Spatial Analysis of Benthic Functional Biodiversity in San Jorge Gulf, Argentina

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ABSTRACT. Anthropogenic pressures on coastal and marine ecosystems are increasing. Current development of spatiotemporal models will improve understanding of how changes to biodiversity distribution resulting from such pressures might affect ecosystem functioning. The objective of this study was to characterize the spatial distribution of benthic biodiversity in San Jorge Gulf (Argentina) to provide insight into the relationship between benthic habitats and biodiversity. First, we characterized the spatial heterogeneity of both sediment types and bottom water variables. Then, we described the ecosystem's functional diversity considering trophic interactions and behavioral and morphological characteristics of benthic organisms, and we explored whether benthic environment variables can predict functional diversity distribution. Our results showed that the distribution of assemblages of epifauna functional groups in San Jorge Gulf is mainly related to oxygen availability in bottom water and organic matter in sediments. Habitat suitability maps enable us to predict this distribution, improving our knowledge of biodiversity-ecosystem functioning in the gulf, and providing information for designing sustainable management and conservation strategies for ocean ecosystem services.

INTRODUCTION

Benthic ecosystems are widely affected by multiple anthropogenic stressors that can modify and fragment their habitats (Breitburg et al., 1998; Crain et al., 2008) and strongly impact the composition and abundances of their species (Cardinale et al., 2006; Stachowicz et al., 2007; Hooper et al., 2012; Grabowski et al., 2014). A decrease in biodiversity can negatively affect ecosystem processes linked to productivity, trophic interactions, and biogeochemical cycles (Loreau et al., 2001; Solan et al., 2004; Balvanera et al., 2006; Gamfeldt et al., 2015), and it can determine ecosystem stability and resilience (Hooper et al., 2005; Worm et al., 2006). These impacts may vary depending on the characteristics of the lost species (Cardinale et al., 2006; Harvey et al., 2013), and may be stronger if multiple ecosystem functions are considered together (i.e., multifunctionality; Byrnes et al., 2014). Temporally and spatially explicit models help us to understand the relationship between the

distribution of biodiversity and benthic habitats, in particular how anthropogenic impacts might affect ecosystem functioning (Lecours et al., 2015, Mokany et al. 2016). This understanding can inform long-term ecosystem management and conservation strategies (Copeland et al., 2011; Mokany et al., 2016).

Traditionally, biodiversity has been analyzed from a taxonomic perspective, following a list of observed species. More recently, a functional approach has been used to explore the connections between biodiversity and ecosystem functioning by focusing on the variety of roles played by different organisms (Díaz and Cabido, 2001; Petchey and Gaston, 2006). Functional diversity considers morphological, physiological, and behavioral characteristics related to how species acquire and use resources and modify trophic webs, as well as their preferences for habitats and their impacts on the occurrence and magnitude of disturbances. In benthic ecosystems, functional diversity has usually been linked with feeding and bioturbation strategies, which are considered the most important biotic factors determining ecosystem structures (Mermillod-Blondin et al.,

2005; Norling et al., 2007, Kristensen et al., 2012). Although functional information is still lacking for most benthic species, particularly regarding phenotypic variability and the effects of positive interactions such as facilitation, a variety of functional trait classifications is available to describe the functional diversity of benthic organisms (Pearson, 2001; Bremner et al., 2003; Petchey and Gaston, 2006; Link et al., 2013).

Our study explored the multifunctionality of organisms by considering the combination of their functional traits in order to analyze the ecological roles of functional groups in benthic biodiversity. The main goal of our investigation was to characterize the spatial distribution of benthic biodiversity within San Jorge Gulf, the largest semi-open basin in the southwestern Atlantic Ocean (Miloslavich et al., 2011). Specific objectives were to: (1) describe the spatial distribution of physicochemical characteristics in the benthic environment, (2) classify benthic species regarding their functional traits and identify the presence of assemblages of epifauna and infauna functional groups, (3) evaluate the relationship between environmental variables and benthic assemblages, and (4) build habitat suitability maps for benthic assemblages, that is, determine the probability of the presence of benthic assemblages on the seafloor. We tested the following hypotheses: (1) spatial variations in the benthic environment determine the composition of benthic communities where distribution is correlated with depth, sediment size, and the concentration of organic matter in the sediment; and (2) areas with higher concentrations of organic matter host the most diverse benthic communities.

STUDY SITE

San Jorge Gulf (SJG) lies between Cape Dos Bahías and Cape Tres Puntas along the Atlantic coast of South America and encompasses an approximate area of 39,340 km² (Figure 1; Reta, 1986). SJG circulation depends on inputs of cold,

nutrient-rich water from the Malvinas Current and on a seasonal plume of low-salinity waters from Magellan Strait (Acha et al., 2004; Palma and Matano, 2012). Semidiurnal tides and westerly winds contribute to vertical mixing in the gulf (Palma et al., 2004). In spring and autumn, tidal fronts have been observed close to the gulf's northern and southern extremes. Glembocki et al. (2015) described another seasonal thermohaline front in the southern area of the SJG that originates from a decrease in water depth and the arrival of the plume from Magellan Strait.

Part of the Patagonian Shelf Large Marine Ecosystem (Miloslavich et al., 2011), the SJG is considered one of the Southern Hemisphere's most productive ecosystems (Longhurst, 2007), where a great diversity of species finds food, shelter, and a place for breeding in the SJG (Roux et al., 1995; Yorio, 2009). Anthropogenic

