boulder field community structure and to assess boulder field community dynamics by proposing possible food webs, taking into consideration predatory and anthropogenic impacts. These aims were achieved by installing predator-exclusion cages outfitted with rocks that were monitored monthly over one year in two study zones, a Management and Exploitation Area for Benthic Resources (MEABR, Playa Chica) and open-access area (OAA, Playa Grande). For both study zones, juveniles were the dominant observed ontogenetic state and invertebrate richness and density were higher inside exclusion cages. Furthermore, the MEABR had a differentiated impact on community structure and dynamics in comparison with the OAA. In conclusion, the roles played by boulder fields in intertidal diversity, especially in recruitment and as a nursery zone, are important to consider in management plans.

**Keywords:** Management and Exploitation Areas for Benthic Resources; intertidal zone; boulder beaches; community structure; food web.

### Depredación e impacto antropogénico sobre la estructura comunitaria de playas de bolones

**Resumen:** El impacto depredador sobre la estructura comunitaria intermareal ha sido estudiado para plataformas rocosas, pero no ha sido abordado en campos de bolones intermareales, un hábitat de mayor extensión y heterogeneidad. Considerando que las perturbaciones son una fuerza importante en determinar la diversidad del hábitat intermareal, los objetivos de este trabajo fueron describir y cuantificar la estructura comunitaria de campos de bolones, y evaluar la dinámica comunitaria de este hábitat proponiendo posibles tramas tróficas; considerando el impacto de depredadores y antropogénico. Estos objetivos se lograron mediante la instalación de jaulas de exclusión de depredadores equipadas con rocas, que fueron monitoreadas mensualmente durante un año en dos zonas de estudio, un Área de Manejo y Exclusión de Recursos Bentónicos (AMERB, Playa Chica) y un área de acceso abierto (AAA, Playa Grande). Para ambas zonas de estudio, los juveniles fueron el estado ontogenético dominante, y la riqueza y densidad de invertebrados fueron mayores dentro de las jaulas de exclusión. Además, el AMERB tuvo un impacto diferenciado sobre la estructura y dinámica comunitaria comparado al AAA. En conclusión, el rol que cumplen los campos de bolones en la diversidad intermareal, especialmente en el reclutamiento y área de crianza, son importantes y debiesen ser considerados en los planes de manejo.

**Palabras clave:** Área de Manejo y Exclusión de Recursos Bentónicos; zona intermareal; playas de bolones; estructura comunitaria; trama trófica.

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## INTRODUCTION

Factors that promote variations in biodiversity are highly important considering the impact that diversity has on ecosystem functioning (Hooper et al. 2012). While all species modify habitats, it is anthropogenic modifications that are frequently associated with diversity loss, resource exploitation, and habitat fragmentation (Chapin III et al. 2000). Indeed, oceans worldwide are facing increased threats, including resource over-exploitation, habitat degradation and destruction, pollution, and climate change (Halpern et al. 2008). These stressors influence population declines of commercially/culturally important species, altered community structures and compromised ecosystem functioning.

The conservation and sustainable-use mechanisms for marine resources include Marine Protected Areas and no-take zones (Agardy 2003). In Chile, Management and Exploitation Areas for Benthic Resources (MEABRs) are another sustainable-use and nearshore marine resource management strategy (see references in Gelcich et al. 2008). Notably, MEABRs complement the biodiversity objectives of fully protected areas by providing important conservation add-on effects for species outside of management policies (Aldana et al. 2014, Molina et al. 2014).

Due to dense, diverse organism assemblages, the rocky intertidal zone is an ideal “natural laboratory” for understanding the factors that govern intertidal community organization, a topic of numerous studies. Steep environmental gradients, rapid organism turnover, and abundant sessile and slow-moving organisms grant this zone experimental tractability (Paine 1994). Furthermore, the physical gradients, spatial heterogeneity, competition, predation/grazing, disturbance, larval dynamics, and recruitment variability of the rocky shore system are ecological interactions and processes that influence community structure and species composition (see references in Paine 1994).

Understanding community dynamics requires a basic knowledge of community interactions between member species, which define community structure and determine how effects are transmitted between species. For instance, predators can directly (e.g. by consumption) and indirectly (e.g. through the trophic cascade) affect community structure (Paine 1966, Werner and Peacor 2003, García-Huidobro et al. 2015). Therefore, all ecological relationships in the community must be considered to gain full understanding. Likewise, marine resource exploitation can directly and indirectly modify rocky intertidal community structure and functioning (Steneck 1998, see references in Castilla et al. 2007). Consequently, in communities where predation is an important structuring process and some predator species are commercially exploited, appropriate conservation plans and resource management should be established by evaluating different predator species (Castilla and Durán 1985).

