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Article

Rocky reef benthic assemblages in the Magellan Strait and the South Shetland Islands (Antarctica)

Ensambles bentónicos de arrecifes rocosos en el Estrecho de Magallanes e Islas Shetland del Sur (Antártica)

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Resumen.- Las comunidades submareales de arrecifes de gran parte de las costas del mundo han sido descritas en detalle, sin embargo, escasa información existe para los extensos arrecifes subantárticos. El objetivo fue describir estos sistemas costeros del sur y medir el grado en que varían en función de las medidas fundamentales de la estructura de la comunidad. La Región Magallánica constituye un sitio intermedio entre sitios relativamente bien estudiados en regiones temperadas y Antártica. Estudios previos sugieren que la especie de alga dominante (dosel) puede reflejar diferentes historias de perturbación así como diferencias en sus comunidades asociadas. Hipotetisamos que la variación en los ensambles submareales sésiles en Magallanes, donde *Macrocystis pyrifera* domina ampliamente, será menor a la que ocurre en sitios en Antártica, donde *Desmarestia* spp. o *Himantothallus grandifolius* dominan dependiendo de los regímenes de disturbios. Los resultados de este estudio muestran que los ensambles bentónicos en el Estrecho de Magallanes fueron similares en aquellos lugares donde la estructura física del arrecife fue similar, pero variaron fuertemente donde la forma del arrecife fue distinta. En los sitios de las Islas Shetland del Sur, los ensambles bentónicos fueron diferentes en términos del alga dominante y la estructura comunitaria. No obstante, la evidencia previa acerca de que sitios dominados por *Desmarestia* presentan mayor evidencia de disturbios fue incorrecta. Probablemente el efecto de sombra producido por *Macrocystis* en Magallanes y el efecto del hielo en Antártica son fuertes factores estructuradores en sus respectivas comunidades, situación que debe ser considerada al comparar las características comunitarias.

Palabras clave: Macroalgas, dosel, sustratos duros, Región Magallánica, Océano Austral

Abstract.- Subtidal reef communities from much of the world's coastline have been described in detail, but data from the world's most extensive subantarctic rocky reefs is scarce. The objective was to describe these southern coastal systems and measure the extent to which they vary in terms of fundamental measures of community structure. The Magellan Region constitutes an intermediate site between relatively well-studied temperate regions and Antarctica. Previous studies suggest that dominant canopy species may reflect different disturbance histories and associated communities may similarly be expected to vary structurally. We hypothesized that variation in subtidal sessile assemblages in the Magellan Strait, where *Macrocystis pyrifera* widely dominates, would be less than at Antarctic sites, where *Desmarestia* spp. or *Himantothallus grandifolius* may dominate depending on disturbance regimes. Our results showed that benthic assemblages in the Magellan Strait were similar where physical structure of the reef was similar, but differed strongly where reef form differed. At sites in South Shetland Islands, benthic assemblages differed in terms of dominant macroalgae and sessile community structure; however evidence that the *Desmarestia* -dominated site was more highly disturbed was equivocal. Shading produced by *Macrocystis* in Magellan Strait and ice effect in Antarctica are likely strong structuring factors in their respective communities, which would need to be considered when comparing community characteristics.

Key words: Macroalgae, canopy, hard substrates, Magellan Region, Southern Ocean

Introduction

Shallow-water rocky reefs are important and productive marine environments, and a large number and diversity of plants and animals are associated with them (Dayton 1985a, Schiel 1990, Steneck *et al.* 2002). It is important to understand the structure and functioning of natural communities so that current variation and future changes can be understood and managed if necessary. It is, however, impossible to address higher level questions if species assemblages have not been described (Schiel & Hickford 2001).

Mainland South America (which extends to nearly 54°S) and the Fueguian Archipelago (to nearly 56°S) constitute a substantial part of the world's subantarctic coastline, but these may be the least-studied near-shore rocky reef communities in the world (Escribano *et al.* 2003). The vast majority of the subtidal studies developed in the Magellan Region has been carried out in soft bottom habitats, and although rocky reefs are common coastal habitats in the Magellan Region, very little is known about communities inhabiting those (Försterra *et al.* 2005). In recent years there have been a number of subtidal rocky reef studies developed in steep fjord environments in the north of the Magellan Region (*e.g.*, Häussermann & Försterra 2007). In the south some work has been developed in the intertidal cobble-boulder fields in sites along the Magellan Strait (*e.g.*, Benedetti-Cecchi & Cinelli 1997, Ríos & Mutschke 1999, Ingólfsson 2005) and Cape Horn Archipelago (*e.g.*, Guzmán & Ríos 1986), and invertebrate communities of the kelp *Macrocystis pyrifera* (Linnaeus) C. Agardh, 1820 were studied in the Magellan Strait (Ríos *et al.* 2007) and the Beagle Channel (Ojeda & Santelices 1984, Adami & Gordillo 1999). Ecological studies are equally scarce (but see Castilla & Moreno 1982, Dayton 1985b, Vásquez & Castilla 1984, Vásquez *et al.* 1984).

Comparative quantitative data from subtidal benthic assemblages have not been published (but see Ríos *et al.* 2007 for work on fauna from *Macrocystis pyrifera* holdfasts), and while substantial between-site variation has been shown in the intertidal (Benedetti-Cecchi & Cinelli 1997), *M. pyrifera* dominance along most of the Magellan Strait may suggest a more homogeneous subtidal community, as the kelp forests may provide structuring features for the communities (Ríos *et al.* 2007).

