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NOTE

A CHARACTERIZATION OF PATAGONIAN SALT MARSHES

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Abstract: We combined literature reviews with an analysis of regional cartography, aerial photographs, and satellite images to identify the locations of heretofore-unknown salt marshes along the Patagonian coastline of Argentina. Subsequent ground surveys confirmed the presence of the marshes. While numerous sites still require verification, our surveys confirmed the existence of 27 large coastal salt marshes, which had estimated areas of between 3 and 2400 ha distributed along ~225 km of coastline. We described the major patterns of landscape physiognomy and community structure at eight of these sites. We classified these marshes as either muddy or rocky marshes, and subdivided them into *Spartina* and *Sarcocornia* marshes depending on the dominant vegetation. Muddy marshes were the most common type and showed a clear regional pattern with *Spartina*-dominated communities in the north (≤ 42°S) and *Sarcocornia*-dominated systems in the south (≥ 42°S). Plant height and standing crop biomass tended to be lower at higher latitudes, but plant cover showed the opposite trend. *Spartina* marshes had a more diverse marine macro-invertebrate fauna than *Sarcocornia* marshes, when the two marsh types occur at similar latitudes. Although the diversity of invertebrates was relatively low along the entire latitudinal range, most marshes supported unique species assemblages.

Key Words: Argentina, invertebrates, *Sarcocornia*, *Spartina*

INTRODUCTION

Salt marshes of the Patagonia region in southern South America (40°S to 55°S latitude; Soriano 1983) have received little attention from ecologists (Chapman 1960, Canevari et al. 1998). This is probably because this region is devoid of great coastal plains like those in the northern coast of Argentina (Buenos Aires province) and the Atlantic and Gulf of Mexico coasts of North America. However, large tidal ranges (up to 14 m amplitude) often combine with low slope terrains to produce areas with muddy marine sediments protected from wave action that are conducive to the formation of salt marshes. Regional botanical reports confirm the occurrence of several halophyte species characteristic of salt marshes in many locations along the Patagonian coast (Hauman 1926, Correa 1998). We reviewed regional botanical literature and used aerial photographs, satellite images, cartography, and multi-scale field-surveys to locate and confirm the existence of Patagonian salt marshes. We also describe some of the major biogeographic patterns of plant and marine invertebrate assemblages and landscape physiognomy of these marshes.

METHODS

Identifying Potential Locations of Salt Marshes

This study was conducted from 2002 to 2006 along the Atlantic coast of Patagonia from San Blas Bay (40° 27′ S, 62° 13′ W) to Río Grande (53° 48′S, 67°43′W). We used records of the presence of salt marsh plants, geomorphology-hydrology, and landscape features to identify the location of Patagonian salt marshes. The flora of Patagonia is well-known (see Correa 1998), thus we considered published records of salt marsh plant species as a leading indicator for potential marsh presence along the coast. However, given that most of the region is inhabited by several halophytes species of the families Chenopodiaceae and Poaceae (Correa 1998), the presence of salt marsh plants by itself is not sufficient to confirm the existence of a salt marsh. In addition, we assumed that the absence of recorded halophytes does not necessarily preclude the presence of a salt marsh. Therefore, following Daehler and Strong (1996) we also listed all estuarine or coastal areas with loamy sediments exposed to tidal action, but protected from wave action, and having a source of sediment and fresh water. We located and selected these areas by examining regional geologic and hydrologic cartography. Finally, all potential sites matching the criteria were located on aerial photographs (scale 1:60,000 and 1:20,000) provided by the Servicio de Hidrografía Naval and the Instituto Geográfico Militar of Argentina, Landsat TM satellite images provided by the Centro Nacional Patagónico (CENPAT), and high-resolution images accessible on the internet from Google Earth. For each of these sites, we looked for the presence of characteristic landscape features such as the presence of meandrous and confluent creeks surrounded by dense vegetation (Chapman 1960). The areas and coastline lengths of all detected marshes were estimated from the aerial photographs and satellite images by using the ruler tool of Google Earth. Using all criteria, a list of potential marshes was compiled, and these sites were visited to confirm the existence of salt marshes. The flora and fauna was sampled in detail at eight sites.

