Vol. 648: 39–49, 2020
https://doi.org/10.3354/meps13441

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published August 27

Functional diversity on rocky shores of the SW Atlantic: sewage effluents influence and mask the effects of the latitudinal gradient

G. V. Garaffo*, E. N. Llanos, M. A. Saracho Bottero, E. Hines, R. Elías, M. L. Jaubet

Instituto de Investigaciones Marinas y Costeras, (IIMyC), Facultad de Ciencias Exactas y Naturales (FCEyN), Universidad Nacional de Mar del Plata (UNMdP)-Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), CC1260, 7600 Mar del Plata, Argentina

ABSTRACT: Rocky shores are a transitional ecosystem between land and marine environments, and, together with other benthic coastal habitats, have a diverse macrobenthic community. Although there is enough information about the taxonomic diversity of Argentinean rocky shores, studies with a functional approach are scarce. We applied biological traits analysis and functional diversity indices to evaluate the geographic variation of the functional diversity of macrobenthic assemblages on rocky shores along a latitudinal gradient in the SW Atlantic (from 37° to 50° S). A total of 11 beaches with rocky hard substrate belonging to 2 biogeographical provinces (Magellanic and Argentinean) were studied during April 2016. The trait composition of macrobenthic assemblages and functional diversity indices (Rao's quadratic entropy) varied significantly along the Argentinean coast, suggesting that the latitudinal gradient influences the distribution of species with respect to combinations of trait modalities. Rao's quadratic entropy, species richness, evenness, and Shannon-Wiener diversity showed a pattern with higher values in the sites located in high latitudes. The functional diversity patterns found coincide with the biogeographical provinces. The presence of intertidal sewage effluents considerably influence functional diversity and mask the effects of the latitudinal gradient on the macrobenthic communities on rocky shores.

KEY WORDS: Functional traits · Biological traits analysis · BTA · Functional diversity indices · Latitudinal gradient · SW Atlantic · Macroinvertebrates · Macrofauna

1. INTRODUCTION

One of the components of biodiversity is functional diversity; it focuses on the species functional traits and, as a consequence, may predict ecosystem functioning more precisely (Díaz & Cabido 2001, Cianciaruso et al. 2009). The functional structure of a community can be represented by a set of traits that describe the morphological and behavioral characteristics of the species. Among the most widely used methods to evaluate the functional diversity of assemblages are biological traits analysis (BTA) (Bremner 2008) and calculation of functional diversity indices (Laliberté & Legendre 2010, Villéger et al. 2008). BTA is a multivariate approach that combines information on species distributions with the multiple traits they exhibit (Bremner 2008), and the functional diversity indices have varying abilities to reflect the different aspects of assemblage functional trait structure. Higher values of functional diversity indices are expected when the species in an assemblage differ greatly in their functional traits.

A growing number of authors consider that the functional composition of biological communities should provide more information about their responses to the environment and their ecosystem effects than species diversity (Grime 1998, Díaz & Cabido 2001, Tilman 2001, Hooper et al. 2005, Hillebrand & Matthiessen 2009). Interest in these topics has increased significantly over the past years, principally because changes

*Corresponding author: garaffo@mdp.edu.ar

in species assemblage can modify or alter ecosystem functions and their resilience to environmental fluctuations (Tilman 1999, Hooper et al. 2012).

In marine environments, studies using a functional approach are now more abundant in the literature, although studies evaluating the latitudinal gradients in functional diversity are scarce. While there is a general trend of increasing biodiversity towards the tropics (Dobzhansky 1950, Mittelbach et al. 2007, Valentine & Jablonski 2015, Chaudhary et al. 2016), the patterns of functional trait diversity at different geographic scales are not consistent with any theory of species diversity distribution (Lamanna et al. 2014). For instance, Berke et al. (2014) found that the assemblages of intertidal-to-outer-shelf bivalves depict a strong decrease in functional richness and a sharp increase in functional evenness with increasing latitude. Therefore, innovative approaches are needed to help understand the relationship between species diversity and functional diversity along latitudinal gradients. Besides, determining major patterns in the global deployment of functional diversity is an urgent need in the face of the current anthropogenic impacts (Berke et al. 2014). Although in coastal areas of the SW Atlantic Ocean, studies on the functional structure of rocky shore communities are scarce, there are studies in which the BTA and functional diversity indices have been successfully applied (Gusmao et al. 2016, Otegui et al. 2016, Garaffo et al. 2018, Llanos et al. 2020). The Argentinean marine coast spans approximately 20º of latitude and is more than 4700 km long (Miloslavich et al. 2016). This coast has mostly sandy beaches and some rocky formations located mainly at Mar del Plata and Peninsula Valdes. In this region, the major threats to marine environments and biodiversity that can promote disturbance and degradation of ecosystems are fishing, dredging, presence of ports, aquatic contamination, presence of exotic species, urban development, and tourist use in coastal areas (Miloslavich et al. 2016). Although there is abundant information about the taxonomic diversity of the Argentinean rocky shores (Lutz et al. 2003, Adami et al. 2018), studies with a functional approach are scarce (Wieters et al. 2012, Garaffo et al. 2018).

This study aimed to evaluate the geographic variation of the taxonomic and functional diversity of invertebrate assemblages of rocky shores on the Argentinean coast (from 37° to 50° S). We addressed functional diversity by applying BTA and the calculation of functional diversity indices (functional richness, functional evenness, functional divergence, and Rao's quadratic entropy), and taxonomic diversity by estimating community parameters (species richness, evenness index, and Shannon-Wiener diversity index). We predict that the functional diversity of macrofaunal assemblages will reflect global trends in marine diversity and decrease towards higher latitudes.

2. MATERIALS AND METHODS

2.1. Study area

The study area included the SW Atlantic coastal area (central and south Argentinean shores), from 37° to 50° S. A total of 11 beaches with rocky hard substrate belonging to 4 provinces (Buenos Aires, Río Negro, Chubut, and Santa Cruz) were surveyed during April 2016. The localities surveyed were Santa Clara del Mar, Emisario Beach, Mar del Plata, Miramar, Quequén, Las Grutas, Puerto Madryn, Bahía Camarones, Comodoro Rivadavia, Puerto Deseado and Puerto San Julián (Fig. 1, Table 1). Two of the sampling sites, Quequén and Comodoro Rivadavia, have sewage effluents that discharge directly into the intertidal zone (López Gappa et al. 1990, 1993, Mazón 2010). A submarine outfall currently operates at Emisario Beach (in Mar del Plata city) that discharges the wastewater 4 km from the coast (Cuello et al. 2019).