Predator impacts on intertidal community structure have been studied for rocky platforms, but intertidal boulder fields—a habitat with a greater extension and heterogeneity—have not yet been considered (Bert-

ness et al. 2001). Species living on and under boulders have greater small-scale spatial variabilities than rocky platform species due to discrete habitat patches separated from other boulders by distinct habit types, such as sand, mud, or smaller rocks (Chapman 2002a,b). Many species living under boulders do not inhabit the surrounding habitats. Furthermore, boulder-inhabiting animals and algae often vary between shorelines due to variations in boulder types and sizes (McGuinness and Underwood 1986) and/or to varied wave-actions and disturbances (Sousa 1979a,b, McGuinness 1987). Additionally, most intertidal boulder field studies focus on relatively exposed open-coast shores, where wave-actions and sand burial (processes that directly influence organisms) determine biological dynamics (Chapman and Underwood 1996, Smith and Otway 1997, Le Hir and Hily 2005).

Rocky platforms have decreased diversity due to space monopolization by highly competitive species (Lubchenco and Menge 1978, Sousa 1984). In contrast, boulder movements involve a frequent renewal of free space, thereby facilitating species coexistence (i.e. the intermediate perturbation hypothesis, Sousa 1979a, b). High vulnerability to disturbances and habitat loss makes boulders analogous to habitat-forming biota, and, depending on the disturbance regime, boulders may be denuded (Lieberman et al. 1979), support few opportunistic species (Littler and Littler 1984) or support diverse assemblages (Sousa 1979a, b, McGuinness 1987). Boulder species are often patchily distributed among and within different fields, with variation mostly existing on individual boulders or among patches than between sites or locations (Chapman 2005, 2012). Considering this variability, in addition to the many characteristics that promote this variability (e.g. spatial heterogeneity, different rock types, wave exposure and boulder size) and the spatial coastal extension of boulder fields, evaluating the predation and anthropogenic impacts on community structure of this habitat becomes all the more important. This aspect has been poorly addressed in the literature, making the development of ecology-based resource management plans more difficult.

Therefore, the aims of this study were (1) to describe and quantify boulder field community structure; and (2) to assess boulder field community dynamics by proposing possible boulder field food webs, taking into consideration predatory and anthropogenic impacts. In the two zones were assessed, a MEABR and an open-access area (OAA), we expected to find notable differences in community structure and trophic web between the evaluated boulder fields.

## MATERIALS AND METHODS

### Sampling

Between the summers of 2008 and 2009, two intertidal zones from Quintay, Chile (33°11'S, 71°1'W) were sampled. The study zones were Playa Chica and Playa Grande, which are respectively a MEABR and an OAA. These study zones represent lower and higher

anthropogenic impact scenarios, respectively (Castilla et al. 2007, Gelcich et al. 2008, Molina et al. 2014). Two sites that showed similar wave exposure and rock and boulder presence were selected per zone. The effect of predators on community structure was evaluated by comparing randomly collected rocks at the study site with treatment rocks maintained within cages that excluded predators (Menge 1976).

Specifically, three exclusion cages (20×30×30 cm) were installed at each site and at similar low-intertidal levels. All cages had an aluminium frame covered with wire mesh (10 mm) that was treated with anti-fouling and anti-oxidant paint (see Ojeda and Muñoz 1999). Six rocks (≈15 cm in diameter each) per cage were randomly selected from the same sampling site and placed within each cage. All exclusion cages were sampled monthly for one year, with the exception of some winter months due to adverse climatic conditions. For sampling, the six rocks within each exclusion cage, as well as six rocks outside each exclusion cage (controls), were collected. The collected rocks were placed in individual plastic bags, labelled with the sampling site and date, and transported to the laboratory for subsequent analysis. The rocks taken from inside the exclusion cages were replaced each month after sampling with similar rocks from each sampling site. A control cage was not used as it was impossible to anchor this structure in the boulder habitats.

In the laboratory, the sampled rocks were analysed using 5×5 cm quadrants divided into 25 sub-quadrants (1 cm each) (see Navarrete and Castilla 1990). Invertebrates and algae were classified and counted (number and coverage, respectively) under an Olympus CX31 stereomicroscope. Using the obtained data, the richness and diversity of each site were estimated. Specific richness (S) was established as the total number of species found for each rock sample, and diversity was estimated using the Shannon-Weaver Index.

### Trophic web representation

The representation of trophic webs for the boulder fields of Quintay was supported by predator-prey relationships described in the literature (Paine 1966, Castilla 1981, Angel and Ojeda 2001). Using the collected data, species were grouped according to trophic status. This enabled an approximation of an overall trophic web (frames) that included all of the potential predators and respective prey in intertidal boulder fields, regardless of the sampling zone (see Castilla 1981, Angel and Ojeda 2001).

### Statistical analyses

Spatial variations in richness, density and diversity were assessed using two-way ANOVA (General Linear Models, GLM) to test for differences between study zones (MEABR and OAA) and between treatments (inside and outside exclusion cages). The study zone and treatment were considered fixed factors as interest was focused on the differences inside and outside exclusion cages and between the study

zones. Insofar as these zones were inside and outside a MEABR, conclusions were limited to these levels (Bennington and Thayne 1994). Prior to GLM analysis, normal distribution was verified and an a posteriori Tukey analysis was performed to determine differences between factor levels.