Salt Marsh Community Structure and Physiognomy

Plant Communities. The eight marshes selected for more detailed analysis were chosen on the basis of accessibility and dispersion along the latitudinal range being studied. In June 2004, we collected the following data from 1-m^2 plots at three different marsh elevation levels (n = 5–15 plots per level per marsh): plant species richness, plant cover (i.e., area covered when viewed from above), plant height (height of one stem randomly chosen within each quadrat), and total standing crop dry biomass (pooling all species within quadrats). Marsh levels were defined as the upper, middle, and low third of the elevation gradient covered by marsh vegetation. However, *Sarcocornia*-dominated marshes were often too narrow and botanically homogeneous to clearly differentiate a middle marsh level, and in these cases only high and low marsh levels were sampled, defined as the upper and lower half of the elevation gradient. In central Patagonia (Valdés Peninsula), plant species richness and cover were estimated in spatially paired marshes dominated by either *Spartina* or *Sarcocornia* (Riacho and Fracasso marshes, respectively) to compare species composition among marsh types independent from latitude.

Aboveground biomass was cut at ground level and material was oven-dried at 70°C to constant weight. Taxonomic identifications were made following the Flora Patagónica identification guide (Correa 1998), updating the taxonomic status of the glasswort *Salicornia ambigua* Michx. to *Sarcocornia perennis* (Mill.) A.J. Scott. (following Zuloaga and Morrone 1999). Specimen vouchers of all species were deposited in the Herbario Ecológico de Costas at the Centro Nacional Patagónico. The correlation between total plant cover, height, and standing crop biomass with latitude were evaluated with Spearman's rank tests for each marsh level. T-tests or Mann-Whitney U-tests were used to compare these variables between or among marsh levels.

Invertebrate Communities. To assess marine macroinvertebrate species richness and relative abundances, core samples (20 cm in diameter and 12.5 cm in depth) were collected in February 2004 at random from the high, middle, and low marsh levels at six of the eight marshes sampled for plants (n = 5–6 per level per marsh). All samples were sieved through 0.5 mm mesh size and the organisms retained on the sieve were fixed in formalin (4%) for 24 hrs, rinsed and preserved in ethanol (70%), sorted under a microscope (60×), and identified to the lowest taxonomic level possible. All specimens were placed in the GEAC reference collection at the CENPAT.

Using the Plymouth Routines in Multivariate Ecological Research (PRIMER) statistical package (Clarke and Warwick 2001), macroinfaunal species of the Patagonian salt marshes were compared across latitudes and marsh levels using a Bray-Curtis (Bray and Curtis 1957) similarity matrix obtained from the raw density data and also a 4th-root transformation ($x' = x^{0.25}$) to down-weight effects of dominant species. Macroinfauna densities were compared using non-metric multidimensional scaling (MDS); following suggestions of Clarke and Warwick (2001), the ordination plot and groups were checked for consistency with a hierarchical cluster analysis. A similarity percentages routine (SIMPER) was then used to determine which species were responsible for differences observed among locations.

The Shannon diversity index and the species richness were calculated for each individual sample and for each marsh, and Spearman's correlation analyses were used to evaluate latitudinal trends. Non-parametric analysis (Mann-Whitney U-test) was used whenever parametric assumptions were violated even after the transformation of the data.

Physiognomy. We characterized marshes by their major edaphic features as measured within 1-m topsoil profiles taken at each of the eight sites. At 5-cm depth intervals, soil redoximorphic features were determined in the field using a Munsell Color Chart, and sediment texture, pH, and salinity were determined in the laboratory using standard methods described in Black (1965), Page et al. (1982), and the Soil Survey Laboratory Methods Manual (Soil

Table 1. Patagonian salt marshes along the SW Atlantic continental coastline. A: area. C: coastline length. MPP: marsh plant presence, G-H: geomorphology and hydrology, L: landscape appearance, PO and PC: personal observations and communications. WCP: wave cut platform rocky marsh. CB: cobble beach rocky marsh. SP: *Spartina*-dominated marsh. SA: *Sarcocornia*-dominated marsh.