pressures in the SJG include fishing and the presence of coastal cities, tourism, and activities related to the transport of fossil fuels (Commendatore and Esteves, 2007; Góngora et al., 2012; Marinho et al., 2013). Some of Argentina's main fisheries are located in the gulf, for example, those of the Patagonian shrimp *Pleoticus muelleri*, the hake *Merluccius hubbsi*, and the southern king crab *Lithodes santolla*. Different fisheries management strategies have been implemented in the SJG, such as restricting fishing to selected areas (e.g., Mazzaredo area), enforcing maximum catch quotas, and establishing a coastal marine national park (2006). The 2014 Pampa Azul initiative and the 2015 law entitled Productive Innovation in Maritime Argentine Zones (PROMAR) established the SJG as a priority region for research, development of sustainable strategies for human use, and biodiversity protection.
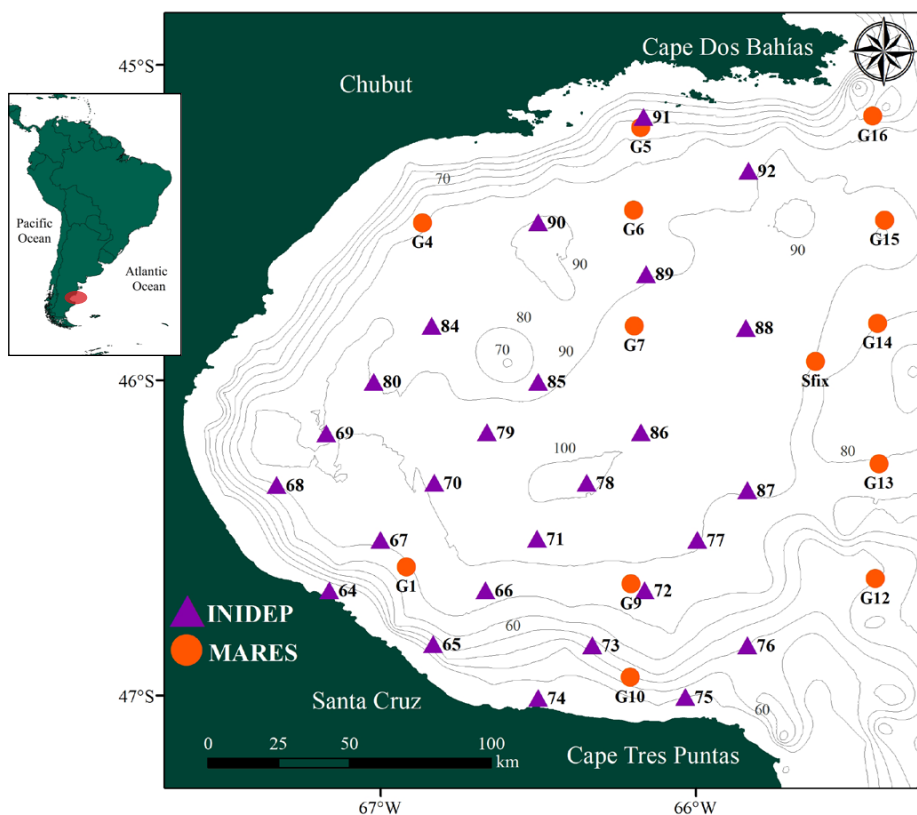
FIGURE 1. Study site in San Jorge Gulf, Argentina, showing sampling stations. Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) data were obtained from the Argentinean National Institute of Fishing, and the MArine ecosystem health of the San Jorge Gulf (MARES) data were acquired from the Programa Multidisciplinario para el Estudio del ecosistema y la geología marina del golfo San Jorge y las costas de las provincias de Chubut y Santa Cruz (PROMESse) Program. *Bathymetry adapted from Carta H-365, Servicio de Hidrografía Naval, Argentina*

DATA ACQUISITION

The environmental and biological data we analyzed were drawn from two main sources. Data from the Instituto Nacional de Investigación y Desarrollo Pesquero (Figure 1, INIDEP stations) were obtained from the Argentinean National Institute of Fishing, and data from the MARine ecosystem health of the San Jorge Gulf: Present status and RESilience (MARES; see this program's stations in Figure 1) were acquired from the Programa Multidisciplinario para el Estudio del ecosistema y la geología marina del golfo San Jorge y las costas de las provincias de Chubut y Santa Cruz (PROMESse, http://coriolis.uqar.ca/). These data included sediment variables such as grain size, total organic matter (TOM), total organic carbon (TOC), and total nitrogen (TN), and bottom water variables including temperature, salinity, percent oxygen saturation, and chlorophyll *a*. Maximal average velocities for bottom current estimated by Vincent Combes and Ricardo Matano of Oregon State University (*pers. comm.*, April 7, 2017) were included in the analyses of the correlation between benthic environments and assemblages. Biological data comprised compositions and abundances of epifaunal species from INIDEP and of infaunal species from MARES. Functional diversity analyses were performed separately for epifauna and infauna data, given that neither the stations nor the sampling method coincided. See the online supplementary materials for a full description of sampling methods and data acquired.

RESULTS

Benthic Environment

In order to create a general picture of the SJG benthic environment, the spatial distribution of sediment types and bottom water variables were plotted using INIDEP and MARES data. The Ordinary Spherical Kriging method of interpolation was chosen to build raster maps with the Spatial Analyst extension on ArcMap. These maps provided a continuous distribution for sediment variables such as grain size, TOM, TOC, TN, and for bottom water variables such as temperature, salinity, percent oxygen saturation, and chlorophyll *a*.

The spatial distribution of sediment environmental variables followed the spatial variation of grain size (Figure 2a). Coarse sediments (with Φ [Phi] values around 2) predominated in the southeast and northern extremes of the gulf close to capes. In contrast, fine sediments (with Φ values around 6) were present in the central region. TOM, TOC, and TN exhibited higher proportions in the fine sediments of the central region while the southeast and northern areas close to the capes showed lower values (Figure 2b–d). Low bottom-water temperatures in the central region contrasted with increased temperatures toward the southern and northern areas of the gulf (Figure 2e), while salinity followed the opposite pattern (Figure 2f). Bottom water in the southeast extreme of the gulf exhibited higher temperature and lower salinity. The mouth of the SJG also had lower salinity values. Chlorophyll *a* concentrations were highest close to the southeast extreme (Figure 2g). Oxygen concentrations were highest close to the southeast area and decreased with depth (Figure 2h).
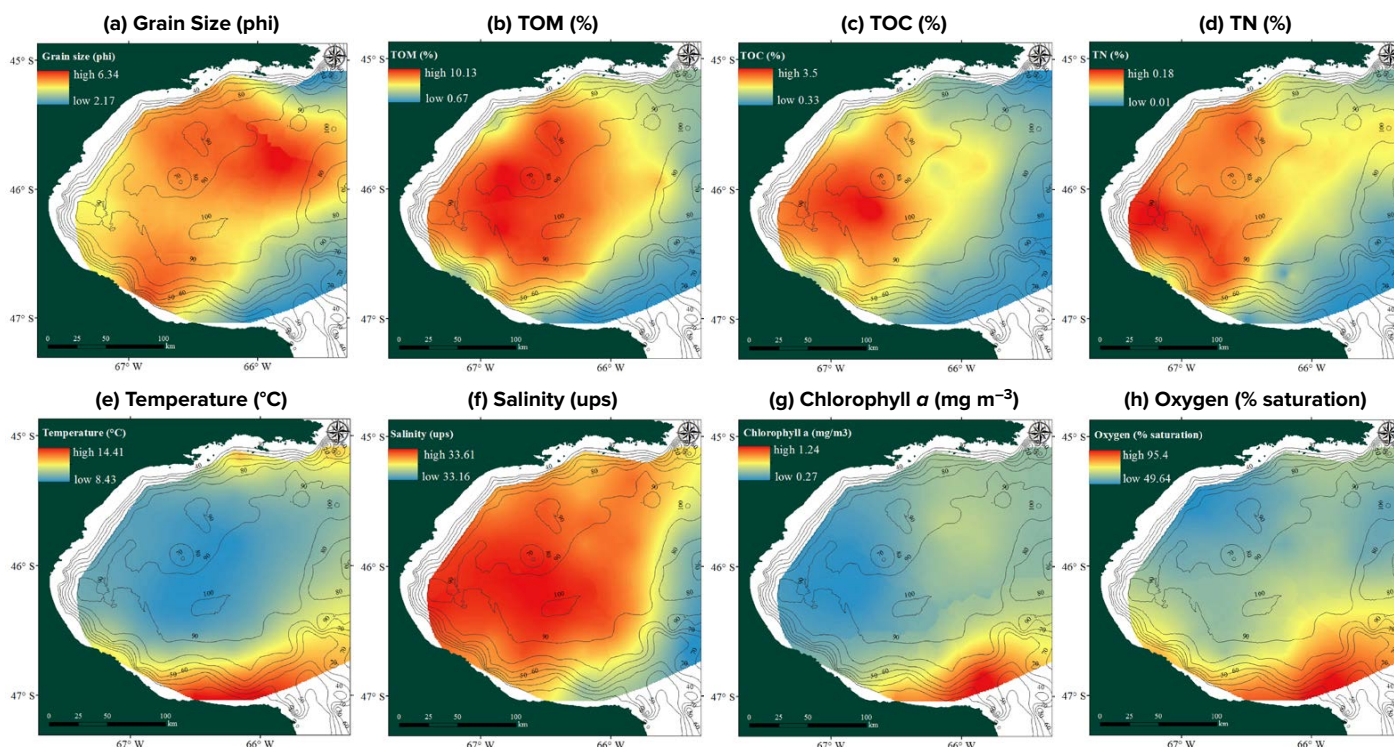

