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ORIGINAL ARTICLE

Intertidal mussel beds from the South-western Atlantic show simple structure and uniform appearance: does environmental harshness explain the community?

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ABSTRACT

Communities of the rocky mid-intertidal zone of the South-western Atlantic are uniform in appearance, dominated by dense monocultures of small-size mussels (*Brachidontes rodriguezii* and *Perumytilus purpuratus*). To explain this, two hypotheses have been advanced in the literature: environmental harshness due to high potential evaporation and historical contingency after the Last Glacial Maximum. In this study of Uruguayan and Argentine shores, we address the implications and predictions of these two hypotheses from a biogeographic perspective by studying the regional distribution and composition of mid-intertidal mussels. We conducted an extensive latitudinal sampling survey (21 locations, 34–54°S), along with a compilation of available information on mussel bed composition and mussel predators present along the coastline. Then we constructed latitudinal profiles of ecologically significant environmental variables with specific emphasis on potential evaporation, a proxy for desiccation stress. The results show that mussel beds are composed of two species of small mussels, which coexist over a biogeographic transition zone (40–42° S) related to sea surface water temperature. The distribution of mussels along the coastline studied is not consistent with the environmental harshness hypothesis. In addition, in the Central Patagonian zone (44–50°S), two invertebrate predators also inhabit the intertidal rocky shores. However, these localities showed higher environmental harshness (potential evaporation rate) than non-Patagonian localities. We suggest that further attention should be given to historical contingency in order to advance towards a hypothesis consistent with current knowledge on the post-glacial biogeographic history of the South-western Atlantic.

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Introduction

Several studies addressing the structure, organization and assembly of communities dominated by mytilids in the intertidal zone of rocky shores (Paine 1994; Menge 2000) were extrapolated and developed by theoretical ecology. However, they were based on local experimental manipulations of interspecific relationships (Paine, 2010). Nevertheless, other works have emphasized that generalizations have much to gain from comparing diverse scenarios which are distinct either because of their environmental drivers (e.g. thermal stress; Helmuth et al. 2006) or their historical contingencies (Jenkins et al. 2008).

The rocky shores of the South-western Atlantic (34–54°S) are interesting from a comparative perspective for different reasons, but most prominently because of their uniform appearance (Whittaker 1962) and relatively simple structure with low diversity of primary space-holding organisms and their associated fauna. First, the mid-intertidal zone consists of dense and extended monocultures of small mussels: *Brachidontes rodriguezii* in the north (Adami et al. 2004) and *Perumytilus purpuratus* in the south (Olivier, Escofet et al. 1966a, 1966b; Bertness et al. 2006). This is attributable to scarcity of mobile invertebrate predators compared with the communities described for the mid-intertidal zone of other temperate regions such as the well-

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studied rocky shores of the North-east and South-east Pacific (Paine 1994; Navarrete & Castilla 2003). Second, previous studies highlighted the low diversity and 'anomalous absences', e.g. barnacles, lygiid isopods, littorinid snails, echinoderms and gastropods in the northern sector of the Argentine coast (Olivier et al. 1966a; Adami et al. 2004). On the other hand, in the southern sector of the Argentine coast (i.e. Patagonian zone), recent experimental studies concluded that starfish predation is not strong enough to control mussels, noting that along Patagonian rocky shores, no native drilling snails live outside the mussel matrix, which results in reduced predation pressure on mussels and barnacles (Bertness et al. 2006; Hidalgo et al. 2007). Conversely, in the sub-Antarctic region in southern Patagonia (53°S), the presence of drilling snails associated with rocky shore mussels beds has been reported, showing different predation rates on mussels (from low to strong) (Gordillo & Amuchastegui, 1998; Curelovich et al. 2016).

An important emerging generalization is that predation by mobile invertebrates on the dominant mussel species moderates competition in the primary substratum among sedentary organisms, thus promoting diversity and heterogeneous appearance in intertidal communities (Paine 1974, 1994). Consequently, according to theory, the physiognomic uniformity observed in the mid-intertidal zone of South-western Atlantic rocky shores is to be expected as a consequence of relatively low predation intensity (Hidalgo et al. 2007; Silliman et al. 2011). This phenomenon has been explained as a consequence of environmental harshness by Bertness et al. (2006), Hidalgo et al. (2007) and Silliman et al. (2011), who suggest that the effects of consumers are weakened evolutionarily and ecologically by an extremely stressful physical environment, measured by potential evaporation. In this context, we examined a compilation of published and unpublished information about mussel predators, including anecdotal and archival sources.

Furthermore, previous experimental studies (op. cit.) and other descriptive studies (e.g. Olivier et al. 1966a, 1966b) were conducted at single locations or in small regions. Generalization by comparison requires zooming-out from small spatial scales and ecological time in order to gain insights into biogeographic and historical contexts. The aim of this study is to evaluate and discuss the implications of environmental harshness on the distribution and composition of the mid-intertidal mussel species from South-western Atlantic rocky shores. To do so, we pieced together a broad picture combining results from an extensive latitudinal sampling survey (21 locations, 34–54°S), a latitudinal profile looking at environmental variables of interest, with specific emphasis on potential evaporation as a proxy for desiccation stress. Finally, the responsibility of historical processes regarding current species distribution in the South-western Atlantic after the Last Glacial Maximum cannot be ignored (Trovant et al. 2015, 2016).

Materials and methods

Study areas

The study region extends over the warm and cold temperate sectors of the South-western Atlantic (Appendix S1, Figure S1a), respectively known as the Argentine and Magellanic Provinces by descriptive biogeographers (Balech & Ehrlich 2008, and references therein). For intertidal and near-shore habitats, the transition occurs in the North Patagonian Gulfs (San Matías, San José, Nuevo) and Valdés Peninsula, between 41° and 43°S (Appendix S1), which we refer to throughout the text as the 'transition zone'. Coastal oceanography in the transition zone is dominated by frontal systems that begin developing in spring and vanish by early autumn (Appendix S1).

The mid-intertidal zone is dominated by mussels, and the low intertidal zone by the red algae *Corallina officinalis* Linnaeus, 1758 (Olivier et al. 1966a, 1966b; Liuzzi & López Gappa 2008). Before 1970, there were no barnacles in the high intertidal south of Rio de la Plata estuary, nor kelp in the low intertidal. However, since then, the exotic barnacle *Balanus glandula* (Darwin, 1854) has spread along the entire Argentine coast and the macroalgae *Undaria pinnatifida* (Harvey) Suringar, 1873 is rapidly expanding along the low intertidal and shallow subtidal zones (Orensanz et al. 2002; Schwindt 2007; Meretta et al. 2012).

The structure and composition of intertidal rocky-shore communities from the region of interest have been described in a number of studies (e.g. Ringuelet et al. 1962; Olivier et al. 1966a, 1966b; Penchaszadeh 1973; Zaixso et al. 1978; Maytía & Scarabino 1979; López Gappa et al. 1990; Adami et al. 2004, 2013; Bertness et al. 2006; Borthagaray & Carranza 2007). Several mytilid species are found in intertidal mussel beds along the coasts of the South-western Atlantic (Figure 1), dominated by two small-sized species: *Brachidontes rodriguezii* (d'Orbigny, 1842) in warmer areas and *Perumytilus purpuratus* (Lamarck, 1819) in cold temperate areas, with both species coexisting in the transition zone (Adami et al. 2013; Trovant et al. 2015). Towards the low intertidal and subtidal zones, small mussels are gradually replaced by larger mytilids: *Perna perna* (Linnaeus, 1758) and *Mytilus* sp., north of Río de la Plata estuary, *Mytilus* sp. alone south of the