	Location		Searching Criteria						
Major Patagonian Salt Marshes	Latitude (-S)	Longitude (-W)	MPP	G-H	L	PO	PC	A (ha)	C (km)
San Blas Complex (SP)	40° 32′ 43″	62° 20′ 46″	X	X	X				117.8
Condor (SP)	40° 43′ 19″	64° 51′ 39″	X	X	X			1041	8
Loros (SP)	41° 00′ 07″	62° 47′ 23″	X	X	X	X		1548	5
San Antonio (SP)	41° 01′ 16″	64° 04′ 37″	X	X	X			602	26
Filiberto Marsh CB (SP)	41° 26′ 10″	65° 02′ 41″				X		~3	
Lobo WCP (SP)	41° 52′ 02″	64° 31′ 52″					X	150	2.5
Puerto Lobos CB (SA)	41° 59′ 38″	65° 04′ 20″		X	X	X		34	5.5
Riacho (SP)	42° 24′ 47″	64° 37′ 21″	X	X	X			159	3.4
Pájaros Island (SP)	42° 25′ 13″	64°30′ 57″	X						
Fracasso (SA)	42° 25′ 39″	64° 07′ 15″	X	X	X			27	1.2
Caleta Valdés Complex	42° 16′ 04″	63° 40′ 23″	X	X	X				
Valdés WCP (SP)	42° 36′ 39″	64° 49′ 35″	X			X	X		
Puerto Madryn WCP (SP)	42° 50′ 0.4″	64° 52′ 13″	X			X			
Rawson (SP)	43° 19′ 49″	65° 04′ 03″	X	X	X			17.5	1
Tombo CB (SP)	43° 58′ 40″	65° 14′ 11″				X			
Bustamante (SA)	45° 05′ 31″	66° 30′ 31″	X		X			12.18	0.8
Malaspina (SA)	45° 09′ 20″	66° 33′ 46″	X	X		X	X		2.2
Puerto Deseado Complex (SA)	47° 44′ 45″	65° 56′ 50″	X	X	X				
Buque (SA)	48° 03′ 31″	65° 59′ 22″		X	X	X		625	2
San Julián Complex (SA)	49° 16′ 13″	67° 43′ 31″	X	X	X			1369	17
Sta. Cruz Complex (SA)	50° 01′ 26″	68° 30′ 49″	X	X	X			116.9	12
Coig Complex (SA)	51° 00′ 20″	69° 18′ 59″		X	X		X		12
Loyola Complex (SA)	51° 37′ 23″	69° 01′ 31″	X	X	X			2400	7.7
Punta Dungeness (SA)	52° 23′ 25″	68° 25′ 41″		X	X			63	1
Puerto Espora Complex (SA)	52° 28′ 44″	69° 27′ 38″	X	X	X				
San Sebastián Complex (SA)	53° 20′ 26″	68° 42′ 32″	X	X		X			
Río Grande (SA)	53° 48′ 50″	67° 43′ 36″	X	X	X		X		

Survey Staff 1999). Topographic measurements were obtained with an optic level (Kern GK1-AC) to determine relative elevations within and among marshes.

RESULTS

Salt Marsh Location

The collective criteria we selected were highly accurate in locating Patagonian salt marshes (Table 1). The first criterion (published records of flora) alone led us to 83% of the salt marshes we identified along the Patagonian coastline. This does not indicate that there were not salt marsh plants in the other 17% percent of the salt marshes we found, merely that there were no official botanical records available for those sites. We also found several salt marshes (11%) in unexpected sites (i.e., sites not identified by one of the preliminary criteria) by following personal communications from local people and/or personal observations. These marshes were not identified by our criteria because they had atypical hydrologic and geomorphologic features. More specifically, they were located on top of exposed wave-cut platforms or in cobble beaches rather than in the typical muddy substrata and/or in estuaries. We classified these sites as rocky marshes. The marshes we located represent a minimum of 8168 ha and 6% (225 km) of the continental West Coast of Patagonia. However, we also identified nearly 130 sites along the coast that were smaller than 5 ha as potential salt marshes, but logistical constraints prevented their verification through field-surveys.