FIGURE 2. Spatial distribution variables in sediment, (a) grain size, (b) total organic matter (TOM), (c) total organic carbon (TOC), and (d) total nitrogen (TN), and in bottom water, (e) temperature, (f) salinity, (g) chlorophyll *a*, and (h) oxygen availability. Bathymetry is indicated by isolines.

Benthic Functional Diversity

Taxa identified from INIDEP and MARES data were classified based on functional traits, including feeding strategy, size, mobility, adult life habits, and bioturbation (Pearson, 2001; Bremner et al., 2003; Link et al., 2013; see Table 1). Taxa were allowed more than one trait in the cases of feeding strategy, adult life habits, and bioturbation. Adult stage functional traits were classified with the best resources available. When species information was not available, traits were classified according to the taxa's family (e.g., Maldanidae), order (e.g., Echiurida), class (e.g., Holothuroidea, Hydrozoa, Priapulida), or phylum (e.g., Bryozoa, Nemertea) to include all species in the functional group analyses. The combination of all levels of traits resulted in designation of a functional group, following Link et al. (2013). Considering all combinations of feeding strategy, size, mobility, adult life habits, and bioturbation, 38 epifauna functional groups and 21 infauna functional groups were recognized in the SJG (see Table S1 for the taxa classified by functional traits).

To identify the presence of assemblages, we pursued the following steps.

First, the Bray-Curtis similarity measure was estimated on the functional group abundance data, representing the number of functional groups identified by station. This similarity matrix was explored by the group average cluster method with the similarity profile analysis (SIMPROF) to identify assemblages, with a significance level of 5% (Clarke and Gorley, 2006). The cluster method considers composition and abundance of functional groups in every station when identifying assemblages, following the approach of Moritz et al. (2013). A similarity percentage (SIMPER) analysis was employed to describe what functional groups contributed to dissimilarity between assemblages and what functional groups explained similarity within assemblages. Functional group richness by station was represented by alpha diversity (α). The average of alpha diversity by assemblage or group of stations represented alpha mean diversity ($\alpha_{assemblage}$). The total number of functional groups at the assemblage scale was the gamma assemblage diversity ($\gamma_{assemblage}$). Data were analyzed using the PRIMER 6 statistical package with PERMANOVA+.

Cluster and SIMPROF analyses of epifauna functional data identified four assemblages (Figure 3a; see Table S2 for composition of functional groups by assemblage). **Assemblage A** was dominated by large and mobile predators with crawl or swimming strategies (e.g., *Austropandalus*

TABLE 1. List of traits used for functional classification of taxa. Functional groups are defined by combinations of traits, for example, opportunist, x-large, mobile, crawl, surface dweller = OXMCS.

| Functional Traits	Level
Feeding Strategies	• Deposit subsurface feeder (S) • Deposit surface feeder (D) • Deposit subsurface and surface feeder (A) • Filter/suspension feeder (F) • Opportunist (O) • Predator (P)
Size	• 0.5 mm < Little (S) < 5 mm • 5 mm < Medium (M) < 10 mm • 10 mm < Large (L) < 50 mm • x-Large (X) > 50 mm
Mobility	• Sessile (S) • Hemimobile (H) • Mobile (M)
Adult Life Habits	• Burrow (B) • Crawl (C) • Sessile (S) • Swim (W)
Bioturbation	• Active burrower (diffusive) (B) • Gallery burrower (G) • Surface dweller (S) • Tube burrower (T)
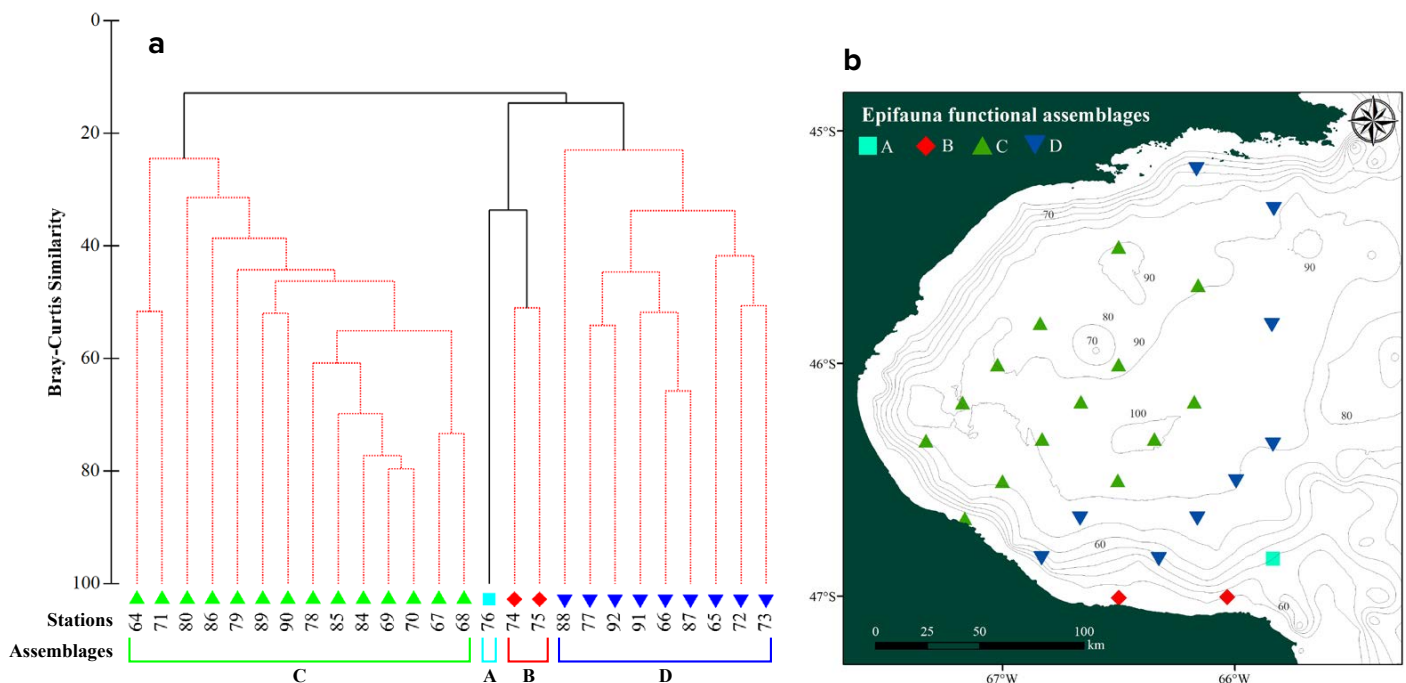
FIGURE 3. Functional assemblages of epifauna. (a) Functional cluster based on Bray-Curtis similarity matrix using functional group abundances of epifauna by station. (b) Locations of epifauna assemblages in San Jorge Gulf.

