

Seasonal changes of macroalgae assemblages on the rocky shores of the Cape Horn Biosphere Reserve, Sub-Antarctic Channels, Chile

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ABSTRACT

The Magellanic Sub-Antarctic Channels ecoregion supports one of the greatest number of macroalgae species in South America. In this ecoregion, the majority of macroalgae research has been associated with spatial ecology. In contrast, the temporal scale has received little attention. Here, we report the seasonal changes of taxa richness, wet biomass and assemblage structure for intertidal macroalgae in Robalo Bay (55°S), situated within the Cape Horn Biosphere Reserve. Overall, forty-nine macroalgae taxa were identified. We found a higher taxa richness and wet biomass in the summer than in the winter, but the strength of seasonal variations varied spatially across intertidal sites and levels. A similar seasonal pattern was detected with multivariate analysis. The seasonal changes are explained by the rise of seasonal algae such as *Adenocystis utricularis*. In turn, we found temporally-persistent algae such as *Ceramium virgatum* and *Nothogenia fastigiata* which did not show sharp seasonal variation. In conclusion, we suggest that macroalgal seasonality might be strongly modulated by coupled factors such as light, nutrient availability, sea surface temperature, relative humidity, and species composition. These factors would support an increase of taxa richness and wet biomass in the summertime on the rocky shores in high latitudes of South America.

1. Introduction

Macroalgae play a fundamental role in the ecological processes of cold temperate coasts (Worm and Lotze, 2006). On the Pacific coast of the American Continent, a characteristic pattern of macroalgae species richness increments towards higher latitudes. For example, in the northern hemisphere, the maximum species richness is found in the latitudes between 45–60°N, specifically in the low intertidal zones and shallow water (< 1 m; Konar et al., 2010). In turn, in the southern hemisphere, species richness increases along southwestern of South America at latitudes 45–55°S (Santelices and Marquet, 1998). Understanding of ecosystems that hold high species richness of primary

producers is crucial because the diversity of macroalgae can influence resilience processes and ecosystem functioning (Allison, 2004; Cardinale et al., 2011). Thus, macroalgae seasonal changes are a key information to understand the ecosystem functioning in rocky shores of cold temperate coasts.

The Magellanic Sub-Antarctic Channels (thereafter the Magellanic Channels) is one of the most extensive coastal areas of South America with several ecological attributes for macroalgae diversity (Rozzi et al., 2012). Currently, around 234 species have been identified, and seventy percent belong to the Sub-Antarctic component (Meneses and Santelices, 2000; Ramírez, 2010). Remarkably, there is a higher number of macroalgae species in the Magellanic Channels compared to

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other marine ecoregions of the Eastern Pacific Ocean of South America and the Antarctic Peninsula (Santelices and Marquet, 1998; Santelices and Meneses, 2000; Ramírez, 2010). Thus, the alpha diversity of macroalgae is a relevant attribute in the Magellanic Channels. At the same time, we can observe a high beta diversity which contributes to a high spatial heterogeneity of intertidal macroalgae assemblages (e.g. Benedetti-Cecchi and Cinelli, 1997; Soto et al., 2012; Rosenfeld et al., 2018). Both alpha and beta diversity should be assessed in temporal terms for a better understanding of rocky shore productivity in high latitudes of South America.

On intertidal rocky shores, environmental factors such as light, temperature, and humidity might modulate the abundance and diversity of macroalgae. From a global and regional perspective, Cruz-Motta et al. (2010) propose that changes of spatial patterns in rocky shore communities are mainly influenced by surface water temperature, precipitation, and photoperiod. Locally, seasonal fluctuations in photoperiod and irradiance might generate marked variations in the intertidal composition and macroalgae coverage (Underwood, 1981). For example, Gunnarsson and Ingólfsson (1995) noted that macroalgae coverage increased at the same rate as rising irradiance during summertime on coastlines of the Northern Hemisphere such as Iceland. In the Southern Hemisphere, on the cold temperate region of the Atlantic Patagonian coast, macroalgae assemblages exhibit a heterogeneous pattern through time and space. Raffo et al. (2014) mention that the macroalgae biomass and richness can vary at each site due to the combined effect of physical and ecological processes. Here, the combination of strong winds, low humidity, and high solar radiation increases desiccation during low tides (Bertness et al., 2006).

Currently, in the Magellanic Channels, the majority of studies have been performed during summertime (e.g. Guzmán and Ríos, 1981; Benedetti-Cecchi and Cinelli, 1997; Ríos and Mutschke, 1999). For this reason, we asked the following question: How does richness and biomass of macroalgae assemblages vary during different periods of the year on rocky shores of the Magellanic Channels? To test this question, we performed seasonal surveys of taxa richness and wet biomass of macroalgae assemblages at different spatial scales on the rocky shores of Róbaló Bay, Navarino Island (55°S, Chile). Our macroalgal study acquires particular relevance today, since the Chilean government established a 15 million ha protected area south of Cape Horn: the Diego Ramírez Islands- Drake Passage Marine Park (Rozzi et al., 2017; MMA, 2018; O'Leary et al., 2018). The new marine park protects 140,000 km² and includes the Diego Ramírez Archipelago (Rozzi et al., 2017). Thus, information about intertidal productivity is crucial for the new Marine Protected Area's planning. Finally, we discuss and link our results with other studies performed in cold temperate coasts of South America.

