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Eduardo Marcelo Acha, María Delia Viñas, Carla Derisio, Daniela Alemany, Alberto R. Piola



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Large-scale geographic patterns of pelagic copepods in the southwestern South Atlantic.

Eduardo Marcelo Acha ^{a,b,#}; María Delia Viñas ^{a,b}; Carla Derisio ^b; Daniela Alemany ^{a,b} and Alberto R. Piola ^{c,d}

^a Instituto de Investigaciones Marinas y Costeras, Universidad Nacional de Mar del Plata-Consejo Nacional de Investigaciones Científicas y Técnicas (UNMDP-CONICET), Mar del Plata, Argentina.

^b Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina.

^c Departamento Oceanografía, Servicio de Hidrografía Naval (SHN), Buenos Aires, Argentina.

^d Departamento de Ciencias de la Atmósfera y los Océanos, Universidad de Buenos Aires, Buenos Aires, Argentina.

[#]Corresponding autor: E.M.A. macha@inidep.edu.ar Postal address: Instituto de Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo V. Ocampo n°1, Mar del Plata (7600), Argentina.

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Authors' e-mails:

Eduardo Marcelo Acha macha@inidep.edu.ar

María Delia Viñas mdvinas@inidep.edu.ar

Carla Derisio cderisio@inidep.edu.ar

Daniela Alemany dalemany@inidep.edu.ar

Alberto R. Piola apiola@hidro.gov.ar

Abstract

We compiled an extensive dataset of copepod presence/absence data to define ecoregions in the southwestern South Atlantic (33°S- 55°S) and to examine their relationships to water mass characteristics. We also investigated the role of mesoscale fronts in determining the boundaries of the ecoregions. Finally, we compared copepod distributions with previously defined biogeographical provinces in the southwestern South Atlantic. The regional copepod community is organized into six assemblages that occupy distinct areas of the shelf, the shelfbreak, and the oceanic realm. These areas are characterized by different water masses. In general, the spatial configuration of the ecoregions matches that of the previously defined regional biogeographic provinces and marine fronts seem to act as boundaries between the ecoregions.

Keywords: zooplankton; ecoregions; water masses; marine fronts; southwestern South Atlantic; Argentina; Uruguay

Highlights

- Ecoregions based on copepods assemblages relate to water mass characteristics
- Marine fronts constitute boundaries of the ecoregions
- Ecoregions match the biogeographic provinces of the southwestern South Atlantic

1- Introduction

Plankton communities are often structured in assemblages that have close relationships to environmental characteristics. Ocean dynamics play a major role in the distribution patterns of marine organisms and the borders of marine bioregionalization schemes take place where the limits of species distributions occur together; therefore, biogeographical frontiers tend to coincide with boundaries between major water masses (Gaines et al., 2009). The idea that marine fronts separate different water masses, and hence different pelagic populations, is not new (Sournia, 1994). However, the role of fronts in marine biogeography is not yet fully understood (Acha et al., 2015). It is clear that some large-scale fronts such as the Antarctic Polar Front constitute biogeographic boundaries for zooplankton (e.g., Boltovskoy et al. (2005); Sournia (1994); Spalding et

al. (2012); but see Fraser et al. (2017)). In addition, several shelf-break fronts mark the neritic-oceanic transition (Longhurst, 1998; Spalding et al., 2007). Nonetheless, fronts that have a smaller spatial scale (e.g. tens or hundreds of kilometers) or are not persistent (e.g. fronts lasting for weeks or being seasonal) do not constitute boundaries between main geographic units (i.e., provinces) in the more recent biogeographic marine schemes, such as those proposed by Longhurst (1998), Spalding et al. (2007), or Spalding et al. (2012). Such partitions have been defined on global scales, so they presumably reflect global scale forcing. The effects of fronts have been recognized in finer resolution regional arrangements, such as ecoregions (Spalding et al., 2007), or when separating species assemblages (e.g., Berasategui et al., 2004; Derisio et al., 2014a). In the southwestern South Atlantic, marine fronts are abundant, covering several scales of space and time. Winds, tides, freshwater discharges, and ocean currents are the forcing factors. The interactions of forcing factors with geomorphological features, such as bottom topography, or changes in coastal orientation produce several frontal types (e.g., tidal fronts, estuarine fronts, shelf-break fronts, etc. Acha et al. (2004)); accordingly, the southwestern South Atlantic is a useful case for studying the role of marine fronts in plankton biogeography.

Previous biogeographic studies focused on the southwestern South Atlantic continental shelf were mainly based on the distribution of benthic invertebrates (echinoderms, crustaceans and mollusks) and fishes (e.g., Balech and Ehrlich, 2008; Boschi, 2000; López, 1964). Two biogeographical provinces have been proposed for the region: the Argentine and the Magellan provinces (Figure 1), which are part of the Subtropical and Subantarctic regions, respectively. The Argentine Province extends from 30°S-32°S to 41°S-44°S and from the coast to *ca.* the location of the 100 m isobath, which lies close to the shelf break. The Magellan Province extends from Valdés Peninsula to the southern tip of South America and from 43°S northward along the eastern boundary of the Argentine Province. This scheme, based on regional studies, has some discrepancies with the global classification proposed by Spalding et al. (2007), which is based on the reconciliation of different boundary systems proposed by several other authors.

In the southwestern South Atlantic, zooplankton distributions have been analyzed at much larger spatial scales than those of the provinces (e.g., over the entire South Atlantic basin, Boltovskoy et al. (1999)) or at smaller scales at which spatial units are defined by the taxonomic composition of communities (Berasategui et al., 2004;

Berasategui et al., 2005; Derisio et al., 2014a; Fernández Araoz et al., 1991; Fernández Araoz et al., 1994; Marrari et al., 2004; Sabatini et al., 2012; Sabatini and Martos, 2002; Santos and Ramírez, 1995; Santos and Ramírez, 1991; Temperoni et al., 2014; Thompson et al., 2013; Viñas et al., 2002). However, there are few studies on zooplankton distributions on the scale of biogeographic provinces. Scaling up to the regional scale would allow to understand the larger patterns and drivers of zooplankton communities of this area, which remains too poorly studied in spite of its large coverage and noteworthy characteristics.

Copepods are dominant components of the marine zooplankton biomass (Kiorboe, 2011) and are one of the taxonomically best known planktonic invertebrates in the southwestern South Atlantic (Bradford-Grieve et al., 1999; Ramirez, 1981; Cepeda et al., 2018). The adaptive characteristics of copepods that cause this dominance include their hydrodynamic body-shape, their muscular and sensory capabilities, which make them highly efficient in attacking prey and escaping predators, and their ability to remotely detect mates (Kiorboe, 2011). Here, we take advantage of their overwhelming abundance and well-known taxonomy in the region, and use copepods as a proxy to study mesozooplankton geographical patterns.

Our main objectives are to 1) determine ecoregions for the southwestern South Atlantic (33°S- 55°S) based on copepod species distributions; 2) study the relationship between ecoregions and water masses characteristics, giving special consideration to marine fronts in setting the boundaries of the ecoregions; and 3) compare the distribution of copepods with previously defined biogeographical units in the study region. To this end, we compiled a dataset of copepods observations on a pluri-annual scale for the region, as well as climatological data, such as temperature and salinity, from the World Ocean Atlas and the mean position of mesoscale fronts as reported in previous studies.

2-Data and methods

2.1. Study area

The continental shelf off Argentina and Uruguay extends over more than 1,000,000 km² and produces an exceptionally large neritic province. The open ocean circulation is dominated by the Brazil (subtropical) and the Malvinas (subantarctic) currents, which flow in opposite directions. The currents meet between 36 and 38°S on

average (Olson et al., 1988). In this area, referred to as the Brazil/Malvinas Confluence, both flows veer offshore and form large amplitude meanders and eddies (Figure 1). Steep gradients in salinity, temperature and dissolved nutrients characterize the Confluence, which is one of the most energetic regions in the world ocean (Olson et al., 1988; Chelton et al., 1999).