grayi, *Diplasterias brandti*, *Alpheus puapeba*), large and mobile opportunists (e.g., *Lithodes santolla*, *Pseudechinus magellanicus*, *Arbacia dufresnii*), and large sessile filter feeders (e.g., *Molgula* sp.; see Table 2). This assemblage was identified at only one station, in the southeast area (Figure 3b).

Assemblage B was characterized by high abundances of large sessile filter feeders (e.g., *Mytilus edulis*, *Renilla* sp.), large and mobile predators with crawl or swimming strategies (e.g., *D. brandti*, Nemerteans, *A. grayi*, *Carolesia blakei*), and small and semimobile deposit surface/subsurface feeders with burrowing strategies (e.g., Echiurida; Table 2). The SIMPER analysis indicated that large and sessile filter feeders (FXSSS) and

small and semimobile deposit surface/subsurface feeders with burrowing strategies (ASHBB) contributed 100% to the average similarity of 50.97% (SIMPER, Table S3) of this assemblage, which was found at the southern coast close to Cape Tres Puntas (Figure 3b).

Assemblage C was dominated by large mobile opportunists with crawl and swimming strategies (e.g., *Pseudechinus magellanicus*, *Munida gregaria*, *Ophiura* sp.), large sessile deposit subsurface feeders with tube burrower strategies (e.g., Pectinariidae), and large mobile predators with swimming strategies (e.g., *A. grayi*). However, the variation in this assemblage between stations was also high (Table 2). The SIMPER analysis indicated that these functional groups

contributed 84.58% to the average similarity of 41.52% (Table S3). Assemblage C was present in the central area and close to the coasts in the west (Figure 3b).

Assemblage D comprised the highest number of functional groups (Table 2). It was characterized by large mobile deposit subsurface and filter burrowers (e.g., *Neilonella sulculata*), large sessile deposit subsurface and filter burrowers (e.g., *Ennucula puelcha*, Pectinariidae), large mobile opportunist crawlers (e.g., *Ophiura* sp.), and large sessile filter feeders (e.g., *Molgula* sp., *Renilla* sp.). Diversity indices showed Assemblage D to be more diverse in terms of functional group composition (Table 2). However, the variation between stations for this assemblage was also high. The SIMPER analysis indicated that large mobile deposit subsurface and filter burrowers (S.FLMBB), large sessile deposit subsurface and filter burrowers (S.FLSBB), and large sessile filter feeders (FXSSS) contributed 69.37% of the average similarity of 36.51% (Table S3). Asemblage D was found in the northern and southern coastal areas and close to the mouth of the SJG (Figure 3b).

Infauna groups with higher abundances were large deposit subsurface and filter burrowers (e.g., *N. sulculata*, *E. puelcha*), medium semimobile deposit subsurface tube burrowers (e.g., Maldanidae), large mobile deposit surface gallery burrowers (e.g., *Notiax brachyophthalma*), and large sessile filter feeders (e.g., *Stylatula* sp). Cluster and SIMPROF analyses of infauna data identified no significant differences between stations that would allow determination of the presence of assemblages (Figure S1).

Relation Between Environmental Variables and Assemblages of Benthic Functional Groups

To determine which set of environmental variables best explained the distribution of assemblages of epifauna functional groups, a distance-based linear model permutation test (DistLM) was performed. The resemblance matrix was

TABLE 2. Functional diversity indices for assemblages of the five dominant epifauna functional groups.

Assemblage A Diversity Indices	
$\alpha_{assemblage}$: 13	$\gamma_{assemblage}$: 13

Dominant functional groups:
- PLMWS: predator, large, mobile, swim, surface dweller
- PXMCS: predator, x-large, mobile, crawl, surface dweller
- PLMCS: predator, large, mobile, crawl, surface dweller
- OXMCS: opportunist, x-large, mobile, crawl, surface dweller
- FXSSS: filter/suspension feeder, x-large, sessile, sessile, surface dweller

Assemblage B Diversity Indices	
$\alpha_{assemblage}$: 8	$\gamma_{assemblage}$: 14

Dominant functional groups:
- FXSSS: filter/suspension feeder, x-large, sessile, sessile, surface dweller
- PXMCS: predator, x-large, mobile, crawl, surface dweller
- PLMWS: predator, large, mobile, swim, surface dweller
- ASHBB: deposit surface and subsurface feeder, little, semimobile, burrow, active burrower
- PLMCS: predator, large, mobile, crawl, surface dweller

Assemblage C Diversity Indices	
$\alpha_{assemblage}$: 8.5	$\gamma_{assemblage}$: 23

Dominant functional groups:
- OXMCS: opportunist, x-large, mobile, crawl, surface dweller
- OXMC.WS: opportunist, x-large, mobile, crawl and swim, surface dweller
- SLSBT: deposit subsurface feeder, large, sessile, burrow, tube burrow
- OLMCS: opportunist, large, mobile, crawl, surface dweller
- PLMWS: predator, large, mobile, swim, surface dweller

Assemblage D Diversity Indices	
$\alpha_{assemblage}$: 13	$\gamma_{assemblage}$: 30

Dominant functional groups:
- S.FLMBB: deposit subsurface and filter/suspension feeder, large, mobile, burrow, active burrower
- OLMCS: opportunist, large, mobile, crawl, surface dweller
- S.FLSBB: deposit subsurface and filter/suspension feeder, large, sessile, burrow, active burrower
- FXSSS: filter/suspension feeder, x-large, sessile, sessile, surface dweller
- SLSBT: deposit subsurface feeder, large, sessile, burrow, tube burrower

calculated based on Bray-Curtis dissimilarity. Benthic environmental data were previously normalized. Maximal average velocities for bottom currents during January were included for this analysis. The best-fit model was estimated considering the AICc (Akaike's information criterion corrected) selection criterion and a minimum of two variables with PRIMER 6. Results were visualized with a distance-based redundancy analysis (dbRDA).