Multivariate analysis was based on density data for collected mobile and sessile species. Density data were fourth-root-transformed and standardized (between 0 and 1) to ensure that all species, abundant or rare, contributed similarly to the analysis. The Bray-Curtis index of similarity was used. Nonmetric multidimensional scaling (MDS) was used to display the similarities of mobile and sessile species between study zones (MEABR and OAA) and between treatments (inside and outside exclusion cages). Differences in mobile and sessile community assemblages were tested a priori for significance with the ANOSIM procedure (randomized permutation test; Clarke and Warwick 2001). Similarity analysis (SIMPER) identified those species that accounted for the largest differences between study zones (MEABR and OAA) and between treatments (inside and outside exclusion cages) (Clarke and Warwick 2001).

Significance was established at  $P < 0.05$ . For analyses concerning descriptors of community structure, the STATISTICA 7.0 (StatSoft.Inc. 2004) and PRIMER 5.0 (PRIMER-E Ltd) statistical software were used.

## RESULTS

### Recorded taxa

A total of 67 taxa were recorded, 27 of them corresponding to algae and 40 to invertebrates (Table 1). In the MEABR, 46 were recorded, 17 of them corresponding to algae and 29 to invertebrates (Table 1). In the OAA, 51 species were recorded, 24 of them corresponding to algae and 27 to invertebrates (Table 1). Mollusca and Rhodophyta were the most abundant taxonomic groups in both study zones.

### Community structure of intertidal boulder fields

Analysis of invertebrates revealed greater species richness and density inside than outside exclusion cages (Table 2, Fig. 1A, B). Additionally, inside the exclusion cages, density was higher in the MEABR (posterior Tukey test  $P < 0.05$ , Fig. 1B). However, invertebrate diversity was higher in the OAA (Table 2, Fig. 1C).

Algae analysis indicated that inside exclusion cages, richness and diversity were greater in the OAA than in the MEABR (Table 2, posterior Tukey test  $P < 0.05$ ; Fig. 2A, C). In terms of algal density, the MEABR showed higher density outside than inside exclusion cages (Table 2, posterior Tukey test  $P < 0.05$ ; Fig. 2B), whereas in the OAA no differences in density were found (posterior Tukey test  $P > 0.05$ , Fig. 2B).

Regarding species composition, no differences were found between study zones (MEABR and OAA) or inside vs outside exclusion cages for either mobile or sessile species.

Table 1. – Taxonomic list of species found in each sampling zone, inside and outside exclusion cages. MEABRs, Management and Exploitation Area for Benthic Resources; OAA, Open-Access Area; IN, inside exclusion cages; and OUT, outside exclusion cages.