Salt Marsh Community Structure and Physiognomy

Plant Communities. With only two exceptions, we found that each Patagonian salt marsh was dominated by only one or two species that commonly composed 95–100% of the total plant cover (Table 1, Figure 1). In general, the marshes could be

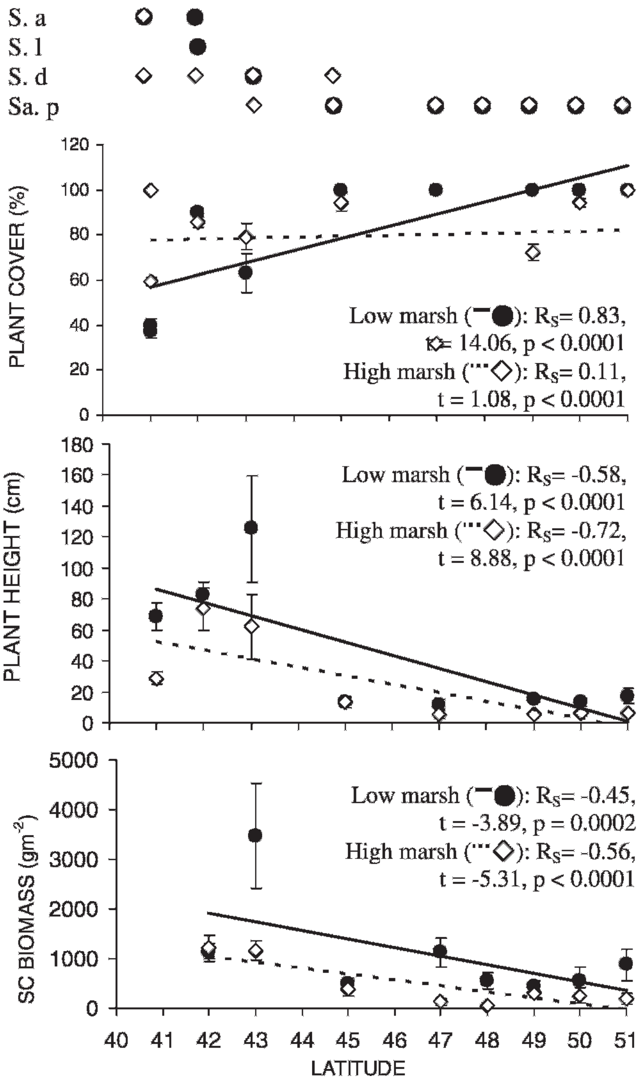

Figure 1. Non parametric correlations (R_s: Spearman's correlation coefficient) of total plant cover and latitude from a survey of eight salt marshes distributed along the Patagonian coast of Argentina and the four associated species comprising the 95–100% of plant cover for each site. The key at the top indicates the dominant plant species present at the different sites and marsh levels (black and white marks are low and high marsh levels respectively). S.a: *Spartina alterniflora*, S.l: *S. longispica*, S.d: *S. densiflora*, Sa.p: *Sarcocornia perennis*.

characterized by four dominant vascular plant species (Figure 1), but four other halophytes (*Limonium brasiliense* (Boiss.) Kuntze, *Atriplex* sp., *Suaeda* sp., and an undetermined Poaceae) also were commonly present. Fourteen of the 27 marshes visited (Table 1) were characterized by the presence of vast monospecific stands of *Sarcocornia perennis* that eventually graded into fleshy dwarf bushes of the genus *Suaeda, Limonium*, and *Atriplex*. The minor species generally occurred as small-scattered patches within a compact carpet of *S. perennis* that grew to ~0.20 m height. Plant species richness was the same in *Spartina*-dominated and *Sarcocornia*-dominated marshes located at the same latitude, but different species were present along a tidal elevation gradient. There was a negative correlation between latitude and both plant height and standing crop biomass (Figure 1). Standing crop biomass (low: $\bar{x} = 1007.5$ g m^{-2}, SD = 931.1, n = 62; high: $\bar{x} = 440.5$ g m^{-2}, SD = 442, n = 63; t = 6.74, df = 123, $p < 0.0001$) and plant height (low: $\bar{x} = 40.6$ cm, SD = 42, n = 77; high: $\bar{x} = 26.2$ cm, SD = 28.2, n = 74; t = 3.44, df = 149, p = 0.0007) were significantly higher in the low marsh than in the high marsh when all sites were pooled. The average area covered by plants in a 1-m^2 plot after pooling all sites was not different between the low ($\bar{x} = 0.81$ m^2, SD = 0.27, n = 91) and high marsh levels ($\bar{x} = 0.79$ m^2, SD = 0.24, n = 92; U = 3646, $p > 0.05$).

