ECOSYSTEMS

Short-term temporal dynamics of morphological and feeder functional groups and species richness in relation to seasonal changes

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Abstract: This study examines the distribution of primary and secondary space holders integrated in morphological and feeder functional groups as well as the species richness over the seasons on northern Patagonian rocky shores. We also evaluated whether the temporal changes in species richness, assemblage structure and species turnover were related to seasonal changes. These patterns were studied by non-destructive samplings between December 2013 and March 2015. Thirty taxa were identified, including six algal morphological functional and three invertebrate feeder groups. The cover of seaweeds and invertebrates was positively correlated with changes in the environmental factors. The marked seasonality in this Patagonian zone changed between two contrasting periods. Species richness and assemblage structure were associated with seasonal changes and were influenced by the more abundant morphological and feeder functional groups. We suggest that habitat-formers, such as articulated calcareous and suspensor feeder groups, can expand and retract over time-scales of months to seasons, generating available space for the colonization and growth of other organisms. We conclude that seasonal changes and the dynamics of articulated calcareous and suspensor feeder groups drive changes in the algal and invertebrate abundances, in turn driving changes in species richness and assemblage structure.

Key words: Spatial and temporal scales, Rocky shores, Seaweeds, Invertebrates.

INTRODUCTION

Seaweeds as primary-space holders are major components of intertidal and subtidal communities in intertidal rocky systems; they contribute significantly to primary marine production and form nursery habitats for a diverse benthic fauna (Lüning 1990). In rocky shore benthic communities, the primary-space holders include primary producers and filter feeders (Menge & Sutherland 1987) and the secondary-space holders include herbivores and carnivores, which are mobile consumers, but many secondary-space holders are also primary producers or filter feeders (Bruno et al. 2003). Species richness expressed as the number of species in a community is one of the main traits of communities because it influences stability, productivity and susceptibility to invasion (Scrosati et al. 2011). Also, temporal variability in primary-space holders richness and their associated secondary-space holders and mobile species can cause variability in a regional species pool (Menge & Sutherland 1987, Bruno et al. 2003). Hence, the species richness in functional groups influences the community functioning (Cardinale et al. 2006, Duffy et al. 2007, Bruno & Cardinale 2008).

From an environmental point of view, different abiotic factors such as desiccation,

seawater temperature and solar radiation emerge as the main drivers of ecological processes and patterns, depending on the spatial and temporal scales in marine ecosystems (Levin 1992, Willig et al. 2003). Determination at different scales, ranging from local patchiness to variation over biogeographical gradients of species richness, diversity and composition of intertidal marine communities, may provide information on community structure and functioning (Kraufvelin et al. 2010, Hooper et al. 2012, Cardinale et al. 2013).

Because the sessile condition of primary-space holders they are constrained to the effects of long-term exposure to environmental stress, resulting in changes in the structure of the assemblages (Eriksson et al. 2002, Karez et al. 2004, Kraufvelin et al. 2006, Pinedo et al. 2007). For this reason, seaweeds are considered useful descriptors of environmental characteristics of coastal habitats, and are being used as ecological quality bio-indicators under the Water Framework Directive (Directive 2000/60/EC). Thus, in order to capture the variability of benthic assemblages and relate it to their environment, biodiversity assessments usually rely on proxy measurements, such as structural components of assemblages based on species level taxonomical identifications. However, the enumeration of all species is a time-consuming task requiring expertise, so extrapolative and other techniques are always sought to optimize biodiversity assessment efficiencies (Gaspar et al. 2017). Thus, in order to optimize time and resources taken in identifying species-level taxa, and to provide insights into the functional structure of benthic communities, species can be grouped into different functional groups, based on their ecological and morphological attributes in the case of seaweeds, and the feeding type in invertebrates (Litter & Litter 1980, Steneck & Dethier 1994, Balata et al. 2011).

Macroalgal functional groups have been widely used, categorizing species differing in morphological features and in how these form-based features are supposedly linked to different ecological functions (Steneck & Dethier 1994). Moreover, biological traits, usually measured at the individual level and used comparatively across species, may be seen as well as a surrogate measure of the (species-level measured) biodiversity (McGill et al. 2006).

Despite the ecological and economic importance of Patagonian coasts, its benthic diversity remains poorly understood, except for some specific sites (Torres & Caille 2009, Irigoyen et al. 2010, Sueiro et al. 2011). In addition, there are difficulties related to the assessment of benthic communities, such as marine invertebrates and seaweeds, which thrive in intertidal rocky shores. Such difficulties include: a) high natural variability across a range of spatial and temporal scales, b) their diversity assessment implying high sampling and laboratory processing effort and good taxonomical expertise, and c) insufficient knowledge about their structural and functional characteristics. Considering these difficulties, the objective of the present work was to study how different functional groups, including seaweeds trait-based thallus morphologies and invertebrate feeding types, respond to temporal gradient in the lower intertidal zone along the Punta Este shore in Western Patagonia.

MATERIALS AND METHODS

Study area

This study was performed on the northern Patagonian coast of Argentina at Golfo Nuevo, on the rocky shore of Punta Este (42°78'S, 64°95'W) (Fig. 1). Golfo Nuevo is a semi enclosed basin of low hydrodynamics, located in the transition zone between the cold-temperate
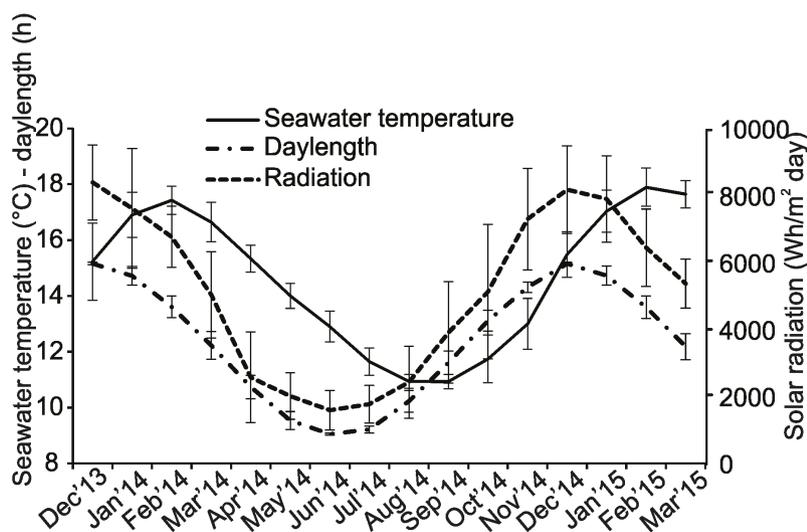
Figure 1. Variation in daylength (hours), solar radiation (Wh/m² day) and surface seawater temperature (°C) monitored between December 2013 and March 2015.

