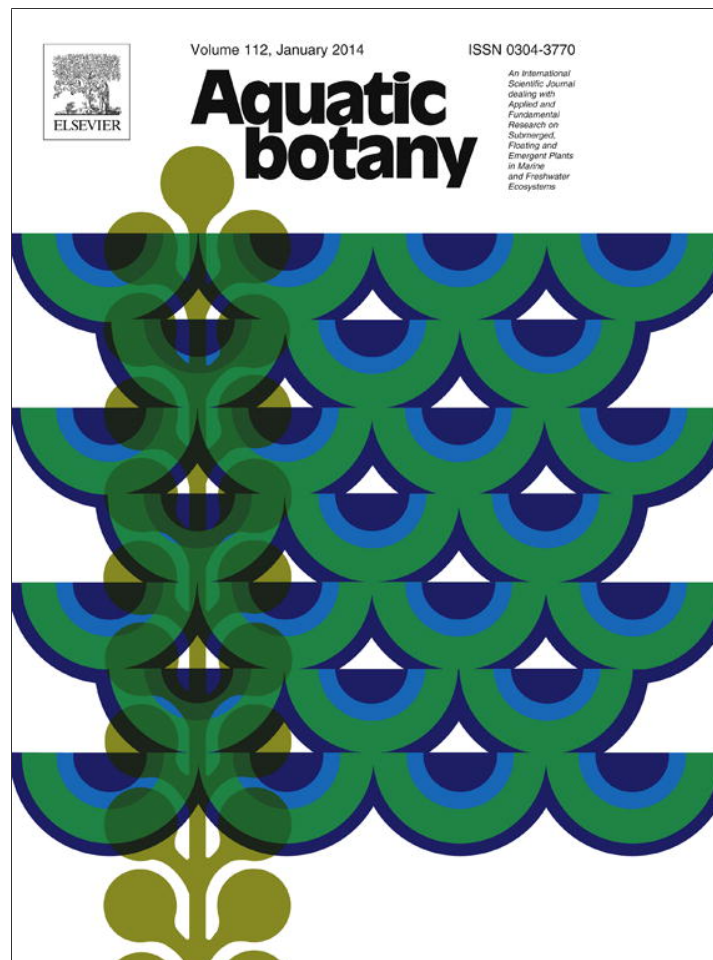


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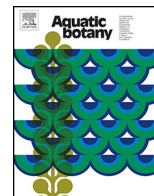
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Introduced and native species on rocky shore macroalgal assemblages: Zonation patterns, composition and diversity



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ABSTRACT

The study of the natural and anthropogenic changes in patterns of species and habitat diversity is important for understanding the organization of natural species assemblages. One of the major threats to native marine biodiversity and resource values is the introduction of exotic species. Rocky intertidal shores are considered among the environments that are susceptible to the introduction of organisms like macroalgae. The scope of this work is to study the spatial variation of the native and introduced intertidal macroalgae in rocky shores of northern Patagonia, Argentina. Seasonal sampling of cover, abundance, richness, biomass and diversity of native and introduced macroalgae at three intertidal levels (high, middle and low) was carried out at four wave-protected rocky shores during one year. We found a conspicuous zonation pattern of the dominant species of algae and invertebrates, with the greatest richness, abundance and algal diversity at the low intertidal level, but these variables were heterogeneous through time and space. These differences were mainly due to the variations in the abundance of ephemeral algae. Introduced species represented around 20–25% of the total richness of each locality, being most abundant in those localities that also showed a greater total diversity. This study provides the first assessment of rocky shore macroalgae assemblages from Argentina that incorporates the presence of introduced species and shows that the number of introduced algae species along Patagonian rocky shores had been underestimated. We also encourage the monitoring of the biodiversity and the study of the processes that are involved in the role that introduced species plays in these environments.

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1. Introduction

Changes in patterns of species and habitat diversity are important to understand the organization of natural species assemblages (Andrew and Mapstone, 1987). Intertidal communities usually have strong zonation patterns represented by bands of different organisms that occur progressively up a shoreline across environmental gradients (Stephenson and Stephenson, 1949, 1972). These patterns are common in many rocky shores and the organisms are influenced by a combination of ecological processes such as grazing, competition, facilitation and recruitment (e.g. Raffaelli and Hawkins, 1996; Underwood et al., 2000) and abiotic factors like nutrient availability, exposure and tidal variation (Connell, 1972; Pedersen and Kraemer, 2008).

On rocky intertidal shores, macroalgae have an important ecological role for the organization of the communities, providing food

for many species of invertebrates that inhabit in their fronds and also offering protection against predation, amelioration of physical extremes and reduction of water movement (Jenkins et al., 1999). Intertidal macroalgae assemblage structure and biomass of the key taxa can vary across multiple spatial scales along the coastline (Smale et al., 2010). Recent investigations have also showed that small-scale spatial variability may override more general patterns of distribution (Liuzzi and López Gappa, 2008; Wieters et al., 2012). The physical features of the environment, and consequently the structure of the local assemblage, may change abruptly over very small spatial scales (Metaxas et al., 1994). In this sense, the detection and monitoring of rare and declining species and the effects of regional and global change are an important issue in long term conservation and management of biodiversity (Lubchenco et al., 1991).

