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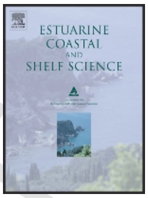

Life between tides: Spatial and temporal variations of an intertidal macroalgal community at Potter Peninsula, South Shetland Islands, Antarctica

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ABSTRACT

Intertidal zones are one of the most studied habitats in the world. However, in Antarctica, further studies are needed for a more complete understanding of these systems. When conspicuous Antarctic intertidal communities occur, macroalgae are a key component. Given that intertidal communities have a fast response to variations in environmental conditions and could reflect climate fluctuations, we conducted a non-destructive study with photographic transects in an intertidal zone at Potter Peninsula, Isla 25 de Mayo/King George Island, over four years and during five months of the warm season. We tested the general hypothesis that macroalgal intertidal communities are mainly structured by the vertical stress gradient and that changes in temperature between seasons and between years have a great influence in the macroalgal community structure. Spatial, seasonal and inter-annual variations were studied using GLM, quantile regression and NMDS ordinations. The vertical stress gradient was the main factor that explained macroalgal cover. The Low and the Middle level shared similarities, but the latter was more variable. The High level had the lowest cover, richness and diversity. The dominant species here was the endemic red alga *Pyropia endiviifolia*, which is strongly adapted to extreme conditions. At the Middle level, there was a significant increase in macroalgal cover during spring months, and it stabilized in summer. Inter-annual variations showed that there is a strong variation in the total macroalgal cover and community structure over the studied years. Environmental conditions have a significant effect in shaping the studied intertidal community, which is very sensitive to climate oscillations. An increase in temperature produced a decrease of annual ice foot cover, number of snow days and - as a result - an increase in macroalgal cover. In a global climate-change scenario, a shift in species composition could also occur. Species with wide physiological tolerance that grow in warmer conditions, like *Palmaria decipiens*, could benefit, while other species will be discriminated. More detailed studies are necessary to predict future changes in Antarctic intertidal communities.

1. Introduction

Macroalgae have a fundamental role in Antarctic benthic communities as they are important primary producers, the direct source of food for consumers associated with benthos (Iken, 1999; Amsler et al., 2005), and contribute significantly to particulate and dissolved organic matter (Reichardt and Dieckmann, 1985; Iken, 1999). Some macroalgal thalli generate microhabitats that provide structural and chemical refuge from predation and reduce water movement (Jenkins et al., 1999; Takeuchi and Watanabe, 2002; Huang et al., 2007). Moreover, they can also act as a substrate for epiphytic diatom communities (Al-Handal and Wulff, 2008; Majewska et al., 2016).

Intertidal habitats are among the most studied environments in the world (Underwood, 2000). However, there is little information on Antarctic intertidal macroalgal assemblages (Kim, 2001). Initially, studies consisted of a list of species or a description of the vertical zonation pattern in qualitative terms (DeLaca and Lipps, 1976; Heywood and Whitaker, 1984; Zielinski, 1990). Few studies have focused on the structure of these communities in relation to environmental or ecological drivers (Kim, 2001; Zacher et al., 2007a,b; Valdivia et al., 2014; Martín et al., 2016). Moreover, most intertidal studies at the Western Antarctic Peninsula focus on zoobenthos (Barnes et al., 1996; Barnes and Conlan, 2007; Waller, 2008; Bick and Arlt, 2013; Martín et al., 2016), which are important components of the communities at this region.

Antarctic intertidal habitats are certainly among the ecosystems with the greatest physical disturbance of the world due to ice foot formation in winter, ice scouring, high ultraviolet radiation and extreme temperature and salinity values (Barnesa, 1999; Peck et al., 2006). Hence, Antarctic intertidal communities are rare, but can be found in

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sheltered locations where there is no ice formation during the warm season (Wulff et al., 2009).

Antarctic seaweeds are almost entirely subtidal, as in the intertidal zone physical conditions are much more extreme (Wiencke et al., 2006). They are adapted to constant low temperatures and a strong seasonality of the light regime (Wiencke and Amsler, 2012). These algae present two life growth strategies: seasonal anticipators and seasonal responders *sensu* Kain (1989). Seasonal anticipators start growing early in winter and spring, under non-optimal light conditions, and can even reproduce in winter. Their maximal growth rate occurs in spring (Wiencke et al., 2006). Most season anticipators are endemic, which is probably an adaptation to the seasonally changing conditions in polar seas (Wiencke and Amsler, 2012). On the contrary, seasonal responders are opportunists; when conditions become favorable they start to grow and reproduce (Wiencke and Clayton, 2002). When intertidal habitats are conspicuous, macroalgae are dominant components of these ecosystems (Kim, 2001). Previous studies have focused on the variation of the community at a spatial scale (Valdivia et al., 2014). However, ecological studies over a long-term period are still very much needed to establish a baseline of the variability at a temporal scale in accordance to macroalgal life strategies of this region.

The following hypotheses have driven our investigation; macroalgal intertidal communities are mainly structured by the vertical stress gradient and, changes in temperature between seasons and between years have a great influence in the macroalgal community structure.

Thus, our aim in this study was: Firstly, to analyze the composition of an intertidal macroalgal community. Secondly, to evaluate the community structure over a vertical stress gradient. Thirdly, to evaluate monthly community changes within the warm season. Finally, to investigate the inter-annual variations in the community in a long-term period (four warm seasons).

2. Methods

2.1. Study site

The study was carried out at an intertidal rocky site at Peñón Uno (62° 14′S, 58° 38′W), Potter Peninsula (62° 14′S, 58° 38′W, Fig. 1a), situated at approximately 1.5 km away from Carlini Station (Fig. 1b). Potter Peninsula is the Antarctic Specially Protected Area Nº143. The Environmental and Tourism Antarctic Management Program of the National Direction of the Antarctic (*Dirección Nacional del Antártico*) in the Argentine Republic, has granted the appropriate permission for all the stages of this research in this site (under art. 7, Annex V of the Madrid Protocol, Law 25260). This permission complied with the regulations in force.

In general, Potter Cove surface waters and its coastal zones freeze from July to October, when sea ice cover breaks up and icebergs reach the shore (Schloss et al., 2012). Peñón Uno is covered with ice and snow from March to October (Pers. obs. 2007, 2009, 2013). In 2008, ice foot lasted until September. Sampling was performed during the austral spring and summer from 2007 to 2013.