The sampling sites were distributed within 2 biogeographical provinces (Magellanic and Argentinean). The Valdés Peninsula delimits these provinces; and the Magellanic Biogeographic Province (43° to 56° S) of cold waters includes the southern part of Chubut Province and the Santa Cruz and Tierra del Fuego Provinces, while the Argentinean Biogeographic Province (36° to 43° S) of warmer waters consists of the Buenos Aires and Río Negro Provinces and the northern part of Chubut Province (Lutz et al. 2003, López Gappa et al. 2006, Balech & Ehrlich 2008, Miloslavich et al. 2016). The transition zone between these biogeographical provinces occurs in the North Patagonian Gulfs (San Matías, San José, Nuevo) and Valdés Peninsula, between 41° and 43° S. Concerning coastal oceanography, this zone is dominated by frontal systems that begin developing in spring and vanish by early autumn (Gagliardini & Rivas 2004).

2.2. Sampling design and field and laboratory routines

At each sampling site, 7 to 10 sampling units were collected using a 10 cm diameter corer (78 cm^2). The corer was buried into the secondary substrate up to

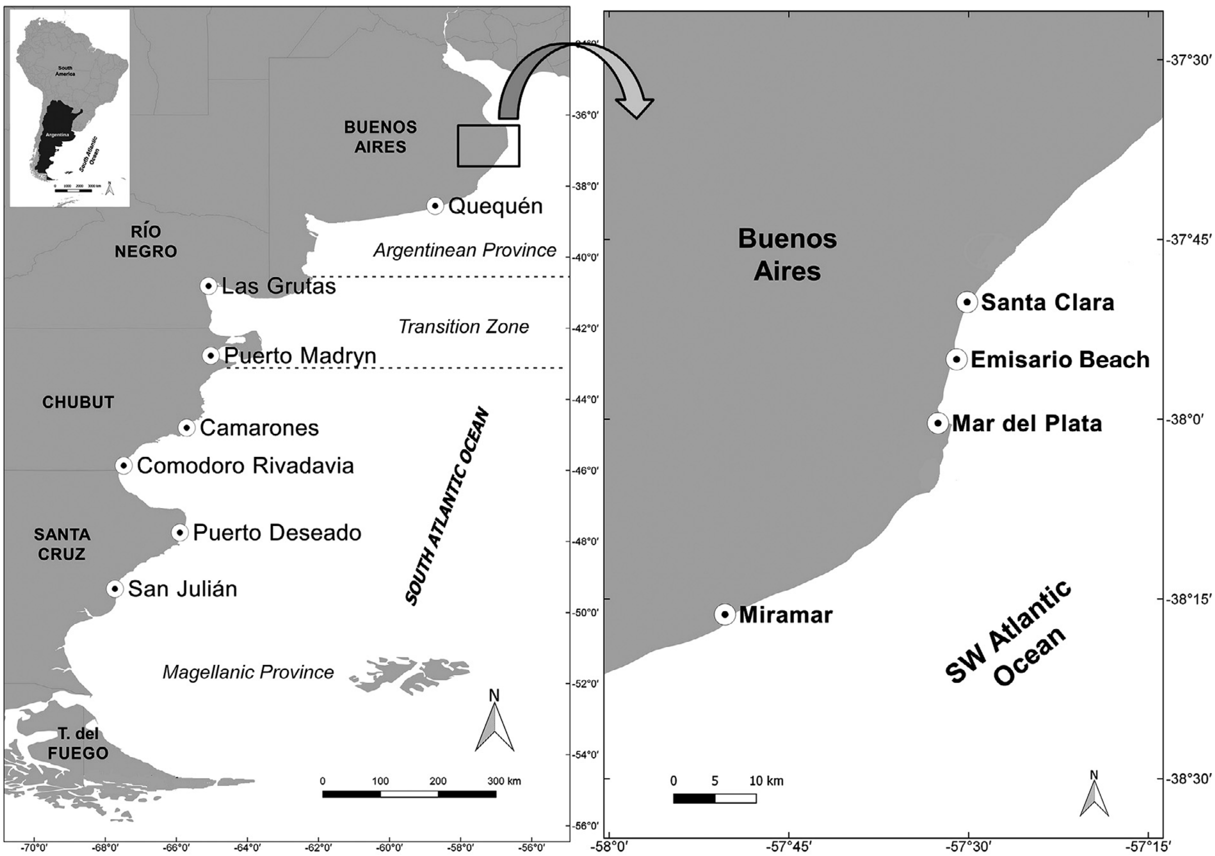

Fig. 1. Study area. Localities in Argentina sampled during the spatial survey. Left: the area extending from Buenos Aires Province (37° S) to Tierra del Fuego Province (54° S); right: localities sampled in the center of Buenos Aires Province

Table 1. General characteristics of the sampling sites

Site	Geographical position	Exposure to waves	Sewage outfall	Dominant secondary substrate
Santa Clara del Mar	37.85° S, 57.50° W	Open	Without effluent	*Brachidontes rodriguezii* (mussels)
Emisario Beach	37.93° S, 57.54° W	Open	With submarine effluent	*Brachidontes rodriguezii* (mussels)
Mar del Plata	38.00° S, 57.54° W	Open	Without effluent	*Brachidontes rodriguezii* (mussels)
Miramar	38.27° S, 57.83° W	Open	Without effluent	*Brachidontes rodriguezii* (mussels)
Quequén	38.57° S, 58.65° W	Open	With intertidal effluent	*Boccardia proboscidea* (auto-ecosystem engineer polychaete, see Jaubet et al. 2015)
Las Grutas	40.81° S, 65.08° W	Closed	Without effluent	*Brachidontes rodriguezii* (mussels)
Puerto Madryn	42.78° S, 65.00° W	Closed	Without effluent	*Brachidontes rodriguezii* (mussels)
Bahía Camarones	44.80° S, 65.71° W	Closed	Without effluent	*Perumytilus purpuratus* (mussels)
Comodoro Rivadavia	45.86° S, 67.48° W	Open	With intertidal effluent	*Boccardia proboscidea* (auto-ecosystem engineer polychaete, see Jaubet et al. 2015)
Puerto Deseado	47.76° S, 65.88° W	Closed	Without effluent	*Perumytilus purpuratus* (mussels)
Puerto San Julián	49.32° S, 67.71° W	Closed	Without effluent	*Perumytilus purpuratus* (mussels)

the basal rocky bottom (approximately 20 cm), and each replicate (sampling unit) was randomly collected from independent rocks. Each sample was fixed in 5% neutralized formalin solution and then sieved through a 0.5 mm mesh. The retained organisms were identified, counted, and preserved in a 70% ethanol solution.