The continental shelf is occupied by relatively cold and fresh waters of subantarctic origin, which are further diluted by different freshwater sources. These diluted waters are derived from the southeast Pacific (a region subject to substantial continental runoff and to excess precipitation over evaporation) and enter the Argentine shelf through the Straits of Magellan and Le Maire, and across the shelf break (e.g. Combes and Matano, 2018). Salinity progressively increases northeastward and offshore, reaching approximately 33.8 at the shelf break, suggesting a northeastward mean flow over the inner and mid-shelf regions, referred to as the Patagonian Current (Figure 1) (Brandhorst and Castello, 1971; Guerrero and Piola, 1997). The San Matías Gulf in northern Patagonia produces high salinity waters because evaporation greatly exceeds precipitation. These high salinity waters spread northeastward onto the inner shelf (Palma and Matano, 2012; Scasso and Piola, 1988). There are no significant continental freshwater discharges into the ocean from Patagonia. On the other hand, the northern zone, near the boundary between Argentina and Uruguay, is characterized by abundant freshwater discharge from the Río de la Plata (approximately $25,000 \text{ m}^3 \text{ s}^{-1}$), which spreads as a low salinity plume all along the Uruguayan coast that reaches southern Brazil beyond 28°S (Piola et al., 2008; Piola et al., 2000). The study region experiences a temperate climate regime, characterized by marked seasonality and the formation of a strong thermocline during spring and summer. The large tidal amplitudes and currents observed south of 40°S induce intense vertical mixing near the shore (e.g., Palma et al., 2004); the continental shelf of Patagonia exhibits one of the highest rates of tidal energy dissipation in the world ocean (Glorioso and Flather, 1995; Palma et al., 2004). Winds north of approximately 40°S are milder and more seasonally variable, while the region farther south is influenced by the intense and more regular southern hemisphere westerlies. All these forcing factors interact with geomorphological features, such as the bottom topography and changes in coastal orientation, producing several types of fronts that develop over a variety of spatial and temporal scales (Acha et al., 2004; Rivas and Pisoni, 2010).

2.2. Data sources

A database on copepod species occurrence was constructed from records from the Zooplankton Laboratory at the Argentine National Institute for Fisheries Research and Development (INIDEP), Argentina. Data from different published sources were also included (Fernández Araoz et al., 1994; Goberna, 1986, 1988; Mazzocchi and Ianora, 1991; Ramirez, 1996; Sabatini, 2008; Sabatini et al., 2001; Sabatini et al., 2004). The database contains information about the presence of adult copepod species from 566 plankton samples taken over 40 years (1966-2006) from a region extending approximately between 33-55° S and 43-68° W. Different samplers, mesh sizes and sampling strategies were employed in different seasons (Table 1). Because of the variety of sampling protocols, the abundance data is hardly comparable across the original datasets; therefore, abundance data were converted to presence/absence and any abundance above zero was converted to presence. Data were obtained from cruises that were not focused on sampling individual species or groups of particular species, but instead focused on sampling sites and in all cases all the species present in each sample were identified. Except for data reported by Goberna (1986; 1988), and Mazzocchi and Ianora (1991), the remaining data (83%) were produced by different researchers at the Zooplankton Laboratory of INIDEP, who employed similar identification and laboratory protocols. The scientific nomenclature of the species was updated following WoRMS (2018) and Cepeda et al. (2016). To relate copepods' distributions to water masses, we employed historical hydrographic data retrieved from the World Ocean Atlas (<https://www.nodc.noaa.gov/OC5/woa18/woa18data.html>). The hydrographic data are provided over a grid with a horizontal resolution of 1° x 1° and a vertical resolution of 5 m in the upper 100 m and 25 m from 125 to 500 m. We ascribed the nearest grid node to each plankton station and averaged the physical data over the same depth range of each plankton tow, which, in most cases, was from the surface to near the bottom or to 100 m in waters deeper than 100 m.

2.3. Data analysis

A multivariate numerical classification was used to identify grouping of stations with distinct copepod species assemblages. A preliminary analysis showed insufficient spatial coverage when data were classified by season; therefore, all the seasons were analyzed together and our results are valid only at an annual time scale. In the general matrix, only those species present in at least 10% of the samples were included.

Hierarchical agglomerative clustering (CLUSTER) was performed on a Sørensen distance similarity matrix of the presence/absence data using a group average linkage (Clarke and Warwick, 2001) to produce dendrograms that depict clusters of stations based on copepod species compositions. This technique is appropriate for delineating groups with distinct community structure and has been used in numerous ecological studies (Clarke and Warwick, 2001). Additionally, a nonmetric multidimensional scaling analysis (MDS) was performed on the similarity matrix to construct a chart of the samples that shows the relative distance between them. The combination of clustering and ordination analysis is an effective way of checking the adequacy and mutual consistency of both representations (Clarke and Warwick, 2001). To test the significance of the groups defined by clustering, a similarity profile (SIMPROF) permutation test was performed ($p < 0.001$) under the null hypothesis that groups of stations with similar copepod composition and distribution do not exist in the study area (Clarke et al., 2008). The groups of stations were mapped to analyze their geographic patterns to determine ecoregions. Ecoregions, *sensu* Spalding et al. (2007), are areas of relatively homogeneous species composition, are determined by the predominance of a well-defined set of oceanographic features, and are large enough to be distinguished by unique characteristics of the ecological or life history processes.

We performed a sensitivity analysis to test the effects of different mesh sizes and seasons on the definition of clusters and their spatial patterns (Supplementary Material). Because most of the samples were taken with 300/330 μm mesh (Table 2), we repeated the analysis by alternatively removing those stations taken using 200 μm mesh, and those taken using 500 μm mesh. Spring was the season best represented in the samples; therefore, we repeated the analysis by alternatively removing samples taken during the summer, fall and winter (Table 2). To test the significance of the groups defined by clustering, SIMPROF tests were performed ($p < 0.001$). The groups of stations were mapped and compared with the results based on all the data.

The indicator species of each assemblage were identified using a similarity percentages (SIMPER) analysis. This method examines the contribution of each species to similarities within a group or dissimilarities between groups (Clarke and Warwick, 2001). The more frequent a species is within a group, the more it will contribute to the intragroup similarity.

The groups of stations were plotted in temperature-salinity (T/S) space to visually examine their relationship with water masses. To statistically test the effects of

salinity and temperature on the groups' species compositions, we determined the Pearson correlations between the temperature, salinity, and the stations scores along the MDS components (which summarize the variation in species composition). Complementarily, we identified a parsimonious model to evaluate the role of temperature and/or salinity on copepod species composition. Draftman plots were performed (Clarke and Gorley, 2006) (see Supplementary Materials) to determine collinearity between the variables. This routine plots variables against each other in scatter plots and evaluates how much one variable is related to another by calculating the Pearson correlation coefficients between all pairs of variables. Once a lack of collinearity was proven, a distance-based linear model (DISTLM) was developed (Anderson et al., 2008) based on the temperature and salinity climatologies and the resemblance matrix, with significance testing based on 999 permutations. A procedure that examines the value of the selection criterion for all possible combinations of predictor variables (BEST) was used to test the significance of temperature and salinity on the assemblages. The Akaike's information criterion (AIC) was used to rank the resulting models.