The Magellan Region constitutes an intermediate site between temperate regions and Antarctica, but there is a scarcity of comparative studies between them (Arntz 2005). The South Shetland Islands off the Antarctic Peninsula are less remote from the Magellan Strait than well-studied sites widely termed «southern Chile» in the ecological literature. Biogeographic affinities have been found between the Antarctic Peninsula and the Magellan Region for different groups of invertebrates (Moyano 1996, Thatje & Brown 2009). It is, however, still unclear to what extent the benthic communities inhabiting both regions are related (Thatje & Mutschke 1999) and more studies are needed in order to have a better understanding of differences and similarities existing between these areas. Perhaps surprisingly, the Magellan Region is the less well-studied region of the two (Arntz 2005).

At Subantarctic Islands and Antarctic Peninsula sites, seaweeds and sessile fauna are largely absent from the intertidal (Castilla & Rozbaczylo 1985, Kim 2001). Subtidally, faunal dominance is common below the ice-affected shallow sublittoral, community structure tends to be dominated by bryozoans, ascidians and sponges (Barnes 1995, Bowden 2005, Smale 2008). Coralline algae and summer growth of annual red macroalgae may be abundant, perennial brown algae are almost always absent in the shallows, but may be abundant below ~5-10 m (Gruzov & Pushkin 1970, Sakurai *et al.* 1996, Quartino & Boraso de Zaixso 2008). Dominant canopy species may reflect different disturbance histories (Dayton 1990) and associated communities may similarly be expected to vary structurally (Clark *et al.* 2011).

For development of comparative studies it is important to have information collected with the same methodology. Moreover, Antarctic sites easily accessible from Chilean bases are likely to be more readily accessible to researchers working in the Magellan Region, and present an opportunity for extending ecological research across a large latitudinal gradient. Here, we take steps to fill the knowledge gap in Magellanic rocky reef macroalgal community ecology by describing the composition and structure of benthic assemblages and measuring variation between locations. We hypothesized that variation in subtidal sessile assemblages along the eastern mainland coast of the Magellan Strait (where *Macrocystis pyrifera* widely dominates (Dayton 1985b, Ríos *et al.* 2007)) would be less than at Antarctic sites (where *Desmarestia* spp. or *Himantothallus grandifolius* may dominate (Dayton 1990, Klöser *et al.* 1996)). We aimed to measure the extent to which these southern coastal systems are similar in terms of fundamental measures of community structure (algal dominance, diversity, composition, abundance).

Materials and methods

Study area

Shallow-water rocky reefs benthic assemblages of the Magellan Region and Antarctica were studied during the austral summer, from December 2008 to February 2009. Sites were selected according to their accessibility and the existence of nearby facilities for sample processing and facilitation of planning and coordination of research efforts (Iken & Konar 2003). Four sites were studied in the Magellan Strait: Puerto del Hambre (53°36’57"S; 70°55’43"W), Fuerte Bulnes (53°37’34"S; 70°55’13"W), Punta Carrera (53°35’10"S; 70°55’32"W) and Punta Arbol (53°43’07 S; 70°57’58"W) (Fig. 1).

In Antarctica, two sites were chosen within Maxwell Bay, King George Island, South Shetland Islands. Maxwell Bay is one of two large fjords of the island, facing south-east to Bransfield Strait (Kim 2001). Nebles Point is located at the entrance of Collins Bay (62°11’02"S; 58°51’14"W) close to Collins Glacier. The Fildes Bay site (62°12’17"S; 58°56’47"W) was on the Maxwell Bay side of Albatross Islet (Fig. 1).

Sample collection

Rocky reef communities were sampled based on the protocols of NaGISA (Rigby *et al.* 2007). Depth-stratified random sampling was carried out in series of 1 m^2 quadrats. At the Magellanic sites, five quadrats were sampled at each depth. Intertidal strata were sampled at high (HT), medium (MT) and low tide (LT) levels. Subtidal sampling was done on SCUBA at 1, 3, 5, 10 and 20 m depth levels, where accessible. The 20 m depth level was sampled only at Fuerte Bulnes where it was accessible due to the steepness of the reef to 30 m. The Puerto del Hambre site was sampled to 10 m. At Punta Carrera and Punta Arbol sandflats began at less than 5 m and 3 m respectively. When placing quadrats, large holdfasts (>10 cm diameter) of *Macrocystis pyrifera* were avoided, as these were studied by Ríos *et al.* (2007), and the associated cryptic organisms would be poorly represented with the methods we employed. At the Antarctic sites, poor weather severely restricted sampling time and scope. Four quadrats were placed at each of 1, 5 and 10 m depths at both sites, and at one level in the intertidal at Fildes Bay.