and warm-temperate biogeographic regions of the south-western Atlantic Ocean. The region is characterized by extreme weather conditions, with a predominance of strong winds from the west and low humidity (Paruelo et al. 1998). These strong, dry winds, combined with low local rainfall, make the Patagonian intertidal zone the place with the highest desiccation stress recorded for rocky shore communities (Bertness et al. 2006). The tide regime is semidiurnal, and the mean amplitude is 3.8 m, reaching 5.7 m in spring. Water temperature and salinity fluctuate between 10 to 19.5 °C and 33.7 to 33.9% in summer and winter, respectively.

Sampling and proceeding

Non-invasive samplings using photography and observational techniques as well as percentage cover estimates of invertebrates and seaweeds were performed between December 2013 and March 2015. Samplings were made every 15 days, at low tide in the lower intertidal zone. The low-intertidal level at Punta Este has a mean height of 2.05 m above sea level and was defined as the zone dominated by dense coralline algal cover. At the lower intertidal level, six quadrats of 0.5 × 0.5 m (*i.e.*, 0.25 m²) were marked exactly.

Each replicate was individually georeferenced and later photographed every fifteen days during the entire sampling period. The quadrats were located in three different positions in the intertidal zone, western, middle and eastern zones, since the air exposure time from west to east is different during low tide, the quadrats located in eastern zone being more exposed. Post hoc species sample analyses indicated that on average 75% ± 5.0 SE of the species pool was sampled each time.

Whenever necessary, multi-layered species assemblages were taken into account by setting aside canopy species for secondary photographic records of understory species.

In each quadrat divided into 25 equal 0.25 m² frame sections we measured each species percentage cover using the digital processing software *ImageJ*. For data analyses, it is important to have abundance data expressed in the same measurement unit for every species. We chose percentage cover to quantify abundance because alternative measures (*e.g.* individual density) cannot always be reliably determined for clonal organisms (Scrosati 2005) or (*e.g.* biomass) would have implied destructive sampling of numerous shore areas.

No organisms were removed from the quadrats. Cover values were obtained from the projection of three-dimensional structures to the plane of the sampling frame. Total percentage cover for a quadrat could exceed 100% because of the assemblage multi-layered structure. When the cover was less than 1% in total for a given species, we recorded it as 0.5% (Dethier et al. 1993, Scrosati 2016). In each photograph, all taxa present in the quadrat were identified.

Taxa assignments

To identify the invertebrates and seaweeds, samples near to the marked quadrats were removed from the substrate and placed in bags. The invertebrates were fixed in 10% formalin and later transferred to 70% ethanol. The algae samples were squeezed by hand to remove excess seawater and subsequently transported to the laboratory in closed plastic bags. Samples were stored overnight at 5 °C. The following day, each specimen was washed thoroughly with seawater to remove adhering sand and the fronds were stored in FAA (ethyl alcohol: formaldehyde: acetic acid at 8:1:1). Invertebrates and algae were identified to the lowest possible taxonomic level. The algae taxa were assigned to different traits: a) growth (fast or slow growth), thallus longevity (annual or perennial) and succession (opportunistic or late successional); and b) thallus morphology (filamentous and leaf-like, fleshy, thick, or calcareous upright, and calcareous and non-calcareous crusts) (Orfanidis et al. 2011). Also, algae taxa were assigned according to the different morphological-functional groups, namely, filamentous, foliose, corticated foliose, corticated, leathery, articulated calcareous, and crustose (Steneck & Dethier 1994).

Each invertebrate organism was assigned to a functional group according to its feeding type: suspension feeder, predator - scavenger and grazer. The mytillids *Perumytilus purpuratus*, *Brachidontes rodriguezii*, *Mytilus edulis* and *Aulacomya atra* were counted and grouped together under the name "mussels" because of their difficult identification in the photographs.

Environmental data

Surface seawater temperature and daylength were measured daily at the sampling location. Radiation data were provided by Automatic Meteorological Station of Climatology Laboratory of CENPAT-CONICET. Monthly average values are reported.

DATA ANALYSIS

The information on species cover was used to construct a comprehensive table where each species is classified as very frequent (recorded 19-32 times), frequent (recorded 10-18 times), or rare (recorded 1-9 times). Frequency of occurrence of each taxon was calculated by counting the number of sampling times in which each species was recorded. Species turnover was calculated by counting how many species were lost or gained from all quadrats between successive sampling times.

Multivariate analysis of morphological and feeder functional group were performed using the statistical package PRIMER 6 with the PERMANOVA add-on (Clarke & Gorley 2006, Anderson et al. 2008). Multivariate relationships were assessed by correlating the similarity matrices (RELATE) of environmental (Euclidean distance) data to each other and to model matrices for cyclicity, testing for seasonality and gradients following individual environmental variables. Cover data based on species and functional groups were used to construct resemblance matrices with a Bray-Curtis similarity index.

Differences in functional group and species richness were assessed by analysing species percent cover with a Permutational Multivariate Analysis of Variance. The analysis had three fixed factors: months, seasons and position and was performed on Bray-Curtis matrix of square-root transformed data, using 9999 permutations of residuals under a reduced model. Pair-wise comparisons were then performed for significant factors with more than two levels. The different seasons were defined by the following months: autumn (March, April and May), winter (June, July and August), spring (September, October and November) and summer (December, January and February). SIMPER test was used to determine the relative contribution of each functional group to the average Bray–Curtis dissimilarity between positions and seasons. This method determines which morphological and feeder group and taxa were responsible for any differences.