CLUSTER/SIMPROF, MDS, SIMPER and DISTLM analyses were performed using a PRIMER v6 multivariate statistics package (Clark and Gorley, 2006). In addition, species richness patterns were studied using Species-Area Relationships (SARs) (Clarke & Gorley, 2006) across clusters. Previously, we looked at the incremental increase in species richness relative to the number of samples to assess the effect of sampling effort on the estimated SARs. Species accumulation curves were constructed with a random sample order permuted 999 times in PRIMER 6 (Clarke & Gorley, 2006).

The locations of the main marine fronts in the region were determined from the climatological distribution of the sea surface temperature (SST) gradient, the salinity, and the Simpson's stratification parameter according to the different types of fronts, as reported in previous studies (Bianchi et al., 2005; Guerrero et al., 2010; Lucas et al., 2005; Piola et al., 2008; Piola et al., 2000; Piola et al., 2005; Piola and Falabella, 2009). Both fronts and station assemblages were mapped to investigate the degree of spatial correspondence between the fronts and the boundaries of the ecoregions.

3-Results

3.1. Grouping of stations

Eighty-six copepod species compose our database (Table 3). Based on copepod species occurrences, the cluster analysis classified the stations into six groups (Figure 2 A) and a SIMPROF test allowed us to reject the null hypothesis of no internal structure in the whole set of samples ($p < 0.001$), which supports the definition of clusters at the 20% similarity threshold. The first separation occurs at 10% similarity and separates the Northern Offshore (yellow) and the Northern Shelfbreak (red) groups from the remaining groups. The second separation separates the Coastal (magenta) and the Summer Northern Shelf (gray) from the remaining groups (14% similarity). The Northern Offshore (yellow) and the Northern Shelfbreak (red) groups separate at a 16% similarity. The Shelf (green) and Southern Offshore (blue) groups are separated from the remaining groups at 18% similarity. At 27% separated Southern Offshore (blue) from Shelf (green). Finally, the Coastal (magenta) and the Summer Northern Shelf (gray) groups are separated at a 29% similarity. In spite of a relatively high stress level (0.17), distinct groups of stations emerge from the 2-dimensional picture produced by the MDS analysis (Figure 2 B) and match well those produced by the CLUSTER analysis.

3.2. Ecoregions

The six clusters defined present distinct spatial distributions (Figure 3). The Coastal ecoregion (magenta in Figure 3), occupies the shallower portions of the northern shelf and is characterized by bottom depths shallower than 50 m between 37° to 43° 30' S and shallower than 20 m between 37° to 35° S. This area includes the northern Patagonian gulfs and the Valdés Peninsula and extends northward to the Río de la Plata estuary. The Shelf ecoregion (green in Figure 3) occupies the more widely spread waters immediately eastwards of the Coastal ecoregion and extends beyond the shelfbreak. This area widens southward and encompasses the shelf around the Malvinas Islands. South of ~ 44° S, the Shelf ecoregion reaches the coastline, and extends all along the Magellan Strait, reaching the Pacific Ocean. The Northern Shelfbreak ecoregion (red in Figure 3) is located east of the shelf and north of 38°S, immediately off the shelfbreak, which falls close to the 200 m isobath. Part of the offshore boundary of the Northern Shelfbreak ecoregion bounds the Northern Offshore ecoregion (yellow dots in Figure 3). The Northern Offshore (yellow dots) and the Southern Offshore ecoregions (blue dots in Figure 3) occupy the oceanic domain to the north and to the south of an oblique line more or less perpendicular to the shelfbreak. The Southern

Offshore and the Shelf ecoregions overlap in a band centered along the shelfbreak; an onshore intrusion of the Southern Offshore ecoregion is also evident between 50 ° and 54° S. Finally, the Summer Northern Shelf ecoregion (gray dots in the inset of Figure 3) overlies the northern portion of the shelf. It is composed of stations solely taken during summer cruises and located at bottom depths shallower than 100 m, approximately between 33° 14' and 37° 00' S. Based on these results the groups are hereafter referred to as ecoregions.

The main sources of potential biases in the data, which could differentially affect the ecoregions' definitions, are presented in Table 2. The Coastal; Shelf and Northern Shelfbreak ecoregions were mainly based on samples taken with 300-330 µm mesh. The Northern Offshore is based on 500 µm mesh tows. The Southern Offshore is based on 300-330 and 500 µm meshes. There are seasonal biases too: the Coastal ecoregion is mainly based on spring (47%) and summer data (14%); the Northern Shelfbreak is mainly based on winter data (70%); and the Northern Offshore is entirely (100%) based on winter data; the Southern Offshore is based on fall, winter and spring data and a small amount (7%) of summer data. The Shelf ecoregion is based on data collected over all seasons and the Summer Northern Shelf is almost entirely based (96%) on summer data. The mean spatial resolution (the number of stations divided by the surface area of each ecoregion) was similar for the Coastal; Northern Shelfbreak; and Summer Northern Shelf ecoregions (approximately 5-6 stations per 10,000 km²), followed by the Shelf ecoregion (2.5 stations per 10,000 km²). The Northern and Southern offshore ecoregions, had the lowest resolution (0.6-0.7 stations per 10,000 km²) (Table 2). To test the impact of the very heterogeneous sampling methods and sampling seasons on the results we carried out a sensitivity analysis based on the elimination of stations linked to a specific mesh or season. Though these tests introduce changes to the percentage of stations integrating each cluster (Supplementary Material, Table S.1), the original ecoregions can be still recognized. In all the cases, the SIMPROF tests supported the clusters defined at a 20% similarity threshold ($p < 0.001$). Samples taken with the 200 µm mesh net had a strong influence in the definition of the Coastal ecoregion, although most of those stations were far from the coastal sector (Figure S.1). Some ecoregions, when fully defined from samples taken with a particular mesh or season removed, were lost, but this did not greatly affect the spatial pattern of the remaining ecoregions; when the samples taken with a 500 µm mesh net were removed, both oceanic ecoregions (Northern and Southern Offshore) were lost (Figure S.2). In

addition, as might be expected the Summer Northern Shelf ecoregion is lost when eliminating the samples collected in summer (Figure S.3). Elimination of samples taken during the fall extended the Coastal ecoregion northward, over the Uruguayan shelf and slope (Figure S.4). Removal of winter samples lead to losing the Northern Offshore ecoregion and produced a southward retraction of the Coastal and Shelf ecoregions (Figure S.5).

3.3. Ecoregions and water masses

The T/S diagram (Figure 4) depicts the association between the six ecoregions and the water mass characteristics. All the ecoregions showed wide thermohaline ranges and though some ecoregions present overlapping T-S properties, they tend to occupy relatively well-defined portions in T-S space. The Coastal ecoregion (magenta) was characterized by a 7.3-16.9 °C temperature range and a 21.92-33.85 salinity range. The Shelf ecoregion (green) also shows wide ranges (5.0-19.7 °C and 30.29-35.07, respectively). The Summer Northern Shelf ecoregion (gray) shows the highest temperatures and a relatively wide salinity range (9.3-19.7 °C and 30.29-34.85, respectively). The stations in the Northern Shelfbreak ecoregion (red) show ranges of 8.9-19.7 °C and 33.76-35.39 for temperature and salinity, respectively. Ranges were narrower in the oceanic areas, especially for salinity; stations of the Southern Offshore ecoregion (blue) were characterized by 4.7-15.7 °C and 32.79-35.05 temperature and salinity ranges, respectively; and those in the Northern Offshore (yellow) by 8.0-18.7 °C and 33.83-35.65 ranges, respectively.

Scatter plots (Draftsman plot routine, PRIMER package) and Pearson correlation coefficients (Figure S.6) did not detected multicollinearity in the predictor variables (temperature and salinity), allowing for their use in the DISTLM analysis to test their effects on the copepods' assemblages. The final model included both temperature and salinity and explained 16% of the variation ($R^2 = 0.16$, AIC = 3783.2; Table 4). Each variable alone explained less than 9% of the variation (marginal tests in Table 4, $p < 0.05$).