2. Materials and methods

2.1. Study area

This study was conducted along rocky shores of the Róbaló Bay (Chile) in the Beagle Channel which is located on the northern coast of Navarino Island, situated inside of the Magellanic Channels (54°55'S; 67°39'W; Fig. 1). From 2008–2009, macroalgae assemblage surveys were performed by extractive sampling for five consecutive days on May (20th - 25th; hereafter autumn), August (10th–15th; hereafter winter), October (20th - 25th; hereafter spring), and January (15th–20th; hereafter summer). Róbaló Bay has a coastline close to 6.5 km long and is adjacent to Omora Ethnobotanical Park, a Long-Term Socio-Ecological Research site in the Cape Horn Biosphere Reserve (Rozzi et al., 2007). Róbaló Bay has different wave exposure due to the predominantly west-east wind direction in the Beagle Channel (Santana et al., 2006), presenting a mix of different types of rocky substrates such as cobbles and small and large boulders (Ojeda et al., 2014).

2.2. Sampling and processing of samples

According to the substrate characterization of Róbaló Bay performed by Ojeda et al. (2014), we divided Róbaló Bay into six sites and each of them was categorized in three intertidal levels (low, mid, and high; Fig. 1). Each site had an approximate extension of 150 m parallel to the coastline, and the distance between each site was around 500 m. Most of the intertidal sites in the Beagle Channel have gently sloping shores with a tidal range average of 1.2 m (SHN, 2018). The intertidal levels were determined with the method used by Benedetti-Cecchi and Cinelli (1997), recording for each site the actual water level at high and low tide as predicted by tide tables during days with similar tidal excursion and calm sea conditions. At each intertidal level, we took four random samples with a 25 x 25 cm quadrat; all the macroalgae within the quadrat were carefully and completely removed. Overall, the sampling design was: 4 (seasons-fixed) x 6 (sites-fixed) x 3 (intertidal levels-fixed) x 4 quadrats = 288 samples. Macroalgal biomass was determined by measuring the wet biomass (g)/species/quadrat (25 x 25 cm). Subsequently, macroalgae were taxonomically identified to the genus or species level through macroscopic and microscopic features, using the best taxonomical literature available (e.g. Skottsborg, 1907; Ramírez and Santelices, 1991; Kim et al., 2004; Guiry and Guiry, 2013) and a reference collection at the cryptogamic herbarium cured at the University of Magallanes (Mansilla et al., 2013). Coralline algae were excluded from the analyses due to their strong attachment to the substrate, hindering their complete removal in the field. According to our field observations, Coralline algae were present at low intertidal level, and *Lithophyllum subantarcticum* (Foslie, 1907) has been observed in a 18% of occurrence at the low intertidal level on the rocky shores of Beagle Channel (Ojeda et al., 2017).

2.3. Data analysis

To provide a general characterization of the macroalgal communities of Róbaló Bay across time and space, we computed the total wet biomass of each species obtained from the sum of the pool of quadrates of each season. Also, the occurrence frequency (Fr) was determined by the total pool of quadrats during the whole period of study. The macroalgal species that contributed 50% of the annual total wet biomass were categorized and visualized according to their annual contribution per season, site and intertidal level.

Seasonal and spatial variability in taxa richness and wet biomass was tested using a multifactorial analysis by Generalized Linear Models (GLM). Both variables fitted to a negative binomial distribution, which can be observed for data with too many zeros (Crawley, 2007). The full model included 3 factors: 'season' (fixed, 4 levels), 'site' (fixed, 6 levels, crossed with season), 'intertidal level' (fixed, 3 levels, nested within site and crossed season). After that, we performed an analysis of deviance, and subsequently run a Tukey *post hoc* test to perform pair-wise comparisons (e.g. Betancourt et al., 2018). As the main objective of the analysis was to test for seasonal variability in taxa richness and wet biomass, we simplified the spatial structure of the model to obtain a denominator for testing the main factor of interest ('season'). All GLMs were performed by the R statistical software R 3.5.0, using the packages 'MASS' and 'emmeans' (R Development Core Team, 2017).

Assessing the macroalgal assemblages on the rocky shore of Róbaló Bay, we ran a Canonical Analysis on Principal Coordinates (CAP; Anderson and Willis, 2003). Following the experimental design above, we transformed the data with square root, fitted the data to a matrix of Bray-Curtis Similarity, and assessed the significance of fits with 9999 permutations. To detect species that may show nonlinear relationships with canonical axes, we used a Spearman rank's correlation. This is an indirect *post hoc* way of identifying possible contributions of individual species to differences among groups (Anderson and Willis, 2003). CAP is a constrained multivariate method, which uses an *a priori* hypothesis to produce an ordination plot. This allows the discovering of patterns