Mean sea surface temperature (SST, °C) for each site was extracted from INIDEP (www.inidep.edu.ar). The SST was obtained from the processing of Aqua-MODIS satellite data corresponding to the 11 and 12 µm (night) band and with a spatial resolution of 4 km.

2.3. BTA, community parameters, and functional diversity metrics

The spatial pattern of the macrofaunal functional trait composition was evaluated using BTA. Seven categorical functional traits that express the life histories of species were used: depth penetration, maximum size, development mode, living habit, feeding mode, relative adult mobility, and tolerance to pollution (Table 2). These traits were chosen since they have the potential to illustrate changes in ecosystem functioning. Information about species traits were obtained from identification guides (Boschi & Cousseau 2004, Vallarino & Elías 2009), scientific journals, and ad hoc information from local specialists. Expert judgment and/or data from the nearest phylogenetic neighbor were considered when reliable information was missing.

Each taxon was classified according to its affinity with different modalities (i.e. trait categories) of functional traits (see the Supplement at www.int-res.com/articles/suppl/m648p039_supp.pdf). This affinity to each trait modality was quantified using a fuzzy coding procedure (Chevene et al. 1994), with scoring ranging from 0 to 3. No affinity for a trait was coded as 0 and complete affinity as 3 (e.g. mytilid *Brachidontes rodriguezii* was assigned the following values for the trait 'living habit': burrow dweller 0; attached 3; tube dweller 0; free-living 0). The scores for each trait, except for development mode, were assigned considering the species adult form. Trait scores of each taxon were multiplied by its abundance for every sample and subsequently summed to generate a matrix with the overall frequency of each trait modality per sample.

The taxonomic diversity indices calculated were: species richness (S), evenness index (J') (Pielou 1969) and Shannon-Wiener diversity index (H') (Shannon & Wiener 1963). To assess different components of functional diversity, the indices functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and relative Rao's quadratic entropy (rRao) were calculated (Rao 1982, Botta-Dukát 2005, Ricotta 2005, Villéger et al. 2008, Laliberté & Legendre 2010). FRic represents the trait space filled by a given species assemblage by calculating the convex hull volume that comprises the entire trait space filled by all species of this assemblage (Villéger et al. 2008). This index can thus be used as a proxy of the range of functional traits of an assemblage (Schuldt et al. 2014). The FEve index measures the regularity of the abundance distribution in trait space by summing the branch lengths of the minimum spanning tree that is required to connect all species in an assemblage weighted by the species abundances (Villéger et al. 2008). The distribution of the species abundances around the gravity center of the functional trait space is measured by FDiv (Villéger et al. 2008). This index describes how abundance is distributed within the functional traits space (Casanoves et al. 2008). The multitrait dispersion was measured by rRao. This index measures the general dispersion of the multivariate trait space of an assemblage. It considers the abundance-weighted pairwise distances among species in the trait space and can be interpreted as a measure of multivariate dispersion (Laliberté & Legendre 2010, Ricotta & Moretti 2011). The indices were calculated based on a matrix of Jaccard distances of species functional traits using the FDiversity software (Di Rienzo et al. 2008). All metrics were calculated per replicate.

Table 2. List of biological traits and respective categories

Biological traits	Trait categories	Labels
Depth penetration	Surface	DS
	0–3 cm	D0-3
	3–8 cm	D3-8
	>8 cm	D>8
Maximum size	Very small (<1 cm)	SVS
	Small (1–3 cm)	SS
	Medium (>3 cm)	SM
Development mode	Planktotrophic	DP
	Lecithotrophic	DL
	Direct	DD
Feeding mode	Deposit feeder	FD
	Filter/suspension feeder	FF
	Opportunist/scavenger	FO
	Grazer	FG
	Predator	FP
Living habit	Burrow dweller	HB
	Attached	HA
	Tube dweller	HT
	Free living	HF
Relative adult mobility	None	MN
	Low	ML
	Medium	MM
	High	MH
Tolerance to pollution	1st order opportunistic	V
	2nd order opportunistic	IV
	Tolerant	III
	Indifferent	II
	Sensitive	I

2.4. Data analysis

A canonical correspondence analysis (CCA) was carried out to determine the correspondence between the species and the sampling sites by weighting the effects of SST, latitude, and the presence or proximity of a sewage outfall. The proximity to a sewage outfall was classified in an ordinal score: with intertidal effluent, value = 3; with subtidal effluent, value = 2; and without effluent, value = 1.

The relationships among sites and each trait modality were also explored by a CCA, considering the matrix with the overall frequency of each trait modality. This analysis considered the same environmental predictors used in the species-based CCA. The final ordination depicted the centroid of each sampling site.

Generalized linear models (GLMs) (Dobson 2002) were used to assess the variability of functional indices and taxonomic diversity indices in relation to each environmental predictor. The explanatory variables evaluated were biogeographical province, SST, and the presence or proximity of a sewage outfall. SST is a continuous variable, and the remaining are categorical variables. Biogeographical province (BP) has 3 categories: Argentinean (A), transition (T), and Magellanic (M); and sewage outfall (SO) has 3 categories: with intertidal effluent (IE), with subtidal effluent (SE), and without effluent (WE). Only the main factors were evaluated, interactions between variables were excluded because of the high number of empty cells in the data matrix due to the lack of data in the intersections between factors. The models were fitted assuming a gamma error distribution, with a log-link function.

The best model for each index was selected using the sample-corrected Akaike's information criterion (AIC_c) (Akaike 1973). Models (for each index) with a difference in AIC_c (ΔAIC_c) < 2 were considered to have equivalent support from the data (Burnham & Anderson 2002). ΔAIC_c and Akaike weights (w_i) were calculated for each model. When more than 1 model had substantial support, model averaging (a form of multimodel inference) was used (Burnham & Anderson 2002). Multimodel inference involves ranking the fitted models from the best to the worst based on the AIC_c, and then scaling to obtain the relative plausibility of each fitted model by a weight of evidence (in this case w_i) relative to the selected best model (lowest AIC_c). Then, a weighted estimate of the predicted value, weighting the predictions by w_i, is computed. In the present study, the fit and complexity of the models were evaluated in successive steps to avoid overfitting until a model with sufficient predictive power was obtained.

The R project software and associated packages (R Core Team 2013) were used for data analyses (version 3.4.0).