3.4. Indicator species and diversity of the ecoregions

The six ecoregions were characterized by typical copepod species derived from the SIMPER analysis (Tables 3 and 5). The dissimilarity among ecoregions analysis, using the SIMPER routine, revealed that all the ecoregions were clearly distinct, with

percentages of dissimilarity in pairwise comparisons higher than 80% (Table 6). The species-area relationships (Figure 5) show that the Northern Shelfbreak ecoregion was the most diverse (122 species per 100,000 km²), followed by the Summer Northern Shelf, and the Coastal and the Northern Offshore ecoregions (50, 16 and 8 species per 100,000 km², respectively). The Shelf and the Southern Offshore ecoregions showed lower values (5 and 3 species per 100,000 km², respectively). The species accumulation curves (Figure 6) indicate that the Northern Shelfbreak was the best-sampled ecoregion. On the other hand, the sampling effort in the Northern Offshore was poor and perhaps far from reaching an asymptotic value. The remaining ecoregions show intermediate conditions and similar patterns between them and the asymptotic values were not reached in these regions.

4-Discussion

4.1. Data constraints and caveats.

Our database contains several potential sampling biases (e.g., samples taken over several decades by different researchers, sampling gears, mesh sizes, seasons and successional stages; Tables 1 and 2), in addition to the inherent noise in plankton data due to the patchy distribution of organisms (e.g., Postel et al., 2000). The use of different mesh sizes and samplers and, in several cases, the use of semiquantitative data prevent carrying out a more quantitative study. The number of species recorded here (n= 86) is lower than the observations of Cepeda et al. (2018) who found 101 species/taxa for a smaller area than what is presented here. This bias could be mainly due to the different mesh sizes employed in both studies. Most of the samples from the Coastal and Shelf ecoregions, where a dominance of small-sized species is expected, were collected with 300/330 µm mesh. However, approximately half of the samples collected in the Southern Offshore ecoregion and all of the samples from the Northern Offshore ecoregion were taken with 500 µm nets. The higher number of species reported by Cepeda et al. (2018) could be due to the smaller mesh size they employed. Another important limitation of our analysis is that the study region undergoes a strong seasonal cycle, but we did not carry out a seasonal analysis and each season was sampled differently in each ecoregion. The Northern Shelfbreak and the Northern Offshore ecoregions (red and yellow clusters in Figure 2) are the first separated from the remaining ecoregions and are based on samples taken mainly during winter (70 and 100%, respectively). The contiguity of these areas and the fact that samples were

collected during the same season probably accounted for the similarities in their copepods' communities, and their separation from the remaining ecoregions. However, a sensitivity analysis (see Supplementary Materials), shows that the effects of different mesh sizes and the sampling seasons and regions did not substantially affect the clusters defined nor the spatial pattern of the ecoregions.

The study region exhibits strong thermal stratification during the warmer months. Moreover, the northern area which is under the influence of the Río de la Plata discharge, shows strong haloclines. Because we averaged physical data from the deepest plankton sampling depth to the surface, we missed the possible impact of the vertical structure of the water column on the plankton distribution. Moreover, temperature and salinity data here employed has a relatively low spatial resolution (1° latitude x 1° longitude). In spite of such shortcomings, statistical analysis revealed that both temperature and salinity have an effect on the copepods' composition of the ecoregions, explaining 16% of their variability (Table 4).

Despite the above-described limitations, the geographic pattern derived from our analysis is consistent, in the sense that few stations (*ca.* 3%) occur at manifestly “wrong” places (Figure 3), and the resulting spatial pattern can be understood based on current knowledge of the oceanography and biology of the region, giving us confidence in our results.

4.2. Ecoregions, water masses and fronts

The Coastal ecoregion occupies waters with an ample thermohaline range (Figure 4). The lower salinities (approximately 22) are associated with the continental runoff, notably due to the Río de la Plata discharge (mean annual runoff $\sim 25,000 \text{ m}^3\text{s}^{-1}$). Much lower salinities exist in this area (Guerrero et al. 1997), but are not captured at the spatial resolution of the hydrographic data employed. Salinities higher than 33.7 correspond to the San Matías Gulf and its surroundings; the gulf is a semienclosed basin where on average evaporation exceeds precipitation by 100 cm year^{-1} , locally generating high salinity waters (Scasso and Piola, 1988). To the east, the Coastal ecoregion is bounded by the Shelf ecoregion. Near the Río de la Plata mouth ($\sim 35^\circ \text{ S}$), the limit between both ecoregions matches the estuarine front, represented by the climatological position of the 27.5 isohaline (E in Figure 7). This is a permanent front, though its shape and location varies seasonally in response to changes in wind direction (Guerrero et al., 1997), while on interannual scales, the front is affected by river runoff

fluctuations associated with El Niño-Southern Oscillation variability (Acha et al., 2008; Matano et al., 2014). Between 38° and 42°S, the boundary between the Coastal and the Shelf ecoregions seems associated with a shallow sea front defined by the critical value of the Simpson parameter during summer ($\Phi_C = 40 \text{ J m}^{-3}$) (Bianchi et al., 2005; Lucas et al., 2005) (D in Figure 7). The southern part of this front is driven by tidal forcing (e.g., Carreto et al., 1986; Glorioso, 1987), while its northern portion is presumably driven mainly by wind mixing (Lucas et al., 2005). This is a seasonal front that depends on the formation of the thermocline; its influence on our dataset could be due to the high proportion of Coastal and Shelf samples taking during the warmer months (61% and 48%, respectively; Table 2), when the front is well developed.

The Shelf ecoregion covers the largest surface area. Between 35° and 44° S it extends immediately offshore the Coastal ecoregion, and reaches the coastline further south. It extends eastwards beyond the shelfbreak. This ecoregion presents a wide thermal range (5.0-19.7 °C) because of its broad latitudinal coverage and because the surface waters over the shelf present a large seasonal amplitude. Two sources of low salinity waters influence the Shelf ecoregion. In the southern portion the Magellan Strait discharges low salinity waters (Krepper and Rivas, 1979), and the northern part of the ecoregion is under the influence of the Plata plume (see below, Piola et al., 2008). On the eastern boundary, subantarctic waters within the Malvinas Current, typically saltier than 34.1 (Guerrero and Piola, 1997; Piola et al., 2010), represent the highest salinities for this ecoregion. North of 36° 30'S, the eastern boundary of the Shelf ecoregion coincides with the offshore boundary of the Plata plume front, represented by the climatological position of the 33.5 isohaline (A in Figure 7) (Piola et al., 2008; Piola et al., 2005). South of 38° S and along the shelfbreak, the maximum SST gradient in January (C in Figure 7) is close to the location of the permanent Patagonian shelfbreak front (Franco et al., 2008; Saraceno et al., 2004). The shelfbreak front marks a relatively sharp transition from comparatively warm-fresh shelf waters to cold-salty Malvinas Current waters (e.g., Piola et al., 2010; Saraceno et al., 2004). Moreover, the shelfbreak front also marks a relatively sharp kinematic transition, as the flow over the shelf is substantially less intense than the flow within the Malvinas Current (e.g., Piola et al., 2013). Contrary to expectations (e.g., Spalding et al., 2007), the shelfbreak front does not represent a sharp boundary between the shelf and the oceanic species. The transition between the Shelf and the Southern Offshore ecoregions forms a band centered at the front, a transitional area where stations of both ecoregions cooccur. The blurred

transition could be due to intrusions of offshore waters onto the continental shelf (Figure 3). Piola et al. (2010) documented recurrent intrusions of slope waters onto the continental shelf near 41° S, extending onshore approximately 150 km from the shelfbreak. It is possible that instead of a continuous exchange, the front accumulates material for a while and then through frontal instabilities leads to relatively large pulses of cross-front exchange (Largier, 1993) that facilitate the co-occurrence of species typical of the shelf and deep ocean realms along the shelf break.