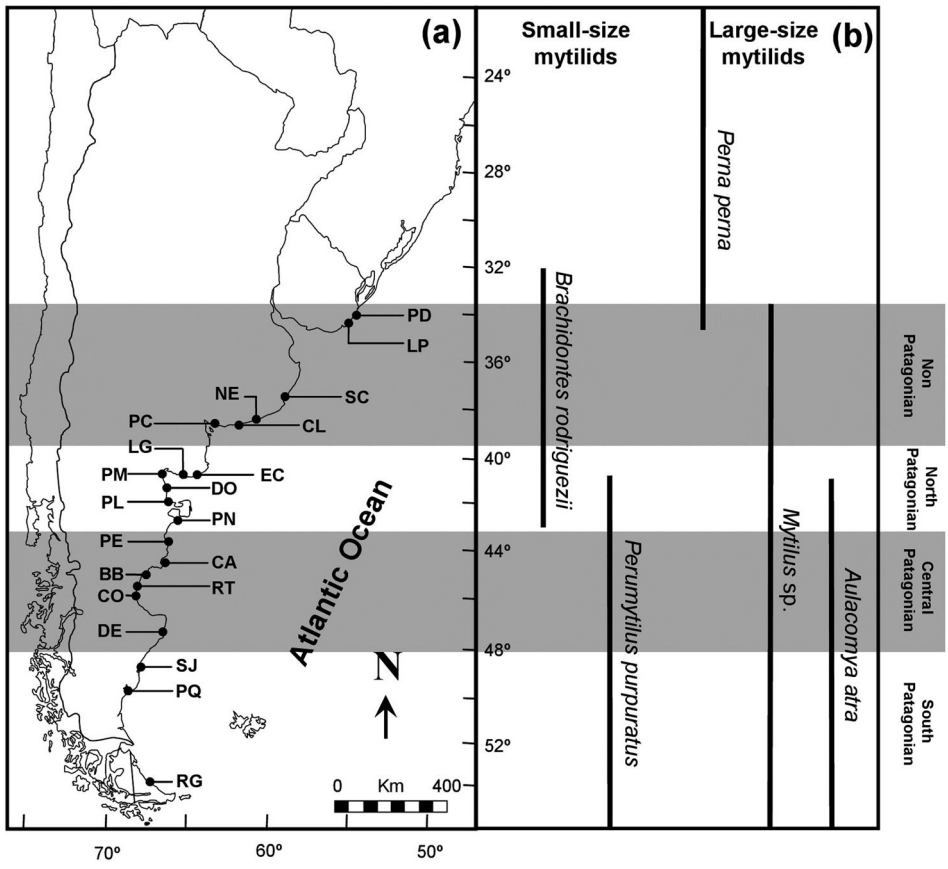

Figure 1. (a) Study region showing sampling survey sites, (b) Latitudinal range of distribution of intertidal bed-forming mussel species within the region of interest. For locality codes see Table I. Grey horizontal bars indicate both Non-Patagonian and Central Patagonian region. White horizontal bars indicate both North and South Patagonian region.

estuary, and *Aulacomya atra* (Molina, 1782) south of ~40°S. The exact number of *Mytilus* species present in South-western Atlantic waters has yet to be resolved (Westfall & Gardner 2010).

Latitudinal variation of environmental variables and calculation of potential evaporation

We compiled information on several environmental variables for the entire study region (21 locations from 34° to 54°S), including tidal regime (source: Argentine Naval Hydrographic Service, http://www.hidro.gov.ar), monthly average of sea surface water temperature (SST, source: Advanced Very-High Resolution Radiometer (AVHRR), www.poet.jpl.nasa.gov, from 1993 to 2002, 9-km resolution), rainfall (annual average) and air temperature (monthly averages, source: WorldClimate, www.worldclimate.com) for the period 1900–1990.

Potential evaporation was used as a proxy of stress (see Bertness et al. 2006) and the potential evaporation rate (PER) was calculated using Reanalysis 2 data (R-2; Kanamitsu et al. 2002). The main advantages of these global data are their continuity in time and space, and physical consistency between the variables analysed, a product of the advanced atmospheric model and the system of data assimilation utilized in their preparation. For data set the Jones (1992) equation was used (see Appendix S2, Table S2.1, supplementary material).

Latitudinal survey of mid-intertidal mussel beds

Mussel beds from the mid-intertidal zone were surveyed and sampled at selected locations along the rocky shores of the South-western Atlantic, which spans almost the entire latitudinal distribution of the species of interest. We excluded the isolated, artificial, rocky enclave of Rio Grande (southern Brazil), where the occurrence of *B. rodriguezii* has been reported (Rios 1986), and the islands at the southern tip of the continent, south of the Beagle Channel, where *P. purpuratus* and *Mytilus* '*chilensis*' are likely to occur. In order to reduce the effect of intermediate scale variation, habitat-related variability of prospective sites was avoided by selecting sites on the basis of substrate, salinity, tidal level and exposure. Samples were always taken from the mid-intertidal zone, aiming at the centroid of patches with 100% mussel cover developed

over gently sloping ('horizontal') platforms. Exposure, following Barrales & Lobban (1975), was characterized by the angle of a circular section open towards the ocean, defined with a 50 km radius; locations with an exposure angle smaller than 90° were considered 'sheltered'. Only sites classified as 'exposed' (angle > 90°) were selected for this study.

The survey included 21 coastal sites spread over ~20 degrees of latitude (Figure 1a, Table I), from 34° to 54°S, and was conducted during January 2004 and January 2005 (austral summer). At each site, 10–15 sampling units were spread randomly over the mid-intertidal zone. The sampling unit was a 200 cm^2 quadrant where all organisms and sediment down to a depth of 10 cm were collected. Samples were fixed in a 4% formaldehyde solution, taken to the laboratory and sieved through a 0.5 mm mesh so that mussels and other microfauna could be sorted from sediment and debris. Samples were then preserved in 70% ethanol for later analysis. Mussels were identified and counted under a dissecting microscope (50×); small or deteriorated specimens that could not be identified were treated as a separate category. Reference specimens (MACN-In 37558–37561) and voucher materials of all the locations included in this study (MACN-In 37614–37638) are kept at the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'.

Mussel predators: historical data recovery

Information on the distribution and composition of mussel beds and their predators along the coasts of the South-western Atlantic is scattered throughout a number of published and unpublished sources, many of which are cryptic or difficult to access. We screened the regional literature, unpublished theses, technical documents, archival sources and anecdotal reports in order to extract and organize relevant information to complement our inquiry (Table II). Of particular significance was the recovery of: (i) field notes from a survey of intertidal communities conducted along the coasts of San Matías Gulf during the austral summer of 1972 (Scarabino 1977; Escofet et al. 1978), and (ii) the personal files of the late Prof. Santiago R. Olivier, who led extensive surveys of intertidal rocky shores between 1962 and 1972 (Olivier et al. 1966a, 1966b; Olivier 1973).

Table I. Names of the sampled localities, codes utilized and their geographic coordinates.

Locality	Code	Coordinates
Punta Del Diablo	PD	34°02′S, 53°32′W
La Paloma	LP	34°40′S, 54°09′W
Santa Clara del Mar	SC	37°50′S, 57°29′W
Necochea	NE	38°37′S, 58°49′W
Claromecó	CL	38°51′S, 60°03′W
Pehuen Có	PC	39°00′S, 61°37′W
El Cóndor	EC	41°03′S, 62°14′W
Punta Mejillón	PM	41°01′S, 64°08′W
Las Grutas	LG	40°50′S, 65°05′W
Playas Doradas	DO	41°37′S, 65°02′W
Puerto Lobos	PL	41°59′S, 65°03′W
Punta Ninfas	PN	42°58′S, 64°19′W
Playa Escondida	PE	43°43′S, 65°11′W
Camarones	CA	44°50′S, 65°35′W
Bahía Bustamante	BB	45°05′S, 66°30′W
Rada Tilly	RT	45°58′S, 67°32′W
Caleta Olivia	CO	46°20′S, 67°33′W
Puerto Deseado	DE	47°44′S, 65°59′W
Bahía San Julián	SJ	49°14′S, 67°40′W
Punta Quilla	PQ	50°07′S, 68°22′W
Río Grande	RG	53°50′S, 67°33′W

Statistical analysis

A Principal Component Analysis (PCA) was performed to identify the environmental variables (tidal amplitude, maximum and minimum monthly SST averages, and maximum and minimum potential evaporation rate) that were important in the characterization of localities. Two-way nested ANOVAs were used on the PCA components to compare sites, with locality nested within zone. In order to meet the assumptions for normality and homogeneity of variance, Lilliefors and Bartlett tests were performed, respectively. Pearson's correlations were used to examine the relationships among principal components, environmental variables, and the relative abundance of each mussel species expressed as r/(r + p) and m/(r + p + m), where r = *B. rodriguezii*, p = *P. purpuratus* and m = *Mytilus* sp. Proportions were transformed according to x′=x + 0.5 in order to avoid the effect of zeros in the analysis (Sokal & Rohlf 1995). Analyses were performed using Statistica v.7 and INFOSTAT version 2015 software (Di Rienzo et al. 2015).