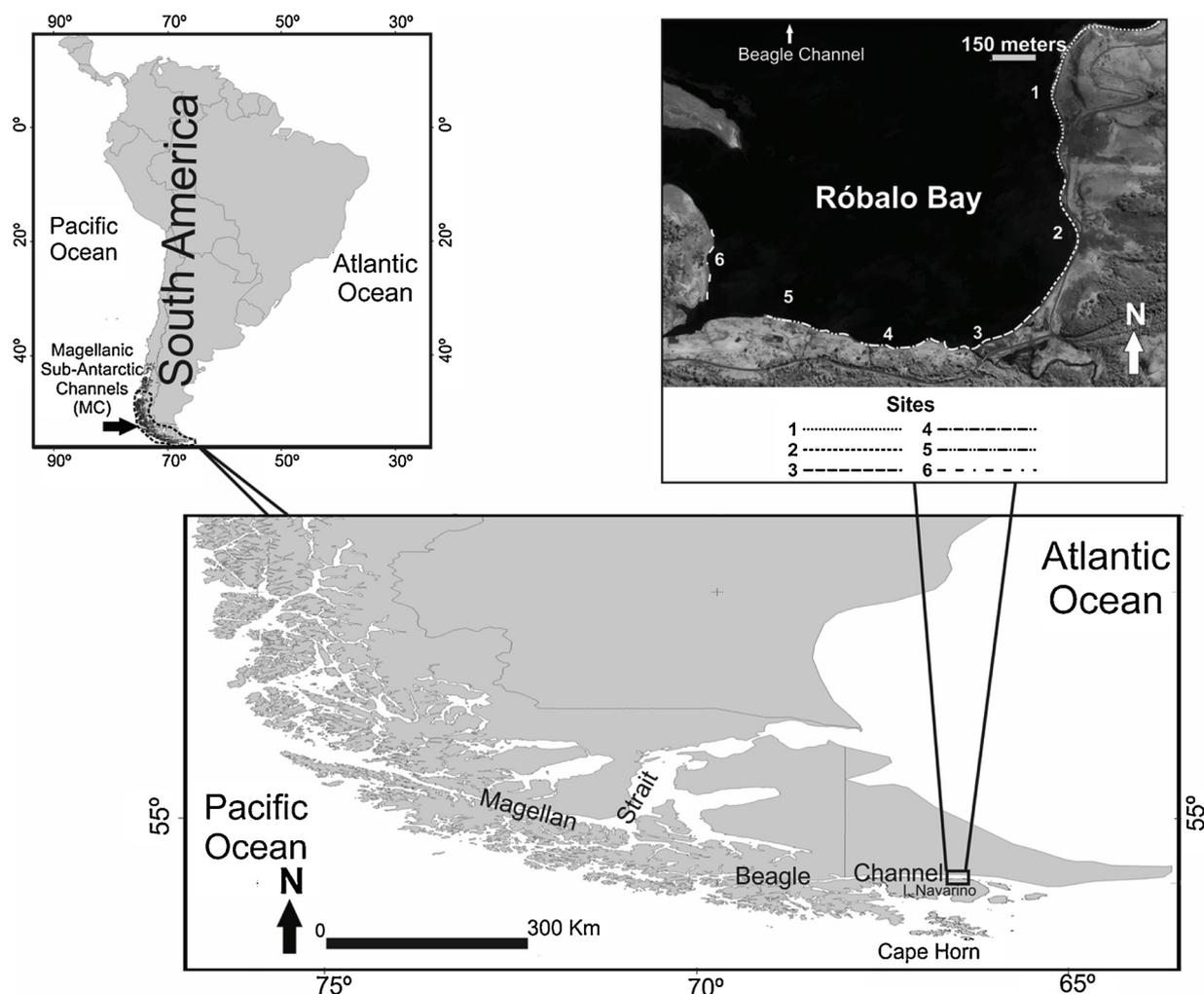


Fig. 1. Location of the study area in Róballo Bay, Beagle Channel ($54^{\circ}55'S$; $67^{\circ}39'W$), Navarino island, Cape Horn Biosphere Reserve, Chile.

that might be masked by overall dispersion in unconstrained methods (Valdivia et al., 2011). A further complementary use of this canonical analysis is that it has the capacity for identifying the species responsible for multivariate patterns (Anderson and Willis, 2003).

We performed Permutational Analysis of Variance PERMANOVA (Anderson, 2005) in order to test the seasonal changes of macroalgae structure in Róballo Bay. We run PERMANOVA with a total of 49 variables (i.e. taxa). The statistical processing was performed by a transformation of the data (fourth root), which were analyzed by Bray-Curtis dissimilarities matrices with 9999 permutations. The full model included 3 factors: 'season' (fixed, 4 levels), 'site' (fixed, 6 levels, crossed with season), 'level' (fixed, 3 levels, nested within site and crossed season). All PERMANOVAs and pair-wise comparisons were done using the FORTRAN program (Anderson, 2005). Finally, we calculated the contribution of each taxon per season in assemblage structures by SIMPER routines (Clarke, 1993). In this procedure, the data were transformed to the fourth square root to reduce the contribution of the more abundant macroalgae compared to that of the less conspicuous macroalgae. SIMPER list was cut off when the accumulated contribution of species reached 90%. The analyses were performed using PRIMER 5 software (PRIMER-E, Ltd. Plymouth, UK).

3. Results

3.1. Characterization of macroalgae assemblages

The taxonomic composition of the macroalgae assemblage of Róballo

Bay contained a total of 49 different taxa: 21 were identified at the genus level and 28 to the species level (Table 1). Overall, the macroalgae assemblage included 34 genera classed in 27 families. Regarding to all quadrats of the study, the best represented group was Rhodophyta with 47% of the taxa, followed by Chlorophyta (33%) and Ochrophyta (20%). *Adenocystis utricularis* showed the highest frequency of occurrence (27.1%), along with *Ceramium virgatum* (23.3%), *Ulva intestinalis* (21.5%) and *Ectocarpus* sp. (12.8%). The lowest frequencies of occurrence were recorded for *Desmarestia ligulata* (0.7%), *Codium fragile* (0.3%), *Polysiphonia morrowii* (0.3%), *Ballia callitricha* (0.3%) and *Dasya* sp. (0.3%) (see Table 1). Six macroalgae contributed 50% of the total wet biomass of the assemblage: *C. virgatum* (16%), *U. intestinalis* (9%), *Ectocarpus* sp. (8%), *Ulva* sp. (7%), *A. utricularis* (6%) and *Pyropia columbina* (4%). The visualization of percentage contribution for these six macroalgae –which were categorized in seasons, sites, and intertidal levels– showed that some of them were seasonal algae and other were temporally-persistent algae (Supplementary material Fig. 1). For instance, *A. utricularis* presented a higher percentage contribution during spring and summer presenting a spatial distribution in different sites and intertidal levels in Róballo Bay (Supplementary material Fig. 1d). In the case of *P. columbina*, the changes over time were more significant: its contribution was higher in summer and around 50% of this contribution was found at the mid-intertidal level (Supplementary material Fig. 1f). In contrast, *C. virgatum* was a temporally-persistent algae recording percentages during autumn, winter, spring, and summer and its highest contribution was observed during wintertime, with 20% contribution (Supplementary material Fig. 1a).