There is a conspicuous and well established macroalgal assemblage at the intertidal zone on Peñón Uno. The study site consists on basaltic and andesitic lava flows from the tertiary (Kraus and del Valle, 2008). The intertidal zone is composed of predominantly solid rock, boulders, pebbles and gravel.

The tide regime is mixed, predominantly semidiurnal. The mean amplitude of syzygy tides is 148 cm and of quadrature tides is 120 cm (Schoene et al., 1998). The intertidal zone is suitable for sampling only for a 2–3 days period per month during the extreme low tides (National Meteorological Service of Argentina, SMN).

The light conditions of the area have been described in Richter et al. (2008) and Zacher et al. (2007b). Maximum atmospheric photo-

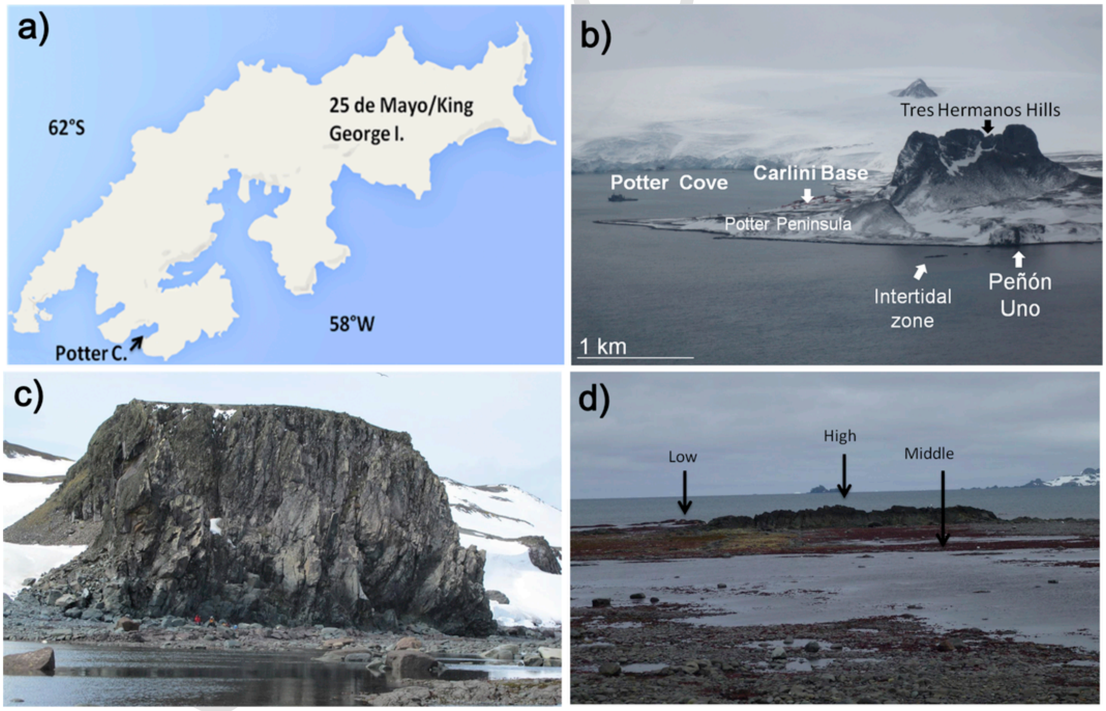

Fig. 1. Study site. a) Isla 25 de Mayo/King George Island, South Shetland Islands and the location of Potter Cove. b) Aerial view of Potter Peninsula showing location of Peñón Uno and Carlini Scientific Station (Arrows). c) Peñón Uno. d) Intertidal zone at the base of Peñón Uno with three levels.

synthetically active radiation (PAR, 400–700 nm) and UV radiation (UVR, 320–400 nm) are usually recorded for late spring-early summer (Zacher et al., 2007b). For the same study site, earlier studies showed mean PAR values of 1136 ± 327 μmolm^{-2}s^{-1}, mean UVA of 24.1 ± 12.6 W m^{-2} and mean UVB of 1.4 ± 0.7 W m^{-2} above surface, between December and February (Zacher et al., 2007b). On average, 30% of PAR, 13% of UVA and 7% of UVB can reach 2 m depth (i.e., approximately the maximum depth at high tide) at Peñón Uno (Zacher et al., 2007b).

2.2. *Sampling*

Three intertidal levels (Low, Middle and High) were identified according to the vertical gradient of tides. The Middle and Low levels are separated by a continuous rocky promontory of different composition (entirely solid rock). This large rock was considered the High level (Fig. 2) and it was almost entirely represented by the red alga *Pyropia endiviifolia*. The upper limit of species distribution is an appropriate indicator of the High level (often extended to the "spray zone"). The use of this species as an indicator has been broadly consented for the whole of the Antarctic shores (Harley and Helmuth, 2003; Wiencke et al., 2006).

Samplings were performed using a 50 × 50 cm quadrat (supplementary data), which was subdivided into 100 smaller sub-quadrats (5 × 5cm). Community structure depends on scale and quadrate sampling has been proven to be accurate to demonstrate differences in community structure (Valdivia et al., 2011, 2014).

A systematic sampling was performed (Krebs, 1989), always starting at the Low level in order to be able to cover a representative area of the three levels. Transects were placed parallel to the shore and the first quadrat was randomly selected. Each quadrat was separated by 3 m, as well as each transect. The High level had one transect in the superior face of the rock and a few quadrats randomly placed on the lateral faces of the rock. Fifteen photographs from the Middle level where randomly selected from the pool of photographs taken every year given the extent of this zone, and given the need to compare similar number of quadrats between the three levels. To assess spatial and inter-annual differences, sampling was performed in late December or early January on four years (2007, 2008, 2009, 2013), which were less than 20 days apart. To assess temporal differences we made monthly samples from October 2008 to February 2009 ("Warm season 2008–2009" here on). Sampling from 2010 to 2012 were not complete for the Low level due to weather conditions. The intertidal zone can be sampled only in extreme low tides once or twice a month, and given the strong wind during those days, significant sampling could not be met.