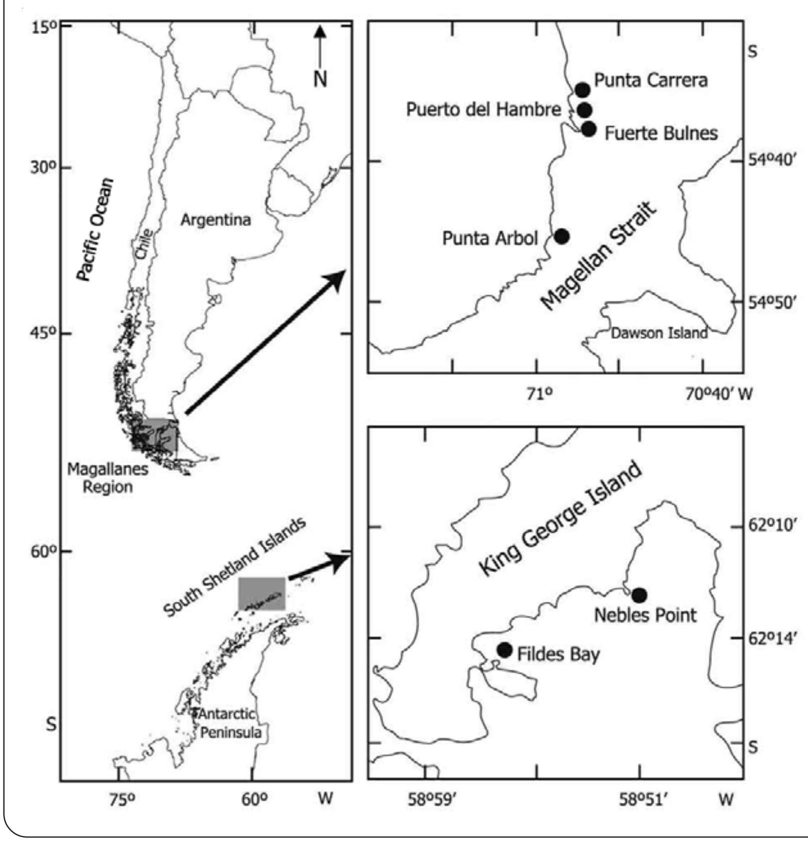

Figure 1. Study sites (black circles) in the Magallanes Region and South Shetland Islands (Antarctica) / Sitios de estudio (círculos negros) en la Región de Magallanes e Islas Shetland del Sur (Antártica)

Each 1 m^2 quadrat was divided in quarters with elastic cord and marked with coloured plastic at 10 cm intervals to assist in assigning close ups to the correct area of the quadrat. Each quarter was photographed from directly above. A series of close ups recorded any reef face obscured by macroalgae or reef form. Additionally, the presence or absence of surface canopy of *Macrocystis pyrifera* was noted in the Magellan Strait sites. Photographs were later analysed for data collection. The dominant substrate type was ranked on a scale of fineness as: Bedrock = 4; Boulders = 3; Cobbles = 2; Gravel = 1, Sand = 0. All organisms larger than 2 cm^2 were identified to the lowest possible taxonomic level and percent cover of sessile invertebrates and macroalgae was estimated. Macroalgal cover (excluding surface canopy of *Macrocystis pyrifera* fronds) and cover of all sessile organisms on the reef face were recorded (percent cover) and mobile fauna were counted. Macroalgae were collected for identification where necessary, and were mostly identified to genus. Specimens were fixed with 10% formaldehyde in seawater (buffered) or in 70% alcohol. The taxonomic status of each species was confirmed according to WoRMS database[1].

The community structure and composition at each site were analysed for species richness (S) and Shannon-Wiener diversity (H'). Differences in number of species and diversity between sites were tested using one-way ANOVA. Shapiro-Wilk's normality test and Levene's test for homogeneity of variances were performed before the analysis.

Percent coverage data were log-transformed in order to downweigh the influence of extreme values (*i.e.*, rare species) to test differences in percent coverage between depths, sites and areas. A similarity matrix was developed based on Bray-Curtis similarity index. Multivariate patterns between regions and sites were visualized in nMDS (non-Metric Multidimensional Scaling) plots. Ordinations with centroids averaged by site were produced to depict variability between regions and sites.

Analyses of Similarity (ANOSIM) were performed to test differences between the different factors where area, site and depth were considered *a priori* factors for the analysis. When the global *R*-value was significant ($P < 0.05$), pairwise comparisons were conducted. Thus, interpretations of pairwise comparisons were based on *R*-values rather than *P* values as recommended by Clarke & Gorley (2006). SIMPER analysis was then performed to assess the contribution of each taxon to observed dissimilarities between groups. The same routine was undertaken for comparisons with mobile data where number of individuals was square root transformed. ANOSIM and SIMPER procedures were run using PRIMER v6 (Clarke & Gorley 2006).

Results

Substrate was largely rocky at two sites in the Magellan Strait (Fuerte Bulnes and Puerto del Hambre) while Punta Arbol and Punta Carrera became sandy at 3 and 5 m, respectively. Sites in Antarctica were also mostly rocky, although bedrock was more common at Nebles Point, and boulders more common at Fildes Bay (Fig. 2).

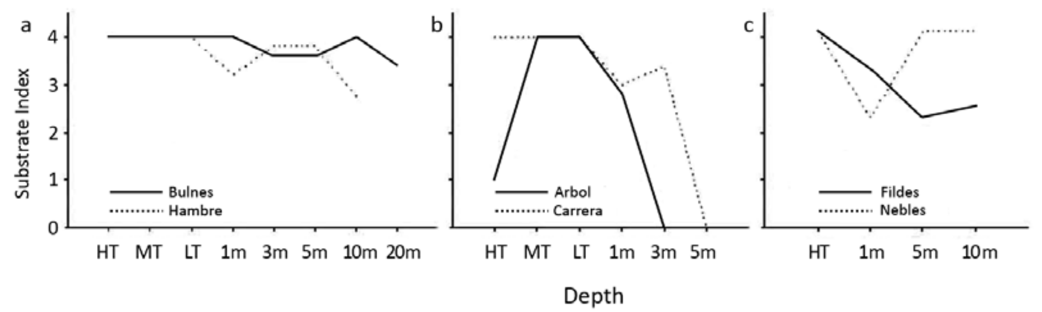

Figure 2. Substrate type with increasing depth in the Magellan Strait (a, b) and South Shetland Islands, Antarctica (c). Indices generated by assigning a number to the dominant substrate in each quadrat (Bedrock = 4, Boulders = 3, Cobbles = 2, Gravel = 1, Sand = 0) and averaging across all quadrats from each depth / Tipo de sustrato de acuerdo a la profundidad en el Estrecho de Magallanes (a, b) e Islas Shetland del Sur, Antártica (c). Índices generados asignando un número según el sustrato dominante en cada cuadrante (Roca = 4, Bolones = 3, Cantos rodados = 2, Grava = 1, Arena = 0) y valores promedios de todos los cuadrantes en cada profundidad

[1]World Register of Marine Species <http://www.marinespecies.org>

A total of 168 taxa (106 in Magallanes, 62 in Antarctica) were recorded from 141 quadrats studied across all sites. Overall species richness was higher in Magellan Strait sites than in Antarctic sites. The highest number of species was recorded in Fuerte Bulnes (83 taxa) whereas Fildes Bay showed the highest value (27 taxa) in Antarctica.