The distance-based linear model showed organic matter concentration in sediments and oxygen availability in bottom water to be the environmental variables that best explained the distribution of assemblages of epifauna functional groups (Figure 4). Assemblages A and B correlated with high concentrations of oxygen and low TOM in sediments. Assemblage C was associated with high concentrations of TOM and low oxygen availability. Assemblage D correlated with low concentrations of TOM and oxygen availability.

Habitat Suitability for Assemblages of Functional Groups

Habitat suitability for assemblages of epifauna functional groups was analyzed at gulf scale, following the approach of Moritz et al. (2013). First, a generalized linear model (GLM) was applied to relate the presence/absence of a given assemblage with the local environmental variables at our stations. Environmental variables from the best model identified in the DistLM and dbRDA were used as predictors. Considering the results, a second set of GLMs was implemented using only significant explanatory variables. The GLMs were performed in the statistical package RStudio, assuming a binomial distribution (presence/absence of assemblages) with a logit-link function. To build continuous raster maps describing the probability of the presence of assemblages, the assemblage-specific estimates were included in the inverse logit function in the Raster Calculator (Spatial Analyst tools, ArcMap) to relate

the model to the distribution of environmental variables at gulf scale. Like the DistLM routine, the GLM models highlighted that Assemblages C and D were correlated with TOM and TOM and oxygen, respectively (Table 3). However, it was not possible to implement the GLM model for Assemblages A and B because of the low number of stations in their area.

The probability of the presence of Assemblages C and D was projected in the habitat suitability maps (Figure 5). Our results show high probabilities for the presence of Assemblage C, characterized by opportunist crawlers and deposit subsurface burrowers, where organic matter concentrations in sediments are high, particularly in the deeper, central zone of the gulf. In contrast, our model predicted high probabilities for Assemblage D, characterized by deposit subsurface feeders, filter burrowers, and sessile feeders in the north, close to the mouth, and along the southern coastal area, associated with low oxygen availability in bottom water and low organic matter concentrations in sediment.
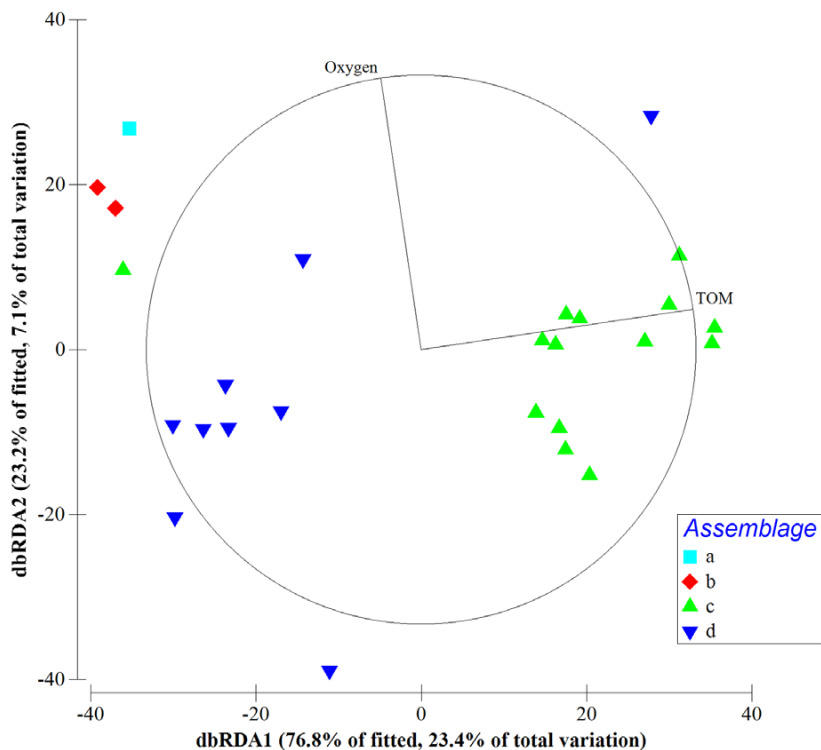
DISCUSSION

Our results show spatial heterogeneity in environmental conditions for the benthic communities, with conditions in the central area distinct from the southern cape, and some areas in the mouth of the

FIGURE 4. Distance-based redundancy analysis (dbRDA) plot of the distance-based linear model permutation test (DistLM) based on the best environmental variables fitted to the variation in assemblages of epifauna functional groups (Best-fit model with 9,999 permutations, AICc = 205.3, R² = 0.305). Vectors indicate direction of the environmental variable in the ordination plot.

TABLE 3. Results for the second set of generalized linear models predicting the probability of the presence of Assemblages C and D of epifaunal functional groups in San Jorge Gulf.

Assemblage C of Epifauna Functional Group				
	Estimate	**Std. Error**	**z Value**	**p**
Intercept	−5.2791	2.0527	−2.572	0.01012*
TOM	0.7872	0.2721	2.893	0.0038**

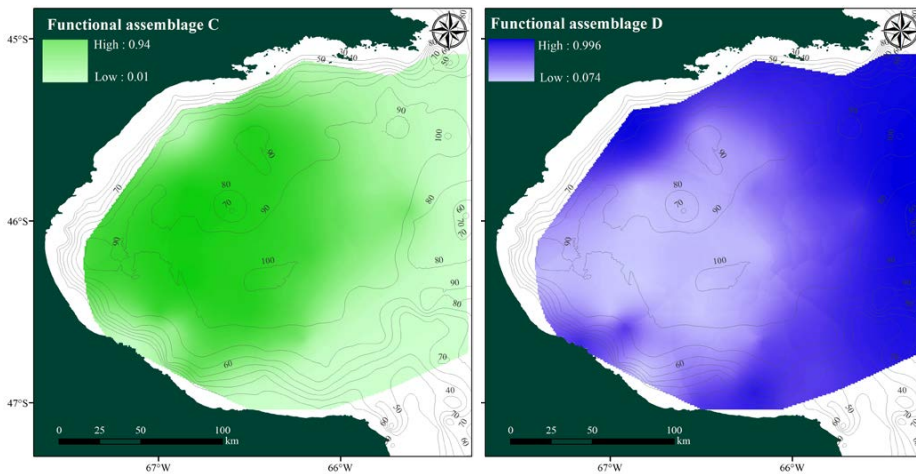| Assemblage D of Epifauna Functional Group				
	Estimate	**Std. Error**	**z Value**	**p**
Intercept	15.77791	7.12044	2.216	0.0267*
TOM	−0.94591	0.38657	−2.447	0.0144*
Oxygen	−0.14556	0.06777	−2.148	0.0317*

Significant codes: * = 0.01, ** = 0.001.