We took two photographs to each quadrat for species identification and its cover, with a digital camera Canon Powershot G11 with a 28 mm lens. Macroalgae were identified according to Wiencke and Clayton (2002) to the lowest possible taxonomic level. We counted the number of limpets *Nacella concinna* (Patellidae, Gastropoda), which is the most abundant benthic macroinvertebrate in the study site. The photographic sampling technique allowed us to take many samples precisely and quickly, which is fundamental in a harsh envi-

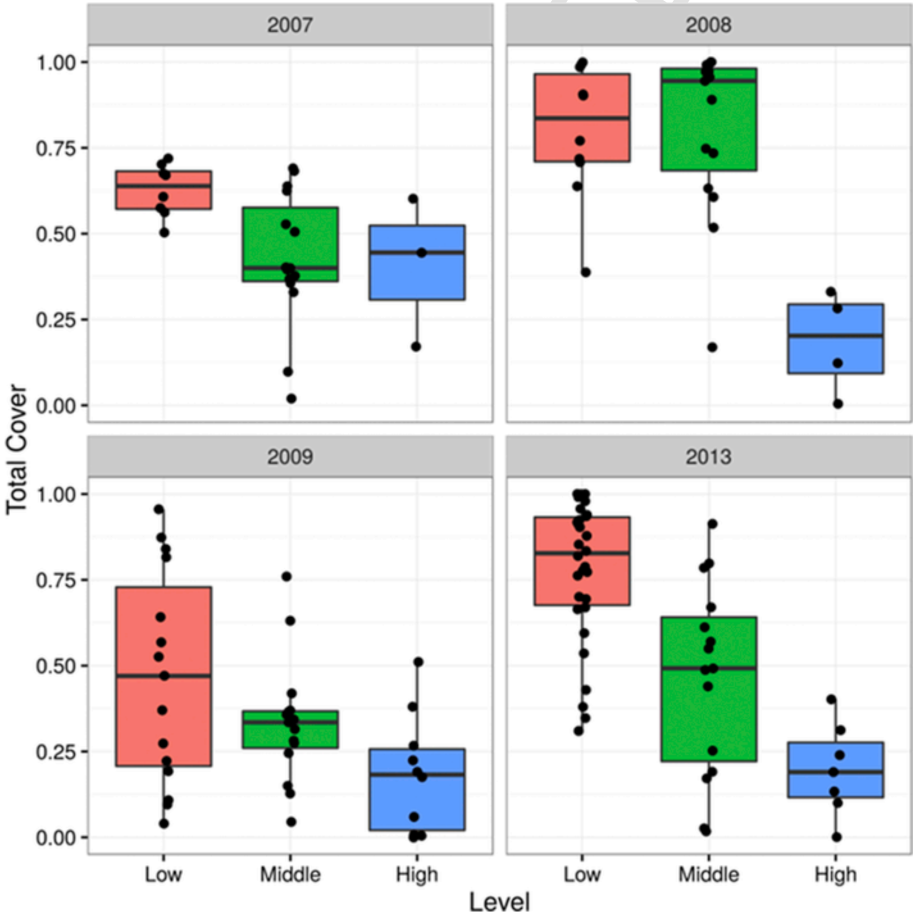

Fig. 2. Boxplot for total macroalgal cover (%) per year and intertidal level.

ronment like an Antarctic intertidal zone. We validated the method using eye inspection to verify that there was no significant over-layering. In some cases, accurate taxonomic identification of seaweed individuals was difficult. This was compensated by field notes and by collecting samples for later identification in the laboratory. This technique has been proven to be highly accurate and has been extensively used in several studies (Beuchel et al., 2006; Peck et al., 2006; Quartino et al., 2013).

Environmental data were obtained from the National Meteorological Service of Argentina; annual number of snow days, average spring temperature and average summer temperature. Annual number of days with ice foot was informed by overwintering scientists in the years of this study.

2.3. *Community characterization*

Percentage cover of species was estimated by analyzing the digital photographs. The minimum percentage cover assigned to a species in a sub-quadrat was 0.25%. We also characterized the community using ecological indexes: diversity, richness and evenness; calculated for each quadrat. Diversity was determined by the Shannon index: $H = \sum p_i \log_2 p_i$ where p_i is the relative abundance of taxon i in the quadrat and evenness was calculated using Pileous Index as $J = H/\log_2 S$. Richness (S) was the total number of species in each quadrat.

2.4. *Statistical analysis*

For total cover and diversity indexes we used Generalized Linear Models (GLM) and quantil regression. We analyzed the changes in the community structure using multivariate techniques for species cover.

Differences among tidal levels for percentage cover were compared using GLM (Crawley, 2013), and for richness, diversity and evenness we used Kruskal Wallis tests. The total macroalgal percentage cover data was transformed to a proportion and a binomial distribution was chosen. The possible explanatory variables tested were: year, number of limpets and intertidal level. The number of quadrats for each intertidal level was: Low = 63, Middle = 60, High = 24. These correspond to combined data of four years.

To analyze species composition patterns, we built a similarity matrix using the Bray-Curtis distance of taxa relative abundance and then applied non-metric multi-dimensional scaling (NMDS) ordinations. The High level was not incorporated in the matrix, given that it shared no species with the other levels for this data set. We fitted explanatory variables into the ordination space by projecting biplot vectors for continuous data or calculating centroids for discrete factors. The vectors represent the directions of the maximum variation and the centroids are the central location of the data. To visualize groups, we showed the convex hulls, which are the smallest area encompassing total variation of the observations and the standard ellipses, which are the bivariate version of the standard deviation and are insensitive to outliers (Jackson et al., 2011). The statistical significance is based on 999 random permutations of the variables or factor levels. The ordination analysis and vector fitting were produced using the R Vegan package (Oksanen et al., 2015).

Differences in the community structure between seasons were tested separately for Middle and Low level. Quantile regressions were performed since the GLM assumptions could not be met for this data set. This technique allows the examination of the maximum response of one variable to a predictor, rather than the average one (Cade and Noon, 2003). The total macroalgal percentage cover was the response variable, and the explanatory variables tested were: month, average monthly temperature, number of snow days per month, richness and evenness. Shannon diversity was highly correlated with evenness and, thus, it was not included. As several univariate tests were performed, p-values were adjusted by a sequential multiple test procedure (Hommel, 1988). NMDS ordinations were constructed to visualize species composition patterns using the explanatory variables as factors.

To see if there were inter-annual differences in community structure, the same procedure described above was performed. We used the Middle level summers' sampling of the four years. We looked for differences in the Middle level because it was the most variable in the intertidal zone. The explanatory variables were: year, richness, evenness, number of limpets, average summer temperature, average spring temperature, annual number of snow days and annual number of days with ice foot. Most of the environmental variables were highly correlated.

All statistical analyses were performed using the R statistical software R 3.1.2 (R Development Core Team, 2015) and scripts and output files available at figshare (https://dx.doi.org/10.6084/m9.figshare.3187483.v2) .