In the Magellan Strait, the sessile fauna in the intertidal was dominated by bivalves (3 taxa) and ciripedians (3 taxa), while the subtidal fauna was dominated by the Ascidiacea (9 taxa), Porifera (6) and Bryozoa (6)[2]. In Antarctica, the sessile fauna was dominated by Porifera (18 taxa) and Ascidiacea (7 taxa). The mobile intertidal fauna in the Magellan Strait was dominated by molluscs (5 taxa) and echinoderms (2 taxa). In the subtidal, the mobile fauna was dominated mainly by molluscs (19 taxa) and echinoderms (12 taxa), especially echinoids and asteroids. At Antarctic sites, the limpet *Nacella concinna* (Strebel, 1908) was the only species found in the intertidal. Subtidal assemblages were dominated by echinoderms (9 taxa) and molluscs (4 taxa).

The mean number of taxa per quadrat (including sessile and mobile organisms) in the intertidal varied significantly across sites ($F_{4,76}$ = 8.812, P < 0.001). The highest value was recorded at Fuerte Bulnes (5.1 ± 0.5 SE) and lowest in Fildes Bay (Fig. 3a). Subtidally, values were also significantly different between sites ($F_{5,82}$ = 3.367, P < 0.001). Species richness per quadrat at the Magellan Strait sites ranged from 10.6 (± 1.5) at Punta Arbol to 6.2 (± 0.5) at Punta Carrera, while in Antarctica, Fildes Bay showed the highest number of species per quadrat (6.8 ± 0.59; Fig. 3a). Diversity varied across sites at the intertidal ($F_{4,76}$ = 2.976, P < 0.01) and subtidal levels ($F_{5,82}$ = 3.686, P < 0.05). In the intertidal, the highest diversity was found at Fuerte Bulnes whereas subtidally the highest diversity at subtidal depths was recorded at Punta Arbol in the Magellan Strait, and Nebles Point in Antarctica. Interestingly, Fuerte Bulnes showed the highest diversity at the intertidal levels (0.8 ± 0.2) and the lowest (0.4 ± 0.1) in the subtidal (Fig. 3b).

Subtidal macroalgal cover (not including the surface canopy formed by *Macrocystis pyrifera* fronds) ranged from < 5 % (Fuerte Bulnes 20 m) to > 80% (Fuerte Bulnes and Puerto del Hambre 1 m, Nebles Point, 5 and 10 m, Fig. 4a-c). These dense canopies were dominated by *Lessonia vadosa* (Searles, 1978) in the Magellan Strait and *Desmarestia* spp., at Nebles Point, South Shetland Islands. *Macrocystis pyrifera* also formed a dense surface canopy at some depths at all sites in the Magellan Strait.

In general, macroalgal cover (non-surface canopy) tended to decrease with increasing depth at the Magellan Strait sites, except at Puerto del Hambre, where there was an increase in coverage at 10 m due to high abundance of *Lessonia flavicans* (Bory de Saint-Vincent, 1826). High cover (> 50%) did not occur below a surface canopy of *Macrocystis* (Fig. 4a, b). At the Antarctic sites, the canopy cover increased with depth, reaching high values where the brown algae *Himantothallus grandifolius* (Gepp & Gepp) Zinova, 1959 and *Desmarestia* spp. dominated at Fildes Bay and Nebles Point respectively. The red algae

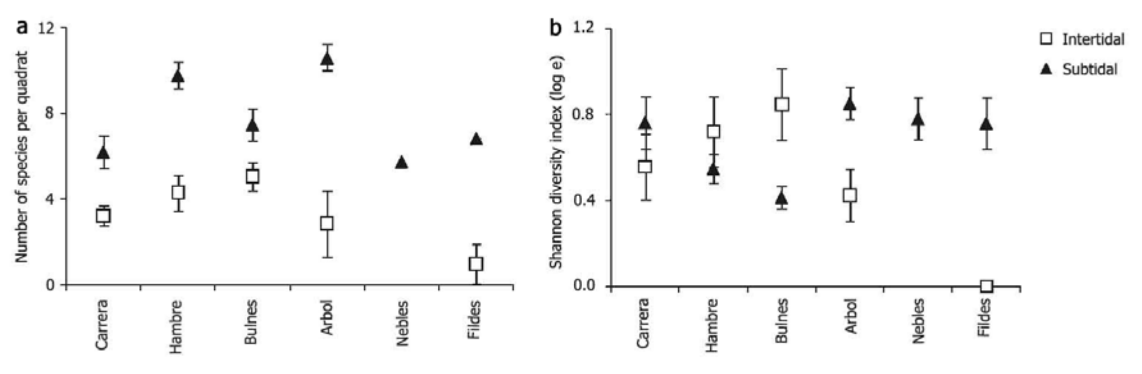

Figure 3. a) Species richness and b) diversity at four sites in the Magellan Strait and two sites in the South Shetland Islands, Antarctica. Error bars indicate 1 SE / a) Riqueza de especies y b) diversidad en cuatro sitios en el Estrecho de Magallanes y dos sitios en las Islas Shetland del Sur, Antártica. Barras de error indican 1 EE

[2]Appendix 1. List of species available by email from authors.