The Summer Northern Shelf ecoregion includes stations occupied solely during summer cruises, and covers a relatively small area. Temperatures at such stations are moderately high (9.3 - 19.7 °C). Salinity spans over a broad range (28.20 - 35.47) because though most of the stations are under the influence of the diluted waters of the Plata plume, some of the offshore stations are placed in the warm and salty waters influenced by the Brazil Current (Piola and Matano, 2001). Species forming this ecoregion could be advected from the north during summer due to seasonal flow reversal of the shelf circulation and the Plata plume driven by winds (e.g., Guerrero et al., 2014; Piola et al., 2008).

The Northern Offshore and Southern Offshore ecoregions clearly present surface water mass properties that correspond to the subtropical-subantarctic transition. On daily/weekly time scales, the transition between the offshore regions is well defined and is associated with sharp thermohaline gradients, particularly in the upper 500 m. However, intense mesoscale variability leads to the wide range of thermohaline properties in both ecoregions. The Northern Offshore ecoregion is located in the oceanic domain north of approximately 40 - 42 °S, a region dominated by tropical/subtropical waters (e.g., Piola and Matano, 2001); however, some stations extend to the south into subantarctic waters, resulting in a relatively broad thermohaline range (8.0 - 18.7 °C and 33.83 - 35.65). The Southern Offshore ecoregion is mostly characterized by subantarctic waters transported northward by the Malvinas Current and its southward return downstream of the Brazil/Malvinas Confluence. However, the upper limit of the salinity range (32.79 - 35.05) is similar to that of the Northern Offshore ecoregion, also revealing the influence of subtropical waters. The temperatures observed in the Southern Offshore ecoregion (4.7 - 15.7 °C) are somewhat lower than those observed in the Northern Offshore ecoregion. The large thermohaline range in these oceanic areas is expected in response to the intense subantarctic-subtropical mixing associated with eddies and meanders in the highly energetic Brazil/Malvinas Confluence (Olson et al., 1988). A

few stations from the Northern Offshore fall in the region dominated by the Southern Offshore ecoregion (Figure 3). These stations may represent sporadic southward penetrations of the Brazil Current which frequently develop into large mesoscale eddies that characterize the Brazil/Malvinas Confluence (e.g., Chelton et al., 1990; Gordon, 1981). The Subtropical Front separates the Subantarctic Water and the Subtropical Water masses. The climatological position of the 35 isohaline (B in Figure 7) represents the location of the Subtropical Front (Piola and Matano, 2001). This isohaline matches the transition between the Northern Offshore and the Northern Shelfbreak ecoregions. Its penetration into the oceanic domain represents the Brazil-Malvinas Confluence (Piola and Matano; 2001) and separates the Northern Offshore and the Southern Offshore ecoregions.

The convergence of water masses of subtropical, subantarctic and shelf origins is frequent in the area occupied by the Northern Shelfbreak ecoregion. Displacements of the Brazil/Malvinas Confluence and the frequent export of shelf waters along the Confluence axis lead to large surface temperature and salinity variations in this region (e.g., Guerrero et al., 2014; Matano et al., 2014). Consequently, despite its relatively small surface area, the Northern Shelfbreak ecoregion exhibits a wide environmental range (8.9-19.7 °C and 33.76-35.39) (Figure 4).

Except for some minor segments, the boundaries between ecoregions match the location of five ocean fronts (Figure 7). Other fronts present in the region (e.g., Acha et al., 2004), however, do not show any appreciable association with the geographic delimitation of the areas. The role of fronts in setting biogeographic boundaries depends on the spatial scale, physical contrast, and persistence. The stronger those properties, the stronger the influence of the front (Acha et al., 2015).

The T/S diagram suggests some degree of mixing across the ecoregion boundaries (Figure 4). This could be due in part to the collection of most of the samples by oblique or vertical tows (and the stratified samples were vertically averaged), that mix the populations occurring at different depths. The plankton sampling technique forced us to vertically average the temperature and salinity data, missing the biological and physical structure of the water column. Given that fronts are slanted, vertical averaging close to a front will lead to a wider range of thermohaline properties and planktonic species characteristic of the water masses at either side of the front. In addition, the spatial resolution (1° latitude x 1° longitude) of hydrographic data is coarse compared to frontal width, which are typically of a few km to a few tens of km may

contribute to rather blurred interfaces. Notwithstanding those limitations, the ecoregions occupy relatively well-defined portions of the T/S space (Figure 4), mirroring the spatial relationships between them in the geographic space (Figure 3).

4.3. Indicator species and diversity of the ecoregions

The differences in body size between the ecoregions' indicator species display a classic coastal to open-sea gradient (Table 5), with the smallest species at the coastal system and the largest ones at the shelfbreak and oceanic waters (e.g., Sourisseau and Carlotti, 2006; Cepeda et al., 2018). Indicator species of the Coastal ecoregion (e.g., *Paracalanus parvus*, *Acartia tonsa*, *Oithona nana*) present a size range of 0.44-1.50 mm (Table 5). Those species are overwhelmingly abundant in the region (Cepeda et al., 2018; Derisio et al., 2014b; Viñas et al., 2013). Most of the Coastal ecoregion is characterized by relatively low phytoplankton concentrations all year round (Carreto et al., 1995) and high concentrations of cyanobacteria, bacterioplankton and ciliates during the warm season (Silva et al., 2009; Viñas et al., 2015; Cepeda et al., 2018); bottom-up processes related to food size and quality prevents the occurrence of large copepods in this region. On the other hand, the shelfbreak is characterized by a highly productive front, dominated by diatom blooms during spring (e.g., Carreto et al., 2016) that can sustain larger grazing copepods (Cepeda et al., 2018). Some indicator species of the Shelf ecoregion, such as *Calanus australis* (2.60-3.59 mm in length; Table 5), are large-bodied. But the largest ones are those of the oceanic areas: the Northern Offshore and the Southern Offshore ecoregions, whose main indicator species are in the 1.60-4.90 mm size range (Table 5). Although larger copepods are expected in those areas, it must be noted that samples were taken mostly with a 500 μ m mesh size (Table 2), thus the results are biased to the larger species due to the sampling technique.

The Northern Shelfbreak ecoregion shares some of its indicator species with adjacent regions: *Oithona atlantica* with the Southern Offshore ecoregion; *Pleuromamma gracilis* with the Northern Offshore ecoregion; and *Calanoides carinatus* with the Summer Northern Shelf. Notwithstanding, most of the Northern Shelfbreak ecoregion characteristic species are restricted to this area; it hosts the most heterogeneous copepod ecoregion, with medium and large sized species (Table 5). This ecoregion shows by far the highest diversity (Figure 5), this could be due in part to the higher sampling effort compared to other ecoregions (Figure 6) and because this ecoregion is bordered by several ecoregions with which it shares species (Figure 3).

Though the Northern Shelfbreak and the Northern Offshore ecoregions differ markedly in species diversity (122 and 8 species per 100,000 km², respectively), those clusters (red and yellow in Figure 2.A) represent the main dichotomy in species composition, and show a relatively low average dissimilarity percentage (Table 6). This is because all but two species in the Northern Offshore ecoregion are also present in the more diverse Northern Shelfbreak ecoregion. The Summer Northern Shelf ecoregion, which is also relatively well sampled, follows in terms of diversity (Figure 6) and is characterized by a tropical and subtropical community (Table 5), and the Coastal ecoregion distinguished by higher habitat heterogeneity, encompassing the Plata and the Bahía Blanca estuaries, and the northern Patagonian gulfs. The remaining of the ecoregions show lower diversity but the species accumulation curves (Figure 6) indicate that the sampling effort was probably insufficient to capture the entire diversity range.