Table 1

Total wet biomass (g) per macroalgae obtained from the sum from the pool of quadrats per season (n = 72). Occurrence frequency (Fr; %) per macroalgae obtained from the total of quadrats (n = 288) in Róbal Bay.

Taxa	Autumn	Winter	Spring	Summer	Fr
Chlorophyta					
<i>Acrosiphonia arcta</i> (Dillwyn) Gain 1912	24.2	14.6	28.3	100.7	6.3
<i>Acrosiphonia</i> sp1.	5.4	0.3	53.4	162.7	6.6
<i>Acrosiphonia</i> sp2.	0	0	0	82.2	3.8
<i>Bryopsis magellanica</i> Hylmö 1919	0.6	13.2	0	24.1	2.4
<i>Cladophora</i> sp.	6.5	5.3	33.4	169.2	3.8
<i>Codium dimorphum</i> Svedelius 1900	0	0	0	320.9	1
<i>Codium fragile</i> (Suringar) Hariot 1889	0	0	0	10.4	0.3
<i>Monostroma</i> sp.	0	12.8	145	0	6.3
<i>Spongomorpha</i> sp.	0	0	0	9.6	0.7
<i>Ulva bulbosa</i> Pasilot de Beauvies 1805	0	0	0	346.9	4.2
<i>Ulva intestinalis</i> Linnaeus 1753	639.3	10.9	194	61.4	21.5
<i>Ulva lactuca</i> Linnaeus 1753	26.9	0.3	80	167	11.1
<i>Ulva linza</i> Linnaeus 1753	0	0	0	0.6	0.7
<i>Ulva prolifera</i> O.F. Müller 1778	1.4	0.9	7	365.3	11.8
<i>Ulva rigida</i> C. Agardh 1823	5.5	0.2	18.3	36.4	5.2
<i>Ulva</i> sp.	0.9	0	1.2	671.8	9
Ochrophyta					
<i>Adenocystis utricularis</i> (Bory) Skottsberg (1907)	2.3	70.6	130.7	363.3	27.1
<i>Caepidium antarcticum</i> J. Agardh 1859	2.7	0	0	25.1	11.1
<i>Chordaria</i> sp.	0	3.3	10	298.4	9.4
<i>Cladostephus</i> sp.	0	0	0	88.6	0.7
<i>Desmarestia ligulata</i> (Stackhouse) J.V. Lamouroux	0	0	0	5.2	0.7
<i>Desmarestia</i> sp.	1.8	0	0.2	14.5	2.8
<i>Ectocarpus</i> sp.	0	242.8	379.7	171.4	12.8
<i>Halopteris</i> sp.	31.5	0	0.1	0	1.4
<i>Scytosiphon lomentaria</i> (Lyngbye) Link 1833	0.3	36	49.6	123.3	1.7
<i>Scytothamnus fasciculatus</i> (Hook & Harvey) Cotton 1915	105.8	0	1.6	68.1	5.9
Rhodophyta					
<i>Ahnfeltiopsis furcellata</i> (C. Agardh) Silva & DeCew 1992	0	0	0	4.5	1.7
<i>Ballia callitricha</i> (C. Agardh) Kützing 1843	0	0	0	0.5	0.3
<i>Bostrychia</i> sp.	87.6	99.8	141.3	19.5	10.4
<i>Callithamnion</i> sp.	22.1	11.1	10.8	28.7	7.6
<i>Callophyllis variegata</i> (Bory) Kützing 1843	18.9	28	24.8	56.6	6.3
<i>Catenella fusiformis</i> (J. Agardh) Skottsberg 1923	0.3	0.2	5.3	1.1	2.1
<i>Ceramium pacificum</i> (Collins) Kylin 1925	10.5	1.1	196.5	0	3.5
<i>Ceramium virgatum</i> Roth 1797	312.3	825.8	195.3	261.6	23.3
<i>Ceramium</i> sp1.	0	0	0	119.3	5.2
<i>Ceramium</i> sp2.	0	1.2	0	0	1
<i>Dasya</i> sp.	0	0	0	11.2	0.3
<i>Griffithsia</i> sp.	0.2	0.8	3.7	0.1	2.1
<i>Heterosiphonia</i> sp.	53.1	26.6	9.2	54.9	7.6
<i>Mazzaella laminarioides</i> (Bory) Fredericq 1993	0	18.2	7.6	0	1.4
<i>Nothogenia fastigiata</i> (Bory) Parkinson 1983	61	72.7	40.8	89.4	9
<i>Plocamium cartilagineum</i> (Linnaeus) Dixon 1967	0	0.1	0	2	1
<i>Polysiphonia abscissa</i> Hooker & Harvey 1845	0	0	4	168.4	2.8
<i>Polysiphonia morrowii</i> Harvey 1857	0	0	0	2.9	0.3
<i>Polysiphonia</i> sp1.	4.9	0.1	3.2	0	3.5
<i>Polysiphonia</i> sp2.	34.8	5.9	11.9	0	4.2
<i>Porphyra</i> sp.	0	0.9	0	85.3	3.5
<i>Pyropia columbina</i> (Montagne) Nelson 2011	11.2	1.7	11.8	386.1	7.3
<i>Sarcothalia crispata</i> (Bory) Leister 1993	0	31.3	0	26	1
N° taxa = 49	Σ = 1471.7	Σ = 1536.5	Σ = 1798.3	Σ = 5005.1	