The marshes with rocky substrata were dominated by pure stands of *Spartina densiflora* or *S. alterniflora* Loisel. with the exception of Puerto Lobos marsh, where *S. perennis* formed a well-defined band in the high marsh (cover range: 70–90%, n = 30) with occasional specimens of *Limonium brasiliense* dispersed across the marsh. Excepting Puerto Lobos, *S. densiflora* was usually the only vascular plant inhabiting the low marsh level, with cover values of 20–60% (n = 30 per site) and an untypical small size. Plant heights in Ameghino marsh and Puerto Madryn marshes averaged 22 (4.6 SD) cm and 30 (5.3) cm, respectively (n = 30 in both cases). Filiberto was the only rocky marsh we found that was exclusively populated by *S. alterniflora* (cover: 25–50%; plant height: 32.3 (8.3) cm, n = 24).

Invertebrate Communities. The marshes surveyed for macroinfauna showed an increase of species richness from high to low marsh (Table 2), but did not show latitudinal trends in diversity ($R_s = -0.12$, $t = -1.01$, p = 0.31) or species richness ($R_s = -0.09$, $t = -0.79$, p = 0.43) (Figure 2a). *Spartina* marsh had a richer and more diverse faunal assemblage than *Sarcocornia* marsh (Table 2, Figure 2a). The only shared species (the cryptogenic amphipod *Orchestia gammarella*) did not differ in abundance between these two marsh types (U = 343, $p > 0.05$). The MDS analysis, together with the cluster analysis, showed five distinct groups within the surveyed marshes (Figure 2b). When MDS analysis included the marsh levels (high and low), the same stress value was observed (0.13) but no separation between levels was evident (Figure 2c). The SIMPER analysis showed that the organisms most responsible for the observed differences among

Table 2. Presence/absence of marine invertebrate taxa found in Patagonian marshes. H = high, M = middle, L = low marsh levels. X indicates presence of the organisms, and empty spaces indicate absence. n.i. = not identified to a lower taxon.

	Riacho			Fracasso		Buque		San Julián		Sta. Cruz		Loyola	
Marine Invertebrates	H	M	L	H	L	H	L	H	L	H	L	H	L
Crustaceans													
Orchestia gammarella (Pallas)		X	X	X	X	X	X	X	X			X	X
Ampithoe valida Smith			X										
Melita palmata (Montagu)			X										
Monocorophium insidiosum (Crawford)			X										
Exosphaeroma sp.			X										
Edotia tuberculata Guerin-Meneville							X						X
Cirolana sp.	X												
Tanais dulongii Audouin			X										
Tanaidacean n.i.			X										
Balanus glandula (Darwin)		X	X				X						
Neohelice granulata Dana			X										
Ostracoda n.i.			X										
Polychaetes													
Namanereis sp.						X	X			X	X	X	X
Phyllodocidae													X
Sabellaridae													X
Bivalves													
Cyamium antarcticum Philippi								X					
Perumytilus purpuratus Lamarck							X		X				
Brachidontes rodriguezii d'Orbigny		X	X										
Mytilus sp.			X				X						
Lasaea spp.	X	X	X			X	X	X	X			X	X
Total Species Richness	2	4	13	1	1	3	7	3	3	1	1	3	6

marshes were the bivalves *Lasaea* spp. and *Perumytilus purpuratus*, the barnacle *Balanus glandula*, the amphipod *O. gammarella*, and polychaetes in the genus *Namanereis* (Table 3). *O. gammarella* is a cryptogenic species and was present in all Patagonian marshes across the entire latitudinal range (Table 2). The only known introduced species found in the salt marshes of this region was the barnacle *B. glandula*, which was found on *Spartina* and *Sarcocornia* stems and leaves in Loros, Riacho, and Fracasso marshes.