3. Results

3.1. *Macroalgal community*

Fifteen macroalgal taxa were found (Table 1, Fig. 3): eight Rhodophyta, five Ochrophyta and two Ulvophyta. In the four summer samplings, the Low and Middle level presented at least 11 and 10 of the 15 taxa respectively, while the High level presented only three taxa. In Warm Season 2008–2009 samplings, four more taxa were observed: *Desmarestia antarctica* in Middle level in summer, *Curdiae racovitzae* at Low level in both seasons, Delesseriaceae spp. at Low level and *Plocamium cartilagineum* at Middle level, both in spring. On late summer (February 2009), *Adenocystis utricularis* appeared on the lateral sides of High level rocky promontory.

3.2. *Spatial characterization*

The community structure of Peñón Uno showed differences between levels (Table 2, Figs. 2 and 3). The Low level presented more total percentage cover than the Middle level, except in 2008 (Fig. 2). In general, the High level presented the lowest macroalgal percentage cover. It had also the lowest richness, diversity and evenness, and showed significant differences with the other levels (Table 2, Figs. 2 and 3). The Middle level presented higher values of total cover, diversity and richness, but there were no significant differences with the Low level. Evenness was the only community-structure feature that had significant differences between the three levels, being highest in the Middle level.

The Low level had 79.4% of non-endemic species, the most abundant were *Iridaea cordata*, followed by *A. utricularis*, the Corallinaceae family and others (Fig. 3). The remaining 20.6% was composed by endemic species with *Phaeurus antarcticus* as the predominant species. The Middle level was almost entirely composed by non-endemic species (98.1%) such as *I. cordata* (35.9%), *Palmaria decipiens* (27.6%), *A. utricularis* (23.1%), Corallinaceae (7%) and *Monostroma hariotii* (4.5%) (Fig. 3). Finally, the endemic red alga *P. endiviifolia* was dominant and almost monospecific of the High level (Fig. 3).

In GLM models, intertidal level was the only significant factor to explain macroalgal cover (Low:Middle $p = 0.048$, Low:High $p = 0.0004$, High:Middle $p = 0.03$, supplementary data). Following

Table 1
List of species (Guiry and Guiry 2016) found in the intertidal zone and at each level.

Phylum	Class	Taxon	Abbreviation	Intertidal level		
				Low	Middle	High
Rhodophyta	Bangiophyceae	*Pyropia endiviifolia* (A.Gepp & E.Gepp) H.G.Choi & M.S.Hwang 1963[a]	Pyr.end.	–	–	X
Rhodophyta	Florideophyceae	Corallinaceae[b]	Cor.spp.	X	X	–
		Curdiea racovitzae Hariot 1900[a]	Cur.rac.	X	–	–
		Gigartina skottsbergii Setchell y N.L. Gardner 1936	Gig.sko.	X	–	–
		Iridaea cordata (Turner) Bory de Saint-Vincent 1826	Iri.cor.	X	X	–
		Palmaria decipiens (Reinsch) R.W.Ricker 1987	Pal.dec.	X	X	–
		Plocamium cartilagineum (Linnaeus) P.S. Dixon 1967	Plo.car.	–	X	–
Ochrophyta	Phaeophyceae	*Adenocystis utricularis* (Bory de Saint-Vincent) Skottsberg 1907	Ade.utr.	X	X	X
		Ascoseira mirabilis Skottsberg 1907[a]	Asc.mir.	X	X	–
		Desmarestia menziesii J. Agardh 1848[a]	Des.men.	X	X	–
		Desmarestia antarctica R.L.Moe y P.C.Silva 1989[a]	Des.ant.	–	X	–
		Phaeurus antarcticus Skottsberg 1907[a]	Pha.ant.	X	X	–
Chlorophyta	Ulvophyceae	*Monostroma hariotii* Gain 1911	Mon.har.	X	X	–
		Ulotrichaceae/Ulvaceae[c]	Ulv.spp.	–	–	X

[a] Endemic.

[b] Probably two species.

[c] Probably Ulothrix sp. and *Urospora penicilliformis*.

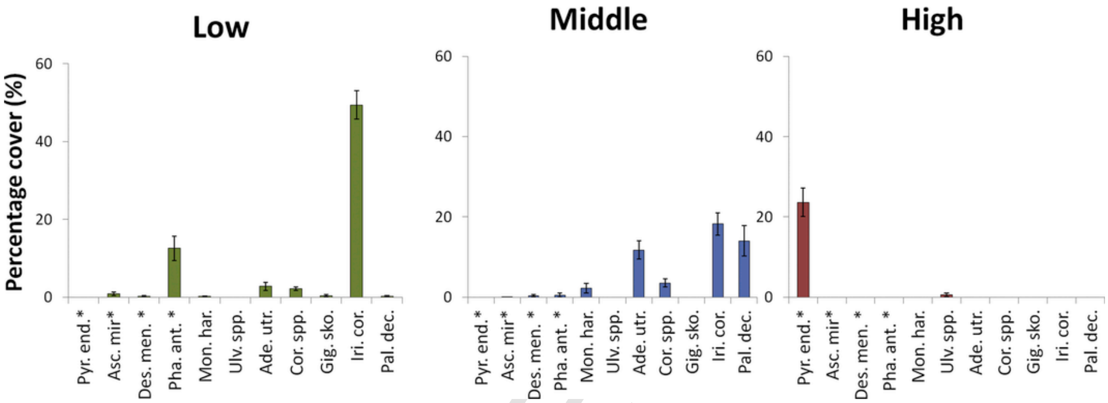

Fig. 3. Spatial taxonomic characterization. Sampling of the four years (2007, 2008, 2009 and 2013) combined. Percentage cover (%) ± SE for each species on three intertidal levels. From left to right: Low (green), Middle (blue) and High level (red). *endemic. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Mean ± Statistical Error of total macroalgal cover (C), richness (S), diversity (H′) and evenness (J') of the intertidal zone: Low, Middle, and High level and Tukey post-hoc pair comparisons test. Sampling of the four years (2007, 2008, 2009 and 2013) combined. **p > 0.05 ***p > 0.005.