3.2. Taxa richness and wet biomass

Overall, the deviance analysis of taxa richness and wet biomass showed significant seasonal fluctuations and spatial changes across Róbal Bay (Table 2). The seasonal fluctuations were significant mainly between summer and the other seasons (Fig. 2). For example, average taxa richness increased from 1.9 ± 0.3 taxa in winter to 4.6 ± 0.4 taxa in summer (Fig. 2). In turn, the average wet biomass tripled from winter to summer (21.3 ± 5.2 g and 69.5 ± 8.6 g, respectively; see Fig. 2).

The deviance analysis revealed a significant interaction between 'site' and 'season' (Table 2). In turn, intertidal sites showed that the magnitude of seasonal changes for taxa richness and for wet biomass varied at each site (Fig. 3). For example, sites 3 and 4 exhibited

significant differences in taxa richness, when compared to summer and the other seasons. However, these seasonal differences were not observed for the sites 5 and 6 (Fig. 3a). A similar trend was observed in wet biomass of macroalgae assemblage, where the magnitude of seasonal variation varied with regard to intertidal sites. For example, site 3 and 4 showed significant differences between summer and the other seasons, while sites 1 and 5 did not registered significant differences along the study period (Fig. 3b). In spite of this, the highest wet biomass averages in all sites were summertime.

The deviance analysis revealed a significant interaction between 'level (site)' and 'season' (Table 2). In turn, the averages –which obtained for each level at each site– showed that the magnitude of seasonal changes for taxa richness and for wet biomass varied depending on the site and intertidal level (Supplementary material Fig. 2). For

Table 2

GLM results for taxa richness and wet biomass of macroalgae variability. Pr (> Chi) indicates P value. The asterisk (*) states significant differences: *P < 0.05, **P < 0.01, ***P < 0.001.

Variable	Source of variability	Df	Deviance. Resid.	Df	Resid. Dev	Pr (> Chi)
Taxa Richness	Season	3	21.797	284	315.02	7.19E-05***
	Site	5	40.483	282	316.74	1.19E-07***
	Season x Site	15	56.092	264	317.71	1.17E-06***
	Season x Level	6	1.095	276	316.11	9.82E-01
	Level (Site) x Season	36	67.311	216	302.15	1.19E-03**
Wet Biomass	Season	3	16.164	284	307.77	1.04E-03**
	Site	5	24.13	282	307.64	2.00E-04***
	Season x Site	15	52.803	264	302.87	4.16E-06***
	Season x Level	6	6.241	276	307.61	3.97E-01
	Level (Site) x Season	36	123.182	216	286.05	1.82E-11***

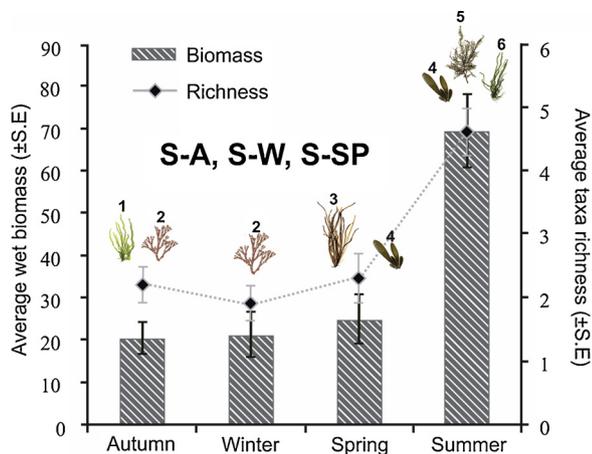


Fig. 2. Averages of wet biomass (g) and taxa richness of the macroalgae assemblages that were found in Róbal Bay during Autumn, Winter, Spring, and Summer. Striped bars correspond to the average wet biomass per quadrat (25 x 25 cm) ± S.E (Standard Error) and black points are average taxa richness per quadrat (25 x 25 cm) ± S.E. Averages were obtained from the pool of quadrat per season (n = 72) performed in Róbal Bay. The macroalgae illustrations display the species that had a higher contribution by season: 1- *Ulva intestinalis*; 2- *Ceramium virgatum*; 3- *Scytosiphon lomentaria*; 4- *Adenocystis utricularis*; 5- *Chordaria* sp.; 6- *Ulva* sp. Deviance analysis, performed from taxa richness and wet biomass in respond to ‘Season’, showed significant differences (P < 0.001). Tukey test was done to evaluate the significant differences. Letters states differences (P < 0.05) among seasons. A = Autumn, W = Winter, SP = Spring, and S = Summer.

example, the low-intertidal level at site 1, the averages for both variables did not show greater differences among seasons (Supplementary material Fig. 2). In contrast, the mid-intertidal level at sites 2 and 4, the averages for both variables increased markedly from winter to summer (Supplementary material Fig. 2). A relevant point to highlight is that the highest average taxa richness was recorded at the mid-intertidal level at the site 1 during summer (7.5 ± 1.8 taxa). In the case of macroalgal wet biomass, the highest averages were found at the mid-intertidal level at site 1 (148.7 ± 27 g) and low-intertidal level at the site 6 (152.6 ± 53 g) in summer (Supplementary material Fig. 2). We did not find macroalgae species at the high-intertidal level at the sites 2, 3, 4 in winter (Supplementary material Fig. 2).