Results

Latitudinal variation of environmental variables and calculation of potential evaporation

All the environmental variables of interest, except evaporation and rainfall, were linearly correlated to latitude along the coasts of the South-western Atlantic (Figure 2). Air temperature and sea surface temperature (SST) decreased with latitude. Annual rainfall decreased across the Non-Patagonian warm temperate zone to the North Patagonian Gulf and then increased again across the cold temperate zone (Figure 2a). SST amplitude (maximum and minimum difference) was widest in the warm temperate zone (Figure 2b). Conversely, average tidal amplitude

Table II. Summary of predators on intertidal mussels reported from the South-western Atlantic and its immediate adjacent areas.

Warm temperate zone			
Predator Common name: Scientific name	Region	Observations	Source
Sea anemones: *Phymactis* sp., *Aulactinia marplatensis* (Zamponi), *A. reynaudi* (Milne-Edwards), and *Oulactis muscosa* Dana	Mar del Plata (38°01′S) and adjacent areas	Passive predators of dislodged mussels	Acuña 1997; Acuña & Zamponi 1995, 1996, 1999; Zamponi 2001
Croaker: *Micropogonias furnieri* (Desmarest)	Buenos Aires Province, mostly nearby Santa Clara (37°50′S)	Bites take a portion of the mussel bed, often creating a patch	J.M. Orensanz (unpublished observations)
Silverside: *Odontesthes argentinensis* (Valenciennes)	"	Bites take single individual mussels	"
Common oystercatcher: *Haematopus palliatus* Temminck	Near Necochea (38°34′S)	Preys on *B. rodriguezii* and *Mytilus* sp.	García & Gómez-Laich 2007
Sanderling: *Calidris alba* Pallas	Between Monte Hermoso and Pehuén-Có (38° 59′S)	*B. rodriguezii* second most frequent prey item	Petracci 2002

Remarks: The only seastar occurring in the intertidal zone is *Asterina stellifera* (Moebius), which like other species of *Asterina* (e.g. Crump & Emson 1978) is an omnivorous scavenger principally dependent for food on surface films of algae, bacteria and detritus, but is not known to prey on live mussels. Salvat (1975) observed bryozoans and small crustaceans among the folds of evaginated stomachs, but never mussels. Intertidal crabs include two varunid grapsoids (*Cyrtograpsus altimanus* Rathbun, and *C. angulatus* Dana) which forage on biofilms, soft-bodied invertebrates and small crustaceans, and the xanthoid *Danielethus crenulatus* A. Milne Edwards, which inhabits pools and upper subtidal rocky habitats but has not been shown to be a mussel predator in the field. Predatory gastropods occurring in the region do not feed on intertidal mussels.

Transition zone			
Predator Common name: Scientific name	Region	Observations	Source
Octopus: *Octopus tehuelchus* d'Orbigny	San Blas Bay to Magaña Beach (~40°30′–43° 25′S)	*Brachidontes* spp. are a significant component of the diet. Predation by this semelparous, short-lived species is seasonal, peaking during the summer. Prey are often recognizable by empty mussel shells left near the entrance	Iribarne et al. 1991; Ré & Gómez-Simes 1992; M.E. Ré & J.M. Orensanz (personal observations)
Red knot: *Calidris canutus* (Linnaeus)	San Antonio Oeste (40° 42′S, 65°0′W)	*Brachidontes* is a prey item	González et al. 1996

Remarks: Native invertebrate predators from the cold-temperate zone (*Anasterias*, *Trophon*; see below) also prey on intertidal mussels in sectors of the transition zone. Birds other than red knots are likely to be mussel predators in the transition zone.

Cold-temperate zone			
Seastar: *Anasterias antarctica* (Lütken, 1897)	Southern South America, northward to San Matías Gulf (41°S)	*B. purpuratus* was main prey item at several locations	Gil & Zaixso 2007; 2008, J.M. Orensanz (personal observations)
Snails: *Trophon* spp., mostly *T. geversianus* (Pallas)	Southern South America, northward to Punta Mejillón, San Matías Gulf (41°S)	Shell-drilling snail	Scarabino 1977; Gordillo & Amuchastegui 1998; Andrade & Ríos 2007.
Green crab: *Carcinus maenas* Leach	44°45′–47°45′S	Recently introduced, potential mussel predator	Hidalgo et al. 2005; 2007; Bertness et al. 2006
Kelp gull: *Larus domicanus* Lichtenstein	42–44°S (three locations surveyed); Punta Arenas, Magellan Strait	Frequency in pellets was 12–53% (two years, three sites)	Hockey et al. 1988; Yorio & Bertellotti 2002
Oystercatcher: *Haematopus* sp.	Cabo Dos Bahías (43°53′–43°55′S)	Predation rate on *Perumytilus purpuratus* very low	Bertness et al. 2006

Remarks: There is no evidence of significant fish predation on intertidal mussels in the cold-temperate region or in the transition zone. The most ubiquitous fish predator on benthic invertebrates along the Patagonian coasts of the South-western Atlantic is the southern blenny (*Eleginops maclovinus* (Cuvier & Valenciennes)), which, however, does not appear to be a significant mussel predator (Gosztonyi 1979; Gordillo & Isla 1991; Isla & San Román 1995; Martin & Bastida 2008; J.M. Orensanz, unpubl. obs.). Another notothenid, *Patagonotothen cornucola* (Richardson), common in rocky shores, does not appear to be a significant predator either (Hidalgo et al. 2007).

increased with latitude, from microtidal in Uruguay (< 0.5 m) to macrotidal near the southern end of continental South America (> 7.5 m), with local maxima in inner San Matías Gulf (Las Grutas, Playas Doradas and Puerto Lobos) (Figure 2c). The highest maximum potential evaporation rates (PER) were found in Central Patagonia from 45° to 47°S, (11.14 mm day^{-1}), while the lowest minimum PER were found in the Non- Patagonian warm temperate zone, from 33° to 40°S, (0.15 mm day^{-1}) (Figure 2d).

The sampling localities grouped into four clusters based on the PCA analysis of environmental variables. These clusters corresponded to the 'Non-Patagonian warm temperate zone' (33–40°S), 'North Patagonian' (40–44°S), 'Central Patagonian' (44–50°S) and 'South Patagonian' (50–55°S) regions (Figure 3).