Taxa	Species	MEABRs		OAA	
		In	Out	In	Out
Annelida	<i>Phragmatopoma</i> spp. Mörch, 1863			×	×
Annelida	<i>Pseudonereis gallapagensis</i> Kinberg, 1866		×		
Annelida	<i>Spirorbis</i> spp. Daudin, 1800	×	×	×	×
Arthropoda	<i>Allopetrolisthes angulosus</i> (Guérin, 1835)	×			
Arthropoda	Amphipoda spp. Latreille, 1816	×	×	×	×
Arthropoda	<i>Balanus flosculus</i> Darwin, 1854			×	×
Arthropoda	<i>Balanus laevis</i> Bruguiere, 1789			×	×
Arthropoda	Copepoda spp.		×		
Arthropoda	Isopoda spp. Latreille, 1817	×	×	×	×
Arthropoda	<i>Jehlius cirratus</i> Darwin, 1854		×		×
Arthropoda	<i>Petrolisthes granulosus</i> (Guérin, 1835)	×			
Arthropoda	<i>Petrolisthes tuberculatus</i> (Milne Edwards, 1837)	×			
Arthropoda	<i>Petrolisthes violaceus</i> (Guérin, 1831)	×			
Arthropoda	<i>Pisoides edwardsii</i> (Bell, 1835)	×			
Arthropoda	<i>Taliepus dentatus</i> (Milne Edwards, 1834)	×			
Bryozoa	Bryozoa spp.	×		×	×
Chlorophyta	<i>Blidingia</i> spp. Kylin, 1947	×	×		×
Chlorophyta	<i>Chaetomorpha</i> spp. Ktzing, 1845	×	×	×	×
Chlorophyta	<i>Codium dimorphum</i> Ktzing, 1845	×	×	×	×
Chlorophyta	<i>Ulva</i> spp. Linnaeus, 1753	×	×	×	×
Cnidaria	<i>Actinia</i> spp.	×		×	×
Cnidaria	<i>Anemonia alicemartinae</i> Sebens and Paine, 1979			×	
Cnidaria	<i>Phymactis clematis</i> (Drayton in Dana, 1846)	×			
Cnidaria	<i>Phymanthea pluvia</i> (Drayton in Dana, 1846)	×			
Echinodermata	<i>Patiria chilensis</i> Verrill, 1870			×	
Echinodermata	<i>Ophiactis kroyeri</i> Lütken, 1856			×	
Echinodermata	<i>Tetrapyrgus niger</i> (Molina, 1782)				×
Mollusca	<i>Chiton cumingsi</i> Frembly, 1827		×		×
Mollusca	<i>Chiton</i> spp. Linnaeus, 1758	×			
Mollusca	<i>Chiton latus</i> Sowerby 1825	×	×	×	×
Mollusca	<i>Echinolittorina peruviana</i> (Lamarck, 1822)	×	×		×
Mollusca	<i>Echinolittorina araucana</i> (d'Orbigny, 1840)		×		
Mollusca	<i>Fissurella maxima</i> Lamarck, 1822		×		
Mollusca	<i>Mitrella</i> spp. Risso, 1826	×		×	
Mollusca	<i>Perumytilus purpuratus</i> (Lamarck, 1819)	×	×	×	×
Mollusca	<i>Prisogaster niger</i> Wood, 1828	×	×	×	×
Mollusca	<i>Protothaca thaca</i> (Molina, 1782)				×
Mollusca	<i>Scurria cecilianae</i> (d'Orbigny, 1841)	×	×	×	×
Mollusca	<i>Semimytilus algosus</i> (Gould, 1850)		×	×	×
Mollusca	<i>Tegula euryomphala</i> (Jonas, 1844)	×	×	×	×
Mollusca	<i>Tegula luctuosa</i> (d'Orbigny) 1841				×
Mollusca	<i>Toncia disjuncta</i> (Frembly, 1827)			×	
Mollusca	<i>Turritella cingulata</i> Sowerby, 1825				×
Ochrophyta	<i>Adenocystis utricularis</i> (Bory de Saint-Vincent) Skottsberg, 1907			×	
Ochrophyta	<i>Colpomenia</i> spp. (Endlicher) Derbès & Solier, 1851	×			
Ochrophyta	<i>Glossophora kunthii</i> (C. Agardh) J. Agardh, 1882			×	×
Ochrophyta	<i>Sphacelaria</i> spp. Lyngbye, 1818			×	
Platyhelminthes	<i>Tythosoceros inca</i> Baeza, Veliz, Pardo, et al., 1997	×			×
Rhodophyta	<i>Ahnfeltiopsis</i> spp. P.C. Silva & DeCew, 1992	×		×	×
Rhodophyta	<i>Anisocladella pacifica</i> Kylin, 1941			×	
Rhodophyta	<i>Centroceras clavulatum</i> (C. Agardh) Montagne, 1846	×			×
Rhodophyta	<i>Chondria</i> spp. C. Agardh, 1817				×
Rhodophyta	<i>Corallina officinalis chilensis</i> (Decaisne) Kützing, 1858		×	×	×
Rhodophyta	<i>Erythrotrichia</i> spp. Areschoug, 1850	×	×	×	×
Rhodophyta	<i>Gelidium</i> spp. Lamouroux, 1813			×	
Rhodophyta	<i>Gelidium lingulatum</i> Kützing, 1868			×	×
Rhodophyta	<i>Lithothamnium</i> spp. Philippi, 1837	×	×	×	×
Rhodophyta	<i>Mazzaella</i> spp. G. De Toni, 1936	×	×	×	×
Rhodophyta	<i>Mazzaella membranacea</i> (J. Agardh) Fredericq, 1993		×	×	×
Rhodophyta	<i>Mesophyllum</i> spp. Lemoine, 1928	×	×	×	×
Rhodophyta	<i>Nothogenia fastigiata</i> (Bory de Saint-Vincent) P.G. Parkinson, 1983			×	
Rhodophyta	<i>Polysiphonia mollis</i> J.D. Hooker & Harvey, 1847		×		
Rhodophyta	<i>Polysiphonia paniculata</i> Montagne, 1842		×		
Rhodophyta	<i>Porphyra</i> spp. C. Agardh, 1824				×
Rhodophyta	<i>Rhodomenia</i> spp. Greville, 1830	×	×	×	×
Rhodophyta	<i>Rhodomenia corallina</i> (Bory de Saint-Vincent) Greville, 1830		×	×	×
Rhodophyta	<i>Schottera nicaeensis</i> (J.V. Lamouroux ex Duby) Guiry & Hollenberg, 1975			×	×