3. RESULTS

3.1. Benthic assemblages

In the sampling period, a total of 94 627 individuals were identified and quantified, corresponding to 44 species from 6 phyla (Annelida: 19, Arthropoda: 14, Mollusca: 7, Nemertea: 2, Nematoda: 1, and Platyhelminthes: 1). The first 2 axes of the CCA depicting changes in taxonomic composition represented 48% of the total inertia (Fig. 2a). Overall, a latitudinal gradient was observed on the horizontal axis and an impact gradient on the vertical axis. The high latitude sites were grouped separately from the low latitude sites (Axis 1). However, Quequén was an exception to this general pattern. According to the latitudinal gradient, *Perumytilus purpuratus*, *Lasaea miliaris*, oligochaetes, and nematodes were associated with high latitudes, while *Brachidontes rodriguezii*, *Siphonaria lessonii*, *Leodamas tribulosus*, *Mytilus platensis*, and *Alitta succinea* were associated with low latitudes. Axis 2 showed a clear separation of Quequén and Comodoro Rivadavia from the rest of the sites, especially from the sites located at the highest latitudes. These 2 sites have sewage effluents that discharge in the intertidal area and were associated with *Boccardia proboscidea*, *Exosphaeroma* sp., and *Monocorophium insidiosum*.

3.2. BTA

The CCA considering the functional structure of the benthos depicted clear differences among sites. Axis 1 explained 57.8% of the total variation and separated Quequén and Comodoro Rivadavia from the other sites. This axis was mostly related to traits such as small size, lecithotrophic development, low relative mobility, deposit feeders, burrow dweller and tube dweller living habits, and opportunistic species. The second axis explained 17.4% of the total variation and mostly reflected the latitudinal gradient, in which high latitudes were associated with organisms which show predator feeding habit and free-living habits and are sensitive to pollution, while low lati-

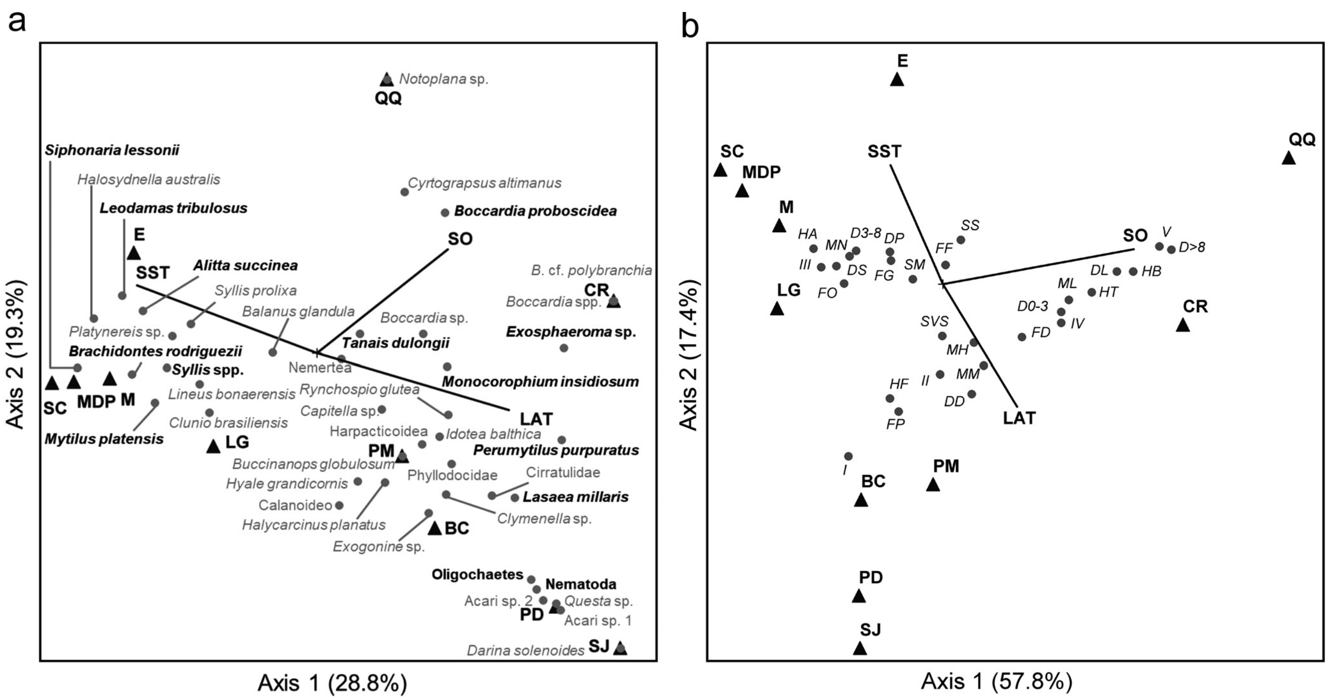

Fig. 2. Canonical correspondence analysis. (a) Correspondence between the species and the sampling sites by weighting sea surface temperature (SST), latitude (LAT), and the presence or proximity of a sewage outfall (SO). Species or taxa with constancy greater than 10% are shown in **bold**. (b) Correspondence between each trait modality and the sampling sites by weighting SST, latitude, and the presence or proximity of a sewage outfall. Site labels: QQ: Quequén; SC: Santa Clara; E: Emisario Beach; MDP: Mar del Plata; M: Miramar; LG: Las Grutas; PM: Puerto Madryn; BC: Bahía Camarones; CR: Comodoro Rivadavia; PD: Puerto Deseado; SJ: San Julián. See Table 2 for trait category labels

tudes were characterized by organisms that are indifferent regarding tolerance to pollution, opportunist feeders, and sessile (Fig. 2b).

3.3. Taxonomic and functional diversity indices

The model with the lowest AIC_c value shows that rRao was significantly related to BP and SO (Tables 3 & 4). This index presented significantly lower values in the sites located in low latitudes (Argentinean Province) (Fig. 3a). The sites with intertidal effluent showed lower values of rRao (Fig. 4a).

The model with the lowest AIC_c for FDiv retained SST. However, this model showed a w_i value of 0.483, which is low. Therefore, the averaged model was calculated considering the models with $\Delta AIC_c < 2$ (Tables 3 & 4). Following model averaging, the lower FDiv values were found in sites with lower SST. The lowest SST was recorded in San Julián (10.6°C). No significant relations with BP and SO ($p > 0.05$) were found.

FRic and FEve were not affected by the explanatory variables evaluated. The models evaluated for these indices showed no improvement in the fit with respect to the null model (Table 3).

The model with the lowest AIC_c value shows that S was significantly related to BP, SO, and SST (Tables 3 & 4). This community parameter presented significantly lower values in the sites located in low latitudes (Argentinean Province), which showed higher SST (Fig. 3b). The sites with intertidal effluent showed lower values of S (Fig. 4b).

The model with the lowest AIC_c for H' retained BP and SO. However, this model showed a w_i value of 0.665, which is low. Therefore, the averaged model was calculated considering the models with $\Delta AIC_c < 2$ (Tables 3 & 4). Following model averaging, lower values were found in the sites located in low latitudes (Argentinean Province) (Fig. 3c) and in the sites with intertidal effluent (Fig. 4c). No significant relation with SST ($p > 0.05$) was found.