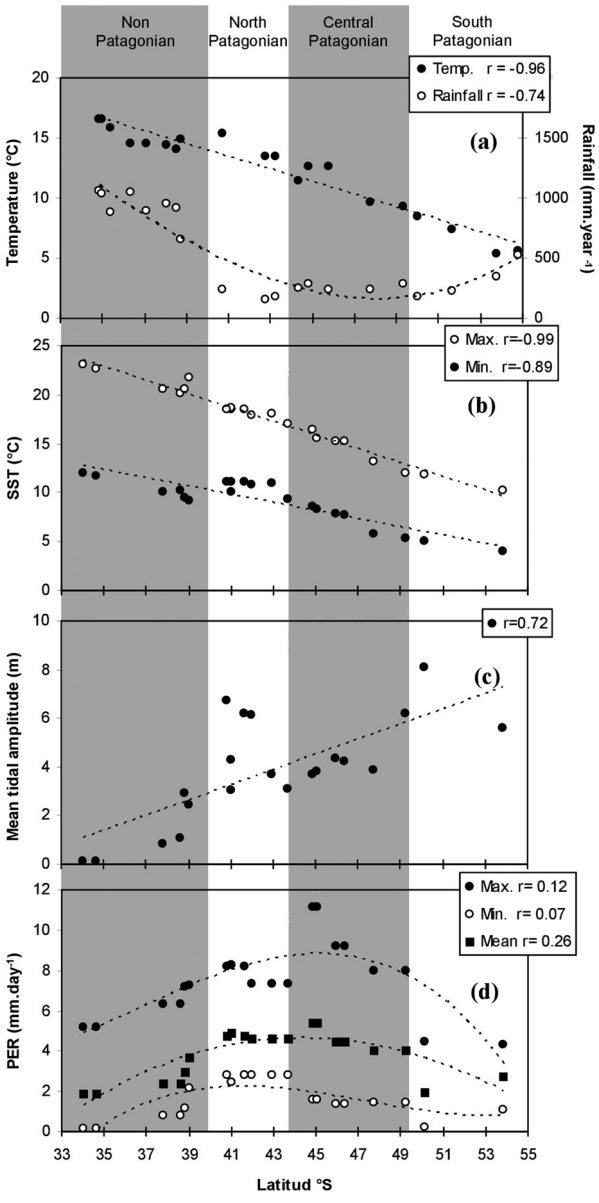

Figure 2. Latitudinal profiles of environmental variables in the region of interest. (a) Environmental temperature and rainfall, (b) SST (Sea surface temperature), (c) Mean tidal amplitude and (d) PER (Potential evaporation rate). Grey stripes indicate Non-Patagonian, corresponding to warm-temperate sector (left) and Central Patagonian (right) localities. Clear stripes indicate North Patagonian (left) and South Patagonian (right) localities. Dotted lines only suggest tendencies of the data to a straight line or a curve (third degree exponential). r: Pearson correlation index.

The two first Principal Components (PC) explained 83.5% of the total environmental data variability (Figure 3 and Table III). PC1 (56.3% of the explained variability) correlated positively and significantly ($P < 0.01$) with maximum (r = 0.98) and minimum (r = 0.89) SST, and correlated negatively and significantly ($P < 0.01$) with latitude (r = −0.99) and tidal amplitude (r = −0.79). PC2 (27.2% of the explained variability) correlated

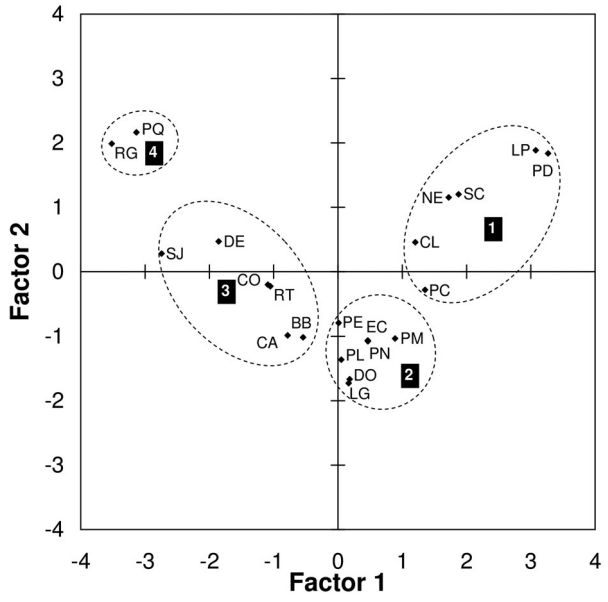

Figure 3. PCA plot showing study localities grouped according to environmental conditions. See locality codes in Table I. Cluster 1: Non-Patagonian localities. Cluster 2: North Patagonian localities. Cluster 3: Central Patagonian localities. Cluster 4: South Patagonian localities.

Table III. Eigenvalues and contribution to variance for each axis of Principal Component Analysis (PCA) calculated on environmental data.

Axis	Eigenvalue	% Variance
1	3.3795	56.3
2	1.6308	27.2
3	0.6931	11.6
4	0.2291	3.8
5	0.0586	1.0
6	0.0089	0.1

negatively and significantly ($P < 0.01$) with maximum (r = −0.75) and minimum (r = −0.91) potential evaporation rate. PC1, representing SST, latitude, and tidal amplitude, was significantly different between zones (two-way nested ANOVA, $F_{3,17}$=27.84, $P < 0.001$) but not among localities within zones ($F_{17,231} = 0.758$, $P = 0.741$). Potential evaporation rate varied non-linearly with latitude. Along the coasts of the South-western Atlantic, mean monthly evaporation rate in central and north Patagonia was 47% higher than along the coasts north of 40°S and south of 50°S (Figure 2d).

Latitudinal survey of mid-intertidal mussel beds

Latitudinal surveys of mid-intertidal mussel beds showed that the dominant mytilid species shifted in a southward direction between 34° and 54°S from *B. rodriguezii* to *P. purpuratus*, to *Mytilus* sp. (Table IV, Figure 4a, b). Transition in dominance between

Table IV. Mean density (ind. m^{-2}) of the mussels for each studied locality.

Localities	Taxa		
	Brachidontes rodriguezii	*Perumytilus purpuratus*	*Mytilus* sp.
Punta del Diablo	13,090	0	370
La Paloma	21,070	0	270
Santa Clara	153,851	0	130
Necochea	84,687	0	70
Claromecó	91,367	0	10
Pehuen Có	16,112	0	30
Las Grutas	36,940	1965	50
Punta Mejillón	46,175	3733	1060
El Cóndor	67,297	0	425
Playas Doradas	8187	20,304	33
Puerto Lobos	0	16,390	40
Punta Ninfas	3144	23,579	10
Playa Escondida	0	63,859	50
Bahía Bustamante	0	61,800	1220
Camarones	0	48,729	0
Rada Tilly	0	69,754	1750
Caleta Olivia	0	51,873	10
Puerto Deseado	0	5040	10
San Julián	0	11,800	2740
Punta Quilla	0	10,670	16,790
Río Grande	0	4470	26,510

B. rodriguezii and *P. purpuratus* occurred between 41° and 43°S (North Patagonian Gulfs, Appendix S1, Figure S1b, Figure 4b). This transition zone is the southern end of the biogeographic range of *B. rodriguezii* (Punta Ninfas) and the northern end of the biogeographic range of *P. purpuratus* (Punta Mejillón).

The relative abundance of *B. rodriguezii* was significantly positively correlated with PC1 ($r = 0.78$, $P < 0.01$), while *Mytilus* sp. was significantly negatively correlated with PC1 ($r = -0.65$, $P < 0.01$). Because the sum of the relative abundances of *P. purpuratus* and *B. rodriguezii* were complementary, when the correlation was positive for one of these species, it was negative for the other.

The shift in dominance between *B. rodriguezii* and *P. purpuratus* occurred over a narrow range of max SST (18.0–18.5°C, Figure 5a). Transition in dominance took place over a wider range of min SST (9.0–11.0°C) than max SST, because *B. rodriguezii* occurred also alone in the winter cold-spot around 39°S (9.2–9.5°C; Figure 5b), located to the north of the transition zone. As a result, when max SST and min SST were considered jointly (Figure 5c), the separation of regions dominated by each species was sharply delineated by max SST.

Mytilus sp. was always present along the whole coastal line studied (Figure 4), but between 39° and 49°S its densities were very low in intertidal mussel beds dominated by the small mussel species *B. rodriguezii* and *P. purpuratus*. Unlike the transition zone between *B. rodriguezii* and *P. purpuratus*, transition in dominance between *P. purpuratus* and *Mytilus* sp. (both cold-temperate species) did not match boundaries of the latitudinal range of distribution of either species. In terms of dominance, the transition was sharply marked by both max SST (11.8–12°C) and min SST (5.0–5.3°C) (Figure 5c). *Mytilus* sp. became dominant over *P. purpuratus* approximately between 49° and 50°S, but our study did not have sufficient resolution to capture the details of this transition, which appeared to be relatively smooth (Figure 5b).