Rocky intertidal shores are susceptible to the introduction of organisms such as macroalgae, since this type of substratum allows their settlement (Arenas et al., 2006). Introduced marine macroalgae are a matter of concern since they may modify both ecosystem structure and function by monopolizing space, developing into ecosystem engineers and changing food webs (Thresher, 2000). There is a limited understanding of the distribution and ecology of

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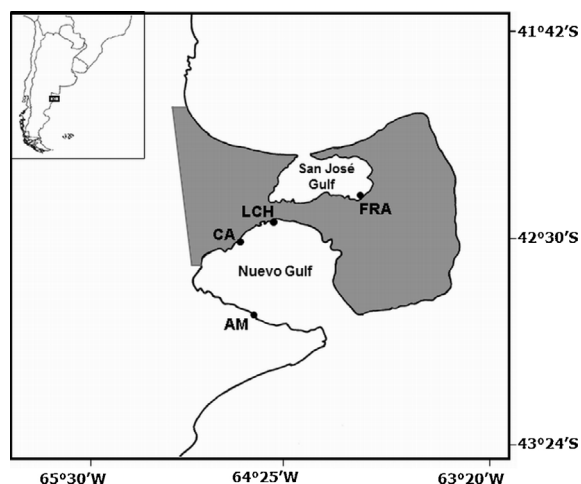


Fig. 1. Map showing locations of the sampling localities: Fracasso (FRA), Las Charas (LCH), Casino (CA) and Ambrosetti (AM). Limits of the Península Valdés Protected Area are shaded in gray.

inconspicuous introduced macroalgae and their introductions are underestimated due to misidentifications (Schaffelke et al., 2006). Three cryptogenic and four introduced species have been reported in Argentina (Raffo and Schwindt, 2011), but this is a very low number compared with other countries such as Australia with 14 species (Ruiz et al., 2000), United States with 20 species in the North-west Atlantic (Mathieson et al., 2008) and France with 45 species (Hewitt, 2003). Macroalgal communities of the rocky shores along the northern Patagonian coast of Argentina are composed of small or medium-size species (between 0.5 and 20 cm high) and different morphological types, including turf forming algae (e.g. *Corallina officinalis*), filamentous algae (e.g. *Polysiphonia*, *Ceramium*), foliose algae (e.g. *Ulva*) and crustose algae (e.g. *Ralfsia*) (Díaz et al., 2002; Liuzzi and López Gappa, 2008).

The goal of our work was to study the spatial variation of the native and introduced macroalgal communities in Patagonian rocky shores. Specifically, the aims of this work were: (1) to describe the zonation patterns of the macroalgae and the associated sessile invertebrates species that inhabit this environment; (2) to determine whether the distributional patterns of macroalgal assemblages vary their composition and diversity in different intertidal levels and localities; and (3) to assess the presence and abundance of the introduced macroalgal species in the context of the native biodiversity.

2. Materials and methods

2.1. Study area

Samples were collected from four similar wave protected rocky shores. These rocky areas were wave-cut siltstone platforms between 100 and 150 m wide, and with slopes varying between 1° and 2° and the same tidal amplitude. Three localities were surveyed inside Nuevo Gulf: Las Charas (42°30' S, 64°36' W), Casino (42°36' S, 64°49' W) and Ambrosetti (42°30' S, 64°30' W), and another one on San José Gulf: Fracasso (42°24' S, 64°05' W). Three of these localities (Casino, Las Charas y Fracasso) are located within the Península Valdés Protected Area, listed as World Natural Heritage Site by the UNESCO in 1999; Fig. 1. Sea water temperature fluctuates yearly between 9.7 and 19.6 °C in Nuevo Gulf, and between 9.3 and 15 °C in San José Gulf (METEOCEAN-CENPAT-CONICET). Salinity usually ranges between 33.7 and 33.9 psu in Nuevo Gulf and between 33.48 and 34.26 psu in San José Gulf (Esteves et al., 1986). Tidal regime

is semidiurnal with mean amplitudes between 3 and 7 m (Servicio de, Hidrografía Naval Argentina).

2.2. Sampling design

At each locality, three intertidal levels were sampled (high, middle and low) set on the basis of different intertidal topographic surveys respect to the Argentinean hydrographic zero. Samples (quadrats of 35 cm × 35 cm) were placed randomly at each level, in four different times: August 2008 (winter), November 2009 (spring), February 2009 (summer) and May 2009 (autumn) to comprise the changes on the algae community structure throughout the year. Cover (%) of all organisms (including sessile fauna and algae) that could be discerned with the unaided eye was recorded in the field for each sample ($N=10$ for each site, level and season, total $N=480$). We did not find any overlapping of algae species during the cover estimations (see also Liuzzi and López Gappa, 2008). Then, all macroalgae within each of six sampling quadrat ($N=6$ for each site, level and season, total $N=288$) were scraped off the surface, bagged, labeled and stored at -13°C . The organisms found were identified in the laboratory to the lowest possible taxonomic level with the help of local taxonomic keys (mollusks: Pastorino, 1995; barnacles: Spivak and L'Hoste, 1976; algae e.g. Boraso de Zaisso, 2004; Piriz, 2009) and complementary specific literature was used to identify those macroalgae species where not found in taxonomic keys (e.g. Hollenberg and Norris, 1977; Hoffmann and Santelices, 1997). Species names and taxonomic classifications were validated with AlgaeBase (Guiry and Guiry, 2012) and updated when necessary. For each quadrat, taxonomic richness (S) was determined as the number of species present in the sample. Macroalgae abundance was obtained as dry biomass (g) of each macroalgae species previously dried in an oven at 60°C for 5 days and weighed to the nearest 0.001 g in a Sartorius analytical balance. Diversity was determined using the Shannon index (H') (Shannon and Weaver, 1949).