In order to relate environmental variables to the community, BEST/BIOENV procedure (Clarke & Gorley 2006) was applied. Environmental variables were correlated with each other in order to detect multicollinearity and exclude it in the analysis since it would not provide additional information. Before applying the method, the environmental variables were log-transformed and were categorised with Euclidean similarities while biological data were square root transformed and categorised using Bray–Curtis similarities. Then data matrices were analysed with BIOENV, estimating Spearman rank correlation between these two matrices.

The relationship between environmental and biological variables (algal and invertebrate assemblages, species richness and abundance of articulated calcareous and suspensor feeder groups) was assessed by Pearson correlation. Principal component analysis (PCA) was used to identify the main environmental gradients across the samples time. The PCA ordination was performed on a correlation matrix after logarithmic transformation to partially reduce the large differences in raw values among environmental variables. Daylength variable was not included in the PCA because it was strongly correlated with radiation and therefore was considered redundant. A subsequent mapping of the biological data from cluster analysis onto the environmental ordination allowed for a visual assessment of the correspondence between major biological patterns and dominant environmental gradients.

RESULTS

Benthic community assemblage

A total of 32 invertebrate and algae taxa were identified from 192 photographic samples. Seaweeds were represented by 18 taxa and the invertebrates by 14 (Tables I and II, respectively). Algal taxa were assigned to six thallus morphology types, two types of growth and successional traits, and seven different morphological functional groups. The annual, opportunistic and fast-growing species were featured as fleshy, filamentous and leaf-like morphologies. The fleshy morphology was represented by five brown algae, while filamentous morphology was observed in brown, green and red algae. The leaf-like morphology was only represented by the genus *Ulva*. Fleshy species comprise the fleshy corticated and fleshy corticated foliose groups, and were only represented by brown algal species. The filamentous functional group exhibited filamentous morphology and was mainly integrated by red algae. Thick, crustose non-calcareous and calcareous upright morphologies corresponded to slow-growing, late succession and perennial species. These categories, consisting of three taxa, *Undaria pinnatifida*, *Ralfsia verrucosa*, and *Corallina* sp., represented three different functional groups,

Table I. Algal taxa assignments in term of growth/thallus longevity/succession, thallus morphology and morphological functional group.

Macroalgal taxa	Growth/thallus longevity/ succession	Thallus morphology	Morphological functional group
Phaeophyceae			
Adenocystis utricularis (Bory) Skottsberg	Fast-annual-opportunistic	Fleshy	Corticated
Colpomenia sinuosa (Mertens *ex* Roth) Derbés & Solier	Fast-annual-opportunistic	Fleshy	Corticated
Dictyota dichotoma (Hudson) J.V. Lamouroux	Fast-annual-opportunistic	Fleshy	Corticated foliose
Leathesia marina (Lyngbye) Decaisne	Fast-annual-opportunistic	Fleshy	Corticated
Myriogloia major Asensi	Fast-annual-opportunistic	Fleshy	Corticated
Ralfsia verrucosa (Areschoug) Areschoug	Slow-perennial-late successional	Crustose non-calcareous	Crustose
Sphacelaria sp.	Fast-annual-opportunistic	Filamentous	Filamentous
Undaria pinnatifida (Harvey) Suringar	Slow-perennial-late successional	Thick	Leathery
Chlorophyceae			
Chaetomorpha sp.	Fast-annual-opportunistic	Filamentous	Filamentous
Cladophora falklandica J.D. Hooker & Harvey	Fast-annual-opportunistic	Filamentous	Filamentous
Ulva spp.	Fast-annual-opportunistic	Leaf-like	Foliose
Rhodophyceae			
Corallina sp.	Slow-perennial-late successional	Calcareous upright	Articulated calcareous
Polysiphonia abcissa J.D. Hooker & Harvey	Fast-annual-opportunistic	Filamentous	Filamentous
Leptosiphonia brodiei (Dillwyn) A.M. Savoie & G.W. Saunders	Fast-annual-opportunistic	Filamentous	Filamentous
Melanothamnus harveyi (Bailey) Diaz-Tapia & Maggs	Fast-annual-opportunistic	Filamentous	Filamentous
Polysiphonia sp.	Fast-annual-opportunistic	Filamentous	Filamentous
Ceramium virgatum Roth	Fast-annual-opportunistic	Filamentous	Filamentous
Ceramium sp.	Fast-annual-opportunistic	Filamentous	Filamentous

leathery, crustose, and articulated calcareous, respectively. The leathery functional group was represented by the introduced kelp, *U. pinnatifida*, which can reach high abundance in the subtidal zone of Punta Este.

Table II shows the invertebrate taxa assignments in term of feeder functional group. Three different feeder functional groups were represented by the invertebrates found in the lower intertidal zone. The suspension feeder group was integrated by the highest number of taxa; it is three molluscan species, the introduced *Balanus glandula* and a non-identified species of sponge. The grazer feeder group was constituted by molluscan species. The third group, predator scavenger, was represented by two taxa, the molluscan *Buccinanops deformis* and the cnidarian *Antholoba achates*.

The abundance (% cover) and occurrence of taxa from each group (invertebrates and algae) are listed in Table III. 56.2% of all taxa were very frequent, 37.5% were rare and only 6.2% of the taxa were frequent. Even though the rare species represented 37.5% of the benthic assemblage, its cover did not exceed 0.12%, whereas the two frequent species covered a greater area of more than 0.57%. The very frequent species assemblages had the greatest contribution to the percentage cover, reaching 73.8%. All the morphological and feeder functional groups recorded in this intertidal zone were represented in the very frequent species. The remaining 25.5% cover was represented by bare substrate.

Temporal variations of environmental parameters, species richness and benthic covers

Environmental parameters

Physical environmental parameters showed a clear seasonal pattern, typical of the transitional

Table II. Invertebrate taxa assignments in term of feeder functional group.