Overall mean density (± SE) was 56,418 (± 5303) individuals m^{-2} for *B. rodriguezii* and 29,044 (± 2630) individuals m^{-2} for *P. purpuratus*; overall mean density of the larger *Mytilus* sp. south of 50°S (where it becomes the dominant species) was 2828 (± 664) individuals m^{-2} (Table IV). Variation in average density in the tightly packed beds (Figure 4a) was due to variation in abundance of recruits (see Appendix S3, supplementary material).

Discussion and conclusions

Relation between regional variation in composition of intertidal mussel beds and environmental factors

The large-scale spatial patterns in the appearance and structure of mid-intertidal mussel beds along the coasts of the South-western Atlantic reveal the link between latitudinal shifts and mesoscale variation of the three dominant mussels and SST. SST is usually treated as a surrogate for the thermal regimes experienced by intertidal organisms (Hutchins 1947) but it is a coarse indicator of those regimes (Helmuth 2009). With due caveats, max SST appears to be a good predictor of range boundaries of intertidal mussels in the South-western Atlantic, but not min SST, because if the *P. purpuratus* distribution range were constrained by min SST, all rocky shores along the warm-temperate sector of the Argentine coast (~37°50′–40°S) would be suitable for this mussel (see Figure 5c). Variability in the timing of low-tide exposure, wave exposure and other locally varying factors has been shown to modulate the effects of latitudinal temperature gradients (Sagarin & Somero 2006), resulting in 'mosaic patterns' of thermal stress (Helmuth et al. 2006). The winter cold-spot around 39°S and the summer cold-spot around Puerto Lobos constitute good examples of mesoscale variability, with implications for patterns of composition and dominance of intertidal communities. Only the cold-temperate *P. purpuratus* was found at Puerto Lobos, while the

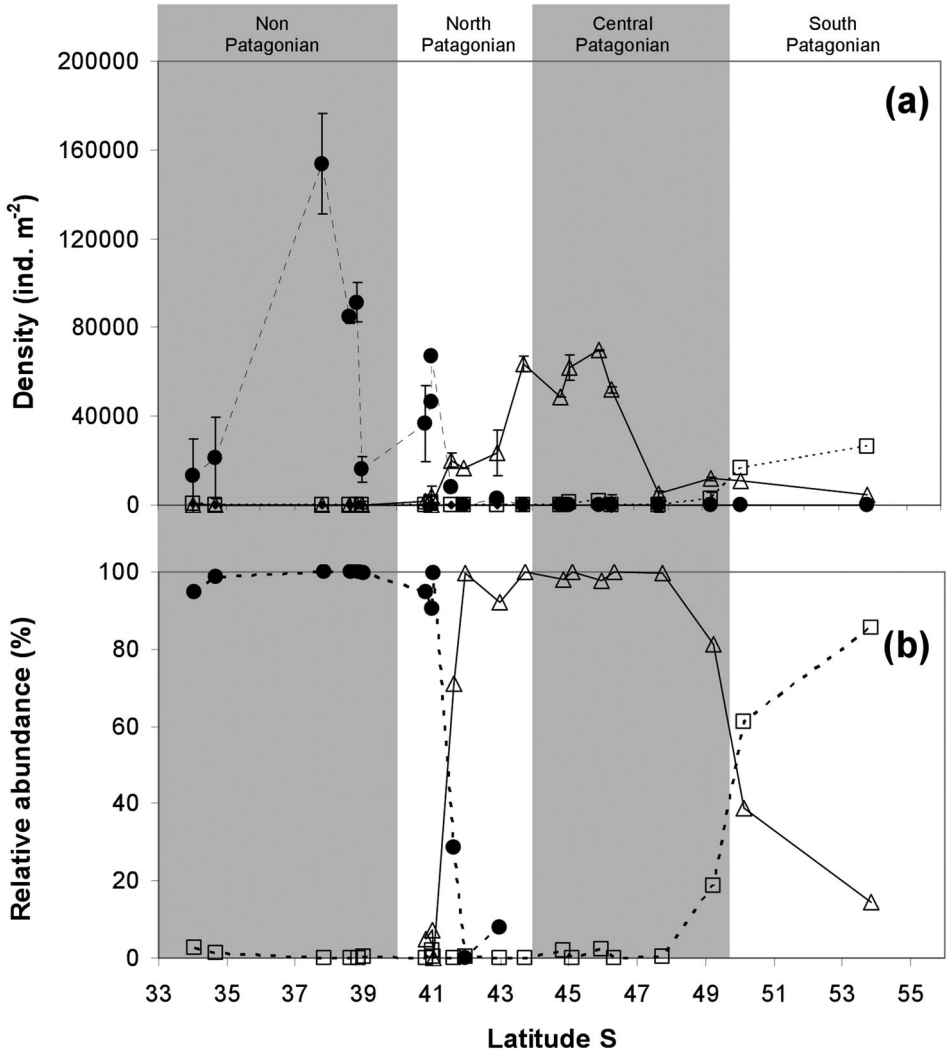

Figure 4. Latitudinal profiles of major biotic elements of mid-intertidal mussel beds. (a) Average density (ind. $m^{-2} \pm$ SE) of *Brachidontes rodriguezii* (●), *Perumytilus purpuratus* (Δ) and *Mytilus* spp. (□). (b) Average relative abundance (%) (same symbols). Grey stripes as in Figure 2.

warm-temperate *B. rodriguezii* is dominant to the north and south. Puerto Lobos is under the direct influence of cold water entering the southern part of San Matías Gulf, and always located south of the thermal front that divides the gulf (Gagliardini & Rivas 2004; Rivas & Pisoni 2010). The condition of Puerto Lobos as a summer cold-spot is apparent in other biogeographic features, such as the occurrence of an isolated population of dwarfed *Macrocystis pyrifera* (Linnaeus) C.Agardh, 1820, the northernmost representative of this ecologically important kelp in the South-western Atlantic (Olivier 1973; J.M. Orensanz, personal observation).

Thermal tolerance has been shown to control the equator-ward distribution of other intertidal mussel species (e.g. blue mussels from the north-west Atlantic; Jones et al. 2009), and has varied reflecting global warming (Jones et al. 2010) or decadal climate oscillations (Hilbish et al. 2010). Olivier et al. (1966b) reported only *P. purpuratus* in their ecological description of the rocky intertidal communities from Puerto Pirámide. Four decades later, Cuevas et al. (2006) reported a mixture of *P. purpuratus* and *B. rodriguezii* for the same location, concluding that the southern limit of the range of the warm-temperate *B. rodriguezii* had expanded pole-ward during the intervening period. Our examination of voucher samples at regional museums (including those from the study conducted by Olivier et al. 1966b) showed, however, that *B. rodriguezii* has been present in the Nuevo Gulf region since at least the early twentieth century. Nevertheless, other recently published authors (Arribas et al. 2013) did not report *B. rodriguezii* south of Playas Doradas (41°37′S) and