Marsh Physiognomy. Marshes occurred on both muddy and rocky substrata (Table 1). Wave-cut platform marshes occurred on sedimentary rocky bottoms in places moderately exposed to wave action and devoid of meandrous tidal/estuarine channels. In this marsh type, the crevices and tide pools across the wave cut platform were literally filled up with *Spartina* rhizomes and roots, shell fragments, and sand. Cobble beach marshes were located in small coves or inlets relatively protected from wave and wind action and grew atop a mixture of small volcanic rock blocks, cobbles, gravels, sand, and mud.

Muddy salt marshes presented two major physiognomies based on their dominant botanic composition: *Spartina* marshes and *Sarcocornia* marshes (Table 1, Figure 1). Three marsh zones (high, middle and low marsh) were clearly present in the muddy *Spartina* marshes but not in *Sarcocornia* marshes, in which only a high and a low marsh were identified. The topographic comparison between *Spartina* (Riacho) and *Sarcocornia* (Fracasso) marshes showed that *Spartina* marsh covers a larger portion of the intertidal frame, going 2 m below the lowest vegetated border in the *Sarcocornia* marsh. This lower marsh level was devoid of *Sarcocornia* plants. The *Spartina* marshes were more common in the northern part of Patagonia (latitudes ≤ 42° S) and were associated with micro- to meso-tidal estuaries characterized by convergent dendritic channels and creeks, and waterlogged substrata with loamy, fine-grain sediments. *Sarcocornia* marshes were more common and larger at latitudes ≥ 42° S

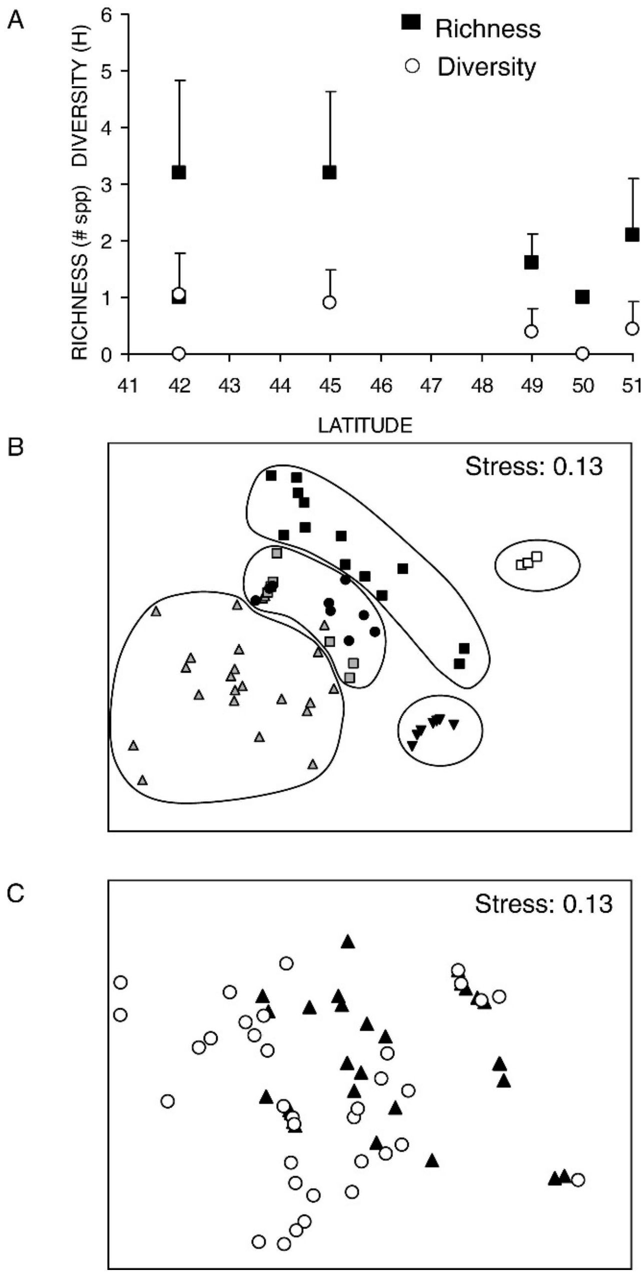

Figure 2. A) Diversity and species richness of marine macroinvertebrates along the latitudinal gradient, B) Non-metric multidimensional scaling (NMDS) analysis of invertebrate communities among the different marsh locations (Riacho: grey triangle, Fracasso: black triangle, Buque: black square, San Julián: grey square, Sta. Cruz: empty square, Loyola: black circle), and C) NMDS analysis of communities among the different marsh levels (high marsh: black triangle, low marsh: empty circle).