	C	S	H′	J′
Low	68.70 ± 3.23	3.24 ± 0.15	0.62 ± 0.05	0.36 ± 0.03
Middle	50.89 ± 3.69	3.03 ± 0.13	0.81 ± 0.06	0.50 ± 0.04
High	21.28 ± 3.47	1.13 ± 0.11	0.13 ± 0.06	0.13 ± 0.06
Low–Middle	0.1	0.7	0.07	0.01**
Low–High	0.001**	<1*e-04***	<0.001***	<0.001***
Middle–High	0.07	<1*e-04***	<0.001***	<0.001***

NMDS ordination, the variations of the community structure were significantly explained ($p < 0.05$) by three variables, in decreasing order of importance: total cover ($R^2 = 0.46$, $p = 0.001$), intertidal level ($R^2 = 0.21$ $p = 0.001$), and year ($R^2 = 0.19$ $p = 0.001$) (Fig. 4). The Middle and Low level shared similarities in community structure. However, the Middle was more variable (Fig. 4a). Although some species were present in both levels, the main difference found was that the cover for each species was different (Fig. 3) and that *P. antarcticus* and *Ascoseira mirabilis* appeared associated with the Low level, while *P. decipiens* was mainly present in the Middle level area (4b).

3.3. Seasonal characterization

3.3.1. Middle level

At the Middle level, total macroalgal cover increased significantly within the spring months, and then on summer there was no significant variation (Fig. 5). Most variation was found in October and November compared to summer months (Figs. 5 and 6).

Macroalgal cover was positively correlated with average monthly temperature, and negatively with the number of snow days per month (quantile regressions, supplementary data). October was the coldest month and the one with more snow days. NMDS ordinations showed that month was a significant factor that explained community composition and abundance (convex hulls). December and February were the most similar, their standard ellipses were overlapped (Fig. 6). Most species were not associated to a particular month. Only *I. cordata* appeared associated with October, whereas *P. decipiens* was found to be related to warmer months, when it increased its cover (Fig. 6b and supplementary data).

3.3.2. Low level

At the Low level the total cover was even throughout the warm season. There were no differences in the total cover among months

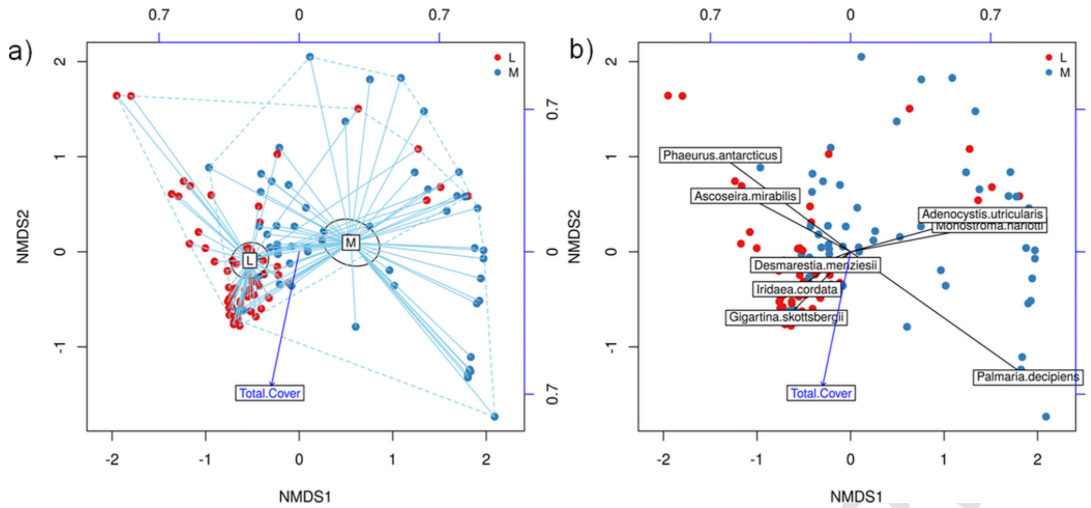

Fig. 4. Non-metric multi-dimensional scaling ordinations (NMDS) for the intertidal zone. Sampling of the four years (2007, 2008, 2009, 2013) combined. a) The ordinations show the centroids convex hulls and standard ellipses for intertidal levels and the fitted vectors are for the variables; total cover and intertidal level (blue). b) Species and vectors of environmental variables (blue arrows) fitted to the ordination. Dots represent single quadrats. Intertidal levels are L = Low, M = Middle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

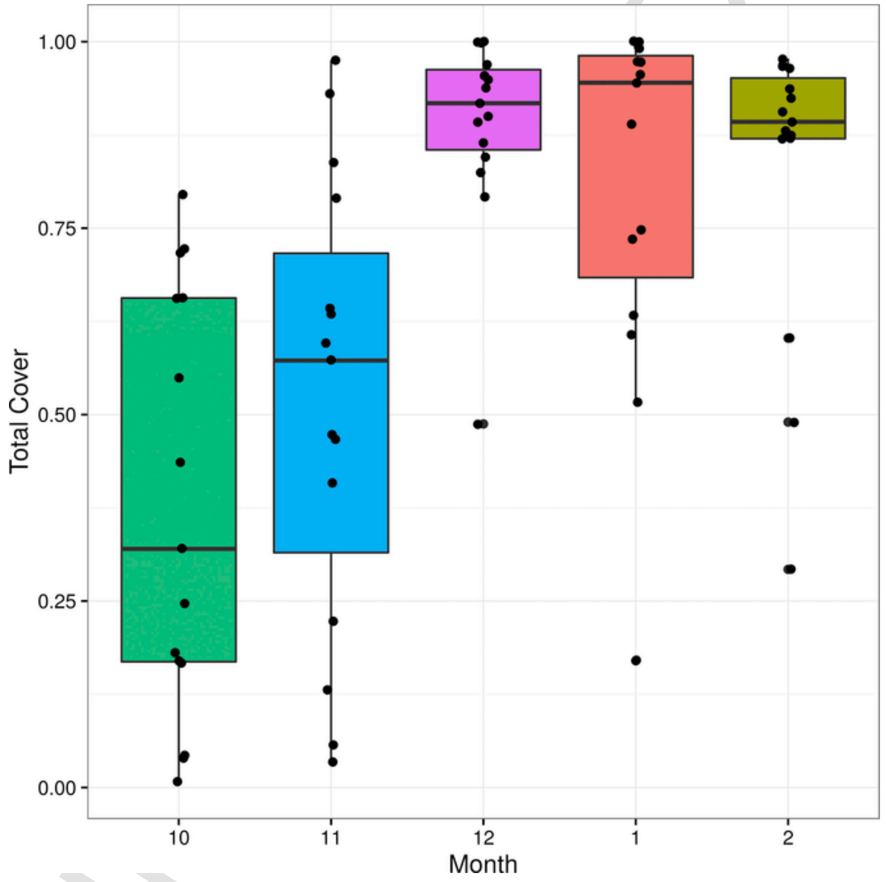

Fig. 5. Boxplot for total macroalgal cover per month in the Middle level. Warm Season 2008–2009. 10 = October, 11 = November, 12 = December, 1 = January, 2 = February.