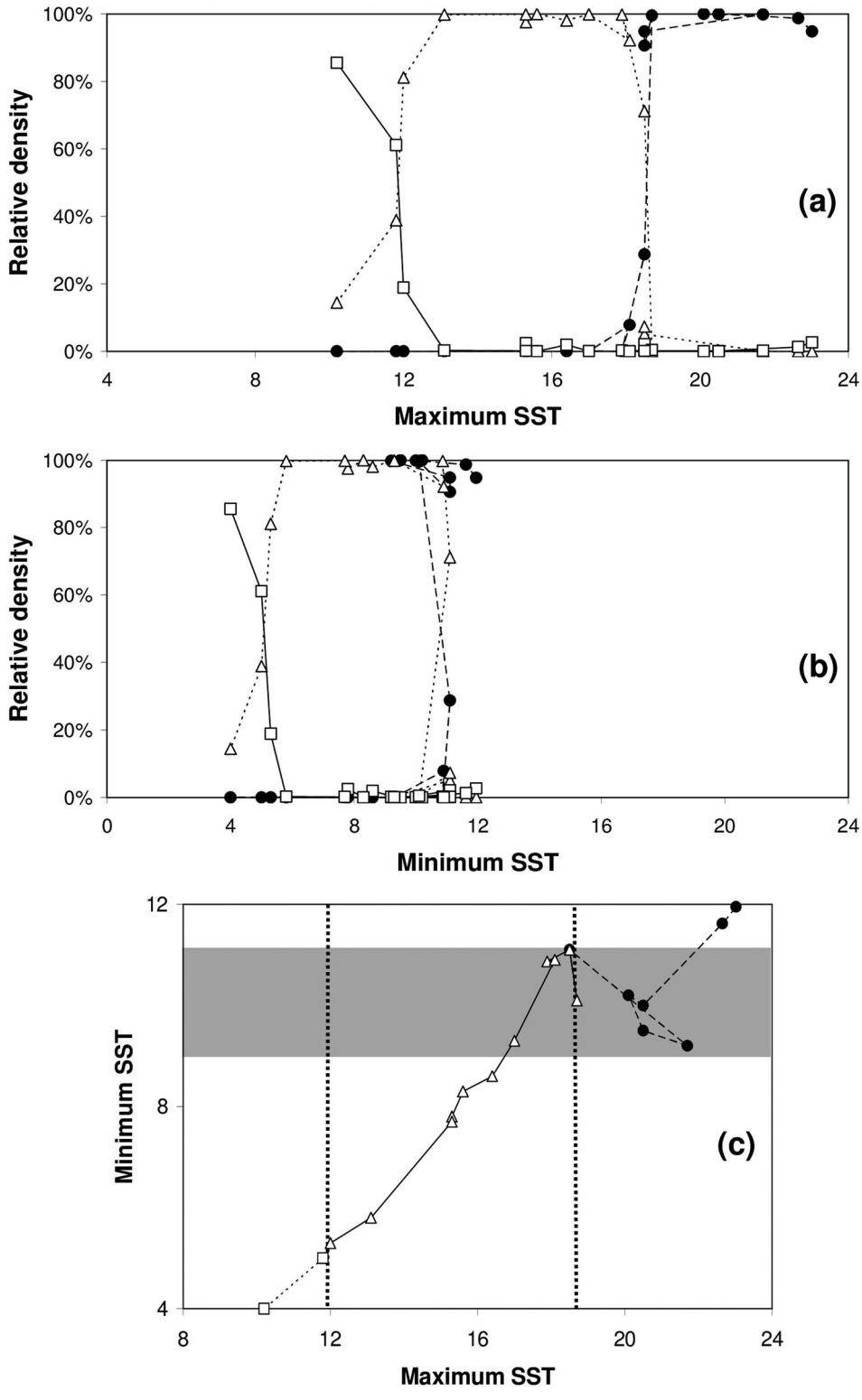

Figure 5. Specific dominance (in numbers) in composition of mid-intertidal mussel beds as related to sea surface temperature (SST). (a) Dominance in relation to the maximum monthly average for *Brachidontes rodriguezii* (●), *Perumytilus purpuratus* (Δ) and *Mytilus* spp. (□). (b) Same for the minimum monthly average. (c) Domains of dominance as related jointly to maximum SST and minimum SST; vertical dotted lines: maximum SST cut-off points between regions dominated by the three species.

suggest a very short overlap of its distribution with *P. purpuratus* only around Lobería (41°09′S). There is therefore no evidence of recent shifts in the range boundaries of *B. rodriguezii* and *P. purpuratus* within the much wider transition zone of the South-west Atlantic, in agreement with Adami et al. (2013).

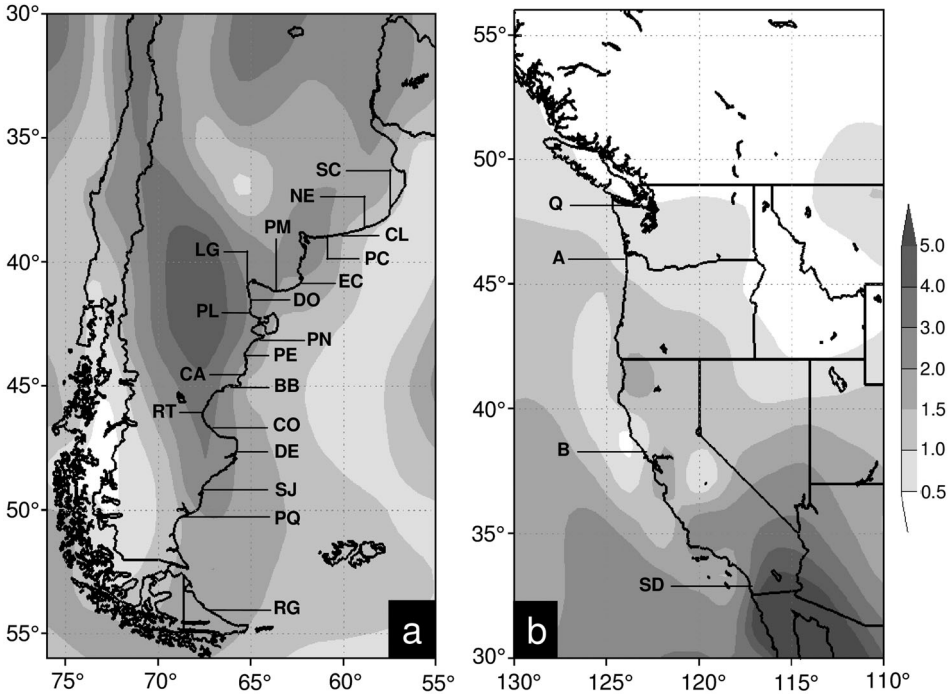

Figure 6. Annual average potential evaporation rate (mm day^{-1}) estimated with Jones' equation, using atmospheric data extracted from global Reanalysis 2 (see text). (a) Southern South America between 30° and 55°S. Arrows indicate the locations where the sampling surveys were performed. Abbreviations are the same as in Figure 1. (b) Western North America between 30° and 56° N; letters indicate locations for which Bertness et al. (2006) calculated potential evaporation: Q: Quillayute (Washington), A: Astoria (Oregon), B: Bodega (central California), SD: San Diego (southern California).

Latitudinal variation in potential evaporation and distribution of mussel predators

The potential evaporation rate (PER) along the Southwestern Atlantic shore from 35° to 55°S is the highest in Central Patagonia. This is primarily due to the steep vertical humidity gradient near the ground (a result of high surface temperature during the summer), and consequently high saturated vapour pressure near the ground and low relative air humidity above the ground.