3.3. Assemblage structure

The CAP ordinations showed a significant effect between macroalgae structure and seasons (P = 0.0001) on the rocky shores of the Róbal Bay (Fig. 4a) with a squared canonical correlation of δ² = 0.795. Structure of macroalgae in summertime was clearly separated of the other seasons (Fig. 4a). A similar trend was observed with PERMANOVA analysis detecting significant differences in macroalgae

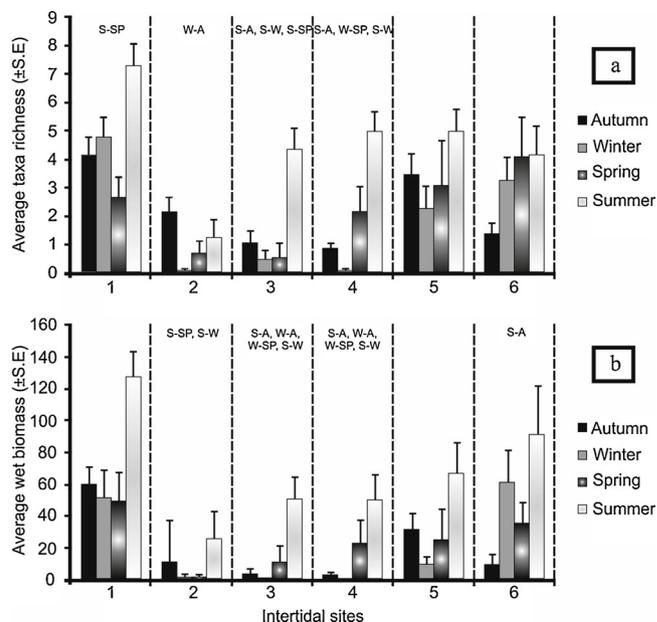


Fig. 3. Average taxa richness and wet biomass (g) of macroalgae assemblages at different intertidal sites along Róbal Bay. The graphic a) shows the average taxa richness ± S.E (standard error) and b) shows the average wet biomass ± S.E in each site during seasons. Analysis deviance, performed for ‘Season’ x ‘Site’, showed significant differences (P < 0.001) for both variables. Tukey test was done to evaluate the significant statistical differences. Letters states significant differences (P < 0.05) between seasons for each intertidal site. A = Autumn, W = Winter, SP = Spring, and S = Summer.

structure among seasons (P = 0.0001). The pairwise test indicated that these differences were mainly detected between summer and the other seasons, and in turn, differences can be observed between autumn versus spring and autumn versus winter (Table 3). In addition, PERMANOVA analysis showed significant interaction between season and site which means that there are differences in the macroalgae structure among intertidal sites (Table 3).

The CAP ordinations exhibited that individual macroalgae such as *Acrosiphonia* sp2., *U. bulbosa*, *U. prolifera*, *Ceramium* sp., *A. utricularis*, *Ulva* sp., and *Chordaria* sp. presented a positive correlation ≥ 0.3 with canonical axis 1. It is necessary to remark that a positive correlation between taxa and axis 1 indicates an increasing wet biomass during summer. This positive correlation was mainly for a growing of seasonal macroalgae, which explains the temporal differentiation in assemblage structure during summer (Fig. 4). In turn, SIMPER analysis helped to identify the main temporal variations of macroalgae between warm (spring-summer) and cold seasons (autumn-winter). In autumn and winter, 4 and 6 taxa, respectively, made up more than 90% of the assemblage, with *U. intestinalis* (autumn) and *C. virgatum* (winter) making up the highest percentage of the assemblage (Supplementary material

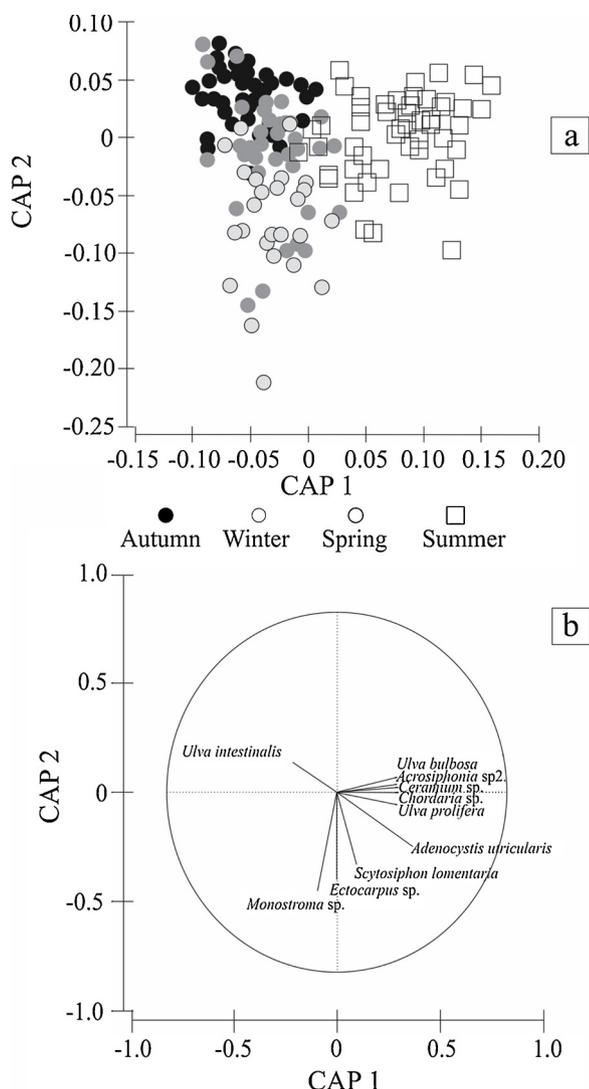


Fig. 4. (a) Constrained ordinations of macroalgae assemblage data from Róbaló Bay, at four different seasons of sampling along annual period. (b) Correlations of several taxa macroalgae variables with the two CAP axes.