The model with the lowest AIC_c value shows that J' was significantly related to BP (Tables 3 & 4). However, this model showed a w_i value of 0.478, which is low (Tables 3 & 4). Therefore, the averaged model was calculated. Following model averaging, this community parameter presented significantly lower values in the sites located in low latitudes (Argentinean Province) which showed higher SST (Fig. 3d).

Table 3. Results of the generalized linear model based on gamma distribution and log-link function of the relationship between functional and taxonomic indices and explanatory variables: AIC_c of models evaluated. The best models are given in **bold**. BP: biogeographic province; SO: presence or proximity of a sewage outfall; SST: sea surface temperature; rRao: relative Rao's quadratic entropy; FRic: functional richness; FDiv: functional divergence; FEve: functional evenness; *S:* species richness, *J'*: evenness index; *H'*: Shannon-Wiener diversity index

Model	rRao	FRic	FDiv	FEve	*S*	*H'*	*J'*
BP-SO-SST	−47.197	**368.961**	−168.827	−32.732	**355.744**	**65.721**	−70.311
BP-SO	**−49.916**	373.278	−164.607	−35.202	359.471	**64.350**	−72.680
BP-SST	−38.361	376.206	**−171.441**	−36.539	365.177	70.941	**−73.920**
SO-SST	−25.202	372.015	**−171.092**	−37.198	361.539	68.926	−71.870
BP	−40.682	373.967	−167.425	−38.821	363.872	68.645	**−75.74**
SO	−9.14	**369.700**	−152.501	−39.265	363.826	77.933	−66.652
SST	−26.674	371.814	**−172.527**	**−40.087**	365.295	72.395	**−74.995**
Null	−12.292	**369.841**	−156.771	**−41.285**	368.222	81.472	−68.740

Table 4. Results of the generalized linear model based on gamma distribution and log-link function of the relationship between functional and taxonomic indices and explanatory variables: the best models. Models with $\Delta AIC_c < 2$ and Akaike weights (w_i) are shown for each index. See Table 3 for abbreviations. Significant values are given in **bold** ($p < 0.05$)

	df	Wald statistic	p
rRao			
BP	2	67.037	**<0.001**
SO	2	13.798	**0.001**
FDiv (M1, w_1 = 0.483)			
SST	1	20.562	**<0.001**
FDiv (M2, w_2 = 0.281)			
BP	2	3.569	0.168
SST	1	6.644	**0.010**
FDiv (M3, w_3 = 0.236)			
SO	2	3.246	0.197
SST	1	24.496	**<0.001**
S			
BP	2	11.131	**0.004**
SO	2	16.182	**<0.001**
SST	1	6.391	**0.010**
***H'* (M1, w_1 = 0.665)**			
BP	2	21.459	**<0.001**
SO	2	9.832	**0.007**
***H'* (M2, w_2 = 0.335)**			
BP	2	8.491	**0.014**
SO	2	10.927	**0.004**
SST	1	1.105	0.293
***J'* (M1, w_1 = 0.478)**			
BP	2	12.575	**0.002**
***J'* (M2, w_2 = 0.329)**			
SST	1	8.848	**0.003**
***J'* (M3, w_3 = 0.192)**			
BP	2	3.495	0.174
SST	1	0.504	0.478

4. DISCUSSION

This study addressed the geographic variation of the functional diversity of macrobenthic assemblages on rocky shores along a latitudinal gradient in the SW Atlantic. Trait composition of macrobenthic assemblages and the rRao index for functional diversity varied significantly along the Argentinean coast, suggesting that the latitudinal gradient influences the distribution of species according to the traits they present. The rRao index and the community parameters (*S*, *H'*, and *J'*) were higher in high latitudes. Highly sewage-impacted sites (Quequén and Comodoro Rivadavia) showed contrasting functional structures, indicating that organic pollution is a highly influential driving force that can blur the general effects of the latitudinal gradient. Therefore, the prediction that the functional diversity of macrofaunal assemblages will reflect global trends in marine diversity and decrease towards higher latitudes was not supported. It indicates that although functional diversity of macrobenthic assemblages presents a spatial pattern, it could be reflecting the inherent differences among sampling sites, which comprise 2 biogeographical provinces (Magellanic and Argentinean). Thus, the observed spatial patterns in functional diversity reflect these differences between biogeographical provinces. On the other hand, the sites located in the Argentinean Biogeographic Province are surrounded by cities with a greater number of inhabitants and more intensive tourist use than the Magellanic Province cities. Therefore, the pattern found could be associated with the anthropogenic impact.

In a study conducted on the Argentinean coast, Wieters et al. (2012) found that the processes that determine the functional structure of intertidal com-