(supplementary data) and macroalgal cover was positively correlated with average monthly temperature only at 0.25 quantile ($p = 0.04$). February appeared different from the rest of the months (supplementary data). Regarding macroalgal composition, a similar pattern to the Middle level was observed: month was a significant factor that explained community structure. The Corallinaceae family and *I. cordata* had less cover (the latter especially in February) whereas *M. hariotii*, *A. utricularis* and *P. antarcticus* increased their cover in summer months (the first two had a peak in February and *P. antarcticus* in January) (supplementary data).

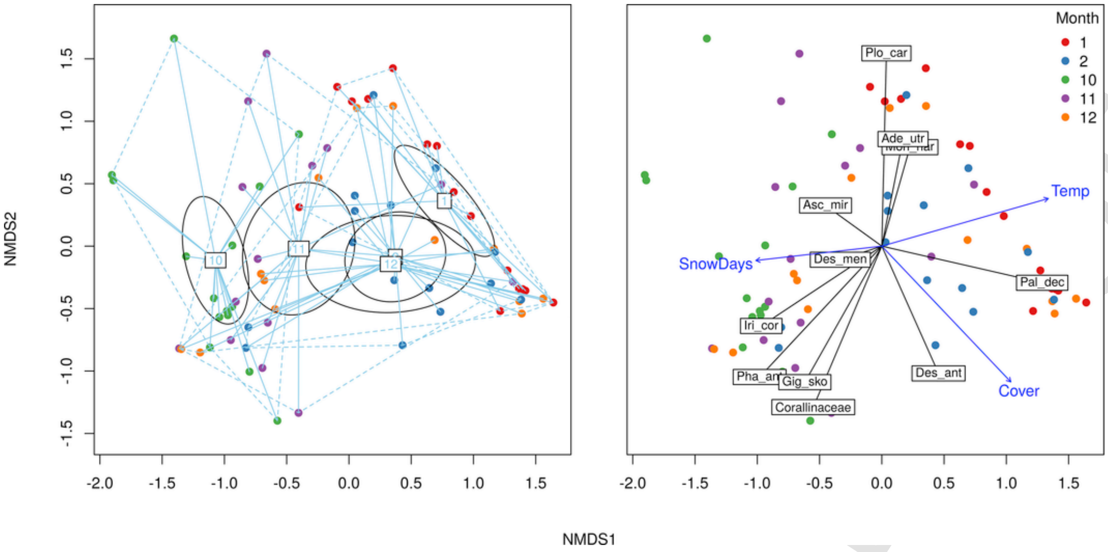

Fig. 6. Temporal scale NMDS ordinations in the Middle level. Warm Season 2008–2009. a) Standard ellipses and convex hulls per month of study from Warm Season 2008–2009. b) Species and vectors of environmental variables (blue arrows) fitted to the ordination. Dots represent single quadrats. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Inter-annual characterization

In the Middle level, macroalgal cover was significantly different among years (Fig. 7). Summer's average temperature was positively correlated with total macroalgal cover in the studied years (supplementary data). 2008 was the year with the highest total macroalgal cover, above 80% in the Middle level (Fig. 7) and also in the Low level (Fig. 2). It was also the year with less snow (119 days) and ice foot, and with the higher annual and seasonal temperature of

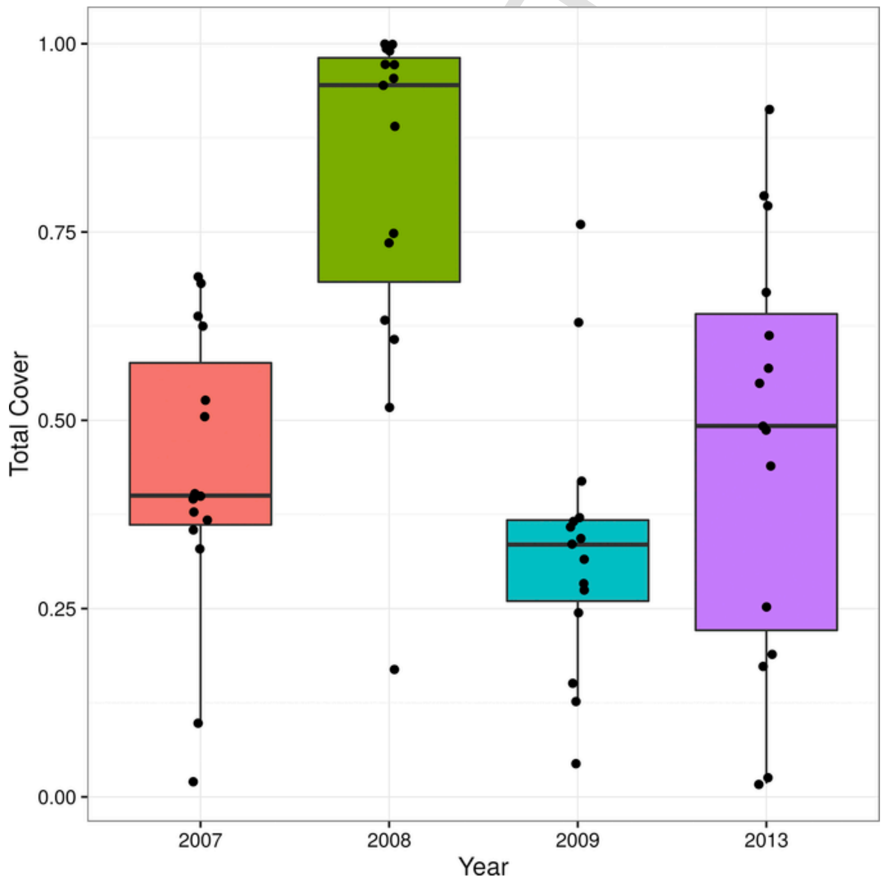

Fig. 7. Boxplot for Middle level total macroalgal cover per year. Sampling from summers 2007, 2008, 2009 and 2013.

the four years (supplementary data). NMDS ordinations showed that year was a significant factor to explain community structure. Regarding the explanatory variables (vectors), snow days and ice foot are in the opposite tendency with spring and summer average temperature (which are all correlated, Fig. 8). It also showed that 2008 was markedly different from the rest of the years, while the community structure was more similar in 2009 and 2013 (Fig. 8). The cover in the year 2008 was mostly characterized by *P. decipiens* (46%), *A. utricularis* (26.5%) and *M. hariotii* (6.2%), and only 1.6% of *I. cordata*, while 2009 and 2013 had 22 and 34% cover of this alga and the absence of *P. decipi*ens. The year 2007 was characterized by *I. cordata* (15.5%), *P. decipiens* (10.1%) and *A. utricularis* (12%) (Fig. 8, supplementary data).