FIGURE 5. Habitat suitability maps representing the probability of the presence of epifauna functional Assemblages C and D in San Jorge Gulf.

gulf and near the coast showing intermediate characteristics. We originally hypothesized that depth, sediment size, and TOM would be the most important environmental variables for explaining functional diversity in the SJG. However, we found that organic matter concentration in sediments and availability of oxygen in bottom waters to be the most important variables for explaining the distribution of assemblages of epifauna functional groups. Future studies should focus on collecting finer-scale data on seafloor topography because it is considered a structuring factor for benthic and pelagic biodiversity and invertebrate growth in coastal ecosystems (Archambault et al., 1999a, 1999b; Brown et al., 2011; Copeland et al., 2011; Carvalho et al., 2017).

The spatial heterogeneity in the distribution of organic matter might be associated with the seasonal variation in productivity and circulation dynamics described for the SJG (Akselman, 1996; Fernández et al., 2003, 2005), as central area environmental conditions promote the deposition of organic matter. Additionally, discarded bycatch of low commercial value species in SJG trawling fisheries could have an impact on the functioning of benthic assemblages by increasing the amount of organic material on the seabed (Varisco and Vinuesa, 2007; Góngora et al., 2012). The accumulation of organic

compounds initially favors opportunistic species and deposit subsurface feeders, which are capable of ingesting the available organic matter. Moreover, the high consumption and degradation of organic matter explain the low availability of oxygen observed in the central area of the SJG. Our results show that a major area of the gulf is occupied by benthic assemblages dominated by organisms that are highly dependent on the recycling of organic matter, for example, *Munida gregaria* (Varisco and Vinuesa, 2007).

The area close to Cape Tres Puntas was characterized by coarse sediments with low concentrations of organic matter and bottom water exhibiting high temperatures, oxygen availability, and chlorophyll *a* concentrations. This might be associated with the presence of fronts in the south where the primary productivity was high (Glembocki et al., 2015; Retana and Lewis, 2017). The abundance of filter-feeding species in assemblages close to Cape Tres Puntas suggests a more direct dependence on primary productivity.

Regarding infauna, stations exhibited great variability in functional group composition, and no spatial patterns were identified. The lack of structure could be related to the low number of stations sampled (13) in a highly variable environment. Data from more stations within the same region would improve descriptions of SJG infauna, and would enable

assessment of whether the functional diversity of infauna is similar over the whole gulf or whether spatial patterns are present. In addition, further studies are required to improve our understanding of these species' functional traits. The combination of our data with data to be collected by future Pampa Azul Programme (Argentina) missions should facilitate description of the composition and structure of these organisms.

Functional Biodiversity Distribution Models

Habitat suitability maps permit determination of zones of particular interest for conservation or identification of indicator species within assemblages for monitoring changes in the ecosystem (Valavanis et al., 2008; Kovalenko et al., 2012; Moritz et al., 2013). In particular, our results provide a more detailed picture of the distribution of functional diversity in relation to spatial variation in the SJG benthic ecosystem. This model can be used to design conservation and management strategies for the SJG and to predict climate change impacts or anthropogenic pressures on habitats and the area's biodiversity (Poloczanska et al., 2008; Maxwell et al., 2009). Further studies may focus on using biogeochemical processes to describe temporal variation of assemblages of epifauna functional groups in an ecosystem, for example, by measuring the rates of degradation of organic matter, oxygen consumption, and biomass production, or the consumption of resources (following Link et al., 2013). Moreover, Robinson et al. (2011) proposed that biodiversity distribution models should include ecological characteristics, such as dispersal, species interactions, ontogenetic shifts, and aggregations of individuals. Model predictions might be improved by integrating habitat data across multiple spatial and temporal scales, for example, including seasonal variations for the SJG ecosystem. Accounting for these factors will result in more robust models for SJG benthic functional biodiversity.

Although the classification of functional traits might be improved in the future with more local information, this was the first study to classify and analyze benthic epifauna and infauna biodiversity in the SJG considering functional traits. Even though a functional traits approach has limitations because the information available is usually insufficient to classify taxa and accurately represent species' functional traits, further SJG studies could focus on improving such classification by using complementary methods to calculate functional diversity, for example, by integrating observational and experimental studies (Hector et al., 2007). Recently, biodiversity-ecosystem function studies have manipulated species richness to deduce changes in functional diversity and in ecosystem processes (Mokany et al., 2016). These studies could consider different trophic levels to determine the effects of trophic cascades in resource utilization dynamics and the relative importance of top-down and bottom-up controls.

SUMMARY AND CONCLUSIONS

In this paper we integrated new and previous data to describe benthic functional diversity in San Jorge Gulf. This is the first study to describe the spatial variation of benthic assemblage distribution in the SJG while considering functional diversity. Our benthic functional biodiversity distribution model identified spatial patterns in benthic assemblage distribution that are highly associated with benthic heterogeneity. We demonstrated that the presence of assemblages of epifauna functional groups is strongly correlated with organic matter concentrations in sediments and oxygen availability in bottom water. Among the environmental variables, bottom current velocities were included in biodiversity analysis for the first time in this coastal ecosystem. Our results reveal that most of the SJG is dominated by a benthic assemblage that depends on organic matter recycling, while assemblage composition in the area close to Cape Tres Puntas reveals a more

direct dependence on primary productivity. Habitat suitability maps representing functional diversity increase understanding of ecosystem functioning and how changes in biodiversity might affect it. The preservation of ecosystem functioning could be incorporated into biodiversity and habitat conservation efforts to sustainably manage the services provided by the San Jorge Gulf ecosystem. 🔁

REFERENCES
Acha, E.M., H.W. Mianzan, R.A. Guerrero, M. Favero, and J. Bava. 2004. Marine fronts at the continental shelves of austral South America: Physical and ecological processes. *Journal of Marine Systems* 44:83–105, https://doi.org/10.1016/j.jmarsys.2003.09.005.

Akselman, R. 1996. *Estudios ecológicos en el Golfo San Jorge y adyacencias (Atlántico sudoccidental). Distribución, abundancia y variación estacional del fitoplancton en relación a factores físico-químicos y la dinámica hidrológica*. PhD thesis, Universidad de Buenos Aires, Buenos Aires, Argentina.

Archambault, P., and E. Bourget. 1999a. Influence of shoreline configuration on spatial variation of meroplanktonic larvae, recruitment and diversity of benthic subtidal communities. *Journal of Experimental Marine Biology and Ecology* 241:309–333, https://doi.org/10.1016/S0022-0981(99)00082-9.

Archambault, P., E. Bourget, and C.W. McKindsey. 1999b. Large-scale shoreline configuration influences phytoplankton concentration and mussel growth. *Estuarine Coastal and Shelf Science* 49:193–208, https://doi.org/10.1006/ecss.1999.0481.

Balvanera, P., A.B. Pfisterer, N. Buchmann, J.S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9:1,146–1,156, https://doi.org/10.1111/j.1461-0248.2006.00963.x.

Breitburg, D.L., J.W. Baxter, C.A. Hatfield, R.W. Howarth, C.G. Jones, G.M. Lovett, and C. Wigand. 1998. Understanding effects of multiple stressors: Ideas and challenges. Pp. 416–431 in *Successes, Limitations, and Frontiers in Ecosystem Science*. M.L. Pace and P.M. Groffman, eds, Springer, New York.