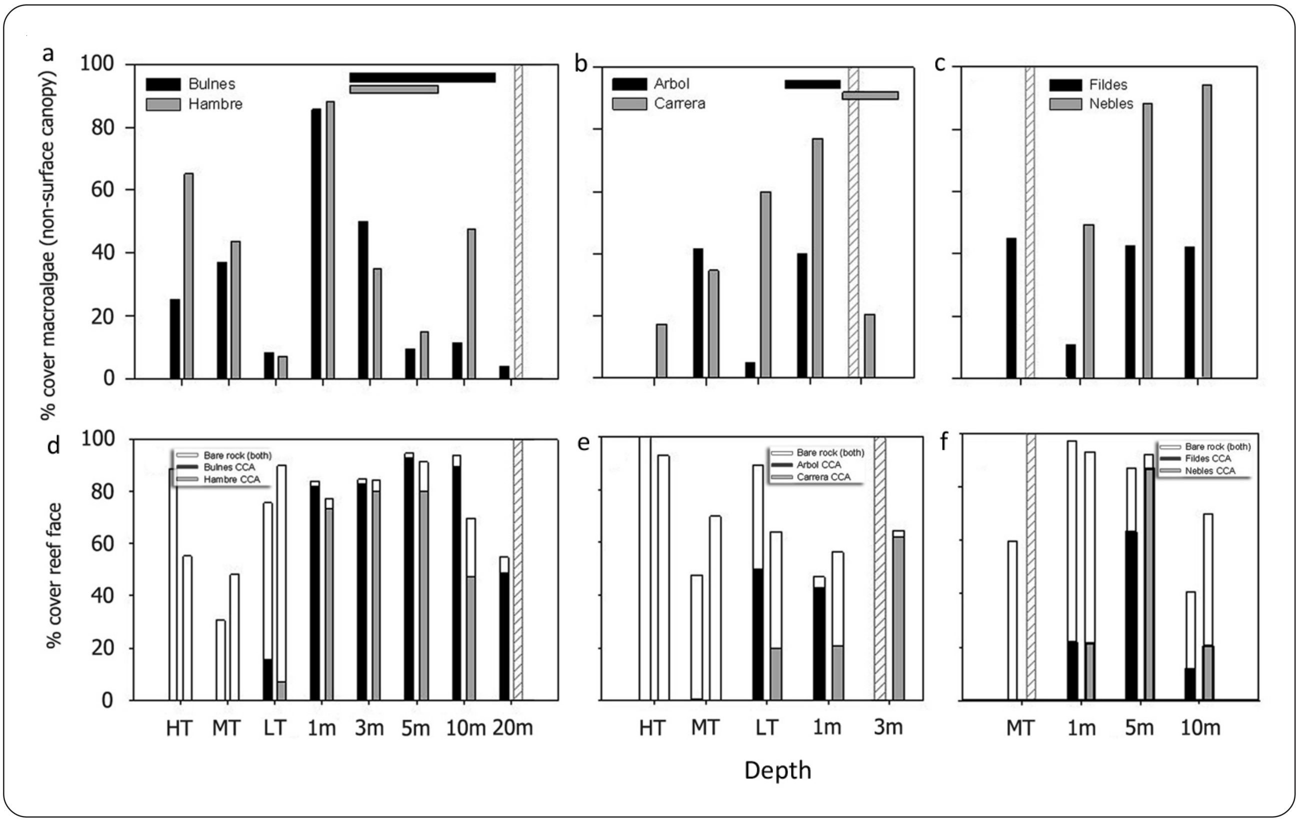

Figure 4. Mean percent cover of fleshy seaweeds (a-c), crustose coralline algae (CCA) and bare rock (d-f) with increasing depth at sites in the Magellan Strait (a, b, d, e) and South Shetland Islands, Antarctica (c, f). Surface canopy of *Macrocystis pyrifera* is indicated by horizontal bars at top of graphs a and b. Grey striped bands indicate data not collected / Promedio de porcentaje de cobertura de algas laminares (a-c), algas coralinas crustosas (CCA) y roca (d-f) en relación al aumento de profundidad en el Estrecho de Magallanes (a, b, d, e) e Islas Shetland del Sur, Antártica (c, f). El dosel de *Macrocystis pyrifera* se indica con las barras ubicadas en la parte superior de los gráficos a y b. La barra gris con bandas indica datos no colectados

Porphyra sp. was the most important species at intertidal levels in Magallanes. Other important species include *Mazzaella laminarioides*, which was dominant at mid-tide in Punta Carrera and Punta Arbol, but dominant at low-tide only at Punta Carrera.

There were large areas of available space (bare rock) in the intertidal, but generally very little (0-36%) in the subtidal in Magellan Strait sites. Encrusting coralline algae were the most important organisms in all sites in the Magellan Strait (Fig. 4d, e). They were highly dominant along the subtidal, especially at Fuerte Bulnes and Puerto del Hambre, covering more than 60% of the substrate. In contrast, the cover of both bare rock and encrusting corallines was similar at the Antarctic sites (Fig. 4f). The area of bare rock was higher than coverage of corallines in Fildes Bay, reaching values of 75% at 1 m while corallines only covered 21% at that depth. The coverage of coralline algae at Nebles Point was slightly higher than bare rock with values near 49% at 10 m. At Magellan Strait sites, the most important organisms after macroalgae were bivalves, cirripedians and ascidians, whereas bryozoans and sponges were important in Antarctic sites.

Fildes Bay had the highest densities of mobile individuals of all sites, reaching an average of over 50 individuals m^{-2} at 5 m depth. The overwhelming majority of these (81%) were the limpet *Nacella concinna*. Densities of mobile animals ranged between 2.6 (± 0.9) individuals m^{-2} at Punta Carrera (1 m) and 61.5 (± 11.8) individuals m^{-2} at Fildes Bay (5 m; Fig. 5). In the Magellan Strait there was generally a more even contribution of molluscs and echinoderms than at the Antarctic sites, except at Punta Arbol where high densities of the small urchin *Pseudechinus magellanicus* (Philippi, 1857) at 1 m depth contributed an average of 80% of the total of 44.2 (± 21.6) individuals m^{-2}.