2.3. Data analysis

To describe the zonation patterns of the macroalgae and sessile invertebrate species that inhabit these intertidal environments we used the percentage cover (%) of each species registered in the field in relation to intertidal levels and times of the year (seasons). Distribution and composition of macroalgae assemblages were tested using the multivariate data analysis, PRIMER (Plymouth Routines In Multivariate Ecological Research) statistical package (Clarke and Warwick, 2001). Differences between intertidal levels (high, middle and low) were tested by a one way ANOSIM test and comparison among localities and seasons inside each intertidal level were analyzed by a two way crossed ANOSIM test, with 999 permutations (seasons × localities). These tests were made by Bray–Curtis similarity matrix applying the square root transformation of the data and using a dummy variable to avoid the differences between the dominant and rare species. In each ANOSIM test, the null hypothesis that there were no significant differences among groups was rejected if the significance level (p) was <0.05 (groups for locality comparison: Las Charas, Casino, Ambrosetti and Fracasso; groups for season comparison: autumn, spring, winter and summer). When significant differences were detected among a priori groups, the R -statistic was used to determine the extent of those differences. Similarity Percentages (SIMPER) were used to explain which species characterized each group and distinguished among each pair of groups.

Variation among abundance, richness and diversity in different seasons was tested independently for each locality with a one-way fixed ANOVA. These variables were tested only for the low intertidal level samples because the highest number of macroalgal

Table 1

List of the taxa found at the different localities (Las Charas, Casino, Ambrosetti and Fracasso) and seasons (W: winter, Au: autumn, Sp: spring, and Sm: summer). Phylum of each species is indicated between brackets (O: Ochrophyta, R: Rhodophyta and C: Chlorophyta) together with the status of Introduced (I) and Cryptogenic (Cr) species. The (x) indicates the presence of the species.

Species	Las Charas				Ambrosetti				Fracasso				Casino			
	W	Sp	Sm	Au	W	Sp	Sm	Au	W	Sp	Sm	Au	W	Sp	Sm	Au
<i>Anotrichium furcellatum</i> (J. Agardh) Baldock. (R) (I)			x	x			x	x	x			x	x		x	x
<i>Antithamnion</i> sp. Nägeli (R)		x	x	x	x		x	x	x	x	x	x	x	x	x	x
<i>Aphanocladia robusta</i> Pujals (R)	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x
<i>Callithamnion gaudichaudii</i> C. Agardh (R)	x		x	x	x		x	x	x	x	x	x	x	x		x
<i>Ceramium tenuicorne</i> (Kützinger) Waern (R)	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x
<i>Ceramium virgatum</i> Roth (R)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Cladophora falklandica</i> (J.D. Hooker & Harvey) J.D. Hooker & Harvey (C)	x	x	x		x	x	x		x	x	x	x		x		x
<i>Cladostephus spongiosus</i> (Hudson) C. Agardh (O)	x		x	x		x			x	x	x	x	x	x	x	x
<i>Codium fragile</i> subsp. <i>novae-zelandiae</i> (J. Agardh) P.C. Silva (C)			x	x					x	x	x	x				x
<i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbès & Solier (O)	x												x	x	x	
<i>Corallina officinalis</i> Linnaeus (R)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Cutleria multifida</i> Greville (Aglaozonia stage) (O) (I)		x				x		x					x	x	x	
<i>Dictyota dichotoma</i> (Hudson) J.V. Lamouroux (O) (Cr)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Ulva prolifera</i> O.F. Müller (C)	x		x	x	x			x	x			x				x
<i>Gelidium</i> sp.1 (R)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Gelidium</i> sp.2 (R)		x							x				x			
<i>Heterosiphonia merenia</i> Falkenberg (R)	x				x	x			x				x			
<i>Leathesia marina</i> (Lyngbye) Decaisne (R)		x	x				x			x	x			x	x	
<i>Lomentaria clavellosa</i> (Turner) Gaillon (R) (I)	x				x		x		x				x	x	x	x
<i>Neosiphonia harveyi</i> (J.W. Bailey) M.S. Kim, H.G. Choi, Guiry & G.W. Saunders (R) (I)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Polysiphonia abscissa</i> J.D. Hooker & Harvey (R)	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Polysiphonia brodiei</i> (Dillwyn) Sprengel (R) (I)	x	x	x	x	x	x	x	x	x			x	x	x		x
<i>Polysiphonia</i> sp. 1 (R)													x		x	x
<i>Polysiphonia</i> sp.2 (R)				x									x		x	
<i>Porphyra linearis</i> Greville (R) (I)									x							
<i>Pyropia columbina</i> (Montagne) W.A. Nelson (R)	x								x				x			
<i>Punctaria</i> sp. Greville (O)	x												x			
<i>Ralfsia</i> sp. Berkeley (1843) (O)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Scytosiphon lomentaria</i> (Lyngbye) Link (O)	x	x							x	x			x	x		
<i>Sphacelaria</i> sp. Lyngbye (O)	x	x		x			x	x	x	x	x	x		x	x	x
<i>Ulva prolifera</i> O.F. Müller (C)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Ulva</i> sp. (C)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Undaria pinnatifida</i> (Harvey) Suringar (O) (I)	x	x			x								x	x		

species was found in this level. The number of macroalgal species at the high and mid-intertidal levels was too low to conduct a statistical analysis (see results). In order to detect differences in ephemeral species, *C. officinalis* was excluded from the analysis due to its high abundance (~95% of the total biomass) in all localities and seasons that hid the differences of the other species. Normality and homogeneity of variance assumptions were evaluated with Kolmogorov Smirnov and Levene tests, respectively. Significant differences among mean values were evaluated with a HSD Tukey post hoc test (Zar, 1999).

Species were classified as native, cryptogenic or introduced following the definitions of Richardson et al. (2011). Native species are those that have evolved in a given area or that arrived there by natural means (through range expansion), without the intentional or accidental intervention of humans from an area where they are native. Introduced species are those whose presence in a region

is attributable to human actions that enabled them to overcome fundamental biogeographical barriers (i.e. human-mediated extra-range dispersal) and cryptogenic species are those of unknown biogeographical history which cannot be ascribed as being native or introduced. We also checked the local and regional literature for traits characteristic of invasive species and in particular, their association with mechanisms of anthropogenic dispersion, dominance or restriction to new or artificial environments, and efficiency of natural dispersal mechanisms (Chapman and Carlton, 1991).