Based on experimental work conducted at Cabo Dos Bahías, central Patagonia, Bertness et al. (2006) and Hidalgo et al. (2007) concluded that the effects of consumers along the rocky shores of Patagonia are weakened, evolutionarily and ecologically, by a highly stressful physical environment. Stress, as indicated earlier, is related to the risk of desiccation as a result of high wind-induced potential evaporation. Cabo Dos Bahías, located near Camarones locality (45°05′S), is indeed located in the most stressful sector of the Patagonian coastline, between Trelew (43°14′S) and Comodoro Rivadavia (45°47′S). Bertness et al. (2006) estimated potential evaporation in Trelew as a surrogate for conditions experienced at their experimental site, and compared it with conditions estimated for other rocky intertidal sites around the world, where earlier ecological studies were conducted. Their estimates, however, appear reasonable in relative terms. To provide a basis for comparison, Figure 6 shows the annual average potential evaporation rate (period 1979–1998) in southern South America and the west coast of North America (where four of the locations listed by Bertness et al. 2006 are located), for equivalent latitudinal ranges (30–56°, respectively S and N). Along the coasts of the North-east Pacific, the lowest rates of potential evaporation occur north of 45°N, and the highest south of 33°N (Figure 6b). Consistently, in the results presented by Bertness et al. (2006), San Diego (southern California) has an evaporation rate 2.9 times higher than Astoria (northern Oregon). This amplitude is comparable to that observed along the Atlantic coast of Argentina (Figure 6a). The highest potential evaporation estimated for central Patagonia, which occurs inland from Trelew to Cabo Dos Bahías, is in the order of that observed along the Pacific coast of northern Baja California (Mexico) (Figure 6), where the intertidal rocky shore communities are similar to those of southern California (Littler, 1980). As in central Patagonia, mean potential evaporation is inflated here by seasonal phenomena. Wind conditions are extremely important in that major reversals occur predominantly during late autumn and winter. This

results in strong, hot, dry 'Santa Ana' winds from the inland desert regions at the time of low tides during the daylight hours, thereby causing extreme heating, desiccation and radiation stress to intertidal organisms (Littler 1980). While environmental harshness (in terms of potential evaporation) is comparable between northern Baja California and Central Patagonia, the significance of invertebrate predators of mussel beds differs radically between the two regions (Blanchette et al. 2006; Wieters et al. 2012; this study).

Potential evaporation declines along the coasts north and south of central Patagonia. North of Patagonia, environmental conditions in the warm-temperate region (Figure 6a: locations SC to PC) are typically mild, with a range of potential evaporation comparable to that estimated for the coasts of central and southern California, from Bodega to San Diego (Figure 6b). Yet mobile invertebrate predators, typically the most significant as structuring agents of intertidal mussel beds, are virtually absent from the warm-temperate region (see Table II). Along the coasts of southern Patagonia (Figure 6a: locations SJ–RG), on the other hand, potential evaporation decreases in spite of the strong prevailing winds, with a range of average annual potential evaporation comparable to that of the California Bight. Decreased evaporation potential estimated by Reanalysis 2 may be counteracted in the intertidal zone by increased exposure due to wider tidal amplitude (Figure 2c). Even though wind speed increases with latitude (Camacho 1979; Bertness et al. 2006), the lower vertical humidity gradient near the ground and lower temperatures in southern Patagonia result in evaporation rates which are much lower than those of central Patagonia: 3.3 mm day^{-1} in Puerto Deseado and Río Gallegos, and just 1.1 mm day^{-1} in Ushuaia (Beagle Channel).

There is little published information for the warm-temperate sector to the north-east of the Río de la Plata estuary. In the Argentine sector of the warm-temperate zone, south of Río de la Plata, there are virtually no mobile invertebrates documented as intertidal mussel predators. There is a sharp contrast between the cold- and warm-temperate sectors in the composition of high-tide assemblages of mobile predators. These consist of mobile invertebrates (*Trophon geversianus* (Pallas, 1774), *Anasterias antarctica* (Lütken, 1857) along the cold temperate sector and fish (*Micropogonias furnieri* (Desmarest, 1823), *Odontesthes argentinensis* (Valenciennes, 1835) along the warm temperate sector (Table II). However, while fish might have been important consumers of *Brachidontes* during the 1970s (Orensanz, unpublished data), their present role may be reduced because croaker and silverside populations have been severely overfished during recent years (Carozza et al. 2004). No significant fish predators of intertidal mussels have been identified in the transition zone or in the cold-temperate sector (Appendix S1, Table II). Additionally, a small octopus, *Octopus tehuelchus* d'Orbigny, 1834, is frequent in the transition zone (Table II). The exotic green crab, *Carcinus maenas* (Linnaeus, 1758), a recent addition to the cold-temperate biota and potentially a mussel predator, currently ranges over three degrees of latitude (44°45′–47°45′S). In addition to mobile invertebrates, passive sessile mussel consumers are a prominent component. In the warm-temperate sector, a guild of four sea anemone species depends largely on mussels dislodged by disturbances as a food item (*Bunodosoma zamponii* Gomes, Schama & Solé-Cava, 2012), *Aulactinia marplatensis* (Zamponi, 1977), *Bunodactis reynaudi* (Milne-Edwards, 1857) and *Oulactis muscosa* (Drayton in Dana, 1846). Two of these species were reported by Bertness et al. (2006) from intertidal mussel beds of Cabo Dos Bahías, where they reach a density of 600 individuals m^{-2}. However, sea anemones rely mostly on dislodged mussels so their structuring role may be limited (Kruger & Griffiths 1998), even if they are a functionally significant component of the intertidal trophic chain.

Shorebirds are the most important low-tide active predators, with kelp gulls (*Larus dominicanus* Lichtenstein, 1823) and oystercatchers (*Haematopus* spp.) being the most ubiquitous. Other documented bird predators are sanderlings (*Calidris alba* (Pallas, 1764)) in the warm-temperate sector and red knots (*Calidris canutus* (Linnaeus, 1758)) in the transition zone (Table II).

Along the cold temperate sector there have been at least two mobile invertebrate predators. *Anasterias antarctica* (seastar) (Gil & Zaixso 2008) and *Trophon geversianus* (snail) (Gordillo & Amuchastegui 1998; Andrade & Ríos 2007; Curelovich et al. 2016) predate on intertidal mussels (see Table II). Bertness et al. (2006) observed in the cold-temperate sector at Cabo Dos Bahías that *A. antarctica* (reaching a density of 80 individuals m^{-2} in the middle to low intertidal of wave-exposed shores) is able to live only in association with the mussel matrix. Although large *A. antarctica* individuals feed selectively on large *P. purpuratus* (up to 30 mm long), their structuring role may be limited because (at least in tidal pools) they may prefer individuals dislodged by wave action (Gil & Zaixso 2008). This contrasts with the rocky intertidal of Central Chile, where experimental studies have shown that *P. purpuratus* populations are controlled by predation by a starfish (*Heliaster helianthus* (Lamarck, 1816)) and

a gastropod (*Concholepas concholepas* (Bruguière, 1789)) (Paine et al. 1985; Moreno 2001; Navarrete & Castilla 2003), whose adults are larger than those of *A. antarctica* and *T. geversianus*, respectively.

Predation by the shell-drilling *T. geversinaus* may be more significant. At many locations it is not constrained to the mussel matrix, and has been observed preying actively on *Mytilus* sp. (Curelovich et al. 2016), even at low tide level. Three or four different mussel species may coexist at the lower edge of intertidal mussel beds from Patagonia, but differential predation by *T. geversianus* has not been assessed.

Wieter et al. 2012 concluded that there are no significant differences in the functional group of the mobile invertebrate predators (including *Trophon* sp. and *A. antarctica*) between the Argentinean and Magellanic biogeographic provinces, but data are missing for sampling sites in the Argentine Biogeographic Province.

Conspicuous absences and historical contingencies

Historical contingency was implicit in the metaphorical notion of 'empty' or 'vacant niches', which was often invoked during the 1960s by Argentine ecologists and biogeographers to explain the conspicuous absence of species expected to occur in the rocky intertidal of the South-western Atlantic (Olivier et al. 1966a). The available pool of species might be limited as a result of historical contingencies, the consideration of which requires a retrospective view of coastal environments.

Invertebrates colonizing the rocky shore substrates that developed in the cold-temperate sector following the LGM (Last Glacial Maximum, ca. 21 KBP) may have originated from indigenous components surviving in enclaves of suitable substrate. In contrast to the Atlantic, the Pacific coast of southern South America was glaciated during the LGM from the Gulf of Ancud (41°S) to the Beagle Channel (Figure 7). There is incipient but consistent phylogeographic evidence indicating that as the glaciers receded, coastal waters were populated by the southward range expansion of species previously circumscribed to non-glaciated shores north of 41°S in the Pacific or from the South-western Atlantic (Ruzzante et al. 2008; Fraser et al. 2010; Trovant et al. 2015). An analogous situation has been reported for rocky intertidal invertebrates in the North Atlantic (Wares & Cunningham 2001).