Invertebrate taxa	Feeder functional group
Mollusca	
Buccinanops deformis (P.P. King, 1832)	Predator -scavenger
Plaxiphora (Plaxiphora) aurata (Spalowsky, 1795)	Grazer
Fissurella radiosa tixierae (Métivier, 1969)	Grazer
Siphonaria lessoni Blainville, 1827	Grazer
Tegula patagonica (d'Orbigny, 1835)	Grazer
Trophon geversianus (Pallas, 1774)	Predator–scavenger
Aulacomya atra (Molina, 1782)	Suspension feeder
Leiosolenus patagonicus (d'Orbigny, 1842)	Suspension feeder
Perumytilus purpuratus (Lamarck, 1819)	Suspension feeder
Mytilus edulis Linnaeus	Suspension feeder
Brachidontes rodriguezii (d'Orbigny, 1842)	Suspension feeder
Cnidaria	
Antholoba achates (Drayton in Dana, 1846)	Predator–scavenger
Arthropoda	
Balanus glandula (Darwin, 1854)	Suspension feeder
Porifera uncertain	Suspension feeder

north Patagonian coastal area. Seawater temperature, daylength and solar radiation peaked in summer (December to February) (Fig. 1). Both summer periods considered in this study were similar over the two consecutive years ($\rho_{cyclicity}$=0.649, p<0.001) (Fig. 2).

Species richness and benthic covers

The total species richness estimated in the sampling time ranged from 14 to 18 taxa. The number of species was variable when comparing both months and seasons (Months: PERMANOVA pseudo-F$_{(11, 191)}$=1.927, p=0.037; seasons: PERMANOVA pseudo-F$_{(3, 191)}$=5.310, p=0.001). The lowest species richness was observed during June and July (Fig. 3). The highest mean species richness difference was noticed between summer and winter (p=0.0003), reaching highest richness during summer period.

Regarding the spatial distribution of species richness, a distribution pattern was not detected by comparing the quadrat positions (PERMANOVA pseudo-F$_{(2, 191)}$=0.077; p=0.925).

The curve of the cumulative species richness showed that during the first six months 18 to 22 taxa were found out of a total of 32, corresponding to from 56.2 - 68.7% of the benthic assemblage. From June onwards, more than 90% of benthic assemblage was observed, gradually reaching the total number of species of the assembly (Fig. 3).

The turn-over of species between successive sampling times was generally low, ranging between 6.6% and 36% of total species richness. The highest number of species gained was reported in May, whereas the highest number of species lost was observed in four months: January, April, August and December 2014 (Fig. 4).

Regarding the benthic fauna, the highest invertebrate cover gained was observed in

November, reaching values near to 9%. Another two high cover increases were noted in December 2013 and April 2014, ranging between 6% and 8%, respectively. The largest loss of invertebrate cover was observed in three months: March, May and June 2014. These cover losses reached values higher than 6% and 9%. Regarding the benthic flora, the highest algal cover gained was observed in May, jointly with the highest gained species number, indicating that the higher percentage was due to the increase in the number of species in the assemblage, especially large-size species, such as *U. pinnatifida*, reaching *c.* 8%, a little lower than that observed in the invertebrate group. Other periods with high increases in algal cover were March and June 2014. The three months with a large loss of cover were: April and November 2014, and January 2015. The first two months coincided with periods characterized by high increases in the cover of invertebrates (Fig. 4). However, most of these events could not be confirmed seasonally due a lack of replication in the second year.

Among the algal functional groups, the articulated calcareous group exhibited the highest cover, reaching 62.7/0.25 m^2. The crustose and corticated groups had intermediate covers, while the remaining functional groups were less abundant. In general, these morphological functional groups cover varied between 0.6 and 6.6/0.25 m^2, representing very low values compared to the calcareous group. The suspensor feeder group presented a considerable cover compared to the other two feeder groups, reaching values of 22.7/0.25 m^2, whereas the predator group reached values of 0.6/0.25 m^2 and the grazer group 1.4/0.25 m^2 (Fig. 5).

Seaweeds and invertebrates covers differed between positions (invertebrates: PERMANOVA pseudo-F$_{(2,191)}$=13.863; p=0.0001; seaweeds: PERMANOVA pseudo-F$_{(2,191)}$=8.465; p=0.0001). The total invertebrates cover was higher in

Table III. Occurrence expressed as the presence at any sampling time or number of samples of rare species (recorded 1-9 times), frequent species (recorded 10-18 times) and very frequent species (recorded 19-32 times). Biomass is cover/0.25 m2 ± standard error; single occurrence denoted by (-), no error is reported.

|	Occurrence by sampling time	Occurrence by samples	Cover %
Rare species	**12 taxa (37.5 % assemblage)**		
Buccinanops deformis	2	2	0.002 ± 0.002
Plaxiphora aurata	6	8	0.009 ± 0.003
Fissurella radiosa tixierae	1	1	0.001 -
Porifera uncertain	1	1	0.001 -
Adenocystis utricularis	1	1	0.001 -
Chaetomorpha sp.	2	1	0.001 ± 0.001
Cladophora falklandica	2	2	0.028 ± 0.026
Polysiphonia abcissa	3	5	0.004 ± 0.017
Leptosiphonia brodiei	2	2	0.039 ± 0.001
Melanothamnus harveyi	1	6	0.028 ± 0.01
Polysiphonia sp.	4	1	0.003 ± 0.012
Sphacelaria sp.	1	1	0.001 -
Frequent species	**2 taxa (6.25 % assemblage)**		
Leiosolenus patagonicus	10	11	0.011 ± 0.004
Ceramium sp.	18	51	0.565 ± 0.128
Very frequent species	**18 taxa (56.25 % assemblage)**		
Antholoba achates	27	96	0.275 ± 0.031
Balanus glandula	32	188	0.559 ± 0.066
Mussels (*)	32	192	16.318 ± 0.579
Siphonaria lessoni	28	80	0.065 ± 0.009
Tegula patagonica	32	181	0.932 ± 0.056
Trophon geversianus	31	95	0.145 ± 0.278
Colpomenia sinuosa	25	94	0.167 ± 0.021
Corallina sp.	32	192	46.565 ± 0.916
Dictyota dichotoma	32	92	0.637 ± 0.072
Leathesia marina	25	125	3.579 ± 0.410
Myriogloia. major	24	79	1.117 ± 0.235
Ralfsia verrucosa	32	167	2.001 ± 0.153
Ceramium virgatum	21	54	0.364 ± 0.036
Ulva spp.	25	52	0.080 ± 0.023
Undaria pinnatifida	26	65	1.001 ± 0.232
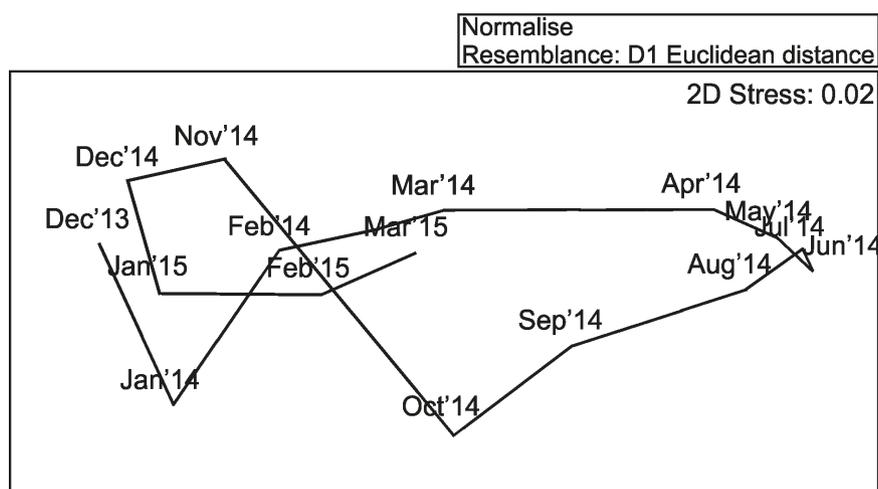
Figure 2.
Ordination nMDS of environmental conditions at each sampling time.