3. Results

3.1. Zonation patterns of the common species of macroalgae and sessile invertebrates

The highest macroalgae cover was in the low intertidal level in all localities and seasons. The high level had a lower cover of

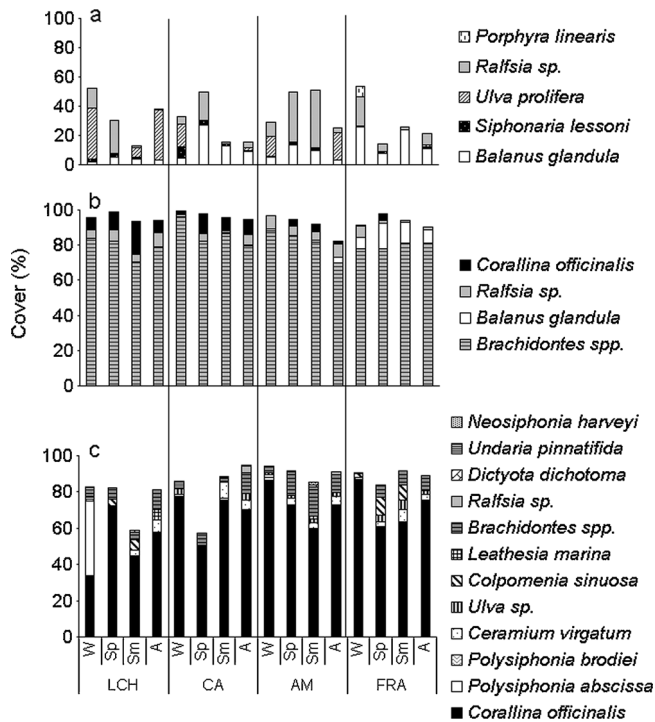


Fig. 2. Variation in the mean cover percentage of the macroalgae and sessile invertebrate species characterizing the high (a), middle (b) and low (c) intertidal levels at each locality by seasons. Localities: Las Charas (LCH), Casino (CA), Ambrosetti (AM) and Fracasso (FRA). Seasons: Winter (W), Spring (Sp), Summer (Sm) and Autumn (Au).

sessile invertebrates and macroalgae (bare substrate >50%, Fig. 2a). The few species found in all seasons and localities were the invasive barnacle *Balanus glandula*, the limpet *Siphonaria lessoni* and the macroalgae *Ralfsia sp.* The green algae *Ulva prolifera* showed a marked seasonality with the greatest abundance in winter and autumn and *Porphyra linearis* in winter in Fracasso (Fig. 2a). The middle intertidal level showed a high cover of the small mussel *Brachidontes spp.* and a low cover of the macroalgae *C. officinalis* and *Ralfsia sp.* (Fig. 2b). The low level had a greater percent cover of *C. officinalis* except for Las Charas in winter, where *Polysiphonia abscissa* showed a high abundance in terms of its cover (Fig. 2c).

3.2. Distributional patterns and composition of macroalgae assemblages

3.2.1. Comparison among intertidal levels

A total of 32 macroalgae taxa (most of which were determined to species level) were recorded across the three intertidal levels in all seasons and localities (Table 1). The number of taxa in the high and in the middle levels was lower than in the low intertidal level ($N=3, 3$ and 29 respectively). The composition of the macroalgal assemblages was significantly different among all intertidal levels ($p < 0.001$). These differences were greater for low vs. high and middle level ($R=0.99$ and $R=0.82$ respectively) and lower for high vs. middle level ($R=0.46$). The high level was different from the middle level because of the greater abundance of *Ralfsia sp.* and by the presence of *U. prolifera* that was absent on the middle level (SIMPER, average dissimilarity = 85.58%). The differences between the low level and both the high and middle levels (SIMPER, average dissimilarity = 99.71% and 79.55% respectively) were attributable to the high abundance of *C. officinalis*. This species was the most dominant in the low intertidal, and its abundance decreased with elevation, being absent high on the shore.

Table 2

Results of the two-way crossed ANOSIM tests (season × locality) showing the significance levels (p), global R and R -statistics for the composition of the macroalgal assemblages for each pair of seasons (a) and localities (b) by intertidal level (high, middle and low). Seasons: winter (W), spring (Sp), summer (Sm) and autumn (Au). Localities: Las Charas (LCH), Casino (CA), Ambrosetti (AM) and Fracasso (FRA).

	High		Middle		Low	
	p	R	p	R	p	R
Season						
Global	0.001	0.75	0.001	0.35	0.001	0.56
W vs. Sm	0.001	0.99	0.001	0.352	0.001	0.71
W vs. A	0.001	0.91	0.001	0.494	0.001	0.66
W vs. Sp	0.001	0.932	0.001	0.467	0.001	0.64
Sm vs. A	0.001	0.544	0.001	0.453	0.001	0.5
Sm vs. Sp	0.001	0.658	0.002	0.302	0.001	0.5
A vs. Sp	0.001	0.623	0.102	0.099	0.001	0.61
Locality						
Global	0.001	0.43	0.001	0.5	0.001	0.58
LCH vs. AM	0.006	0.27	0.002	0.39	0.001	0.59
LCH vs. FRA	0.001	0.63	0.001	0.67	0.001	0.67
LCH vs. CA	0.002	0.45	0.001	0.41	0.001	0.68
AM vs. FRA	0.001	0.53	0.001	0.24	0.001	0.47
AM vs. CA	0.001	0.37	0.001	0.5	0.001	0.7
FRA vs. CA	0.003	0.31	0.001	0.79	0.001	0.81