4.4. Copepods' ecoregions and the biogeography of the southwestern South Atlantic

The separation between the Northern Offshore and the Southern Offshore ecoregions is clearly identified in the large-scale biogeographical views, focused in the oceanic domain (Longhurst, 1998; Boltovskoy et al. 1999; Spalding et al. 2012). The Northern Offshore and the Southern Offshore ecoregions defined here correspond respectively to the South Atlantic Subtropical Gyre and the South Subtropical Convergence defined by Longhurst (1998); to the Transitional Oceanic and the Subantarctic Oceanic defined by Boltovskoy et al. (1999) and Boltovskoy and Correa (2016); and to the South Central Atlantic and the Southern Subtropical Front defined by Spalding et al. (2012). All these studies show that in the oceanic domain, the boundaries between biogeographical units present a zonal orientation, as we observed in this work. However, in the shelf domain of our study region, those boundaries are more closely oriented along a meridional direction. Such differences in orientation were previously indicated by Bisbal (1995), and probably denotes the effects of bathymetry and along shore winds on circulation and stratification processes that in turn affect plankton distributions.

Regarding the biogeography of the shelf ecosystems, two faunistic provinces have been identified for the region (Figure 1): the Magellan Province featured by temperate-cold waters, which involves most of the southern Patagonian shelf (including the Malvinas area) to the latitude of Valdes Peninsula (~ 43° S). Further north, this

province extends eastwards and includes the continental slope reaching it at approximately 34°S. The second province is the Argentine Province, which consists of temperate-warm waters, extending from Cape Frio in southern Brazil (23°S) to Valdes Peninsula (Balech and Ehrlich, 2008; Boschi, 2000; López, 1964). The southernmost boundary between the Argentine and the Magellan Provinces set around Valdes Peninsula, *ca.* 41-43° S, but this limit is admittedly variable in the meridional direction (e.g., Balech and Ehrlich, 2008).

Due to the fluid nature of ocean boundaries, and the noise that arises from their temporal variability, the limits of the biogeographic units remain both uncertain and mobile on several time scales. Despite of these shortcomings, a relatively good correspondence between the established biogeographic provinces and the geographic patterns of copepods emerges, and confirms early findings by Ramirez (1981). It is worth noting that previously reported biogeographic patterns on the continental shelf were based on the distributions of benthic invertebrates and demersal fishes (Boschi, 2000; López, 1964). The similarities between the geographic patterns of copepods and the abovementioned taxa could be established during the planktonic larval stages of the benthic invertebrates and bony fishes, when copepods and meroplanktonic larvae are subject to the same advective and retention processes.

5-Conclusions

Copepods in the southwestern South Atlantic can be grouped into distinct ecoregions that are related to the properties and spatial distribution of water masses. Several marine fronts appear to function as boundaries for most of the ecoregions; however, several of these fronts, such as the Subtropical front, which features strong eddies, are permeable. In addition, the shelfbreak front is characterized by the intrusion of offshore waters on the shelf. Other fronts in the region, however, do not show any appreciable effect on copepod distribution patterns. The ecoregions based on copepod distributions closely match the biogeographic provinces of the continental shelf, which suggests the presence of common drivers for plankton, benthos and nekton.

Because climate change may lead to instability of many boundaries in the ocean, due to expected changes in circulation; stratification; continental runoff etc., studying the spatial patterns of ecoregions is particularly valuable for analyzing long-term trends (Spalding et al., 2012; Spalding et al., 2007). Our results can be used as a baseline for future studies on the effects of climate change on regional biogeography. Moreover, the

spatial partitioning of the southwestern South Atlantic Ocean is valuable for marine ecosystem management policies. The relatively large size of the units defined here is driven by the great connectivity between marine ecosystems and will aid in understanding the spatial scales at which management actions must be applied.

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Authors' roles:

E.M.A.: study design, analysis and interpretation of data.

M.D.V.: analysis and interpretation of data, mainly copepods' ecology.

C.D.: data compilation; analysis and interpretation of data, mainly copepods' ecology.

D.A.: statistical analysis and interpretation of results.

A.R.P.: analysis and interpretation of data, mainly physical oceanography.

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Table 1: Data employed to study the distribution of copepods in the southwestern South Atlantic. Data sources; sampling strategy; number of samples; sampler types; sampling period and geographic coverage. The database contains information about the presence of adult copepod species from 566 plankton samples taken over 40 years (1966-2006) from a region extending approximately between 33-55° S and 43-68° W.

Table 2: Summary of different potential bias sources for each ecoregion, expressed as percentage of different mesh sizes employed, seasons sampled and sampling effort.

Table 3: Occurrence percentage of copepod species by sampling stations at each ecoregion. The six ecoregions are based on cluster analysis and nonmetric multidimensional scaling analysis (MDS), on copepod species presence/absence. The significance of the groups defined was tested performing a similarity profile (SIMPROF) permutation test. Grayed background indicates the indicator species of each ecoregion, as identified by the SIMPER analysis. The more frequent a species is within a group, the more it will contribute to the intragroup similarity.

Table 4: Effects of temperature (T) and salinity (S) on the copepods' composition of the ecoregions. A distance-based linear model (DISTLM) analysis was developed based on climatological temperature and salinity data from the World Ocean Atlas, and the resemblance matrix based on copepods' presence/absence. DISTLM produced a final model including both temperature and salinity, explaining 16% of the variation ($R^2 = 0.16$).

Table 5: Indicator species for each ecoregion. The percentage contribution to the average similarity within each ecoregion, the mean length range of species, the reported inshore/offshore distribution, and water masses/regions inhabited are indicated. Information was taken from Bradford-Grieve et al. (1999), and updated following Cepeda et al. (2018) and Razouls et al. (2019).

Table 6: Average dissimilarity (%) between groups of stations conforming the ecoregions. SIMPER pair-wise tests reveal that all the ecoregions were clearly distinct, with percentages of dissimilarity in pairwise comparisons higher than 80%.

Figure 1: Schematic ocean circulation of the southwestern South Atlantic (modified from Matano et al., 2010) and continental shelf biogeographic provinces (background shading, modified from Balech and Ehrlich (2008) and Boschi (2000)). The red dotted line represents the boundary between the provinces from Spalding et al. (2007), referred to by those authors as Warm Temperate Southwestern Atlantic and Magellan provinces. **M.S.** = Magellan Strait.

Figure 2: Assemblages of sampling stations. **(A)** Dendrogram based on hierarchical agglomerative clustering (CLUSTER) performed on a Sørensen distance similarity matrix of presence/absence data using a group average linkage and **(B)** ordination based on non-metric multidimensional scaling (MDS) analysis performed on the similarity matrix. Colors represent the different ecoregions.

Figure 3: Ecoregions based on copepods' presence/absence data. Map of the sampling stations assemblages defined by CLUSTER and MDS analysis. Colors as in Figure 2.

Figure 4: Relationships of the ecoregions with water masses. Sampling stations assemblages defined by CLUSTER and MDS analyses in a temperature-salinity (T/S) space. Temperature and salinity climatological data from the World Ocean Atlas. Colors as in Figure 2.

Figure 5: Species richness of the ecoregions as Species-Area relationships. The number of species present in each ecoregion was taken from Table 3. The surface area (km²) covered by each ecoregion was calculated from Figure 3. Colors as in Figure 2.

Figure 6: Incremental increase in species richness relative to the number of samples taken in each ecoregion. Species accumulation curves were constructed with a random sample order permuted 999 times. Note the different x-axis scale for the Shelf ecoregion.