Table 1). In spring and summer, however, 11 and 12 taxa, respectively, made up 90% of the assemblage, with *A. utricularis* giving the highest percentage (Supplementary material Table 1). Finally, we can categorize the macroalgae temporal patterns in three: i) Temporally-persistent algae that were present and abundant over the year such as *Bostrychia* sp., *C. virgatum*, *N. fastigiata*. ii) Seasonal algae that were present over year, but they increase their abundance in one season such as *A. utricularis*, *Chordaria* sp. or *P. columbina*. iii) ephemeral algae that were present only in one season such as *U. bulbosa* (see Table 1).

4. Discussion

On the rocky shores of the Cape Horn Biosphere Reserve, macroalgae assemblages have only been examined in spatial terms, particularly in attributes associated with species composition and zonation patterns during austral summer (e.g. Guzmán and Ríos, 1981). This study describes for the first time the seasonal variation of macroalgae intertidal assemblages. On average, the highest taxa richness and wet biomass were found in summer, while the lowest averages were in autumn and winter. Macroalgae structure showed marked differences between summer and the other seasons. This was mainly caused both by the growth of ephemeral and seasonal algae (e.g. *U. bulbosa* and *A. utricularis*, respectively) and by the contribution of temporally-persistent algae (*C. virgatum*). However, although the averages for taxa richness and for wet biomass were higher during summer than in winter, the seasonal statistical differences did not show a general pattern in every single site or intertidal level. Thus, the seasonality differed across space which was observed a significant site x season interaction across Róbaló Bay. In composition terms, macroalgae assemblage in Róbaló Bay comprised a total of 49 taxa, accounting for 8.5% of the total diversity reported for the Magellanic Channels (see Ramírez, 2010). This percentage is high compared to that on other macroalgae checklists that have been reported for Cape Horn Biosphere Reserve (see Guzmán and Ríos, 1981; Mansilla and Navarro, 2003). Our study provides a baseline of intertidal biomass dynamics and a detailed macroalgae checklist. These findings are relevant for management plans of the new Marine Protected Area south of Cape Horn and for the understanding of rocky shore ecology at high latitudes of South America.

On cold temperate coasts, the seasonality of macroalgal biomass can vary according to environmental factors prevailed at the local context. For example, at high latitudes in the northern hemisphere, macroalgae coverage increases in summer and decreases in winter. This is correlated with the irradiance and nutrients (Gunnarsson and Ingólfsson, 1995). In turn, irradiance and nutrient availability play an important role in the life cycle of algae. For instance, *A. utricularis*, which

Table 3
PERMANOVA results for macroalgae structure in Róbaló Bay. The asterisk (*) states significant differences: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Source	df	Macroalgae Assemblage (49 taxa)		
		MS	Pseudo-F	P (perm)
Season	3	37653.6276	12.0362	0.0001***
Site	6	13809.9910	4.4145	0.0001***
Season x Site	15	6788.3909	2.1700	0.0001***
Level (Site) x Season	36	3476.0436	1.1111	0.1357
Post-hoc	Macroalgae Assemblage (49 taxa)			
		t	P (perm)	
Autumn vs. Winter		2.5597	0.0002***	
Autumn vs. Spring		3.8611	0.0001***	
Autumn vs. Summer		3.1679	0.0001***	
Winter vs. Spring		1.5449	0.0506	
Winter vs. Summer		3.4965	0.0001***	
Spring vs. Summer		4.1460	0.0001***	

possesses a Sub-Antarctic/Antarctic distribution (Martín et al., 2016), has opportunistic life strategies in terms of growth and it responds to seasonal environmental changes (Wiencke et al., 2007). However, a higher irradiance and temperature not always promote higher wet macroalgal biomass. For instance, in cold temperate coasts of the northern hemisphere, in summer months the macroalgal growth and abundance can be affected by desiccation, particularly high intertidal level (e.g. Cubitt, 1984). In the southern hemisphere, macroalgae assemblages of Atlantic Patagonian coasts are also affected by high desiccation rates produced by strong dry winds, low rainfall, and low humidity – which is close to 50% in summertime (Paruelo et al., 1998; Bertness et al., 2006; Raffo et al., 2014). Certainly, if we compare both the Atlantic Patagonian coasts and the Magellanic Channels, the desiccation on the intertidal community is lower in the Magellanic Channels. Therefore, this could be a cause to observe an increase in macroalgal richness and biomass in summer.