3.2.2. Comparison among seasons and localities inside each intertidal level

Species composition in each of the three intertidal levels was influenced significantly by seasons and localities (Table 2). The global R -statistic values within each intertidal level were more variable for season than those for locality, ranging from 0.35–0.75 and 0.43–0.58, respectively (Table 2). When the seasons were analyzed for each intertidal level, macroalgae composition was significantly different each season, except between autumn and spring in the middle level ($p > 0.05$). The greater differences in the high level were among winter and the other seasons (Table 2) due to the high abundance of *U. prolifera* in winter. The middle level showed no difference between autumn and spring ($p > 0.05$, Table 2) and low differences among other seasons (R -statistics ranged between 0.3 and 0.49). The species responsible for these differences were *C. officinalis* and *Ralfsia sp.* Both taxa showed a similar abundance in winter and spring seasons, while *Ralfsia sp.* was greater in summer and *C. officinalis* was lower in winter (Table 2). The low level showed significant differences in species composition among all seasons with the greatest value between winter and summer (Table 2). *C. officinalis* had a lower abundance in summer than in winter, while the ephemeral algae *Leathesia marina* and *Ceramium tenuicorne* showed a marked seasonality, with their abundance higher in summer than in the rest of the seasons. *P. abscissa* and *P. brodiei* showed a higher abundance in winter (Table 3a).

When the localities were analyzed for each intertidal level, the macroalgae composition was significantly different at the four localities. High on the shore, Fracasso showed the greatest differences with Las Charas and Ambrosetti (R -statistic: 0.63 and 0.53 respectively, Table 2). Macroalgae composition in Fracasso was distinguished from that at Las Charas by a lower abundance of *U. prolifera* and a greater abundance of *Ralfsia sp.*, and from Ambrosetti by a lower abundance of both species. The greatest differences in the middle level were between Fracasso respect to Las Charas and Casino (Table 3b) and were driven by a lower abundance of *C. officinalis* in Fracasso. The greatest differences in the low intertidal level were among Casino and the rest of the localities (R -statistic: Casino vs. Las Charas 0.68, Ambrosetti 0.7 and Fracasso 0.81 respectively, Table 2). These differences were explained by the low abundance of *C. officinalis* in Casino. There was also a low abundance of *L. marina*, *P. abscissa* and *Ulva sp.* in Fracasso. Las Charas was distinguished from Casino by the high abundance of *P. abscissa* and *P. brodiei*

Table 3

Species characterizing macroalgae assemblages in the low intertidal level at each season (a) and locality (b) are indicated by non-shaded boxes. Species of macroalgae assemblages responsible for significant differences in pairwise tests (SIMPER) between seasons (a) and localities (b) are indicated by shaded boxes. Similarity percentage (non-shaded boxes) and dissimilarity percentage (shaded boxes) between samples of each locality and season are indicated between brackets.

(a)				
	Winter	Spring	Summer	Autumn
Winter	<i>C. officinalis</i> <i>P. abscissa</i> <i>P. brodiei</i> <i>C. virgatum</i> (77%)			
Spring	<i>C. officinalis</i> <i>P. abscissa</i> <i>P. brodiei</i> <i>C. virgatum</i> <i>Ulva</i> sp. <i>Sphacelaria</i> sp. <i>U. pinnatifida</i> <i>C. multifida</i> <i>L. marina</i> (35%)	<i>C. officinalis</i> <i>Ulva</i> sp. <i>C. virgatum</i> <i>P. brodiei</i>		
Summer	<i>C. officinalis</i> <i>P. abscissa</i> <i>L. marina</i> <i>C. tenuicorne</i> <i>U. pinnatifida</i> <i>P. brodiei</i> <i>C. virgatum</i> <i>Ulva</i> sp. (39%)	(82%) <i>C. officinalis</i> <i>P. brodiei</i> <i>L. marina</i> <i>Ulva</i> sp. <i>C. tenuicorne</i> <i>Sphacelaria</i> sp. <i>D. dichotoma</i> <i>C. virgatum</i> <i>N. harveyi</i> (28%)	<i>C. officinalis</i> <i>L. marina</i> <i>C. tenuicorne</i>	
Autumn	<i>C. officinalis</i> <i>P. abscissa</i> <i>P. brodiei</i> <i>Gelidium</i> sp.1 <i>U. pinnatifida</i> <i>N. harveyi</i> <i>Ulva</i> sp. <i>Antithamnion</i> sp. (35%)	<i>C. officinalis</i> <i>P. brodiei</i> <i>Sphacelaria</i> sp. <i>Ulva</i> sp. <i>Gelidium</i> sp.1 <i>N. harveyi</i> <i>C. virgatum</i> <i>Antithamnion</i> sp. <i>P. abscissa</i> (25%)	(77%) <i>C. officinalis</i> <i>L. marina</i> <i>Gelidium</i> sp.1 <i>N. harveyi</i> <i>Ulva</i> sp. <i>C. tenuicorne</i> <i>P. abscissa</i> <i>C. virgatum</i> <i>Antithamnion</i> sp. <i>D. dichotoma</i> (27%)	<i>C. officinalis</i> <i>Ulva</i> sp. (85%)
(b)				
	LCH	AM	CA	FRA
LCH	<i>C. officinalis</i> <i>P. abscissa</i> <i>P. brodiei</i> <i>C. virgatum</i> <i>L. marina</i> (73%)			
AM	<i>C. officinalis</i> <i>P. abscissa</i> <i>P. brodiei</i> <i>Ulva</i> sp. <i>L. marina</i> (36%)	<i>C. officinalis</i> <i>Ulva</i> sp. (86%)		
CA	<i>C. officinalis</i> <i>P. abscissa</i> <i>P. brodiaei</i> <i>C. virgatum</i> <i>L. marina</i> <i>C. multifida</i> <i>Ulva</i> sp. (39%)	<i>C. officinalis</i> <i>Cutleria</i> sp. <i>P. brodiei</i> <i>P. abscissa</i> <i>Ulva</i> sp. <i>C. virgatum</i>	<i>C. officinalis</i> <i>Ulva</i> sp. <i>C. virgatum</i>	
FRA	<i>C. officinalis</i> <i>P. abscissa</i> <i>Ulva</i> sp. <i>P. brodiei</i> <i>L. marina</i> <i>C. virgatum</i> (38%)	<i>C. officinalis</i> <i>L. marina</i> <i>Ulva</i> sp. <i>P. abscissa</i> <i>D. dichotoma</i> <i>Gelidium</i> sp. 1 <i>Antithamnion</i> sp. <i>C. virgatum</i> <i>N. harveyi</i> <i>Sphacelaria</i> sp. (21%)	<i>C. officinalis</i> <i>L. marina</i> <i>P. abscissa</i> <i>Ulva</i> sp. <i>C. multifida</i> <i>P. brodiei</i> <i>N. harveyi</i> (83%)	<i>C. officinalis</i> <i>Ulva</i> sp. <i>C. virgatum</i> (83%)