Bremner, J., S.I. Rogers, and C.L.J. Frid. 2003. Assessing functional diversity in marine benthic ecosystems: A comparison of approaches. *Marine Ecology Progress Series* 254:11–25, https://doi.org/10.3354/meps254011.

Brown, C.J., S.J. Smith, P. Lawton, and J.T. Anderson. 2011. Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuaries, Coastal and Shelf Sciences* 92:502–520, https://doi.org/10.1016/j.ecss.2011.02.007.

Buchanan, J.B. 1984. Sediment analysis. Pp. 41–64 in *Methods for the Study of Marine Benthos*. N.A. Holme and A.D. McIntyre, eds, Blackwell Scientific Publications.

Byrnes, J.E.K., L. Gamfeldt, F. Isbell, J.S. Lefcheck, J.N. Griffin, A. Hector, B.J. Cardinale, D.U. Hooper, L.E. Dee, and J.E. Duffy. 2014. Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods in Ecology and Evolution* 5:111–124, https://doi.org/10.1111/2041-210X.12143.

Cardinale, B.J., D.S. Srivastava, J.E. Duffy, J.P. Wright, A.L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443(7114):989, https://doi.org/10.1038/nature05202.

Carvalho, L.R.S., M. Loiola, and F. Barros. 2017. Manipulating habitat complexity to understand its influence on benthic macrofauna. *Journal of Experimental Marine Biology and Ecology* 489:48–57, https://doi.org/10.1016/j.jembe.2017.01.014.

Clarke, K.R., and R.N. Gorley. 2006. *PRIMER v6: User Manual/Tutorial*. PRIMER-E Ltd, Plymouth, UK, 192 pp.

Commendatore, M.G., and J.L. Esteves. 2007. An assessment of oil pollution in the coastal zone of Patagonia, Argentina. *Environmental Management* 40(5):814–821, https://doi.org/10.1007/s00267-005-0221-3.

Copeland, A., E. Edinger, R. Devillers, T. Bell, P. LeBlanc, and J. Wroblewski. 2011. Marine habitat mapping in support of Marine Protected Area management in a subarctic fjord: Gilbert Bay, Labrador, Canada. *Journal of Coastal Conservation* 17(2):225–237, https://doi.org/10.1007/s11852-011-0172-1.

Crain, C.M., K. Kroeker, and B.S. Halpern. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters* 11(12):1,304–1,315, https://doi.org/10.1111/j.1461-0248.2008.01253.x.

Díaz, S., and M. Cabido. 2001. Vive la difference: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16(11):646–655, https://doi.org/10.1016/S0169-5347(01)02283-2.

Fernández, M., J.I. Carreto, J. Mora, and A. Roux. 2005. Physico-chemical characterization of the benthic environment of the Golfo San Jorge, Argentina. *Journal of the Marine Biological Association of the United Kingdom* 85:1,317–1,328, https://doi.org/10.1017/S002531540501249X.

Fernández, M., A. Roux, E. Fernández, J. Caló, A. Marcos, and H. Aldacur. 2003. Grain-size analysis of surficial sediments from Golfo San Jorge, Argentina. *Journal of the Marine Biological Association of the United Kingdom* 83:1,193–1,197, https://doi.org/10.1017/S0025315403008488.

Gamfeldt, L., J.S. Lefcheck, J.E.K. Byrnes, B.J. Cardinale, J.E. Duffy, and J.N. Griffin. 2015. Marine biodiversity and ecosystem functioning: What's known and what's next? *Oikos* 124:252–265, https://doi.org/10.1111/oik.01549.

Glembocki, N.G., G.N. Williams, M.E. Góngora, D.A. Gagliardini, and J.M. Orensanz (Lobo). 2015. Synoptic oceanography of San Jorge Gulf (Argentina): A template for Patagonian red shrimp (*Pleoticus muelleri*) spatial dynamics. *Journal of Sea Research* 95:22–35, https://doi.org/10.1016/j.seares.2014.10.011.

Góngora, M.E., D. González-Zevallos, A. Pettovello, and L. Mendía. 2012. Characterization of the main fisheries in San Jorge Gulf, Patagonia, Argentina. *Latin American Journal of Aquatic Research* 40(1):1–11, https://doi.org/10.3856/vol40-issue1-fulltext-1.

Grabowski, J.H., M. Bachman, C. Demarest, S. Eayrs, B.P. Harris, V. Malkoski, D. Packer, and D. Stevenson. 2014. Assessing the vulnerability of marine benthos to fishing gear impacts. *Reviews in Fisheries Science & Aquaculture* 22(2):142–155, https://doi.org/10.1080/10641262.2013.846292.

Harvey, E., A. Séguin, C. Nozais, P. Archambault, and D. Gravel. 2013. Identity effects dominate the impacts of multiple species extinctions on the functioning of complex food webs. *Ecology* 94:169–179, https://doi.org/10.1890/12-0414.1.

Hector, A., J. Joshi, M. Scherer-Lorenzen, B. Schmid, E.M. Spehn, L. Wacker, M. Weilenmann, E. Bazeley-White, C. Beierkuhnlein, M.C. Caldeira, and others. 2007. Biodiversity and ecosystem

functioning: Reconciling the results of experimental and observational studies. *Functional Ecology* 21(5):998–1,002, https://doi.org/10.1111/j.1365-2435.2007.01308.x.

Hooper, D.U., E.C. Adair, B.J. Cardinale, J.E.K. Byrnes, B.A. Hungate, K.L. Matulich, A. Gonzalez, J.E. Duffy, L. Gamfeldt, and M.I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486(7401):105–108, https://doi.org/10.1038/nature11118.

Hooper, D.U., F.S. Chapin, J.J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J.H. Lawton, D.M. Lodge, M. Loreau, S. Naeem, and others. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75(1):3–35, https://doi.org/10.1890/04-0922.

Kovalenko, K.E., S.M. Thomaz, and D.M. Warfe. 2012. Habitat complexity: Approaches and future directions. *Hydrobiologia* 685(1):1–17, https://doi.org/10.1007/s10750-011-0974-z.

Kristensen, E., G. Penha-Lopes, M. Delefosse, T. Valdemarsen, C.O. Quintana, and G.T. Banta. 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series* 446:285–302, https://doi.org/10.3354/meps09506.

Lecours, V., R. Devillers, D.C. Schneider, V.L. Lucieer, C.J. Brown, and E.N. Edinger 2015. Spatial scale and geographic context in benthic habitat mapping: Review and future directions. *Marine Ecology Progress Series* 535:259–284, https://doi.org/10.3354/meps11378.

Link, H., D. Piepenburg, and P. Archambault. 2013. Are hotspots always hotspots? The relationship between diversity, resource and ecosystem functions in the Arctic. *PLoS One* 8(9):e74077, https://doi.org/10.1371/journal.pone.0074077.