the western position quadrat, whereas the total seaweeds cover was higher in the central quadrats.

Regarding invertebrates, the suspensor group had a considerably greater coverage compared to the remaining invertebrate groups and was more abundant in the west (PERMANOVA pseudo-$F_{(2,191)}$=52.655; p=0.0001). The cover of the predator-scavenger group was higher in the central quadrat (PERMANOVA pseudo-$F_{(2, 191)}$=4.463; p=0.005), whereas the grazers were more abundant in the east (PERMANOVA pseudo-$F_{(2, 191)}$=2.670; p=0.025). Hence, an interesting decrease of grazers was observed from east to west (Fig. 6). The SIMPER test showed a greater dissimilarity between the quadrats located in the central and western positions. This dissimilarity was determined by the higher abundance of the suspensor feeder group, represented by the "mussel" group, in the western position. The lower presence of grazer in that position also contributed to this dissimilarity (Table IV).

Regarding seaweeds, in the western quadrats all groups showed the lowest covers, with the exception of corticated group, which had the highest cover in that position (PERMANOVA pseudo-$F_{(2, 191)}$=7.241; p=0.0001) (Fig. 7). The SIMPER test showed that the greatest

dissimilarity occurred between the central and eastern positions; such dissimilarity was given by a higher cover of corticated, articulated calcareous and crustose functional groups in the central position, mainly determined by higher covers of *Leathesia marina*, *Corallina* sp. and *Ralfsia verrucosa*, respectively (Table IV).

Feeder groups cover varied between seasons (PERMANOVA pseudo-$F_{(3, 191)}$=11.243; p=0.0001). The highest invertebrate covers were observed during summer and autumn. The suspensor was the most abundant group and dominated during all four seasons, being however more abundant in summer and autumn (PERMANOVA pseudo-$F_{(3, 191)}$=13.106; p=0.0001). Winter was also characterized by the highest grazer cover (PERMANOVA pseudo-$F_{(3, 191)}$=2.038; p=0.037), while in spring the predator group was the least represented (PERMANOVA pseudo-$F_{(3,191)}$=12.759; p=0.0001) (Fig. 8). SIMPER test indicated that the greatest dissimilarity was given between autumn and spring. The higher cover of both suspensor feeder and predator scavenger groups in autumn was responsible for such dissimilarity (Table IV). This dissimilarity was given by the mussels and *Antholoba achates*, respectively.

The algal morphological functional groups varied between seasons (PERMANOVA pseudo-$F_{(3, 191)}$=17.836; p=0.0001). Articulated
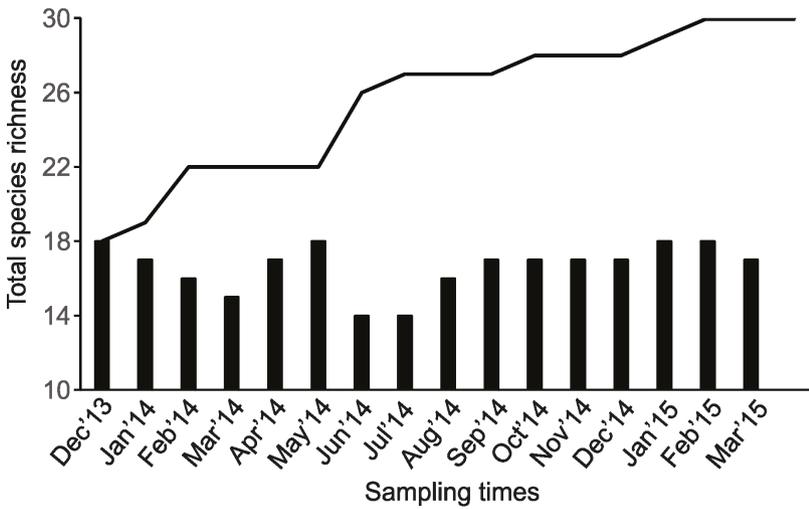
Figure 3. Total number of species found in all six quadrants (0.25 m²) considering a total area analysed of 1.5 m² per sampling time (black bars) and cumulative total species richness (line).
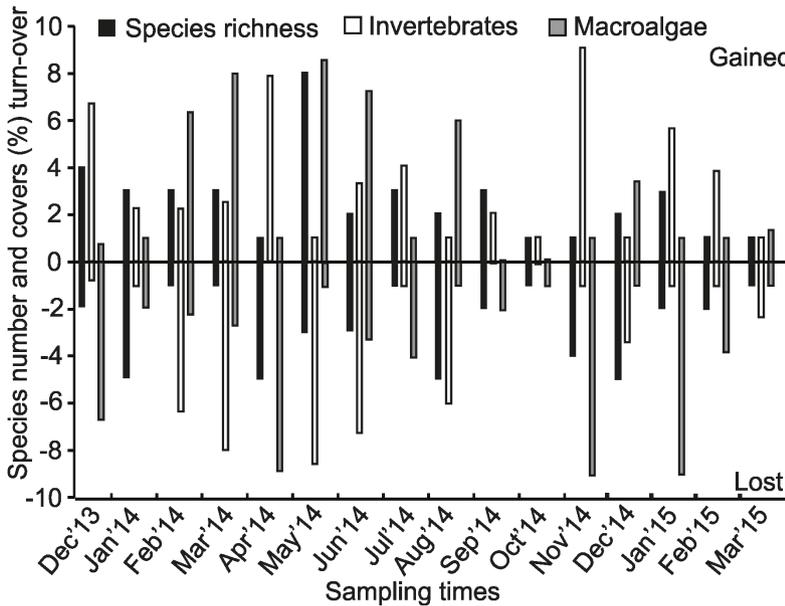