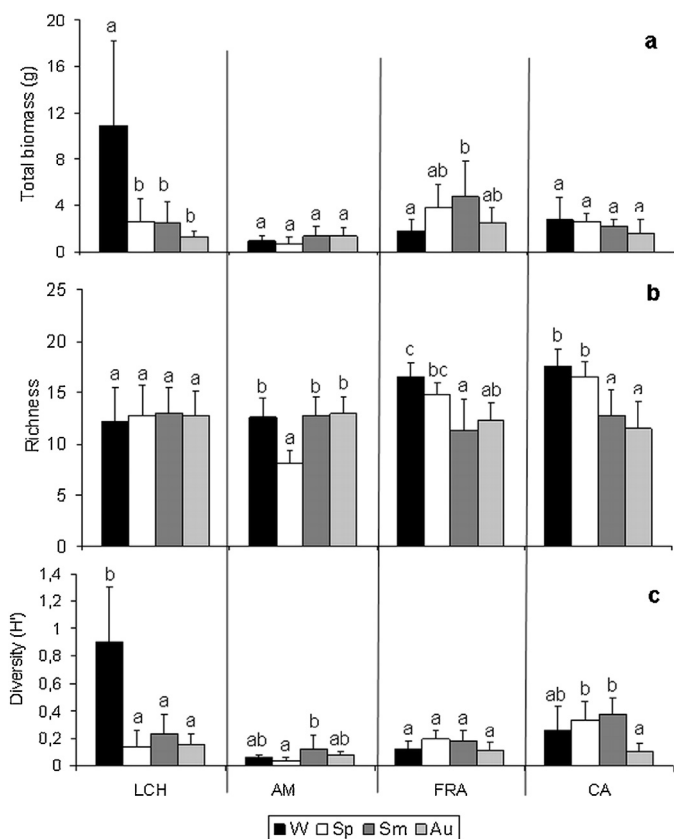


Fig. 3. (a) Total biomass (g), (b) richness (number of species), and (c) diversity (H') at each locality by seasons. Bars represent mean value and whiskers the standard error. Different letters indicate significant differences (estimated with HSD Tukey post hoc test). Localities: Las Charas (LCH), Casino (CA), Ambrosetti (AM) and Fracasso (FRA). Seasons: winter (W), spring (Sp), summer (Sm) and autumn (Au).

(Table 3b) and Ambrosetti was distinguished by the high abundance of *Cutleria multifida* (Agalozonia stage) and *P. brodiei*.

3.2.3. Diversity of macroalgae assemblages

Abundance, species richness and diversity varied in the four localities studied, and each locality showed a different seasonal pattern (Fig. 3a–c). Macroalgae abundance (excluding *C. officinalis*) showed no significant differences among seasons at Ambrosetti and Casino, while at Las Charas the abundance of macroalgae was higher in winter than in the other seasons. There was a lower abundance of macroalgae at Fracasso in the winter than in the summer, while the abundance was not statistically different in autumn and spring (Table 4 and Fig. 3a).

Species richness showed no significant differences among seasons at Las Charas, whereas at Ambrosetti richness was significantly lower in spring. Lowest richness occurred during summer and autumn at Casino, and was significantly higher during winter and

Table 4

Results of the one-way ANOVA evaluating differences in macroalgae biomass, richness and diversity in the low intertidal level among seasons at each locality (p : significance value, df : degrees of freedom and F values). Localities: Las Charas (LCH), Casino (CA), Ambrosetti (AM) and Fracasso (FRA).

	Biomass			Richness			Diversity		
	df	F	p	df	F	p	df	F	p
LCH	23	8.47	0.0008	23	0.1	0.9579	23	8.64	0.0007
CA	23	1.76	0.1879	23	10.61	0.0002	23	6.9	0.0023
FRA	23	3.28	0.0424	23	8.61	0.0007	23	2.53	0.0866
AM	23	2.24	0.1148	23	12.85	0.0001	23	3.62	0.031

spring. The highest species richness at Fracasso was in winter and the lowest was in summer. No significant differences were found between winter and spring, spring and autumn, or autumn and summer (Table 4 and Fig. 3b).

Diversity at Fracasso showed no significant differences among seasons, whereas in Las Charas, diversity was significantly higher in winter than in other seasons. Summer diversity was significantly higher than spring diversity at Ambrosetti, while no differences were found between either of these seasons and autumn or winter. The winter diversity was not different from other seasons at Casino, but in autumn was significantly lower than during spring and summer (Table 4 and Fig. 3c).