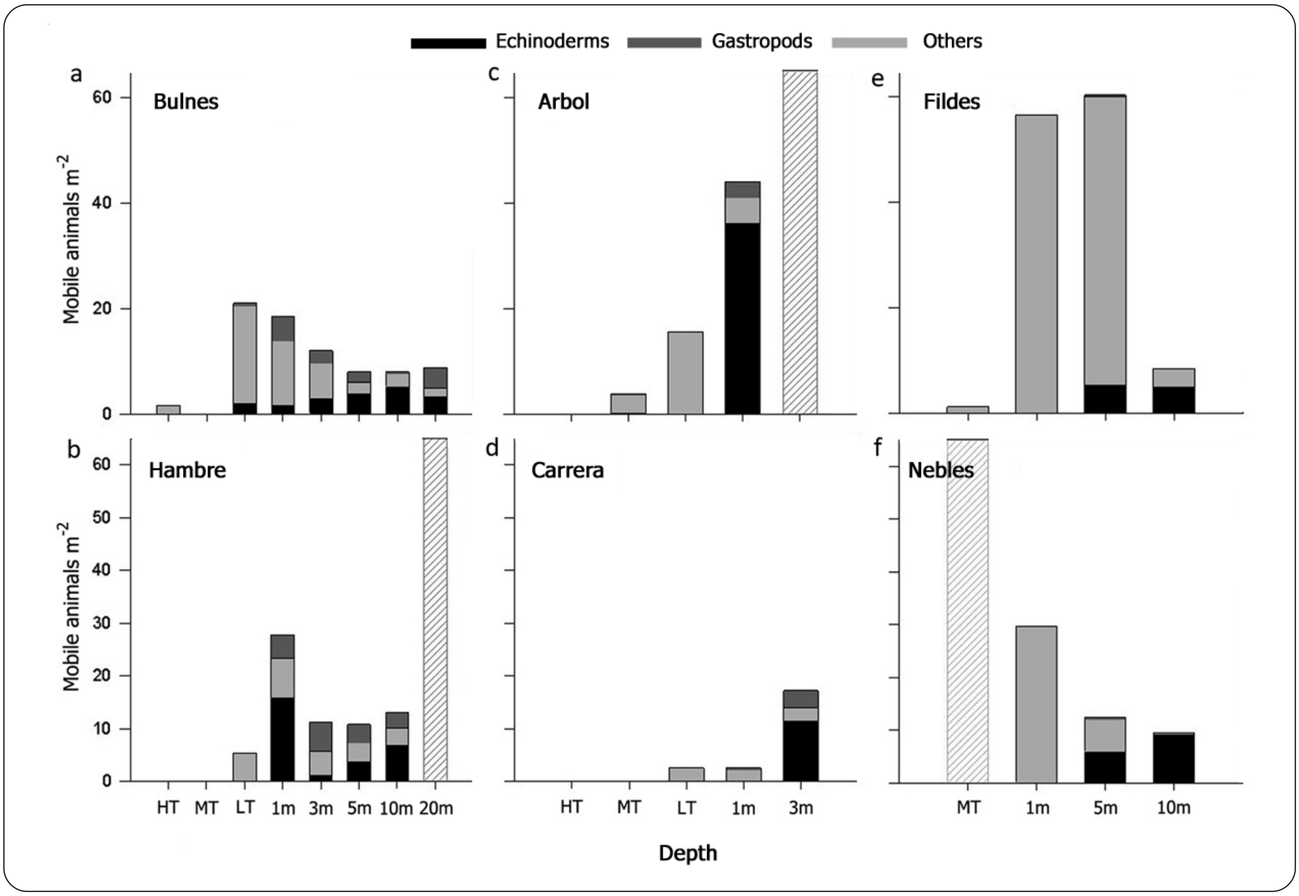

Figure 5. Number of mobile individuals (Gastropoda and Echinodermata) with increasing depth at sites in the Magellan Strait (a-d) and the South Shetland Islands, Antarctica (e, f). Grey striped bands indicate data not collected / Número de individuos móviles (Gastropoda y Echinodermata) en relación al aumento de la profundidad en sitios del Estrecho de Magallanes (a-d) e Islas Shetland del Sur, Antártica (e, f). La barra gris con bandas indica datos no colectados

Clear differences in community structure of sessile assemblages (across all intertidal or subtidal depths) between regions were identified by the nMDS (ANOSIM Global R: 0.85 P = 0.05; Fig. 6). Differences between sites were highest in Antarctica, while Magellan Strait sites were grouped into pairs for subtidal assemblage data. The composition of sessile assemblages differed significantly between sites across studied levels/depths (ANOSIM Global R: HT = 0.52, MT = 0.35, LT = 0.56, 1 m = 0.48, 3 m = 0.45, P = 0.001; 5 m = 0.43, 10 m = 0.55, P = 0.01). Pairwise tests showed high dissimilarities between Punta Carrera and Punta Arbol when compared to other sites in the Magellan Strait (Table 1), whereas Fuerte Bulnes and Puerto del Hambre showed significant differences in the subtidal from 3 to 10 m but not in the intertidal.

Several sessile taxa were responsible for dissimilarities between sites and levels/depths[3]. In Magallanes, the red algae *Porphyra* sp. was the most important species in terms of cover at high-tide while the cirripedian *Notochtamalus scabrosus* (Darwin, 1854), the bivalve *Perumytilus purpuratus* (Lamarck, 1819), and the macroalgae *Mazzaella laminarioides* were the most discriminant species at mid- and low-tide between sites. Percent cover of the kelp *Lessonia vadosa* was the main differentiator between sites at 1 m, as observed differences are explained by the absence of this species at Punta Arbol and Punta Carrera. Dissimilarities between Fuerte Bulnes and Puerto del Hambre at 10 m were mainly caused by differences in coverage of encrusting corallines and *Macrocystis pyrifera*[3]. This species was more abundant at this depth at Fuerte Bulnes, while *Gigartina*

[3]Appendix 2. Detailed analyses available by email from authors.