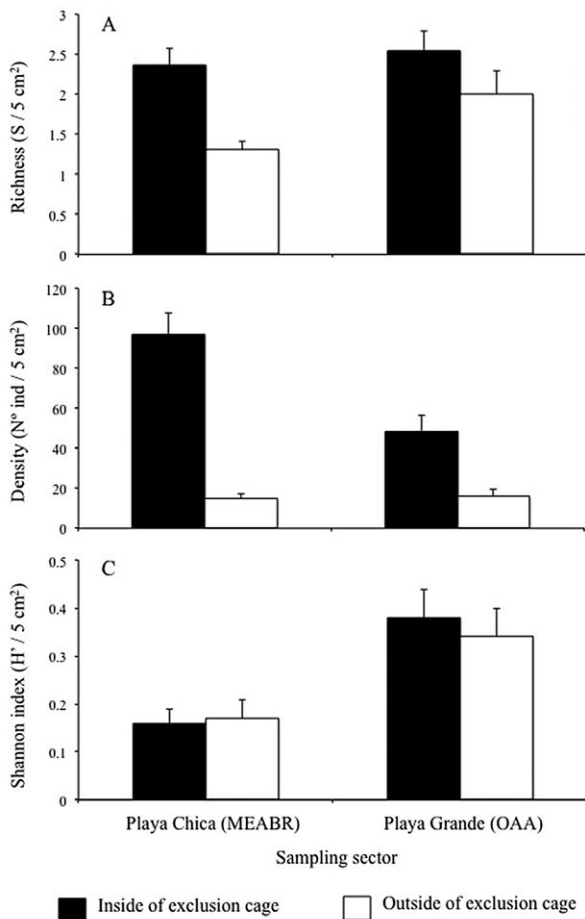
### Trophic web for Playa Chica (MEABR)

The carnivorous predators registered in the MEABR were Actiniaria (*Actinia* spp., *Phymactis clematis* and *Phymanthea pluvia*) and Polycladida

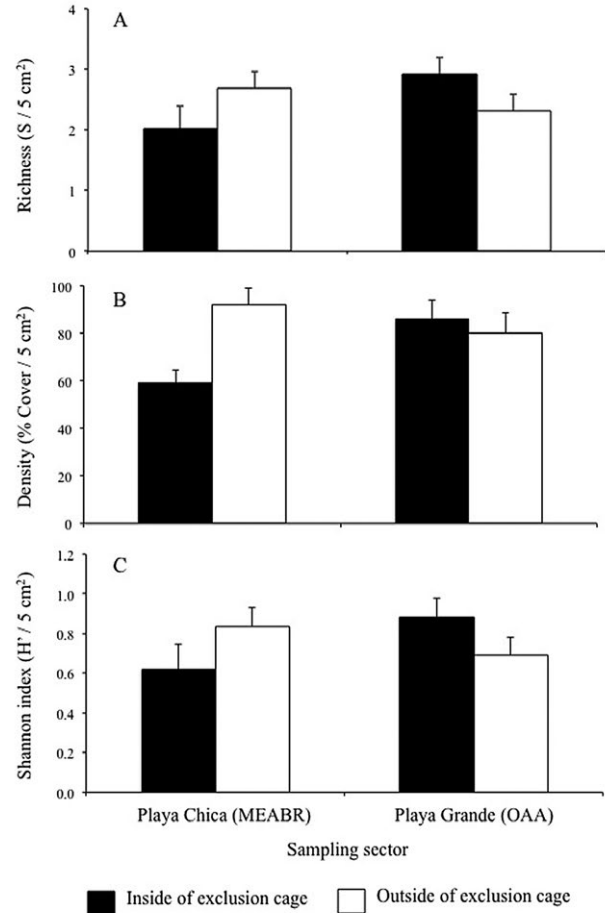
(*Tythosoceros inca*) (Table 1). Herbivorous species included amphipods (Amphipoda spp.), herbivorous decapods (*Taliepus dentatus*), isopods (Isopoda spp.), gastropods (*Austrolittorina peruviana*, *Austrolittorina araucana*, *Fissurella* spp., *Mitrella* spp., *Prisogaster*

Table 2. – General linear model (two-way analysis of variance) results comparing richness, density and diversity between study zones (Management of Exploitation Area of Benthic Resources and Open-Access Area) and treatments (“inside” and “outside” exclusion cages).

Variable	Effect	Invertebrate	Algae
Richness	Study zone (S)	$F_{(1, 169)}=3.31, P=0.070$	$F_{(1, 169)}=4.07, P=0.045$
	Treatment (T)	$F_{(1, 169)}=11.45, P<0.001$	$F_{(1, 169)}=0.67, P=0.412$
	(S) * (T)	$F_{(1, 169)}=1.16, P=0.282$	$F_{(1, 169)}=7.77, P=0.005$
Density	Study zone (S)	$F_{(1, 169)}=14.66, P<0.001$	$F_{(1, 169)}=0.29, P=0.589$
	Treatment (T)	$F_{(1, 169)}=85.05, P<0.001$	$F_{(1, 169)}=37.9, P=0.053$
	(S) * (T)	$F_{(1, 169)}=16.27, P<0.001$	$F_{(1, 169)}=74.58, P=0.006$
Diversity	Study zone (S)	$F_{(1, 169)}=13.21, P<0.001$	$F_{(1, 169)}=3.49, P=0.063$
	Treatment (T)	$F_{(1, 169)}=0.06, P=0.803$	$F_{(1, 169)}=1.14, P=0.287$
	(S) * (T)	$F_{(1, 169)}=0.34, P=0.557$	$F_{(1, 169)}=6.70, P=0.01$

Fig. 1. – Invertebrate community descriptors “inside” and “outside” exclusion cages in the MEABR and the OAA. (A) Species richness, (B) density and (C) invertebrate diversity. Bars indicate SEM ( $\pm 1$ ).