Figure 4. Species richness and cover (%) of algal and invertebrate taxa gained or lost between successive sample times between December 2013 and March 2015.

calcareous group, represented by *Corallina* sp., had the highest cover during all the period examined, being statistically different between seasons; *i.e.,* more abundant in winter and spring (PERMANOVA pseudo-$F_{(3, 191)}$=18.249; p=0.0001). The corticated group, integrated by four brown algae, was statistically more abundant during summer time (PERMANOVA pseudo-$F_{(3, 191)}$=24.508; p=0.0001). The crustose group, represented by the brown algae *R. verrucosa,* was more abundant in autumn (PERMANOVA pseudo-$F_{(3, 191)}$=3.177;

p=0.010) and the leathery morphological group was more abundant in winter (PERMANOVA pseudo-$F_{(3, 191)}$=9.222; p=0.0001) (Fig. 9). The greatest dissimilarity indicated by the SIMPER analysis was observed between summer and winter. These differences were given by the corticated, articulated calcareous and leathery groups (Table IV). Summer was characterized by high abundance of *Leathesia marina* and the lowest cover of *Corallina* sp and *U. pinnatifida.*

Relationships of morpho-functional and feeder benthic groups with environmental factors

BEST/BIOENV analysis revealed that the most important variables structuring morphological and feeder functional groups were seawater temperature and radiation (ρ=0.866, p=0.01). Several permutations were performed to test if there were any changes in the BIOENV outcome. In particular, this test gave the following correlation when the variables were considered separately: daylength (ρ=0.840), temperature and daylength (ρ=0.642), and temperature (ρ=0.272).

In the PCA analysis, the first two axes explained 75.6% of the joint variation of environmental factors and biological variables. PC 1 was related mainly to the seasonal variability of the samples and morphological and feeder groups. Samples from warmer months (December - March) were grouped on the more positive side of the PCA axis I, whereas samples from the cold period (April - October) were on the more negative side of PCA axis I. In addition, the right side of PC 1 was characterized by high species richness, high seawater temperatures, high radiation and high cover of algal assemblages and suspensor group. The left side of PC 1 grouped the colder months and was characterized by high cover articulated calcareous (Fig. 10).

Interesting results were observed when the correlation between environmental parameters and benthic attributes were performed. An inverse relationship was seen between the articulated calcareous group and seawater temperature (ρ=-0.854), radiation (ρ=-0.688), species richness (ρ=-0.781), presence of suspensor feeder group (ρ=-0.746) and the algal assemblage (ρ=-0.873). On the other hand, a positive relationship was observed between the suspensor feeder group and seawater temperature (ρ=0.806) and radiation (ρ=0.709).