Table 1. ***R* values of pairwise tests for comparisons between sessile assemblages at different sites studied in the Magellan Strait. (* = significant differences). High (HT), medium (MT) and low tide (LT) levels** / Valores *R* de las pruebas de comparación pareadas entre ensambles sésiles de diferentes sitios estudiados en el Estrecho de Magallanes (* = diferencias significativas). Niveles de alta (HT), media (MT) y baja marea (LT)

	Puerto del Hambre		Punta Arbol		Punta Carrera	
Fuerte Bulnes	HT	0.05	HT	0.54*	HT	0.61*
	MT	0.02	MT	0.06	MT	0.64*
	LT	0.05	LT	0.56*	LT	0.55*
	1 m	0.15	1 m	0.91*	1 m	0.59*
	3 m	0.63*			3 m	0.2
	5 m	0.43*				
	10 m	0.55*				
Punta Carrera	HT	0.67*	HT	0.90*		
	MT	0.77*	MT	0.56*		
	LT	0.36*	LT	0.33*		
	1 m	0.62*	1 m	0.08		
	3 m	0.51*				
Punta Arbol	HT	0.62*				
	MT	0.21*				
	LT	0.33*				
	1 m	0.77*				

skottsbergii and *Lessonia flavicans* were more abundant at Puerto del Hambre.

Significant differences in sessile community structure were found between sites along depths in Antarctic sites (Table 2). Observed differences at 1 m across sites were caused by differences in abundance of encrusting corallines and red turf algae, which accounted more than 62% of dissimilarities between sites. Dissimilarities at 5 m and 10 m are explained by the higher abundance of the bryozoan *Inversiula nutrix* Julien, 1888 and the brown algae *Desmarestia* sp. at Nebles Point[3]. These species together contributed ~55% of the differences at 5 and 10 m. All comparisons showed high dissimilarities between sites with 40% + dissimilarity of community composition[3].

No differences were shown in the composition of mobile assemblages between sites across intertidal levels in the Magellan Strait (ANOSIM R > 0.1 $P = 0.1$), however, significant differences were found between sites across most subtidal depths (ANOSIM Global *R*: 1 m = 0.54, 3 m = 0.49, 10 m = 0.48; 5 m ≥ 0.1 $P = 0.1$; Table 3). Differences in the shallows were mainly due to the higher abundance of *Pseudechinus magellanicus* at Puerto del Hambre and Punta Arbol compared with the other sites[3]. At 10 m, the

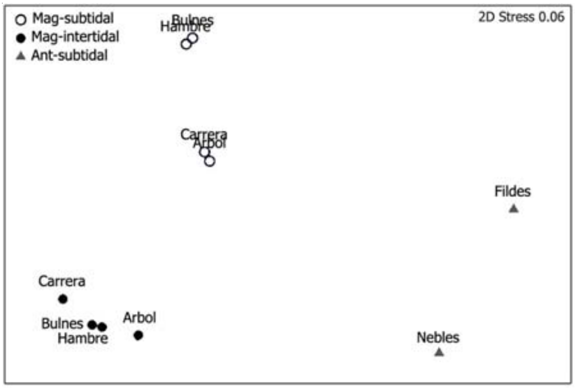

Figure 6. Non-metric multidimensional scaling (nMDS) ordination of sessile assemblages (including macroalgae) across regions (symbols) and sites (labels). Plot is based on a Bray-Curtis similarity matrix. Centroids represent site averages / Escalamiento multidimensional no-métrico (nMDS) de ensambles sésiles (incluyendo macroalgas) entre regiones (símbolos) y sitios (rótulo). El gráfico está basado en un matriz de similitud de Bray-Curtis. Centroides representan valores promedios por sitio

Table 2. ***R* values for comparisons between sessile and mobile assemblages at different sites studied in Antarctica. (* = significant differences)** / Valores *R* para las comparaciones entre ensambles sésiles y móviles de diferentes sitios estudiados en Antártica (* = diferencias significativas)

		Nebles Point
Sessile		
Fildes Bay	1 m	0.35*
	5 m	0.50*
	10 m	1.00*
Mobile		
Fildes Bay	1 m	0.22
	5 m	0.42*
	10 m	0.49*

sea urchins *P. magellanicus* and *Arbacia dufresnii* (Blainville, 1825) constituted the majority of between-site differences as *P. magellanicus* was more abundant at Puerto del Hambre while *A. dufresnii* dominated at Fuerte Bulnes. At Antarctic sites, differences increased with depth (Table 2). Differences were produced mainly by changes in abundance of *N. concinna* between sites in the shallows, and echinoderms at 5 and 10 m depth[3].

Table 3. *R* **values of pairwise tests for comparisons between mobile assemblages at different sites studied in the Magellan Strait (* = significant differences) /** Valores *R* de las pruebas de comparación pareadas entre ensambles móviles de diferentes sitios estudiados en el Estrecho de Magallanes (* = diferencias significativas)

	Puerto del Hambre		Punta Arbol		Punta Carrera	
Fuerte Bulnes	1 m	0.34*	1 m	0.55*	1 m	0.87*
	3 m	0.05			3 m	0.73*
	10 m	0.48*				
Punta Carrera	1 m	0.86*	1 m	0.75*		
	3 m	0.63*				
Punta Arbol	1 m	0.18				

Discussion

Subtidal reef communities have been described in most temperate and boreal regions (Schiel & Hickford 2001), but data from the world's most extensive subantarctic coastline is scarce. Here we presented benthic assemblage data (organisms > 2 cm^2) from easily accessible sites in Magallanes and the South Shetland Islands.