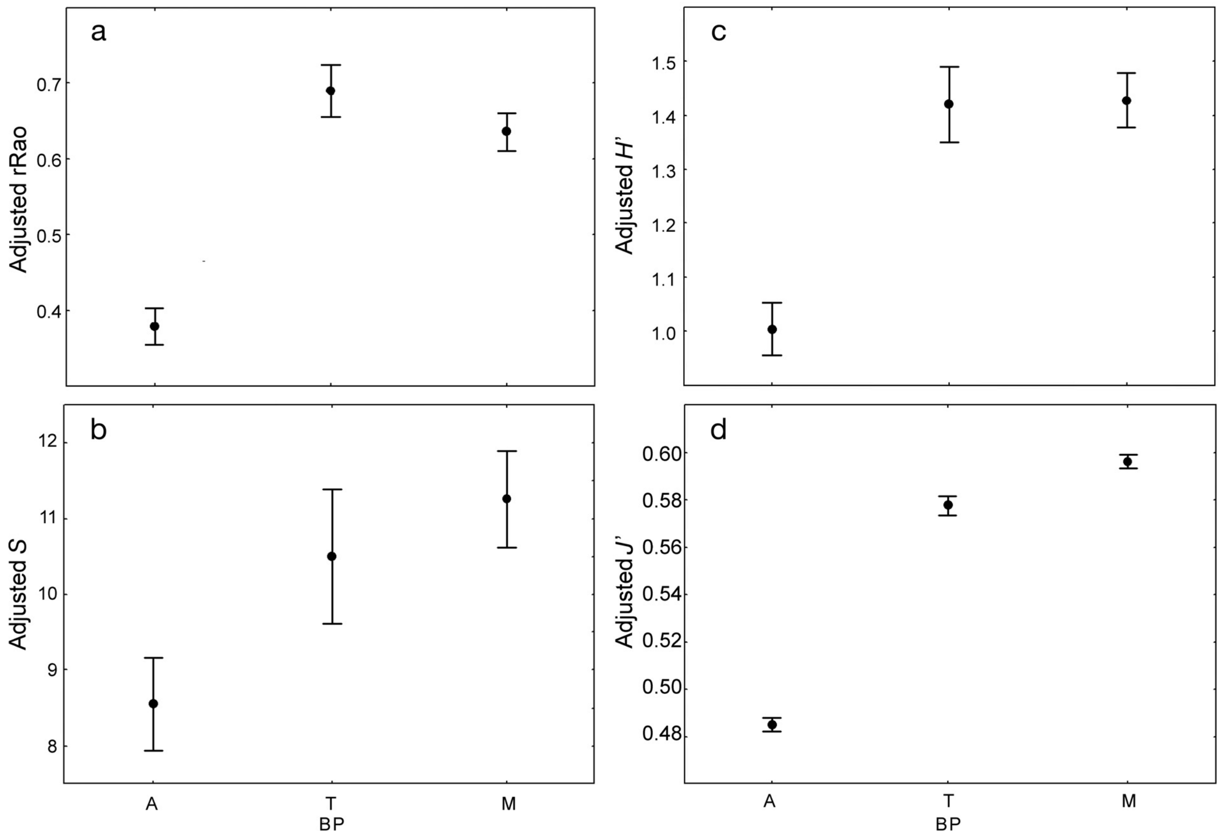

Fig. 3. Mean value of indices adjusted by best model (or averaged model) and biogeographical province (BP). A: Argentinean; T: transition; M: Magellanic. Bars indicate 95% confidence intervals. (a) rRao, (b) *S*: richness, (c) *H'*: diversity, and (d) *J'*: evenness

munities on rocky shores are insensitive to biogeographical boundaries. However, it is important to note that this study only considers the abundance of functional groups that arise from a sampling based on percentage cover and density of macroscopic sessile and mobile species visible to the naked eye. The methods of coverage are useful because the time of sampling and analysis of data are shorter compared to other methodologies, but the results are not as accurate as of those that arise from analysis based on the quantification of all macrofauna. On the other hand, Wieters et al. (2012) propose that their ability to detect and quantify differences between biogeographical regions may have been hampered by the low number of sites sampled in the Argentinean Province (only 2).

Other studies have described patterns that are in line with our observations. Berke et al. (2014) found a substantial decrease in functional richness and a strong increase in functional evenness of bivalves with increasing latitude. Wouters et al. (2018) found that polychaete functional diversity in shallow marine habitats was not related to the latitudinal gradient but negatively correlated with grain size and beach slope; polychaete trait composition changes along the latitudinal gradient but their functional diversity remains relatively constant.

The BTA allowed the recognition of spatial changes in functioning on rocky shore macroinvertebrate communities within the latitudinal gradient. In addition, the analysis separated Quequén and Comodoro Rivadavia from the rest of the sites. The dominance of predators, free-living species, and species sensitive to pollution in the high latitudes could be related to increased sediment quality, which allows the establishment of species with different feeding habits (Rosenberg 2001). An opposite pattern was found in the low latitudes, which were dominated by the trait modalities opportunist, sessile, and indifferent to pollution. Finally, Quequén and Comodoro Rivadavia present functional trait composition characteristics of areas that show organic enrichment (small size, lecithotrophic development, low relative mobility, deposit feeders, burrow dweller and tube dweller living habits, and opportunistic species). Small organisms are found in sites with organic enrichment,

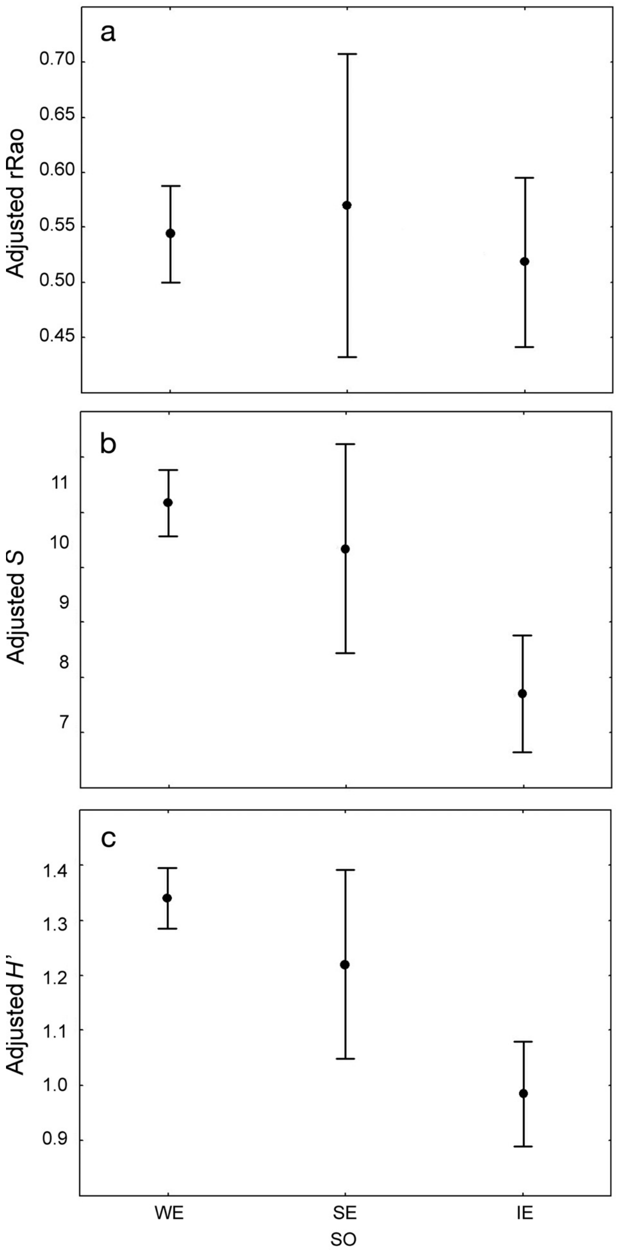

Fig. 4. Mean value of indices adjusted by best model (or averaged model) and presence or proximity of a sewage outfall (SO). WE: without effluent; SE: with subtidal effluent; IE: with intertidal effluent. Bars indicate 95% confidence intervals. (a) rRao, (b) *S* (richness), and (c) *H'* (diversity)

which could be an indicator of disturbance within the system (Pearson & Rosenberg, 1978). This is in line with the findings of Cloern (2001) and Llanos et al. (2020).