The composition of extant intertidal assemblages of the South-western Atlantic reflects the history of coastal ecosystems in post-LGM times. During the

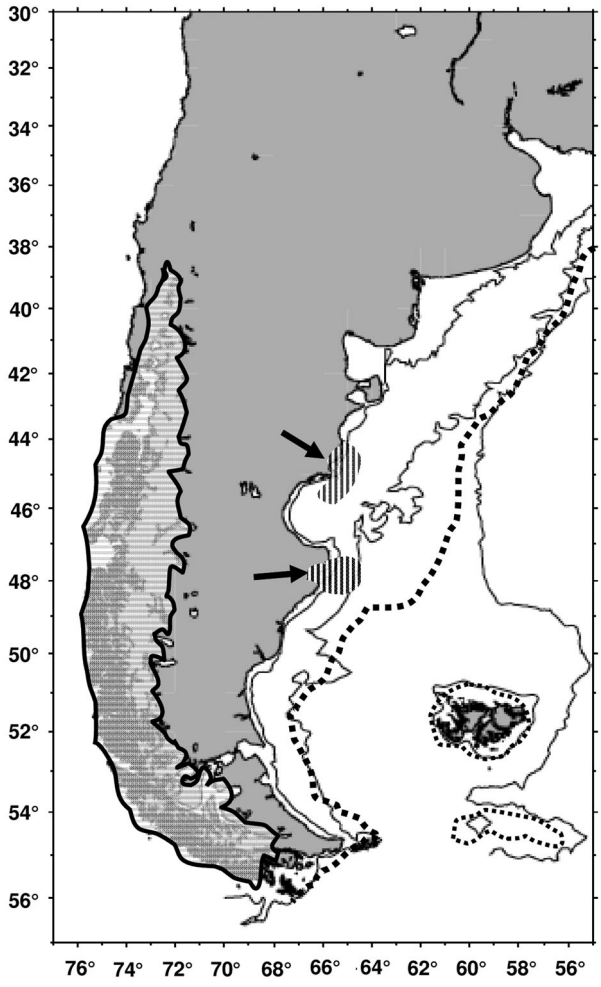

Figure 7. Geographic features of southern South America during the Last Glacial Maximum (LGM), 21 KYA (after Rostami et al. 2000). Shading: area covered by ice; dotted line: approximate position of the coastline; vertical shading (marked by arrows): enclaves of volcanic rock extending beyond the present coastline. Isobaths represented correspond to 50 m, 100 m and 1000 m.

LGM, the coast, which was never glaciated during the Quaternary, ran far to the east of its present location (Figure 7; Rostami et al. 2000, Ponce et al. 2011), and most of the Patagonian shelf was exposed and shallow. As the Patagonian shelf was gradually flooded subsequent to the LGM, coastscapes were dominated by low coastlines and depositional environments (Fray & Ewing 1963). Stretches of hard-rock coastline were, as they are today, 'insular' ecological enclaves. Granitic rock intertidals were most likely limited to the eastward projection of the volcanic rock outcrops that currently dominate the coastline from 44° to 45°15′S and 47°45′–49°S. A survey of fishing grounds (Cousseau & Perrotta 1998) indicates that those structures extend well into the inner shelf (Figure 7).

On the other hand, in a recent phylogeographic study, Trovant et al. (2015) reported that the biogeographic replacement between *P. purpuratus* and *B. rodriguezii* may prove a case of 'high density blocking' (Waters 2011; Waters et al. 2013). The lineage leading to the extant *B. rodriguezii* seems to have been present in that region since at least the upper Miocene (Trovant et al. 2013, 2016), while *P. purpuratus* was a recent expansion in the South-western Atlantic during post-LGM times, which might explain why it did not expand its range northwards in the Atlantic.

Consistent with that reconstruction, there was minimal presence of *Brachidontes* or *Perumytilus* in cores covering large sectors of the shelf, from 35° to 57°S (Richards & Craig 1963); *B. rodriguezii* was found in only one core, off Mar del Plata (68 m depth). *Trophon geversianus*, currently the primary shelled predator of intertidal mussels, was also poorly represented (only three cores, two of them near the entrance to Magellan Strait). Although rocky shore molluscs do not fossilize well *in situ*, they are usually transported to nearby sedimentary environments where they can be well preserved (Vermeij 2001). In fact, both *Brachidontes* and *Trophon* are conspicuous components of fossil assemblages found in marine terraces corresponding to the last interglacial (terraces IV and V) and the post-LGM (Holocene, terrace VI) along the coasts of Argentina (Feruglio 1950), particularly in the vicinity of rocky shores, e.g. the area of Camarones-Cabo Dos Bahías (Pastorino 2000; Aguirre et al. 2006).

Accidental species introductions as a strong test of alternative hypotheses

The two competing hypotheses advanced to explain conspicuous absences in rocky intertidal habitats from the South-western Atlantic make different predictions about the success and specificity of potential immigrants. Candidates to fill in conspicuous vacancies should not prosper under the Environmental Harshness Hypothesis, but would succeed under the Historical Contingency Hypothesis. The pandemic of invasions by exotic species in temperate seas worldwide offers the opportunity of a hard, though qualitative, test of these predictions at the appropriate operating scale, which would not be feasible by way of manipulative experiments. Successful invasion of rocky shores from the South-western Atlantic by ecologically 'significant' species has occurred in both the warm- and cold-temperate regions (Orensanz et al. 2002). Invaders have selectively filled 'niches' previously indicated as 'vacant'. Olivier et al. (1966a) listed ligiid isopods among the absentees from rocky shores in the Mar del Plata area, where *Ligia (Megaligia) exotica* is currently abundant. The absence of a 'barnacle belt' was also highlighted by Olivier (1966a, 1966b); while currently *B. glandula*, introduced around 1970 in Mar de Plata, is present at variable densities on consolidated substrates of the middle-high intertidal zone along the entire Argentine coast (Schwindt 2007). Successful invaders of South-west Atlantic intertidal environments have originated in regions that are not particularly stressful in terms of potential evaporation. *Balanus glandula* came from the west coast of North America (Geller et al. 2008), the sea slug *Pleurobranchaea maculata* (Farias et al. 2016) and the predator/scavenger *Carcinus maenas* from the North-east Atlantic. The recent rapid spread of *Carcinus* indicates that it is possible for a relatively large species, which does not depend on the mussel matrix for refuge, to thrive in this environment, even when it was not naturally selected to cope with the harsh prevailing conditions in the region.

Concluding remarks

While environmental stress (as indicated by potential evaporation) may be a significant driver of local variation in intertidal community composition along the rocky shores of the South-west Atlantic (as has also been well demonstrated in other temperate regions), it does not explain the regional scarcity or low diversity of mobile invertebrate predators. These are virtually absent in the warm-temperate sector, where environmental stress is relatively low. We concur with Hidalgo et al. (2007) on the need for further research to clarify the possible roles of predation (e.g. differential vulnerability of coexisting mussels to predation by *Trophon*), substrate (e.g. granitic outcrops vs. abrasion platforms of friable sedimentites) and environmental stress. Generalizations may be premature. Indicators of stress need to be refined and measured *in situ*. Estimates of SST from remote sensors or evaporation potential based on measurements from meteorological stations are poor surrogates for conditions encountered by organisms in the intertidal zone (Helmuth 2009). Finally, ecological processes cannot be explained solely in terms of environmental drivers and must be placed in historical context. This is not easy in the South-west Atlantic due to the poor representation of marine Pliocene sediments (Martínez & del Río 2002), and because much of the marine record of the post-LGM is submerged (Rostami et al. 2000) and thus difficult to access. Yet the fact that despite their uniform appearance, geographically

adjacent biotas (warm- and cold-temperate) differ in their assemblages, suggests that further attention should be given to the post-glacial biogeographic history of the South-western Atlantic.

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