Longhurst, A.R. 2007. *Ecological Geography of the Sea*, 2nd ed. Academic Press, 560 pp., https://doi.org/10.1016/B978-0-12-455521-1.X5000-1.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J.P. Grime, A. Hector, D.U. Hooper, M.A. Huston, D. Raffaelli, B. Schmid, and others. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294:804–808, https://doi.org/10.1126/science.1064088.

Marinho, C.H., M.N. Gil, and J.L. Esteves. 2013. Distribution and origin of trace metals in sediments of a marine park (Northern San Jorge Gulf) from Argentina. *Marine Pollution Bulletin* 72(1):260–263, https://doi.org/10.1016/j.marpolbul.2013.04.019.

Maxwell, D.L., V. Stelzenmuller, P.D. Eastwood, and S.I. Rogers. 2009. Modelling the spatial distribution of plaice (*Pleuronectes platessa*), sole (*Solea solea*) and thornback ray (*Raja clavata*) in UK waters for marine management and planning. *Journal of Sea Research* 61:258–267, https://doi.org/10.1016/j.seares.2008.11.008.

Mermillod-Blondin, F., F. François-Carcaillet, and R. Rosenberg. 2005. Biodiversity of benthic invertebrates and organic matter processing in shallow marine sediments: An experimental study. *Journal of Experimental Marine Biology and Ecology* 315(2):187–209, https://doi.org/10.1016/j.jembe.2004.09.013.

Miloslavich, P., E. Klein, J.M. Diaz, C.E. Hernandez, G. Bigatti, L. Campos, F. Artigas, J. Castillo, P.E. Penchaszadeh, P.E. Neill, and others. 2011. Marine biodiversity in the Atlantic and Pacific coasts of South America: Knowledge and gaps. *PLoS One* 6:e14631, https://doi.org/10.1371/journal.pone.0014631.

Mokany, K., S. Ferrier, S.R. Connolly, P.K. Dunstan, E.A. Fulton, M.B. Harfoot, T.D. Harwood, A.J. Richardson, S.H. Roxburgh, J.P.W. Scharlemann, and others. 2016. Integrating modelling of biodiversity composition and ecosystem function. *Oikos* 125(1):10–19, https://doi.org/10.1111/oik.02792.

Moritz, C., M. Lévesque, D. Gravel, S. Vaz, D. Archambault, and P. Archambault. 2013. Modelling spatial distribution of epibenthic communities in the Gulf of St. Lawrence (Canada). *Journal of Sea Research* 78:75–84, https://doi.org/10.1016/j.seares.2012.10.009.

Norling, K., R. Rosenberg, S. Hulth, A. Grémare, and E. Bonsdorff. 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Marine Ecology Progress Series* 332:11–23, https://doi.org/10.3354/meps332011.

Palma, E.D., and R.P. Matano. 2012. A numerical study of the Magellan Plume. *Journal of Geophysical Research* 117, C05041, https://doi.org/10.1029/2011JC007750.

Palma, E.D., R.P. Matano, and A.R. Piola. 2004. A numerical study of the southwestern Atlantic shelf circulation: Barotropic response to tidal and wind forcing. *Journal of Geophysical Research* 109, C08014, https://doi.org/10.1029/2004JC002315.

Pearson, T. 2001. Functional group ecology in soft-sediment marine benthos: The role of bioturbation. *Oceanography and Marine Biology* 39:233–267.

Petchey, O.L., and K.J. Gaston. 2006. Functional diversity: Back to basics and looking forward. *Ecology Letters* 9:741–758, https://doi.org/10.1111/j.1461-0248.2006.00924.x.

Poloczanska, E.S., S.J. Hawkins, A.J. Southward, and M.T. Burrows. 2008. Modeling the response of populations of competing species to climate change. *Ecology* 89:3,138–3,149, https://doi.org/10.1890/07-1169.1.

Reta, R. 1986. *Aspectos Oceanográficos y Biológicos Pesqueros del Golfo San Jorge*. Seminario de Grado de Licenciatura en Oceanografía. Universidad Nacional del Sur, Bahía Blanca, Argentina, 135 pp.

Retana, M.V., and M.N. Lewis. 2017. Suitable habitat for marine mammals during austral summer in San Jorge Gulf, Argentina. *Revista de Biología Marina y Oceanografía* 52(2):275–288, https://doi.org/10.4067/S0718-19572017000200007.

Robinson, L.M., J. Elith, A.J. Hobday, R.G. Pearson, B.E. Kendall, H.P. Possingham, and A.J. Richardson. 2011. Pushing the limits in marine species distribution modelling: Lessons from the land present challenges and opportunities. *Global Ecology and Biogeography* 20:789–802, https://doi.org/10.1111/j.1466-8238.2010.00636.x.

Roux, A.M., M. Fernandez, and C.S. Bremec. 1995. Preliminary survey of the benthic communities of the Patagonian shrimp fishing grounds in San Jorge Gulf, Argentina. *Ciencias Marinas* 21:295–310.

Sargent, J.R., C.C.E. Hopkins, J.V. Seiring, and A. Youngson. 1983. Partial characterization of organic material in surface sediments from Balsfjorden, northern Norway, in relation to its origin and nutritional value for sediment-ingesting animals. *Marine Biology* 76:87–94, https://doi.org/10.1007/BF00393059.

Solan, M., B.J. Cardinale, A.L. Downing, K.A.M. Engelhardt, J.L. Ruesink, and D.S. Srivastava. 2004. Extinction and ecosystem function in the marine benthos. *Science* 306(5699):1,177–1,180, https://doi.org/10.1126/science.1103960.

Stachowicz, J.J., J.F. Bruno, and J.E. Duffy. 2007. Understanding the effects of marine biodiversity on communities and ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 38:739–766, https://doi.org/10.1146/annurev.ecolsys.38.091206.095659.

Valavanis, V.D., G.J. Pierce, A.F. Zuur, A. Palialexis, A. Saveliev, I. Katara, J.J. Wang. 2008. Modelling of essential fish habitat based on remote sensing, spatial analysis and GIS. *Hydrobiologia* 612:5–20, https://doi.org/10.1007/978-1-4020-9141-4_2.

Varisco, M., and J.H. Vinuesa. 2007. La alimentación de *Munida gregaria* (Fabricius, 1793) (Crustacea: Anomura: Galatheidae) en fondos de pesca del Golfo San Jorge, Argentina. *Revista de Biología Marina y Oceanografía* 42(3):221–229, https://doi.org/10.4067/S0718-19572007000300002.

Worm, B., E.B. Barbier, N. Beaumont, J.E. Duffy, C. Folke, B.S. Halpern, B.C. Jackson, H.K. Lotze, F. Micheli, S.R. Palumbi, and others. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314(5800):787–790, https://doi.org/10.1126/science.1132294.

Yorio, P. 2009. Marine protected areas, spatial scales, and governance: Implications for the conservation of breeding seabirds. *Conservation Letters* 2:171–178, https://doi.org/10.1111/j.1755-263X.2009.00062.x.

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