We propose that coupled factors such as light, nutrient availability, sea surface temperature (SST), and relative humidity might regulate the intertidal macroalgae in the Magellanic Channels. For instance, the photoperiod has shown significant changes over the year, with a minimum of 8 h of light in winter and a maximum of 18 h in summer (Butorovic, 2009). A similar trend has been detected by meteorological and oceanographic sensors in the Beagle Channel where luminosity factors –such as Photosynthetically Active Radiation– can fluctuate on average from 129 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in winter to 547.8 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (PAR) in summer (see Supplementary material Table 2). The hours of light, and PAR light seem to be excellent promoters of macroalgal growth during warm months. For example, in the Magellanic Channels, *Macrocystis pyrifera* increases its growth rate and its concentration of accessory pigments (fucoxanthin) during summer significantly (Tala et al., 2016; Marambio et al., 2017). In the Magellanic Channels, there are no studies related to the importance of seasonal nutrient availability with macroalgae. However, reports associated with phytoplankton show that nitrogen is critical in the generating of blooms during spring and summer (Aracena et al., 2011). Fast-growing species such as *Ulva* sp. are quite sensitive to changes in nutrient availability as they have really high N requirements (Pedersen and Borum, 1997). Seasonal changes in nitrate or nutrients may thus be an important driver in the Magellanic Channels. Locally, in Beagle Channel, the average SST can vary from 4.5 °C in winter (August) to 8.9 °C in summer (January; Supplementary material Table 2), and the relative humidity fluctuates from 70% to 90% annually (Santana et al., 2006). Both temperature and relative humidity would support that the desiccation might not be a key factor in summer for intertidal communities in the Magellanic Channels.

Our results are in concordance with other seasonal trends observed recently in the Magellanic Channels where in combination with environmental factors mentioned above, the species composition also would play an essential role in macroalgal seasonality (see Rosenfeld, 2016; Rosenfeld et al., 2018). For example, Rosenfeld (2016) performed a study about the trophic ecology of intertidal limpets, observing a substantial rise in macroalgal biomass during summer in comparison with winter. This author mentioned that the range of difference in macroalgal biomass between winter and summer varied at each intertidal site. Furthermore, Rosenfeld (2016) suggested this difference can be associated with the presence of temporally-persistent red algae (*Iridaea cordata*, *N. fastigiata*, and *M. laminarioides*). We propose that species composition plays an important role in the magnitude of macroalgal seasonality in every intertidal site and level. Our data show that when macroalgae assemblage are structured by high abundance of temporally-persistent algae and in combination with the presence of seasonal and ephemeral algae, the macroalgal seasonality shows a gentle variation in richness and biomass terms. This seasonal pattern would change when macroalgae assemblages are predominantly composed of seasonal and ephemeral algae which is why it is possible to observe significant differences among seasons. Although our observational data

support this hypothesis, we think that experimental field studies should be conducted to underpin it.

Although our study focused on the characterization of macroalgae seasonal fluctuations, we found a marked heterogeneity of macroalgae assemblages in small spatial scale. This heterogeneity has already been reported in intertidal communities in the Magellanic Channels (Benedetti-Cecchi and Cinelli, 1997; Soto et al., 2012; Rosenfeld et al., 2018), and also, it has been observed along the Argentinean coast (Wieters et al., 2012; Arribas et al., 2019). In the case of Róbal Bay, PERMANOVA analysis showed there are significant differences in the assemblage composition among sites (Table 3). Multiple factors might explain these differences. On a small spatial scale, we hypothesize that the type of substrate, wind exposition, freshwater input, and species composition are relevant factors to consider in future studies. For instance, in Róbal Bay, site 1 presented the highest taxa richness and wet biomass. This site was structured by a mix of big and medium boulders with a high abundance of foundation species as *Mytilus platensis* (Ojeda et al., 2014). These attributes generate a higher three-dimensionality of the substrate which increases the habitat complexity promoting a higher macroalgae diversity (Tokeshi and Arakaki, 2012), whereas rocky shores with prevalence and uniformity of small boulders could have a lower diversity. Also, wave exposure caused by west-east wind direction in the Beagle Channel (Santana et al., 2006; Ojeda et al., 2014) might be a relevant factor by promoting dispersal and availability of propagules on coasts with westward orientation (e.g. Gagnon et al., 2015). Finally, small-scale heterogeneity is apparently important in South American rocky shores, both along the Argentinean coast and at the southern tip of the continent (Chile).

Our study has shortcomings related to spatiality, temporality, and sampled species. We performed this study in one bay over one year. This limitation was due to logistics. To work in Cape Horn Biosphere Reserve during wintertime is a challenge. Snow storms and shortened light hours reduce hours of field activities. Future seasonal investigations must consider a higher spatial scale and sample seasonally for more than one year. Another shortcoming is that we did not assess the taxa richness and wet biomass of corallinaceans. This was due to the fact that we worked with an extractive method, which hindered the removal of corallinaceans in the field. So far, ecological studies about corallinaceans have not been performed in detail in the Cape Horn Biosphere Reserve. Future studies should consider it because corallinaceans play an important role at low-intertidal level: they can modify the habitat and can increase the stability of macroalgae and mollusks (Kelaheer et al., 2007).

5. Conclusion

In general, seasonal changes were observed for taxa richness, wet biomass, and macroalgae structure on the rocky shores of Róbal Bay. These changes were mainly marked between winter and summer. One of the main causes of these variations was the rapid growth of seasonal algae during summertime (e.g. *A. utricularis*). The seasonal changes of taxa richness and wet biomass did not show significant differences at all sites and intertidal levels. The role of temporally-persistent algae might be important in these subtle seasonal changes. For example, when algae such as *Ceramium virgatum* and *Nothogenia fastigiata* were present, the intertidal sites exhibited a lower seasonal difference in wet biomass and taxa richness. In the Magellanic Sub-Antarctic Channels, summertime plays a fundamental role in the productivity of the intertidal community of the southern tip of South America.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.aquabot.2019.06.001>.

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