Finally, the tolerance to pollution reflects the response of communities to environmental stress. The patterns in the traits assemblage found in Quequén and Comodoro Rivadavia were driven by the dominance of invasive polychaete *Boccardia proboscidea* (Jaubet et al. 2018, Llanos et al. 2020, Saracho Bottero et al. 2020). In extreme conditions of organic pollution, *B. proboscidea* builds reefs formed by thousands of tubes per square meter (Jaubet et al. 2011, Garaffo et al. 2012, Elías et al. 2015). This species is also characterized by a facultative feeding strategy (i.e. they can be deposit feeders and filter/suspension feeders) (Fauchald & Jumars 1979). The development mode of *B. proboscidea* involves a poecilogonous development (production of more than 1 type of offspring with 2 kinds of larvae) and includes adelphophagy (nurse egg ingestion) (Hartman 1941, Blake & Kudenov 1981, Petch 1989, Gibson 1997, Simon & Booth 2007, Jaubet et al. 2015). Therefore, *B. proboscidea* is an opportunistic species since it has a high tolerance to organic pollution and its functional traits reflect adaptation to environmental stress. Quequén and Comodoro Rivadavia can be considered as having a lower environmental quality.

The rRao index presented higher values at high latitudes; therefore, the sites located at high latitudes present macrobenthic communities with a greater degree of heterogeneity of the functional traits, which might be related to greater ecosystem differentiation, occupation of niches, and resistance to invasive species (Mason et al. 2005). Thus, rRao reveals differences in macrobenthic functional structure between low and high latitudes. In addition, this index shows patterns similar to community parameters, indicating that both taxonomic and functional diversity are greater at high latitudes. Thus, these taxonomic and functional metrics together with BTA represent complementary, informative, and useful tools to describe the different aspects of benthic assemblages on rocky shores.

The functional traits considered in this study are mainly related to the response of the benthos to the environmental quality of the rocky shores. Hence, one can suggest that the sites located in higher latitudes presented a higher environmental quality. This higher environmental quality is associated with these sites being less affected by human impacts. At these sites, there was a greater occurrence of species sensitive to contamination (I), with greater mobility, and being free-living and predators. On the other hand, a higher functional dispersion (rRao) indicates high variation in the trait values across different species, indicating a high functional diversity. In this way, communities with high functional dispersion improve the functioning of the ecosystem through more efficient use of resources (Mason et al. 2005). At the local scale (Quequén and Comodoro Rivadavia), the functional traits used showed a high potential to reveal changes in ecosystem functioning and the responses of the benthos to organic matter pollution (sewage outfall presence).

Acknowledgements. This research was funded by the Agencia Nacional de Promoción Científica y Tecnológica (FONCyT-PICT 2446/14; responsible researchers: G.V.G. and M.L.J.). The authors thank Dr. Julio Di Rienzo for helping with the installation of the FDiversity software and the anonymous referees for their contributions that greatly improved the quality of the manuscript. E.N.L., M.A.S.B., and E.H. were supported by a PhD fellowship from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) of Argentina.

LITERATURE CITED

Adami M, Schwindt E, Tablado A, Calcagno J, Labraga JC, Orensanz JM (2018) Intertidal mussel beds from the south-western Atlantic show simple structure and uniform appearance: does environmental harshness explain the community? Mar Biol Res 14:403–419

Akaike H (1973) Information theory and an extension of maximum likelihood principle. In: Petran BN, Csàaki F (eds) Proc 2nd Int Symp Inf Theory. Akadémiai Kiadó, Budapest, p 267–281

Balech E, Ehrlich MD (2008) Esquema biogeográfico del mar argentino. Rev Invest Desarr Pesq 19:45–75

Berke SK, Jablonski D, Krug AZ, Valentine JW (2014) Origination and immigration drive latitudinal gradients in marine functional diversity. PLOS ONE 9:e101494

Blake JA, Kudenov JD (1981) Larval development, larval nutrition and growth for two *Boccardia* species (Polychaeta, Spionidae) from Victoria, Australia. Mar Ecol Prog Ser 6:175–182

Boschi EE, Cousseau MB (2004) La vida entre mareas: vegetales y animales de las costas de Mar del Plata. Publicaciones especiales INIDEP, Mar del Plata

Botta-Dukát Z (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J Veg Sci 16:533–540

Bremner J (2008) Species' traits and ecological functioning in marine conservation and management. J Exp Mar Biol Ecol 366:37–47

Burnham KP, Anderson DR (2002) Model selection and multimodel inference, 2nd edn. Springer-Verlag, New York, NY

Casanoves F, Di Rienzo JA, Pla L (2008) User manual F-Diversity: statistical software for the analysis of functional diversity, 1st edn. www.fdiversity.nucleodiversus.org

Chaudhary C, Saeedi H, Costello MJ (2016) Bimodality of latitudinal gradients in marine species richness. Trends Ecol Evol 31:670–676

Chevene F, Doléadec S, Chessel D (1994) A fuzzy coding approach for the analysis of long-term ecological data. Freshw Biol 31:295–309

Cianciaruso MV, Batalha MA, Gaston KJ, Petchey OL (2009) Including intraspecific variability in functional diversity. Ecology 90:81–89

Cloern JE (2001) Our evolving conceptual model of the coastal eutrophication problem. Mar Ecol Prog Ser 210: 223–253

Cuello G, Llanos EN, Garaffo GV, Jaubet ML (2019) Emisario submarino de Mar del Plata (Argentina): ¿Cómo impactó su construcción en la comunidad bentónica intermareal? Ecol Austral 29:28–40

Di Rienzo JA, Casanoves F, Pla L (2008) FDiversity, version 2008. Cordoba. www.fdiversity.nucleodiversus.org

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646–655

Dobson AJ (2002) An introduction to generalized linear models. Chapman & Hall/CRC, Boca Raton, FL

Dobzhansky T (1950) Evolution in the tropics. Am Sci 38: 209–221

Elías R, Jaubet ML, Llanos EN, Sánchez MA, Rivero MS, Garaffo GV, Sandrini-Neto L (2015) Effect of the invader *Boccardia proboscidea* (Polychaete: Spionidae) on the richness, diversity, and structure of the SW Atlantic epilithic intertidal community. Mar Pollut Bull 91:530–536

Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. Oceanogr Mar Biol Annu Rev 17:193–284

Gagliardini DA, Rivas AL (2004) Environmental characteristics of San Matías Gulf obtained from LANDSAT-TM and ETM+ data. Gayana (Concepc) 68:186–193

Garaffo GV, Jaubet ML, Sánchez MA, Rivero MS, Vallarino EA, Elías R (2012) Sewage induced polychaete reefs in a SW Atlantic shore: rapid response to small scale disturbance. Mar Ecol 33:272–279