*niger*, *Scurria cecilians* and *Tegula euryomphala*), and chitonids (*Chiton cumingsi*, *Chiton* spp. and *Chiton latius*). These herbivores prey on the benthic algae group found in the MEABR (*Blidingia* spp., *Chaetomorpha* spp., *Codium dimorphum*, *Ulva* spp., *Colpomenia* spp., *Ahnfeltiopsis* spp., *Centroceras clavulatum*, *Corallina officinalis chilensis*, *Erythrotrichia* spp., *Lithothamnium* spp., *Mazzaella* spp., *Mazzaella membranacea*, *Mesophyllum* spp., *Polysiphonia mollis*, *Polysiphonia paniculata*, *Rhodomenia* spp. and *Rhodomenia coraline*) (Fig. 3A, Table 1). Filter feeders recorded in the MEABR included mobile annelids (*Pseudonereis galapagensis*), sessile annelids (*Spirorbis* spp.), bryozoa (Bryozoa spp.), cirripedes (*Jehlius cirratus*), copepods (Copepoda spp.), filtering decapods (*Allopetrolisthes*

Fig. 2. – Algae community descriptors “inside” and “outside” exclusion cages in the MEABR and the OAA. (A) Species richness, (B) density and (C) algae diversity. Bars indicate SEM ( $\pm 1$ ).

*angulosus*, *Petrolisthes granulatus*, *Petrolisthes tuberculatus*, *Petrolisthes violaceus* and *Pisoides edwardsii*) and Mytilidae (*Perumytilus purpuratus* and *Semimytilus algosus*) (Fig. 3A, Table 1).

### Trophic web for Playa Grande (OAA)

Three carnivorous predator groups were recorded for the OAA: Asterozoa (*Patiria chilensis* and *Ophiactis kroyeri*), Actiniaria (*Actinia* spp. and *Anemonia alicemartinae*) and Polycladida (*T. inca*) (Fig. 3B, Table 1). Among herbivorous species were amphipods (Amphipoda spp.), isopods (Isopoda spp.), Echinoidea (*Tetrapygyus niger*), gastropods (*A. peruviana*, *Mitrella* spp., *P. niger*, *S. cecilians*, *Tegula euryomphala*, *T.*

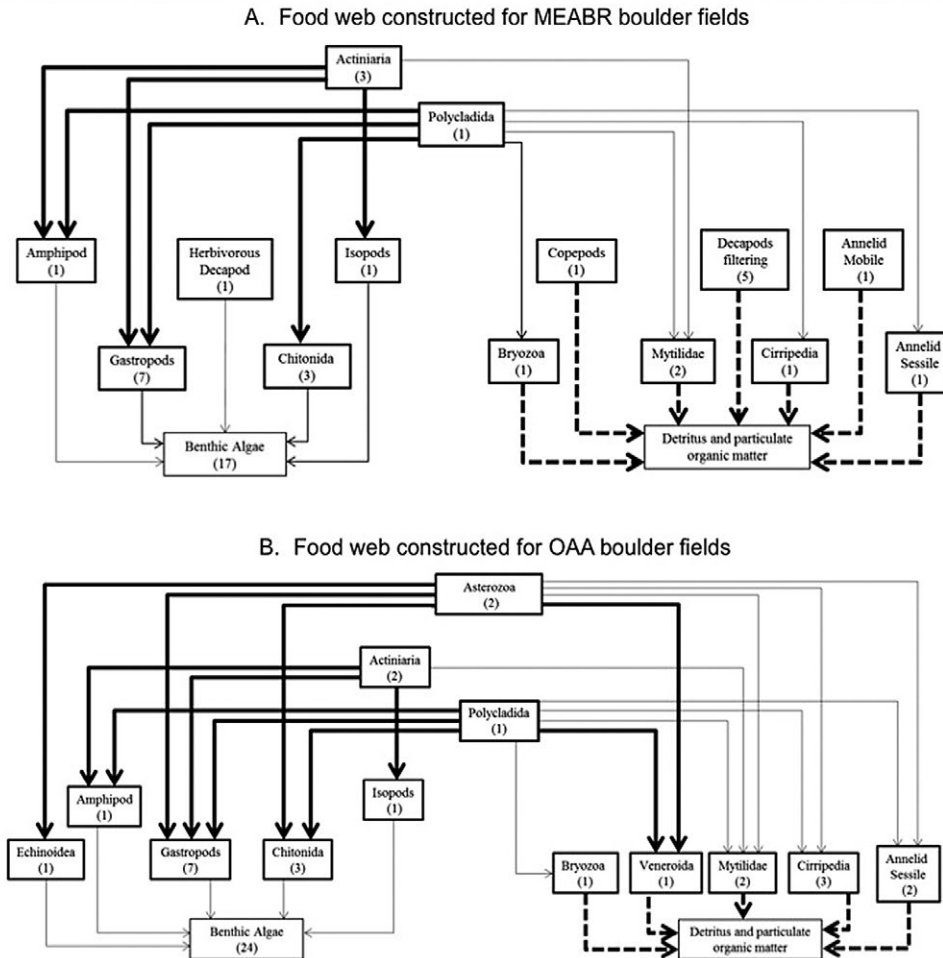


Fig. 3. – Food web constructed for (A) MEABR and (B) OAA boulder fields. Numbers within each box represent the quantity of individuals recorded for each species. Bolded lines indicate predation on mobile organisms. Unbolded lines indicate predation on sessile organisms. Dotted lines represent filtering activities.