DISCUSSION

Two main biogeographical provinces have been proposed for the Atlantic coast of Argentina: the Magellan province, with cold-water covering southern Patagonia, and the Argentinean province, with warmer waters extending from North Patagonia northwards (Lutz et al. 2003). Punta Este is located to the north of this latter province. In general, the species richness is relatively poor in this area and the intertidal rocky shores are characterized by a diminished seaweed flora, mainly due to harsh physical conditions (Bolton 1994, Paruelo et al. 1998, Bertness et al. 2006). Moreover, it is a zone characterized by the presence of calcareous algae covering the low tidal level in wave-protected sites (Bertness et al. 2006). In this study we coincidentally observed low species richness and the highest covers of the articulated calcareous group in the Punta Este low intertidal zone, as well as the presence of ephemeral occurrence endemic species, such as *M. major*. Rocky intertidal communities on Argentinean coasts are characterized by the dominance of mytillids, particularly *B. rodriguezii* in the warm temperate region and *P. purpuratus* in the cold temperate sector, coexisting in the same beds along the transition zone (41-43º S) (Trovant et al. 2013, Van der Molen et al. 2013). In the low intertidal zone of Punta Este, we noted the presence of *P. purpuratus* and *B. rodriguezii* forming a conspicuous mussel bed, mixed with the articulated calcareous group. This region was also characterized by a high abundance of the grazer gastropod *T. patagonica* and predator species, this high grazer abundance was coincident with the highest abundance
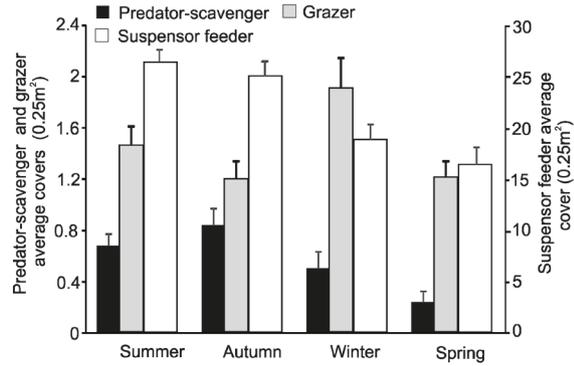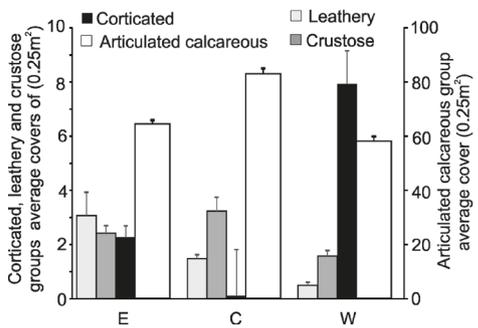
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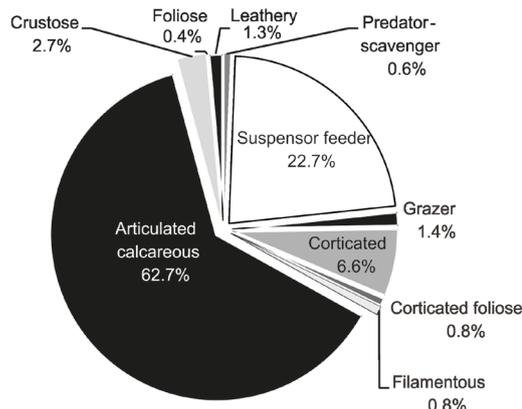
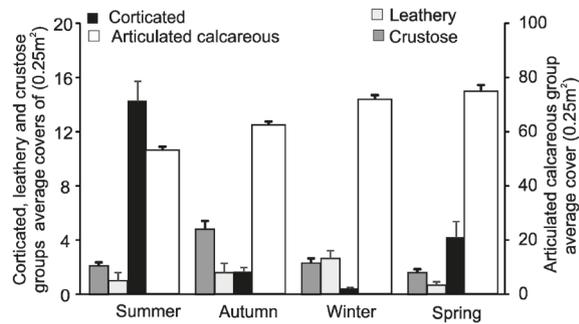**6**
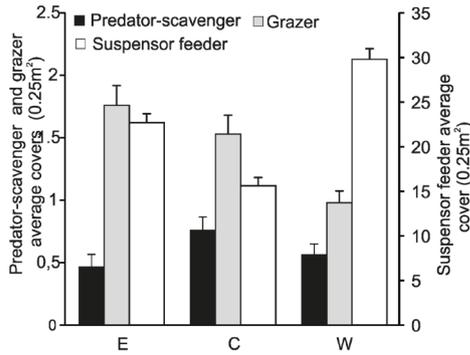
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Figure 5. Distribution in abundance (cover %) of macroalgal morphological and invertebrate feeder functional groups during the whole sampling period.

Figure 6. Distribution of abundance (cover %) of feeder groups in quadrats located at three different sampling sites (E: east; C: centre; W: west).

Figure 7. Distribution of abundance (cover %) of algal morphological functional groups in quadrats located at three different sampling sites (E: east; C: centre; W: west).

Figure 8. Distribution of abundance (cover %) of feeder groups over the seasons.

Figure 9. Distribution of abundance (cover %) of algal morphological functional groups over the seasons.
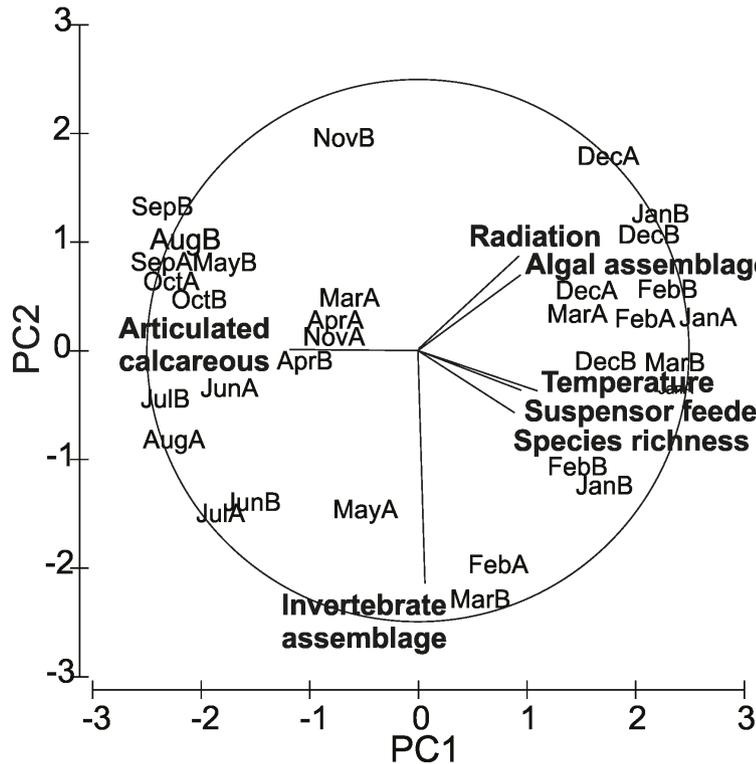
Figure 10. PCA biplot: association between biological and environmental variables. Biological variables: species richness, algal and invertebrate assemblages, suspensor and articulated calcareous groups. Environmental variables: seawater temperature and radiation. Months sampled were indicated by abbreviations: January (Jan), February (Feb), March (Mar), April (Apr), May, June (Jun), July (Jul), August (Aug), September (Sep), October (Oct), November (Nov) and December (Dec). The letters A and B indicate successive sampling times in the same month.

of the leathery morphological functional group, integrated exclusively by *U. pinnatifida*. Rechimont et al. (2013) also associated the dominance of grazers with *U. pinnatifida*.

Ecological studies on seaweeds from the southeast South American region are scarce; thus, seaweed distribution, abundance patterns and functional roles in these ecosystems are poorly known. In particular, seaweeds benthic assemblages are considered to be variable in terms of distribution and abundance. For such studies, it is essential to choose a non-destructive sampling method that guarantees accurate results of the intertidal assemblages. Assignment and use of morphological and feeder functional groups can considerably reduce the time and resources needed to monitor wide geographical areas and, simultaneously, it allows comparisons to be made between regions with different species assemblages (Vandewalle

et al. 2010). Moreover, trait-based approaches in morphologies or feeder preferences can improve biodiversity understanding, reflecting the species' ecological roles (Díaz & Cabido 2001). Such approach has also been used by other authors, such as Gaspar et al. (2017), and proven to be efficient in detecting differences in the algal and invertebrate assemblage patterns in terms of species composition and species cover measured at small scales.