(Table 1), and they usually occurred as elongated bands (often less than 100 m wide) bordering steep shores with macrotidal amplitudes. These areas were often lined with narrow and deep tidal channels (1–4 m deep) that, although meandrous, rarely converged in a common mouth within the vegetated area of the intertidal zone. The geographic distribution of these two marsh physiognomies overlapped between 42° S and 43° S. The presence of abundant cobbles in deep soil layers (≥ 0.5 m depth) was associated with a decrease in the presence of anoxic sediments with depth, and with areas where the Eh varied between 216 mV and 290 mV ($\bar{x} = 172.9$ mV, SD = 6.8, n = 10). Soil pH was circumneutral and similar between marsh levels and among latitudes ($R_s = 0.14$, $t = 0.55$, $p = 0.59$). Soil salinities varied between 41.0 g/L and 13.1 g/L, and decreased with increasing latitude ($R_s = -0.50$, $t = -2.28$, $p = 0.036$).

DISCUSSION

The presence of *Spartina*-dominated marshes on shores exposed to wave action was among the unexpected findings of our survey. The small size of the *Spartina* plants found in rocky marshes, especially those developed on top of wave cut platforms, may help to reduce the impact of strong local winds and tidal erosion, as was observed for *S. densiflora* growing in exposed low marsh areas of Southern Spain (Nieva et al. 2003, Bortolus 2006). Carefully designed and executed experiments are required to determine whether the small-size of these plants is caused by the harsh conditions imposed by the environment (e.g., high wind and wave exposure and low availability of soft substratum) or if there is a genetic explanation. Our results also showed that the muddy *Spartina* and *Sarcocornia* marshes were the most abundant coastal marsh types, and that they occupied the northern and southern portions of the Patagonian coast, respectively (Table 1).

Salt marshes are more extensive in northern Argentina (Isacch et al. 2006) than in Patagonia and this is probably due to the presence of larger estuarine systems and the prominence of muddy and salty substrata along that coast. Most articles referring to southern South American salt marshes include them in the West Atlantic group (sensu Adam 1990), with muddy substrata and typically characterized by *Spartina* species. This is mostly because of the presence of *Spartina* species in the lowest marsh levels, and *Sarcocornia*, *Distichlis*, *Limonium*, and other assorted halophytes recorded in the high marsh (Isacch et al. 2006). Our results show that this generalization is consistent with the physiognomy of *Spartina* marshes, but that it does not adequately describe *Sarcocornia* marshes or rocky marshes. Based on plants (all from the Chenopodiaceae family), the *Sarcocornia* marshes of southern Patagonia are more similar to the

Table 3. SIMPER analysis showing the average dissimilarity for each pair-wise comparison and the percentage contributions for each species. The list of species was truncated after the cumulative percentage reached 50%. Asterisks mark percentages for those species contributing to that 50%. R: Riacho, B: Buque, F: Fracasso, SC: Sta. Cruz, SJ: San Julián, L: Loyola.

MARSHES	*Lasaea* spp.	*Balanus glandula*	*Orchestia gammarella*	*Perumytilus purpuratus*	*Namanereis* sp.	Average Dissimilarity
R vs. F	28.3*	23.7	24.0*			87.3
R vs. B	21.7*	14.2	8.9	15.5*	10.2	79.2
R vs. SJ	21.5*	28.4*	16.7*	3.5		59.7
R vs. SC	26.3*	21.7	7.0		23.1*	100.0
R vs. L	22.3*	24.6*	13.6*		7.9	62.4
F vs. B	33.0*		14.1	19.2*	15.2	80.8
F vs. SJ	64.4*		31.4			72.7
F vs. SC			55.0*		45.0	100.0
F vs. L	58.0*		27.4		8.9	82.0
B vs. SJ	30.2*		13.5	21.2*	15.0	65.2
B vs. SC	33.8*		14.0	19.6*	13.7	81.5
B vs. L	29.2*		13.3	20.9*	14.5	62.0
SJ vs. SC	50.1*		16.5		30.1	100.0
SJ vs. L	31.5*		34.0*	6.4	17.0	35.1
SC vs. L	57.9*		12.5		24.0	87.5