*luctuosa* and *Turritella cingulata*) and chitonids (*Chiton cumingsi*, *Ch. latus* and *Tonicia disjuncta*). The observed benthic algae group for the OAA included *Blidingia* spp., *Chaetomorpha* spp., *C. dimorphum*, *Ulva* spp., *Adenocystis utricularis*, *Glossophora kunthii*, *Sphacelaria* spp., *Ahnfeltiopsis* spp., *Anisocladella pacifica*, *C. clavulatum*, *Chondria* spp., *C. officinalis chilensis*, *Erythrotrichia* spp., *Gelidium* spp., *Gelidium lingulatum*, *Lithothamnium* spp., *Mazzaella* spp., *M. membranacea*, *Mesophyllum* spp., *Nothogenia fastigiata*, *Porphyra* spp., *Rhodomenia* spp., *Rhodomenia corallina* and *Schottera nicaeensis* (Fig. 3B, Table 1). Filter feeder species included Bryozoa (Bryozoa spp.), Veneroida (*Protothaca thaca*), Mytilidae (*P. purpuratus* and *S. algosus*), cirripedes (*Balanus flosculus*, *Balanus laevis* and *J. cirratus*) and sessile annelids (*Phragmatopoma* spp. and *Spirorbis* spp.).

## DISCUSSION

### Species composition, richness, density and diversity

The species composition of the Quintay boulder fields showed patterns similar to those from other re-

ported intertidal zones, such as platforms (Alveal 1971, Santelices et al. 1977, Castilla 1981, see Table 1). The study zones (MEABR and OAA) displayed taxonomic groups typical of the rocky intertidal zone (Castilla 1981). However, important differences in community structure were recorded. Both boulder fields lacked top predators described for rocky platforms. Additionally, taxonomic groups that strongly attach to primary substrates were found, including benthic algae (e.g. *Lithothamnium* spp.), Mytilidae (e.g. *P. purpuratus*), Cirripedia (e.g. *J. cirratus*) and sessile annelids (e.g. *Spirorbis* spp.). Interestingly, intertidal boulder fields were a nursery habitat for all species, as evidenced by the presence of juveniles for all registered taxonomic groups (see Table 1). This finding highlights the importance of boulder fields for studying species development and the relationship of boulder fields with intertidal and subtidal diversity.

The differences in community structure between study sites are likely associated with coastal morphology and the environmental protection status of MEABRs. Moreover, the studied OAA is a well-described retention zone that, due to seawater circulation and coastal morphology, has increased phytoplankton abundance (Mace and Morgan 2006, Henríquez et al.

2007, Palma et al. 2009), which might help to explain the greater diversity of invertebrates in comparison with the MEABR (Fig. 1C). On the other hand, the Quintay MEABR may have had a differential impact on study zones.

General analyses of MEABRs have found greater species diversity and density than in OAAs, as well as different species composition (Durán and Castilla 1989, Gelcich et al. 2008, Molina et al. 2014). Similarly, greater benthic resource abundances in MEABRs than in OAAs could impact various species, even those not considered within management plans, through the direct and indirect effects of interspecific interactions such as competition and predation (for details see Castilla and Gelcich 2008, Gelcich et al. 2008). For example, some taxonomic groups, such as Arthropoda (e.g. crabs from the *Petrolisthes* genus) and Actiniaria (e.g. *P. clematis* and *P. pluvia*), may be favoured on the boulders of Quintay MEABR, (Fig. 3A, Table 1).

Studies evaluating the impacts of MEABRs on abundance and diversity have focussed on the subtidal system, a more stable habitat than boulder fields. Previous studies indicate significantly greater abundance and diversity in MEABRs than in OAAs (Gelcich et al. 2008, Molina et al. 2014). Additionally, the regular extraction of top predators (e.g. *C. concholepas*) (Molina et al. 2014) may promote increased diversity by preventing the monopolization of major environmental resources by species with higher competitive capabilities (Paine 1966). This finding was supported by observations at the Quintay OAA, thus revealing a different functional dynamic related to the combined impact of top predator extraction and boulder field variability.

The greater richness and density of invertebrates within exclusion cages (Fig. 1A, B) suggests that the cage might have provided shelter against predators, thereby acting as an additional protective measure within the MEABR, which would explain the high density at this site (Fig. 1B). Echinodermata and Mollusca showed higher species diversity and density in the Quintay MEABR than in the OAA (see Table 1), an observation consistent with results obtained by Molina et al. (2014). Most molluscs and sea urchins are generalist grazers that scrape the substratum, thus removing spores, macroalgae plantlets, epiphytes and microalgae. The diet of these species is considerably similar (Aguilera 2011), with important impacts on benthic algae populations (Contreras and Castilla 1987). Therefore, the MEABR and exclusion cages promoted a protected area for mostly herbivorous invertebrate recruits (Fig. 3A). This protective status (i.e. MEABR regulations and exclusion cages) would differentially impact algae and invertebrates (Figs 1 and 2).