A variation in the assemblage structure (species composition and species cover) throughout the year was observed. In fact, it was more marked than the variability at horizontal fine-scale; *i.e.*, between eastern, central and western sites. Such horizontal fine-scale variability was only seen in the distribution of feeder groups, as the eastern quadrats presented higher grazer cover than the central and western ones. These results are difficult to

Table IV. SIMPER test showing morphological and feeder functional groups that most contribute to dissimilities.

Groups	Group Av. Abund.	Group Av. Abund.	Contrib. (%)
Feeder functional	**Middle**	**Western**	
Suspensor-feeder	3.27	4.79	63.33
Grazer	1.59	0.54	83.66
	Autumn	**Spring**	
Suspensor feeder	4.21	3.29	60.48
Predator-scavenger	0.64	0.21	24.29
Morphological functional	**Middle**	**East**	
Corticated	2.04	0.90	26.86
Articulated calcareous	6.87	5.63	17.22
Crustose	1.57	0.91	15.53
	Summer	**Winter**	
Corticated	2.94	0.44	35.19
Articulated calcareous	6.20	7.41	18.70
Leathery	0.30	1.06	14.78

interpret, but cannot be ignored because the high sample size and statistical results show a strong significant difference between the three invertebrate functional group covers. A possible explanation of this variation could be that the grazer group prefers sites with greater air exposure. In fact, air exposure time between the three quadrats hardly differs, but the eastern quadrats were slightly more exposed than western ones. Horizontal fine-scale variation in species assemblages has been reported as a common attribute of marine benthic habitats and can often occur at fine resolutions, *i.e.* with a small (10s to 100s of centimetres) to middle scale (10s to 100s of meters) variation (Valdivia et al. 2011, Fraschetti et al. 2005).

Both biological and physical factors, such as substrate availability, recruitment, grazing,

competition, wave and aerial exposure, irradiance, temperature or nutrient exchange, have been mentioned as being potentially responsible for the variability at these spatial scales (Benedetti-Cecchi 2001, Lobban & Harrison 1994, Choi & Kim 2004).

In this study, we determined that intertidal seaweed communities are strongly regulated by physical and biological factors which vary according to season, detecting temporal dynamics of both algal and invertebrate assemblages. Regarding the physical factors, given the co-varying nature of seawater temperature, daylength and solar radiation, it is difficult to separate their individual effect contribution. With respect to biological factors, the abundance of grazers was low; indicating low grazing pressure. Similarly, Bertness et al.

(2006) found low grazing pressure on the western Patagonian rocky shores due to the absence of common predaceous crabs and snails and the limited impact of limpets.

However, competition was an important biological factor at Punta Este since temporal dynamics in algal richness, seaweeds assemblage and invertebrate structures and species turnover was a function of the complex interplay between the environmental factors and the abundance of *Corallina* sp. On the one hand, the presence of articulated calcareous groups directly affected the area of available substrate for colonization by other seaweeds, thereby regulating the species richness. On the other hand, the articulated group only favoured the development of crustose algae, such as *L. marina* and *C. sinuosa*, which only grow attached to *Corallina* thalli.

Articulated calcareous cover was directly correlated with environmental variation, whereas species richness of algae was associated with temporal changes in the calcareous groups. Seasonal change in the cover of *Corallina* sp. was negatively correlated with all of the environmental variables considered, and in particular with seawater temperature. In contrast to temporal patterns in calcareous cover, species richness was not well correlated with any of the environmental factors, suggesting that they are not the main driver of species seasonality *per se*.

Species losses and gains over time were very variable. This variability probably reflects the reproduction, recruitment and growth of many species, particularly those with ephemeral life cycles. However, we agree with Wernberg et al. (2005) who affirmed that the broad range in individual responses to seasonal environmental changes of understory algae and the presence of a canopy layer make it very difficult to identify specific factors or threshold values that control temporal patterns in species richness.

Mussel beds characterized by suspension-feeders are critical in the structure and function of the intertidal community (Silliman et al. 2011). This feeding type is favoured in this environment due to plankton abundance in the water around the rocky shores and wave movement that contributes to nutrient circulation (Bertness 1999).

In several coastal ecosystems, diversity decline is evident due to mussel dominance, but at the same time, beds development creates a secondary substratum enriched in fauna and epibenthic assemblages (Dittman & Robles 1991, Lohse 1993, Ragnarsson & Raffaelli 1999). However, in this study, species richness was not correlated with suspensor feeder group dominance.

It has already been confirmed, that the turf forming coralline alga also provides a more benign habitat for recruitment and survival of several tiny invertebrate species (Kelaher et al. 2007); nonetheless, articulated calcareous group abundance did not favour mussel beds. Our result indicated that there is competition for the substrate between the articulated calcareous and the suspensor feeder groups.

This study represents an important baseline on morphological and-feeder functional groups since studies incorporating both algae and invertebrates in Patagonian Argentina are very scarce. Under this point of view, this study also represents a species-level baseline in the literature, so that future researchers will have solid data for comparison if benthic composition changes in response to global climate change, or other anthropogenic factors. As a future perspective, it would be appropriate to implement the same method, but on a larger scale at different sites on the Patagonian coast.

We conclude that the dominating interactions at the lower intertidal level and small-scale spatial variation jointly with abiotic

factors promote a better environment, preventing other species from extreme physical stress, thus leading to community development. We consider that this pattern is common to a wide range of natural systems where assemblages (algae and invertebrates) are influenced by complex sets of physical and biological processes, such as those operating in the marine ecosystems. However, additional experimental investigations are required in order to have a clear picture of the mechanisms underlying assemblage patterns on the rocky shores of Punta Este and along the Patagonian coast.

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MCG, CF and JFE, conceived of the presented idea; JFE, MCG and CF performed the measurements, MCG and CF, performed the analysis, written and drafted the manuscript and designed the figures; ERP were involved in supervised and provided funding acquisition, MCG and CF aided in interpreting the results. All authors discussed the results and commented on the manuscript.