4. Discussion

4.1. Spatial characterization

We found an intertidal with a conspicuous macroalgal community, similar to other intertidal rocky shores of Isla 25 de Mayo/King George Island (Kim, 2001; Valdivia et al., 2014), but different to most studied intertidal zones of other Antarctic regions, which mostly consist of ephemeral assemblages or species found in protected crevices (Amsler et al., 2005; Wulff et al., 2009).

Our findings showed a visible vertical zonation, with changes in species composition, and in community structure among intertidal levels. There was a decrease in macroalgal cover from the Low to the High level. The vertical stress gradient as main factor structuring the community is in agreement with most previous studies about intertidal communities (Menge and Branch, 2001) and previous studies in nearby areas (Valdivia et al., 2014). Total cover was the second factor in decreasing order of relevance; this implies that inter-specific algal interactions are also important in structuring the community (Menge and Branch, 2001). Year is the third factor, this shows that global environmental factors are important, these will be analyzed in the proper section.

The species composition and community structure is similar to other nearby areas; species like *I. cordata, P. decipiens, M. hariotii, A. utricularis, P. antarcticus*, *P. endiviifolia* are present and highly abundant in the intertidal zone (Kim, 2001; Martín et al., 2016; Valdivia et al., 2014). The number of macroalgal species found in this study per quadrat is similar to other studies (Kim, 2001; Valdivia et al., 2014). In Antarctica, macroalgal richness is low (Clayton, 1994; Wulff et al., 2009) which agrees with our findings.

The Low level presented species of the shallow subtidal habitat like the brown algae *P. antarcticus, A. mirabilis* and the red alga *I. cordata*, with presence of large individuals (Pers. obs). These algae generate a noticeable canopy layer among solid rocks. These species, together with *Desmarestia mensiezii* inhabit shallow waters, and are able to colonize the intertidal system (Kim, 2001; Quartino et al., 2001; Martín et al., 2016). This pattern agrees with a recent study of Valdivia et al. (2014) from several intertidal habitats in a nearby area.

In the Middle level, *I. cordata, P. decipiens*, *A. utricularis*, *M. hariotii* and the Corallinaceae family were the most abundant species. This coincides with other intertidal assemblages reported by Heywood and Whitaker (1984) and Westermeier et al. (1992). Species of the Middle and the High level are adapted to the intertidal zone, where conditions are more extreme, with high irradiance and constant low temperature, in comparison with the subtidal zone (Wiencke et al., 2006), as it was observed in our study. *Iridaea cordata* and *P. decipiens* inhabit tide pools and crevices and extend to the shallow subtidal zone (Wiencke et al., 2006). The geographic distribution of the Corallinaceae family and *I. cordata*, present even in the high latitudes of the Ross Sea, indicate that these macroalgae have a wide range of adaptation to different environmental conditions (Wiencke and Amsler, 2012). Plus, *P. decipiens*, *M. hariotii* and *A. utricularis* have physiological adaptations to the extreme conditions of the intertidal zone (Becker et al., 2011; Zacher et al., 2007b).

The High level showed the lowest values of abundance, richness, diversity and evenness, which agrees with the zonation pattern, as in this level the most unfavorable conditions prevail (i.e. heat and desiccation), and it is at the end of the vertical gradient of physical conditions (Raffaelli and Hawkings, 1996; Menge and Branch, 2001). The endemic red alga *P. endiviifolia* was dominant, and was occasionally accompanied by filamentous green algae that could not be identified, but most likely corresponded to *Ulothrix* sp. and *Urospora penicilli-*

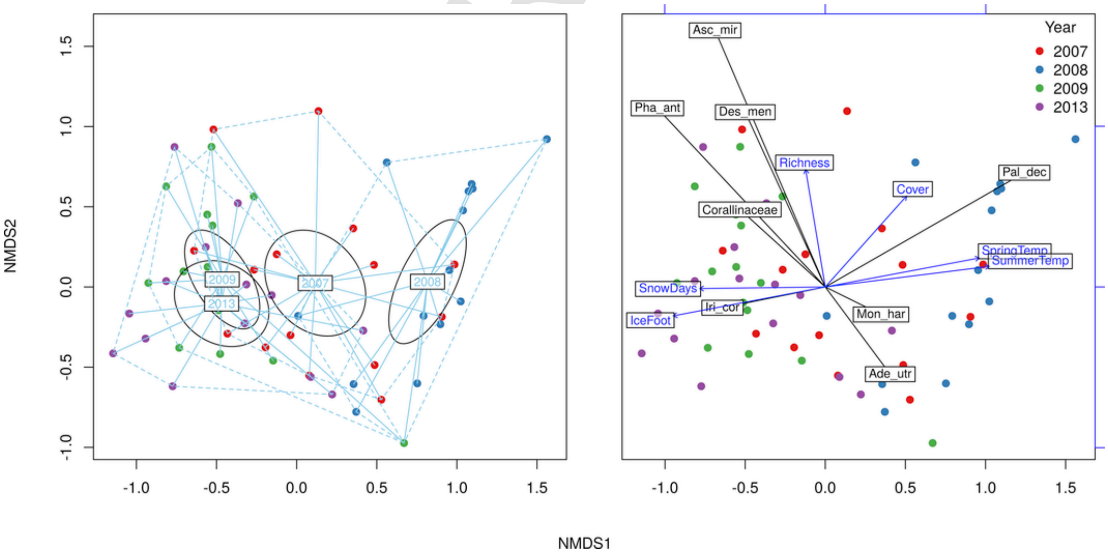

Fig. 8. NMDS ordinations for inter-annual variations in the Middle level. Sampling from summers of the years 2007, 2008, 2009, 2013. a) Centroids, convex hulls and standard ellipses for each year. b) Factors in blue and macroalgal taxa abbreviations. Dots represent single quadrats. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

formis, which were found in nearby areas (Roleda et al., 2009; Valdivia et al., 2014). *Pyropia endiviifolia* is a well-known Antarctic alga that inhabits the highest levels of the intertidal, even in the "spray zone" (Wiencke and Clayton, 2002). This species probably dominates this habitat because it presents a photo-protective mechanism that dissipates excessive light energy, preventing thermal stress (Hanelt and Nultsch, 1995; Hanelt et al., 1997).