marshes on the Pacific coast of northern California, USA. or in northern Europe. Chapman (1960) and Adam (1990) both suggested this some decades ago despite a lack of tangible information. Adam (1990) conjectured that marshes located along the Patagonian coast would be arid environments dominated by fairly open and succulent stemmed shrubby vegetation. While our results generally support this, we also showed that total plant cover increased with latitude, commonly resulting in 100% coverage of the substratum (Figure 1). This slight discordance between our results and Adam's predictions may be attributable to climatic conditions along the coast, where it is less arid than inland portions of Patagonia. The South American continent narrows and the Andes Mountains almost reach the Atlantic as one approaches Tierra del Fuego. As a result, persistent cloudiness, snow presence, high precipitation rates, and glacial melt all tend to elevate the humidity in the air and lower the salinity of the coastal seawaters at increasingly southern latitudes (Prohaska 1979, Sabatini et al. 2004). This macroclimatic pattern is consistent with the increasing abundance of coastal systems dominated by glycophytes (Moore 1983, Correa 1998).

We found that in our austral salt marshes, *Sarcocornia perennis* was taller and stouter in lower compared to higher marsh levels. A similar spatial zonation is well described for the tall and short forms of *Spartina alterniflora* (respectively) in the East Coast of the USA. (Weinstein and Kreeger 2000). Our comparisons between two marshes at same latitude (i.e., Fracasso and Riacho marshes) suggest that the *Sarcocornia* marsh may be analogous to the higher intertidal portion of the *Spartina* marsh because the relative altitude at which the *Sarcocornia* marsh is located corresponds to the high marsh level in the *Spartina* marsh. Faunal assemblages occurring in these two marshes also support this hypothesis. We found that the amphipod *Ochestia gammarella* was broadly distributed across the *Sarcocornia* marshes (both high and low levels) but was restricted to only the high marsh in the *Spartina*-dominated systems. Relatively low overall species richness of marine macroinvertebrates is another characteristic that *Sarcocornia* marsh shares with *Spartina*-dominated high marsh (see review in Adam 1990).

The absence of the burrow beds formed by burrowing crabs (*Uca* spp., *Neohelice* sp.) that commonly covering vast intertidal areas along the coasts of northern Argentina, Uruguay and Brazil (Bortolus and Iribarne 1999, Bortolus et al. 2002, Costa et al. 2003) suggests important differences between the austral Patagonian marshes and other coastal marshes of South America. Crabs are important ecosystem engineers that affect many aspects of the marsh structure and function including plant zonation (Bortolus and Iribarne 1999, Costa et al. 2003), plant reproduction (Bortolus et al. 2004), and nutrient cycles (Botto et al. 2005), and their absence is likely associated with strong differences in the ecosystem functioning between the austral Patagonian marshes and those further north. In addition, most Patagonian marshes have unique species compositions (Figure 2), which suggests the presence of barriers that limit exchange. The destruction of any of these marshes might lead to one or more species extinctions.

Our soil surveys showed that when marshes grew atop old gravel beach ridges, the typical pattern of rapidly increasing anoxic conditions with depth in marsh soils was inverted. Instead, anoxic conditions near the surface of the marsh substratum occurred above oxidized layers at depth. Oxygenated and nutrient-rich seawater easily flows horizontally across the gravel banks and beach ridges at considerable depth under the soil surface in other marine environments along the Patagonian coast (Esteves and Varela 1991), and this seems to be the case for salt marshes. The importance of this inverted edaphic pattern lies in the fact that it may favor the proliferation of rich aerobic meio- and micro-faunal communities in deep soil layer, typically absent in most salt marshes, and these biotic communities may affect soil nutrient cycles and energy flows (Levin et al. 2001). There are clearly many questions that remain to be explored in the largely-overlooked slat marsh ecosystems of Patagonia. The information provided here should encourage ecologists and geo-ecologists to conduct additional studies that will contribute to a better understanding of these ecosystems and their functional importance along austral shorelines.

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