Despite substantial *M. pyrifera* forests at each site, and a similar aspect and exposure across sites, subtidal sessile benthic assemblages within Magallanes varied as much as in Antarctic sites. High heterogeneity in fauna directly associated with *Macrocystis* in Magallanes has been found by other researchers (Adami & Gordillo 1999, Ríos *et al.* 2007) and Benedetti-Cecchi and Cinelli (1997) found high between-site heterogeneity in intertidal assemblages along the Magellan Strait. At our sites in Magallanes, however, there was high similarity in community composition within each of two pairs of sites with similar physical characteristics. Fuerte Bulnes and Puerto del Hambre are close to each other, and both have reef extending to over 20 m depth. Punta Arbol and Punta Carrera are located either side of the Bulnes-Hambre site pair, and at both sites reef gives way to sand at < 5 m depth. Landscape factors could drive differences in community structure any number of ways, from hydrodynamics or ecosystem boundaries mediating food or nutrient supplies, to scouring by adjacent sands, through to predator refuge or access.

Subtidal community composition was very different at our two Antarctic sites. The dominant macroalgae was *Himantothallus grandifolius* at Fildes Bay, and *Desmarestia* spp. at Nebles Point. These macroalgae are often found at deeper and shallower sites respectively, a pattern ascribed to different disturbance histories (Dayton 1990, Klöser *et al.* 1996, Clark *et al.* 2011). Our sites differed in many factors which may drive differences in community structure, and limited spatial replication disallowed any analysis of causal factors in between-site differences. Factors such as type and inclination of the substrate, ice impact and water turbulence may result in the dominance of *Desmarestia* or *Himantothallus* over the other (Klöser *et al.* 1996). The sites have similar relief, but Nebles Point was closer to the Collins Glacier, and communities may therefore be expected to show the effects of more severe ice damage (Klöser *et al.* 1996, Dayton 1990, Gutt 2001). *Desmarestia* dominance may indicate higher disturbance (Dayton 1990, Clark *et al.* 2011), however many of these plants appeared well established, and had thick stipes and large complex holdfasts. While Clark *et al.* (2011) also suggested that the higher sponge abundance and diversity under *Himantothallus* may indicate a more stable community; we found a higher abundance and diversity of sponges under *Desmarestia*. Moreover, at depth (10 m) the substrate at Fildes Bay site was more broken up than the solid bedrock found at Nebles Point. Again this may be causal of variation in benthic assemblages (Klöser *et al.* 1996, Smale 2008) but is in conflict with the theory that *Himantothallus* is associated with more stable environments.

Many described shallow benthic communities from the Antarctic Peninsula have been dominated by encrusting organisms (Barnes 1995, Bowden 2005, Smale 2008) rather than seaweed-dominated, although robust and diverse macroalgal communities are known (Quartino & Boraso de Zaixso 2008). The sites we describe have substantial seaweed cover from only 5 m depth. The dominance of large perennial subtidal seaweeds that form dense cover is a key element of community structure that is shared between these Antarctic and the Magellan Strait rocky reef communities. Large macroalgae can play a fundamental role in the distribution patterns and diversity of other organisms modifying physical factors such as light or water movement (Reed & Foster 1984, Bulleri *et al.* 2002). The abundance of large macroalgae is likely an important aspect of the production and fate of primary productivity within these benthic systems. Macroalgae can be substantial contributors to local primary productivity in the South Shetland Islands, and can reach biomasses of greater than 10 kg m^{-2} wet weight (Quartino & Boraso de Zaixso 2008). Furthermore secondary productivity will be strongly affected by seaweed-dwelling crustacea (Taylor 1998) which can reach densities of at least 3750 and 10, 600 kg (wet weight) $seaweed^{-1}$ in the Magellan Strait and Fildes Bay respectively, and constitute a biomass of at least 4.6 and 5.4 g AFDW kg (wet weight) $seaweed^{-1}$ (Newcombe, unpubl. data).

Our findings (across rocky substrate) do not support the pattern of higher species richness with increasing depth (and changing substrate) found by Ríos (2007) for benthic communities in Magallanes. At our Antarctic sites we found increasing species richness with increasing depth, consistent with past findings from Antarctica, an effect generally attributed to the decrease in ice damage with depth (Barnes 1995, Smale 2008).

Ice is a major force structuring Antarctic benthic communities (Barnes 1995, Gutt 2001, Smale 2008) but at our sites there was little evidence of recent ice damage below 5 m depth (it is likely that prevailing winds or storms cause greater iceberg damage on the west-facing coasts). In the shallows (< 5 m to intertidal), sessile growth is limited largely to relatively fast-growing algal taxa, whereas at 10 m, sessile invertebrate such as bryozoans, encrusting and massive sponges are more abundant. In the Magellan Strait the surface canopy of *Macrocystis pyrifera* apparently limits the growth of understory algae, most likely due to shading (Reed & Foster 1984, Graham *et al.* 2007). Ice damage in Antarctica, and shading by *Macrocystis* in Magellan Strait are likely strong structuring factors in their respective communities, which would need to be considered when comparing community characteristics with increasing depth.

Variation in structure and species dominance means that care needs to be exercised in site selection for future studies. Further detailing of sites by other researchers would build up a substantial base for development of future studies in what could be a useful site in latitudinal studies, or as a comparative system to northern hemisphere sites. Accessible sites in Magallanes and the South Shetland Islands present prime opportunities to extend ecological studies of seaweed forests to southern latitudes. The provision of basic benthic assemblage and community structure descriptive data is an important precursor to the development of more ecological studies in these areas. Key ecological questions to be addressed in these systems include the causes of *Desmarestia* or *Himantothallus* dominance on Antarctic reefs, and the role of landscape in driving structural differences in Magallanes. Annual cycles of productivity in Magallanes may be informative in comparison with Antarctic seasonal dynamics.

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