Figure 7: Ecoregions and marine fronts at the southwestern South Atlantic. Blue lines represent fronts associated with the boundaries of the ecoregions. A= Plata plume front (33.5 surface isohaline, Piola et al., 2008; Piola et al., 2005); B= Subtropical front and Brazil-Malvinas Confluence (35 surface isohaline, Piola et al., 2000); C = Patagonian shelfbreak front (maximum SST gradient for January, Piola and Falabella, 2009); D= Shallow sea front (Simpson' s parameter critical value for summer $\Phi_C = 40 \text{ J m}^{-3}$, Bianchi et al., 2005); E= estuarine front of Río de la Plata (27.5 surface isohaline for November-March, Guerrero et al., 2010).

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Table 1: Data employed to study the distribution of copepods in the southwestern South Atlantic. Data sources; sampling strategy; number of samples; sampler types; sampling period and geographic coverage. The database contains information about the presence of adult copepod species from 566 plankton samples taken over 40 years (1966-2006) from a region extending approximately between 33-55° S and 43-68° W.

Cruise or Bibliographic Source	Towing Type	N	Net Type and Mesh Aperture (μm)	Season (Month Year)	Sampled Region
Cruise PESQUERIAS II	Vertical	35	Hensen net Ø= 72 cm; 330 μm	Spring (November 1966)	Northern Argentine continental shelf (35-39.9 Lat S; 52.5-58.8 Long W)
Cruise PESQUERIAS III	Vertical	50	Hensen net Ø= 72 cm; 330 μm	Summer (February- March 1967)	Northern Argentine and Northern Patagonia continental shelf (34.5-45 Lat S; 52.5-64 Long W)
Cruise PESQUERIAS XI	Vertical	59	Hensen net Ø= 72 cm; 330 μm	Fall (March- April 1969)	Patagonian continental shelf (42.5-52.3 Lat S; 58.2-68.5 Long W)
Cruise SHINKAI MARU I	Vertical	27	Hensen net Ø= 30 cm; 300 μm	Fall (April- May 1978)	Most of the Argentine continental shelf and shelf-break (37-55 Lat S; 54.5- 69 Long W)
Cruise SHINKAI MARU II	Vertical	20	Hensen net Ø= 30 cm; 300 μm	Fall (May- June 1978)	Most of the Argentine continental shelf and shelf-break (40-54 Lat S; 56-68 Long W)
Cruise SHINKAI MARU VIII	Vertical	13	Hensen net Ø= 30 cm; 300 μm	Spring (November- December 1978)	Northern Argentine and Northern Patagonia continental shelf (39.9-45.8 Lat S; 56.2-65.3 Long W)
Cruise WALTER HERWIG III	Vertical	16	Hensen net Ø= 30 cm; 300 μm	Winter (July- August 1978)	Most of the Argentine continental shelf and shelf-break (36-54 Lat S; 53.5-

					66.2 Long W)
Cruise WALTER HERWIG IV	Vertical	21	Hensen net Ø= 30 cm; 300 µm	Winter (August- September 1978)	Most of the Argentine continental shelf and shelf-break (40.7-54.7 Lat S; 57-64.8 Long W)
Cruise WALTER HERWIG V	Vertical	18	Hensen net Ø= 30 cm; 300 µm	Spring (September- October 1978)	Most of the Argentine continental shelf and shelf-break (37.1-53.1 Lat S; 54.2-66.7 Long W)
Cruise WALTER HERWIG VI	Vertical	24	Hensen net Ø= 30 cm; 300 µm	Spring (October- November 1978)	Most of the Argentine continental shelf and shelf-break (35.9-54.8 Lat S; 54.8-65.2 Long W)
Cruise R.V. EVRIKA	Oblique	58	Bongo net Ø= 60 cm; 500 µm	Winter- Spring (August- November 1988)	Oceanic region (36.5-50 Lat S; 43.7-60.9 Long W)
Cruises SAMBOROMBÓN	Oblique	17	Mini Bongo net Ø= 20 cm; 200 or 300 µm	All the year round (March 1987-March 1988)	Samborombón Bay (Plata estuary) (35.6-36.6 Lat S; 56.8-57.3 Long W)
Cruises NICOP-La Plata	Stratified	18	Motoda net Ø= 60 cm; 300 µm	Winter (Aug.-Sept. 2003) Summer (February 2004)	Southern Brazil to northern Argentina, shelf and shelf- break (33-39.2 Lat S; 51- 56.9 Long W)
Cruise CC-12/99	Stratified	18	Multi Net Ø= 50 x 50 cm; 300 µm	Spring (October 1999)	Plata estuary and adjacent continental shelf (35.8-38 Lat S; 56- 57.4 Long W)
Cruise CC-17/99	Stratified	7	Multi Net Ø= 50 x 50 cm; 300 µm	Spring (December 1999)	Plata estuary (35.3-36.4 Lat S; 55.8-56.9 Long W)
Cruise EH-09/01	Stratified	11	Motoda net Ø= 60 cm; 200 µm	Spring (November 2001)	Transect from shelf- break to the inner Plata estuary (35.3-36.9 Lat S; 53.8-56.6 Long W)

GEF PAT (3)	Stratified	12	Motoda net Ø= 60 cm; 200 µm	Winter (September 2006)	Shelf-break (40.8-47.3 Lat S; 55.9-61.4 Long W)
Goberna (1986)	Oblique	66	Bongo net Ø= 60 cm; 330/500 µm	Summer (February 1981) Winter (July 1983)	Uruguayan shelf (35-35.8 Lat S; 51.7-55.5 Long W)
Goberna (1988)	Oblique	14	Bongo net Ø= 60 cm; 300 µm	Winter (July- August 1981)	Northern outer shelf and shelf-break 34.6-39 Lat S; 52- 55.6 Long W)
Mazzocchi & Ianora (1991)	Vertical	19	WP2 net Ø= 57 cm; 200 µm	Spring (November 1989)	Magellan Strait (52.3-53.9 Lat S; 63.6-74 Long W)
Fernández Aráoz (1994)	Oblique	9	Bongo net Ø= 60 cm; 300 µm	Winter (July 1985) Summer (January 1985)	San Jorge Gulf (45.2-46.7 Lat S; 65.4-67 Long W)
Ramírez (1996)	Vertical	18	Bi-conical net Ø= 40 cm; 300 µm	All the year round (April 1974- February 1975)	San Matías Gulf (41-42.1 Lat S; 63.5-65 Long W)
Sabatini et al. (2001)	Oblique	6	Nackthai net Ø= 20 cm; 400 µm	Spring (November 1996)	Southern Patagonian shelf (51-54.9 Lat S; 64.8-68.9 Long W)
Sabatini et al. (2004)	Oblique	4	Nackthai net Ø= 20 cm; 400 µm	Summer (March 1994)	Southern Patagonian shelf (51 Lat S; 64-65.7 Long W)
Sabatini et al. (2008)	Oblique	7	Nackthai net Ø= 20 cm; 390 µm	Fall (March- April 2000)	Southern Patagonian shelf (51-53.1 Lat S; 65.5-68.2 Long W)

Table 2: Summary of different potential bias sources for each ecoregion, expressed as percentage of different mesh sizes employed, seasons sampled and sampling effort.