3.3. Presence and abundance of the introduced species

3.3.1. Determination of native, introduced and cryptogenic species

Over the 32 algae species found in all localities and seasons sampled, a total of seven introduced and one cryptogenic species were recorded. Three of these species (*Anotrichium furcellatum*, *Undaria pinnatifida* and *Neosiphonia harveyi*) were previously reported in the literature as introduced species (Boraso and Zaixso, 2008). The four additional species considered as introduced in this study (*Lomentaria clavellosa*, *Polysiphonia brodiei*, *C. multifida* and *P. linearis*) and a cryptogenic species (*Dictyota dichotoma*), were historically reported as native in Argentina. All the introduced and cryptogenic species were present at all localities, except *U. pinnatifida* and *C. multifida* (Agalozonia stage) which were absent at Fracasso and *P. linearis* which was found only at this locality.

L. clavellosa was first collected in Argentina in 1876 (Papenfuss, 1964) and its distribution ranges between 40° to 54° S (Boraso and Zaixso, 2008). This species is considered native to the eastern North Atlantic, where it has a wide distribution. There are only four isolated records in America (two in North America and two in South America, Boraso and Zaixso, 2008; Mathieson et al., 2008) and it is currently considered as an introduced species in USA (Mathieson et al., 2008). *P. brodiei* was first collected in Argentina in 1979 (Lazo, 1982) and presently occupies the same latitudinal range as *L. clavellosa* (Boraso and Zaixso, 2008). *P. brodiei* has a disjunct geographical distribution, it is being widespread in Europe and having isolated records in North America, Japan, Australia and New Zealand, where it has been reported as an introduced species (Scagel et al., 1989; Yoshida et al., 1990; Adams, 1991; Womersley, 2003). *Cutleria multifida* was first collected in Argentina in 1964 (Asensi, 1971) and its distribution ranges between 42° to 44° S. This species is widely distributed in Europe and is reported as an introduced species in other countries from the Southern Hemisphere such as Australia and New Zealand (Adams, 1994; Aquenal, 2008). *P. linearis* was first collected from Northern Patagonia, Argentina in 1980 (Piriz, 1988) and the current study represents the second record for Argentina. This species is widely distributed in the Northern Hemisphere (Europe and North America) but there are only two disjunct records in the Southern Hemisphere (Chile and Argentina). In Chile this species is actually considered cryptogenic (Castilla and Neill, 2009). Finally, *D. dichotoma* was first collected in Argentina in 1957 (Herbarium Collection, MACN BA-C 9775) and it is distributed along the coast between 42° to 48° S. This is a very widespread species, but is reported as an introduced species in Australia (Glasby et al., 2007).

3.3.2. Distribution and abundance of introduced species

The contribution of the introduced species in all localities was relatively low (<1%) with respect to the total abundance when *C. officinalis* was included in the analysis. When *C. officinalis* was excluded from the analysis, the contribution of the introduced species among localities was low for Fracasso, intermediate for Ambrosetti and Las Charas and high for Casino (Table 5). The

Table 5

Contribution (%) of native (N) and introduced (I) species over the total macroalgae biomass in the different localities (LCH: Las Charas, AM: Ambrosetti, FRA: Fracasso, CA: Casino), diversity (H') (considering and excluding *C. officinalis* from the analysis) and richness of introduced and native species found in each locality.

Locality	Including <i>C. officinalis</i>					Excluding <i>C. officinalis</i>		
	I %	N %	(H')	I richness	N richness	I %	N %	(H')
LCH	1.45	98.55	0.39	7	24	22.10	77.90	0.35
AM	0.18	99.82	0.06	6	17	21.55	78.45	0.07
FRA	0.21	99.79	0.17	6	22	8.33	91.67	0.15
CA	1.48	98.52	0.23	7	25	41.59	58.41	0.26

contribution of the cryptogenic and introduced species in terms of richness showed similar values in all localities and represented between 20 and 26% of the total richness at each locality (Table 5). The highest diversity was found at Las Charas and Casino and these localities also had the highest values of abundance of cryptogenic and introduced species (Table 5).

4. Discussion

This study provides the first assessment of rocky shore macroalgae assemblages on the Atlantic coast of Southern South America that incorporates the presence and distribution of introduced species with a quantification of diversity throughout different intertidal levels and seasons. Although the rocky shores of this region showed similar patterns to other cold temperate areas (e.g. Stephenson and Stephenson, 1972; López Gappa et al., 1990; Sánchez and Zaiuso, 1995; Broitman et al., 2001; Boaventura et al., 2002; Díaz et al., 2002), the specific ecological processes shaping these intertidal communities are still understudied. Some works showed that communities are influenced by the environmental stress due to a combination of strong winds and high solar radiation which increase desiccation during low tides (Bertness et al., 2006; Silliman et al., 2011). A more recent study showed that when functional groups are compared, the differences in the zonation patterns from site to site are not fully explained by environmental stress (Wieters et al., 2012). Either way, physiologically the intertidal communities of Northern Patagonia are very simple if compared with other well studied rocky shores, especially due to the absence of conspicuous mobile predators affecting these communities (Paine, 2002; Navarrete and Castilla, 2003; Bertness et al., 2006; Jenkins et al., 2008). The wave protected high intertidal is mainly devoid of organisms, with the exception of the invasive barnacle *B. glandula*, a species native of the west coast of North America and introduced to Argentina more than 40 years ago, being nowadays the dominant barnacle on rocky shores (Schwindt, 2007). Mussels are the common taxa in the middle intertidal level and the perennial algae *C. officinalis* is the dominant species in the lower level. *Corallina* and mussels are important bed-forming organisms considered as foundation species since they provide shelter to all invertebrates and small algae that inhabits in the intertidal (Watt and Scrosati, 2013), which is particularly important in these southern rocky shores where no other organism lives on the top of these beds (Bertness et al., 2006; Liuzzi and López Gappa, 2008).