Garaffo GV, Jaubet ML, Llanos EN, Saracho Bottero MA, Elías R (2018) Assessing functional diversity of macrobenthic assemblages in sewage-affected intertidal shores. Int Aquat Res 10:333–347

Gibson GD (1997) Variable development in the spionid *Boccardia proboscidea* (Polychaeta) is linked to nurse egg production and larval trophic mode. Invertebr Biol 116: 213–226

Grime JP (1998) Benefits of plant diversity to ecosystems: inmediate filter and founder effects. J Ecol 86:902–910

Gusmao JB, Brauko KM, Eriksson BK, Lana PC (2016) Functional diversity of macrobenthic assemblages decreases in response to sewage discharges. Ecol Indic 66:65–75

Hartman O (1941) Some contributions to the biology and life history of Spionidae from California. Allan Hancock Pac Exped 7:289–324

Hillebrand H, Matthiessen B (2009) Biodiversity in a complex world: consolidation and progress in functional biodiversity research. Ecol Lett 12:1405–1419

Hooper DU, Chapin FS, Ewel JJ, Hector A and others (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35

Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK and others (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486: 105–108

Jaubet ML, Sánchez MA, Rivero MS, Garaffo GV, Vallarino EA, Elías R (2011) Intertidal biogenic reefs built by the polychaete *Boccardia proboscidea* in sewage-impacted areas of Argentina, SW Atlantic. Mar Ecol 32:188–197

Jaubet ML, Garaffo GV, Vallarino EA, Elías R (2015) Invasive polychaete *Boccardia proboscidea* Hartman, 1940 (polychaeta: spionidae) in sewage-impacted areas of the SW Atlantic coasts: morphological and reproductive patterns. Mar Ecol 36:611–622

Jaubet ML, Saracho Bottero MA, Hines E, Elías R, Garaffo GV (2018) *Boccardia proboscidea* (Polychaete: Spionidae) in the SW Atlantic: how far has the invasion spread? Aquat Invasions 13:351–363

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305

Lamanna C, Blonder B, Violle C, Kraft NJB and others (2014) Functional trait space and the latitudinal diversity gradient. Proc Natl Acad Sci USA 111:13745–13750

Llanos EN, Saracho Bottero MA, Jaubet ML, Elías R, Garaffo GV (2020) Spatial-temporal variability of the functional diversity in the intertidal macrobenthic community at sewage-affected shores from Southwestern Atlantic. Mar Pollut Bull 157:111365

López Gappa JJ, Tablado A, Magaldi NH (1990) Influence of sewage pollution on a rocky intertidal community dominated by the mytilid *Brachidontes rodriguezi.* Mar Ecol Prog Ser 63:163–175

López Gappa J, Tablado A, Magaldi NH (1993) Seasonal changes in an intertidal community affected by sewage pollution. Environ Pollut 82:157–165

López Gappa J, Alonso GM, Landoni NA (2006) Biodiversity of benthic Amphipoda (Crustacea: Peracarida) in the Southwest Atlantic between 35° S and 56° S. Zootaxa 1342:1–66

Lutz VA, Boschi EE, Bremec CS, Cousseau MB and others (2003) Perspectives of marine biodiversity studies in Argentina. Gayana (Concepc) 67:371–382

Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111:112–118

Mazón HR (2010) Cambios en las comunidades intermareales y su relación con la contaminación. Aportes para la gestión de efluentes urbanos de la ciudad de Comodoro Rivadavia. PhD thesis, National University of Patagonia San Juan Bosco, Comodoro Rivadavia

Miloslavich P, Cruz-Motta JJ, Hernández A, Herrera C and others (2016) Benthic assemblages in South American intertidal rocky shores: biodiversity, services, and threats. In: Riosmena-Rodríguez (ed) Marine benthos: biology, ecosystem functions and environmental impact. Nova Science Publisher, New York, NY, p 2–56

Mittelbach GG, Schemske DW, Cornell HV, Allen AP and others (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol Lett 10:315–331

Otegui MPB, Brauko KMB, Pagliosa PR (2016) Matching ecological functioning with polychaete morphology: consistency patterns along sedimentary habitats. J Sea Res 114:13–21

Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr Mar Biol Annu Rev 16:229–311

Petch DA (1989) Variation in the spionid polychaete *Boccardia proboscidea* Hartman. PhD thesis, University of Melbourne

Pielou EC (1969) An introduction to mathematical ecology. Wiley-Interscience, New York, NY

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rao CR (1982) Diversity and dissimilarity coefficients: a unified approach. Theor Popul Biol 21:24–43

Ricotta C (2005) A note on functional diversity measures. Basic Appl Ecol 6:479–486

Ricotta C, Moretti M (2011) CWM and Rao's quadratic diversity: a unified framework for functional ecology. Oecologia 167:181–188

Rosenberg R (2001) Marine benthic faunal successional stages and related sedimentary activity. Sci Mar 65: 107–119

Saracho Bottero MA, Jaubet ML, Llanos EN, Becherucci ME, Elías R, Garaffo GV (2020) Spatial-temporal variations of a SW Atlantic macrobenthic community affected by a chronic anthropogenic disturbance. Mar Pollut Bull 156:111189

Schuldt A, Bruelheide H, Durka W, Michalski SG, Purschke O, Assmann T (2014) Tree diversity promotes functional dissimilarity and maintains functional richness despite species loss in predator assemblages. Oecologia 174: 533–543

Shannon CE, Wiener W (1963) The mathematical theory of communication. University Illinois Press, Urbana, IL

Simon CA, Booth AJ (2007) Population structure and growth of polydorid polychaetes that infest the cultured abalone *Haliotis midae.* Afr J Mar Sci 29:499–509

Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80: 1455–1474

Tilman D (2001) Functional diversity. In: Levin SA (ed) Encyclopaedia of biodiversity. Academic Press, San Diego, CA, p 109–120

Valentine JW, Jablonski D (2015) A twofold role for global energy gradients in marine biodiversity trends. J Biogeogr 42:997–1005

Vallarino EA, Elías R (2009) La vida en las costas rocosas. Guía de campo, 1st edn. Dunken, Buenos Aires

Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89: 2290–2301

Wieters EA, McQuaid C, Palomo G, Pappalardo P, Navarrete SA (2012) Biogeographical boundaries, functional group structure and diversity of rocky shore communities along the Argentinean coast. PLOS ONE 7:e49725

Wouters JM, Gusmao JB, Mattos G, Lana P (2018) Polychaete functional diversity in shallow habitats: shelter from the storm. J Sea Res 135:18–30

Editorial responsibility: Pei-Yuan Qian, Kowloon, Hong Kong SAR

Submitted: January 10, 2020; Accepted: July 23, 2020
Proofs received from author(s): August 21, 2020