The Middle level was the more diverse and even in terms of community structure. This level had more heterogeneous substrate (supplementary data), which provides microhabitat for small and medium macroalgae to settle (Richardson, 1979), and could be related to an increase in diversity (Schluter and Ricklefs, 1993). In other studies, it was found that in polar Middle levels there is intermediate disturbance due to ice scouring and herbivory (Kim, 2001). The intermediate disturbance hypothesis could be applied to the three levels (Menge and Sutherland, 1987; Scrosati and Heaven, 2007). Plus, ice scouring has an important effect on the community structure (Barnes 1999). An experimental study of ice disturbance should be performed in order to test this hypothesis.

4.2. Seasonal characterization

There were significant monthly variations in the community structure within the warm season. At the Middle level, macroalgal cover increased from December onwards. Most variation was found in early spring, and it stabilized in summer. This shows the importance of earlier conditions to the succession of the assemblage (Campana et al., 2009), especially regarding season responders, which were the most abundant in this intertidal community.

In the Middle level, *I. cordata* and the Corallinaceae family appeared more related to the colder months. The seasonal responders *M. hariotii* and *A. utricularis* (Wiencke et al., 2006) were more abundant in warmer months. This is in accordance with their life strategies (Wiencke et al., 2006). The Low level was more stable and showed no significant changes in macroalgal cover. However, it showed a similar pattern to the Middle level; colder months had less cover and were mostly composed by season anticipators such as *D. mensieziii* and *A. mirabilis*, together with Corallinaceae family and *I. cordata,* which are resistant to colder conditions. The season anticipator *P. antarcticus* increased its abundance in December and January, while the season responders' *A. utricularis* and *M. hariotii* were more abundant in February.

The general pattern agrees with the literature (Wiencke and Clayton, 2002), but two cases require further attention. Although *I. cordata* is a season responder (Wiencke et al., 2006), it is pseudo-perennial, i. e. parts of the blade are shed each year but re-growth is possible from the basal parts (Wiencke and Clayton, 2002), which could explain its dominance at this intertidal. Moreover, *P. decipiens* was also abundant in warmer months and was similar in abundance with *I. cordata* in the Middle level. This alga has been described as a season anticipator (Wiencke et al., 2006; Becker et al., 2011), but has no photo-inhibition and can continue growing in extreme light and irradiance conditions (Gómez et al., 1997; Deregibus et al., 2016). These two algae seem key components of the intertidal community, so a detailed characterization of more warm seasons is needed to conclude if this pattern would occur every year.

4.3. Inter-annual characterization

There is a strong variation in the total macroalgal cover and community structure over the studied years. Environmental conditions are a major factor for this intertidal community, which is very sensitive to climate oscillations (Bers et al., 2013). This agrees with our hypothesis, given that both seasonal and inter-annual changes influence the community structure. In the whole, the community arrives at a maximum development in summer, but total cover on a particular year depends on the conditions of that year.

It is remarkable that, in 2008, total macroalgal cover in Peñón Uno's Middle and Low level was 50% more compared to the same period in 2009. It was probably related to an important La Niña event, which produced warmer conditions and therefore a less ice-foot cover that year (Stammerjohn et al., 2008; Schloss et al., 2012). The year 2009, on the contrary, was particularly cold (Schloss et al., 2012). Furthermore, in Antarctica, temperature could be regarded as an indirect indicator of ice foot dynamics. This was confirmed in our study, where these two factors had opposite tendencies. Ice foot absence is related not only to more light availability, but also it may facilitate an earlier colonization of the substrate in the intertidal zone (Barnes and Conlan, 2007). When the substrate is released from ice, it affects the germination of overwintering macroalgal propagules (Kim, 2001). This could strongly determine the moment at which the colonization process starts over a particular year (Campana et al., 2009).

The differential plasticity and strategies of the Antarctic macroalgal species to cope with environmental changes, stress and disturbance (Wiencke and Amsler, 2012) is in accordance with the cover variations of the macroalgal community in our study. Some season responders maintain their patterns and increase their cover when conditions are favorable, e.g. *M. hariotii* and *A. utricularis*, but others do not. For example, in our results, the abundant and common species *P. decipiens* was associated to higher temperatures and higher total cover in general, while *I. cordata* seemed to be better adapted to colder conditions. The latter can survive prolonged dark periods in areas with unpredictable light conditions (Weykam and Wiencke, 1996). In 2008, *P. decipiens* is representative of the intertidal zone but it was no longer so after the low temperatures of 2009. This could be related to its eco-physiological response to light conditions (Becker et al., 2011); with the cooling effect, there may be more ice foot and therefore less light penetration (Wiencke and Amsler, 2012). Other environmental factors, such as UVB radiation, which augmented due to ozone depletion in the WAP (>50% increase), were proven to affect Antarctic macroalgal intertidal structure (Zacher et al., 2007b).

Our results show that the structure of macroalgal community could be strongly influenced by environmental factors, such as temperature and ice foot period. In an intensely cold year like 2009, when there was a longer period of ice foot, there was a strong decrease in total macroalgal cover.

Climate change is affecting the Antarctic biota, not only as a consequence of an increase in temperature, but because it triggers other indirect changes such as, glacier retreat, which leads to a rise in sediment input in the subtidal zone (Pasotti et al., 2015; Sahade et al., 2015; Deregibus et al., 2016). Moreover, it can produce a reduction in sea ice cover and an increase of the frequency and intensity of ice scour (Clarke et al., 2007; Barnes et al., 2014). Annual temperature averages increased 0.66 °C in two decades (1991–2009, Schloss et al., 2012). At the intertidal zone, species with wide physiological tolerance and increased growth in warmer conditions, like *P. decipiens*, would benefit from this, and would probably dominate in these conditions. Given that macroalgal intertidal communities have a fast response to variations in environmental conditions (Menge and Branch, 2001; Wiencke and Amsler, 2012) and, therefore, they could reflect climate fluctuations (Bers et al., 2013), more studies of this kind of habitats are needed in the context of the global change scenario.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2016.12.023.

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