When the intertidal levels were compared, the lower level showed the highest richness, abundance and diversity of macroalgae as it was found in other studies (Lubchenco et al., 1984; Raffaelli and Hawkins, 1996; Scrosati and Heaven, 2007). However, while *C. officinalis* is always present, some small macroalgae showed differences in diversity among localities. Although experimental studies are needed to understand these differences, it has been shown that small macroalgae are susceptible to small-scale heterogeneities of the biotic and abiotic factors such as recruitment and substrate surface structure (e.g. Benedetti-Cecchi and Cinelli, 1997;

Chapman and Underwood, 1998; Benedetti-Cecchi et al., 2000). In a similar vein, ephemeral algae such as *L. marina* and *Polysiphonia* spp. showed differences over time, being abundant in summer and winter respectively. These algae are important components of the macroalgae communities since they might modulate the mortality of the coralline algae recruits by buffering lethal heat stress (Coleman, 2003). Coralline algae are known to be the first type of algae to recruit into these assemblages (Konar and Foster, 1992). However, we found that when the cover of *P. abscissa* was high in winter, the cover of *C. officinalis* was low, suggesting that other processes than positive interactions are driving the macroalgae composition of these rocky shores (Daleo et al., 2006).

Although few field studies were performed along the South-western Atlantic rocky shores, all of them agreed that macroalgae diversity vary strongly over time and space, as the result of the combined effect of several physical and ecological processes. The combination of different functional groups and the presence of certain type of species, as the habitat modifier *C. officinalis*, can be determinants in how the algae community develops and its distribution in time and space (Daleo et al., 2006; Liuzzi and López Gappa, 2008; Wieters et al., 2012). The dominance of the turf forming algae *C. officinalis* in the low intertidal level of Patagonian assemblages contrasts with other rocky shores like the Southeastern Pacific or the Northwestern Atlantic coasts where canopy-forming bio-engineer species, like *Lessonia* spp. and *Ascophyllum* spp. are the dominant macroalgae in the low intertidal level (Santelices, 1990; Lubchenco, 1993; Watt and Scrosati, 2013). In these intertidals, negative interactions such as herbivory, play an important role in structuring benthic algal communities and its importance tends to diminish with increasing environmental harshness (Santelices, 1990; Lubchenco and Menge, 1978). In contrast, it has been shown that the effect of herbivory is weak in the northern rocky shores of Patagonia (Bazterrica et al., 2007) and the organisms can be affected by desiccation stress as a result of high tidal amplitude and strong SW winds (Bertness et al., 2006). Consequently, the surface microtopography seems to be critical to ameliorate the environmental stress (Benedetti-Cecchi and Cinelli, 1997). The results of this work adds more evidences that support the importance of small-scale variability of the ecological patterns in complex systems such as the rocky shores and the need for more experimental studies, which should be taking into consideration in the design and management of marine protected areas (Wieters et al., 2012).

Seven introduced and one cryptogenic species were recorded among the 32 algal species found inhabiting the rocky intertidal shores of Northern Patagonia. Three of these species (*U. pinnatifida*, *N. harveyi* and *P. brodiei*) have been commonly reported in the literature because of their significant ecological impacts on native biota, ecological processes, economic activities and human health (Mc Ivor et al., 2001; Casas et al., 2004; Schaffelke and Hewitt, 2007). With the exception of *U. pinnatifida*, most of the introduced and cryptogenic species found in this work are inconspicuous and rarely exceed a few centimeters in height. Small invasive algae may remain unnoticed for long periods due to their morphological similarities with native species (Meinesz, 2007). For example, *N. harveyi* has a long history of misidentifications. It was previously mistaken for the native *P. strictissima* in New Zealand and as *P. japonica* in Japan (Mc Ivor et al., 2001; Sears, 2002). In Argentina *N. harveyi* was misidentified as *Polysiphonia argentinica* and are considered in this study as synonyms following Guiry and Guiry (2012). We suspect that there may be additional introduced species among the rocky shore macroalgae studied here, especially in the genera *Ceramium* and *Ulva*, but we prefer to treat them conservatively since a critical taxonomic review is required prior to the assessment of their status as native, cryptogenic or introduced species.

Five of the eight introduced and cryptogenic species found in this work belong to the Phylum Rhodophyta and three to the

Ochrophyta. These results agree with Williams and Smith's conclusions (Williams and Smith, 2007) that the highest number of introduced macroalgae are in the Phylum Rhodophyta, then in the Phylum Ochrophyta and the lowest number in the Phylum Chlorophyta. This tendency was proposed to be a consequence of the family size or the greater evolutionary diversity and physiological strategies, which enhance the invasion potential of species from larger groups (Williams and Smith, 2007). The number of introduced and cryptogenic macroalgae previously reported in Argentina is low compared with other regions of the world (Boudouresque and Verlaque, 2002; Hewitt et al., 2004; Mathieson et al., 2008) and represents only a 3% of the total richness of the macroalgae listed for this country (Raffo and Schwindt, 2011), suggesting that the real number of exotic species remains unknown to ecologists and managers as well.

The localities with the highest macroalgae diversity also showed the highest abundance of cryptogenic and introduced species. This is an important issue since species diversity may change in different ways and at different spatial scales as a consequence of the invasion by introduced species (Sax and Gaines, 2003). Several studies suggest that a high native biodiversity decreases the invasibility of communities (Lodge, 1993), because fewer resources are available over time. However, other works suggested that resource availability does not affect the invasion processes of these communities, and there are other ecosystem processes determining their diversity by favoring the establishment of exotic invasive species (Stachowicz and Byrnes, 2006). Therefore, the integrative studies of the ecological patterns and processes require a real estimation of the marine invasive species and their role on benthic communities. These studies are an important step toward understanding the ecosystem functioning and the planning of biodiversity monitoring programs (Schaffelke et al., 2006; Schaffelke and Hewitt, 2007).

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