Indeed, the protection given to herbivorous invertebrates inside exclusion cages in the MEABR would increase foraging pressure, explaining the decreased algae density inside exclusion cages (Fig. 2B). This would additionally explain the lower richness and diversity of algae within the exclusion cages in the MEABR than in the OAA (Fig. 2A, C). Although there are no significant differences between zones (MEABR vs OAA), there was a tendency outside exclusion cages

towards lower algae richness and diversity in the OAA, a zone where the *Tetrapyrgus niger* sea urchin was also recorded (see Table 1). The grazing activities of this species have been described as intense, generating large halos in the bed of intertidal benthic algae (Contreras and Castilla 1987).

In both study zones, the high abundance of red algae could be associated with the trophic morphology of the herbivores detected on boulders (*Chiton* spp. and *Fissurella* spp.) (Santelices and Correa 1985, Santelices et al. 1986, Camus et al. 2008) and of species that tolerate high habitat variability. Studies on intertidal rocky platforms have primarily addressed adult individuals with completely developed mouthparts, which prefer Calcarea algae species and other species resistant to grazing (Steneck and Dethier 1994). In boulder fields, only juveniles and invertebrate recruits were found (e.g. *T. niger*, *C. cumingsi*, *C. latus*; Fig. 1B), which may lead to the dominance of the Rhodophyta algae group in this habitat (Santelices 1990, Muñoz and Ojeda 2000, Aguilera 2011). On the other hand, species such as red crustose algae (e.g. *Lithothamnium* spp.) showed traits that would promote success in the highly variable boulder field habitat, which, in turn, would result in greater abundance.

### Food webs

The OAA boulder field food web revealed the presence of Asterozoa predators such as the sea stars *P. chilensis* and *O. kroyeri*. Similar predator species were found for intertidal platforms (Castilla 1981). Asterozoa species have a significant impact on community structure and dynamics since they prey on almost all of the sampled species (Castilla 1981, Navarrete et al. 2000, Navarrete and Manzur 2008, Fig. 3B). Sea stars are a determinant factor in species coexistence, with the predation of dominant community species by sea stars decreasing competitive impacts by preventing competitive exclusion, thereby increasing local diversity (Paine 1966). Moreover, the evidence obtained revealed the presence of other carnivorous groups such as anemones (*Actinia* spp. and *A. alicemartinae*) and planaria (*T. inca*), species with a broad trophic spectrum whose effects on boulder field communities are as yet unknown but should be considered (Sebens and Paine 1978, Zamponi 1979, Acuña and Zamponi 1996).

The MEABR boulder field trophic web revealed the presence of two carnivorous groups (Actiniaria and Polycladida) (Fig. 3A). In turn, the OAA showed three predator groups (Asterozoa, Actiniaria and Polycladida). The Asterozoa group was absent from the MEABR, which may be the result of an increased abundance of commercial predator species that would force Asterozoa to other intertidal or subtidal habitats; however, interactions between predators were not evaluated in this study. Interestingly, both boulder fields lacked the top predators described for rocky platforms, including *C. concholepas* and *Sicyases sanguineus* (Castilla 1981). Moreover, species of the intertidal boulder fields that used primary substrates included benthic algae (e.g. *C. dimorphum*, *G. lingulatum*,

*Lithothamnium* spp. and *Ulva* spp.), Mytilidae (e.g. *P. purpuratus* and *S. algosus*), Cirripedia (e.g. *B. flosculus*, *B. laevis* and *J. cirratus*) and sessile annelids (e.g. *Spirorbis* spp.). In turn, the rocky platforms of central Chile only contain benthic algae and invertebrates such as Mytilidae and Cirripedia (Castilla 1981).

In conclusion, rocks sampled from both Quintay zones showed similar invertebrate compositions and algae patterns to those of other intertidal habitats (e.g. Alveal 1971, Santelices et al. 1977, Castilla 1981). The most abundant taxonomic group was Mollusca, as was found for rocky platforms, and a comparable result was obtained for algae species (Otafaza and Santelices 1985, Santelices et al. 1986, Aguilera 2011). The analysed boulders of the MEABR and OAA showed taxonomic groups characteristic of intertidal zones (Castilla 1981). Evidence of diversity and food web structure variability likely associated with MEABR protection was detected. Moreover, the high diversity observed in the OAA revealed a different functional dynamic that is likely associated with the combined impact of top predator extraction and boulder field variability. Finally, boulder fields are a necessary habitat for the recruitment of, and as a nursery for, all intertidal species, as is supported by the present findings of only juvenile invertebrate individuals. Therefore, the functional impact of boulder fields on the structural dynamics of intertidal communities should be considered in any management plans.

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