Groups	% 200µm	% 300/330µm	% 400µm	% 500µm	% vertical	% oblique	% stratified	Summer		Fall		Winter		Spring		Stations x 10,000 km ²
								% stations	N° species	% stations	N° species	% stations	N° species	% stations	N° species	
Coastal	17	83	0	0	44	22	34	14	13	30	14	9	7	47	20	5.48
Shelf	10	85	5	0	77	14	9	13	25	28	24	24	37	35	42	2.53
Northern shelfbreak	3	97	0	0	26	53	21	15	36	0	0	70	65	15	41	5.60
Northern offshore	0	3	0	97	0	100	0	0	0	0	0	100	30	0	0	0.78
Southern offshore	3	51	4	42	46	51	3	7	13	35	22	36	30	22	15	0.64
Summer Northern shelf	2	98	0	0	89	0	11	96	36	2	4	0	0	2	7	6.40

Species	Journal Pre-proof						mer northern shelf
	Coastal	shelf	shelfbreak	offshore	offshore	offshore	
<i>Acartia (Acanthacartia) tonsa</i>	71.4	17.9	29.4	0.0	0.0	14.9	
<i>Acartia (Acartia) danae</i>	0.0	0.3	52.9	0.0	0.0	0.0	
<i>Acartia (Acartia) negligens</i>	0.0	0.3	17.6	3.4	0.0	0.0	
<i>Acartia (Acartiura) clausi</i>	3.9	1.0	0.0	0.0	0.0	0.0	
<i>Aetideus armatus</i>	0.0	3.3	17.6	0.0	37.5	6.4	
<i>Aetideus giesbrechti</i>	0.0	0.0	17.6	0.0	1.4	6.4	
<i>Agetus flaccus</i>	0.0	0.0	11.8	0.0	0.0	8.5	
<i>Calanoides carinatus</i>	35.1	17.6	47.1	3.4	5.6	44.7	
<i>Calanus australis</i>	3.9	53.1	44.1	10.3	12.5	10.6	
<i>Calanus simillimus</i>	1.3	36.8	14.7	6.9	80.6	2.1	
<i>Calocalanus pavo</i>	0.0	0.3	11.8	0.0	0.0	0.0	
<i>Candacia bispinosa</i>	0.0	0.0	20.6	0.0	0.0	0.0	
<i>Candacia cheirura</i>	0.0	1.6	5.9	27.6	1.4	0.0	
<i>Candacia longimana</i>	0.0	0.0	17.6	10.3	0.0	0.0	
<i>Candacia pachydactyla</i>	0.0	0.0	17.6	27.6	0.0	0.0	
<i>Candacia simplex</i>	0.0	0.0	14.7	0.0	1.4	2.1	
<i>Centropages brachiatus</i>	0.0	35.8	67.6	20.7	13.9	2.1	
<i>Centropages bradyi</i>	0.0	1.0	23.5	0.0	1.4	0.0	
<i>Centropages furcatus</i>	0.0	1.6	2.9	0.0	0.0	23.4	
<i>Centropages velificatus</i>	0.0	0.0	0.0	0.0	0.0	70.2	
<i>Clausocalanus brevicornis</i>	0.0	5.9	11.8	0.0	0.0	0.0	
<i>Clausocalanus brevipes</i>	7.8	41.7	20.6	3.4	40.3	0.0	
<i>Clausocalanus laticeps</i>	0.0	18.2	8.8	6.9	44.4	0.0	
<i>Corycaeus (Corycaeus) speciosus</i>	0.0	0.0	8.8	0.0	0.0	4.3	
<i>Ctenocalanus citer</i>	0.0	6.8	8.8	0.0	0.0	0.0	
<i>Ctenocalanus vanus</i>	45.5	39.1	29.4	3.4	16.7	21.3	
<i>Ditricorycaeus amazonicus</i>	50.6	1.3	14.7	0.0	0.0	23.4	
<i>Drepanopus forcipatus</i>	9.1	58.0	11.8	0.0	9.7	4.3	
<i>Eucalanus attenuatus</i>	0.0	0.3	23.5	3.4	0.0	0.0	
<i>Eucalanus elongatus elongatus</i>	0.0	0.3	47.1	0.0	1.4	0.0	
<i>Euchaeta acuta</i>	2.6	0.7	0.0	48.3	0.0	0.0	
<i>Euchaeta marina</i>	0.0	0.0	52.9	3.4	4.2	4.3	
<i>Euchirella rostrata</i>	0.0	0.0	26.5	0.0	11.1	0.0	
<i>Euterpina acutifrons</i>	44.2	4.9	8.8	0.0	0.0	6.4	
<i>Farranula gracilis</i>	0.0	0.0	14.7	0.0	0.0	0.0	
<i>Gaetanus tenuispinus</i>	0.0	0.3	8.8	3.4	1.4	2.1	
<i>Goniopsyllus rostratus</i>	2.6	0.0	11.8	0.0	0.0	2.1	
<i>Haloptilus acutifrons</i>	0.0	0.0	14.7	3.4	4.2	0.0	
<i>Haloptilus longicornis</i>	0.0	0.3	23.5	0.0	1.4	0.0	
<i>Haloptilus oxycephalus</i>	0.0	0.3	8.8	0.0	8.3	0.0	
<i>Hemicyclops thalassius</i>	13.0	0.0	0.0	0.0	0.0	0.0	
<i>Heterorhabdus austrinus</i>	0.0	0.7	14.7	13.8	2.8	0.0	
<i>Heterorhabdus papilliger</i>	0.0	0.0	17.6	0.0	0.0	0.0	
<i>Labidocera fluviatilis</i>	54.5	7.8	8.8	0.0	0.0	51.1	
<i>Lucicutia flavicornis</i>	0.0	0.0	41.2	0.0	0.0	0.0	
<i>Macrosetella gracilis</i>	0.0	0.0	14.7	0.0	0.0	2.1	
<i>Mecynocera clausi</i>	0.0	0.3	70.6	0.0	1.4	4.3	

<i>Metridia lucens lucens</i>	2.6	8.5	32.4	82.8	47.2	0.0
<i>Metridia lucens pacifica</i>	0.0	2.9	0.0	0.0	0.0	0.0
<i>Microcalanus pusillus</i>	0.0	4.2	0.0	0.0	0.0	0.0
<i>Microsetella norvegica</i>	0.0	3.9	8.8	0.0	0.0	0.0
<i>Nannocalanus minor</i>	0.0	1.6	44.1	17.2	0.0	19.1
<i>Neocalanus gracilis</i>	0.0	0.0	38.2	79.3	2.8	2.1
<i>Neocalanus robustior</i>	0.0	0.0	14.7	0.0	0.0	2.1
<i>Neocalanus tonsus</i>	1.3	2.9	0.0	44.8	23.6	0.0
<i>Oithona atlantica</i>	0.0	37.8	73.5	3.4	34.7	14.9
<i>Oithona nana</i>	55.8	13.0	14.7	0.0	0.0	6.4
<i>Oithona plumifera</i>	1.3	13.4	14.7	0.0	8.3	6.4
<i>Oithona setigera</i>	0.0	0.7	26.5	0.0	0.0	0.0
<i>Oithona similis aff. helgolandica</i>	18.2	71.0	32.4	0.0	5.6	6.4
<i>Oncaea curvata</i>	0.0	4.6	0.0	0.0	0.0	0.0
<i>Oncaea venusta</i>	0.0	1.3	35.3	0.0	0.0	0.0
<i>Onychocorycaeus giesbrechti</i>	0.0	0.3	2.9	0.0	0.0	8.5
<i>Paracalanus parvus</i>	83.1	18.9	23.5	0.0	0.0	4.3
<i>Paraeucalanus sewelli</i>	0.0	0.0	11.8	0.0	0.0	0.0
<i>Paraeuchaeta antarctica</i>	0.0	3.6	0.0	0.0	0.0	0.0
<i>Parvocalanus crassirostris</i>	33.8	0.3	0.0	0.0	0.0	0.0
<i>Pleuromamma abdominalis</i>	0.0	0.0	32.4	65.5	0.0	0.0
<i>Pleuromamma gracilis</i>	0.0	0.3	55.9	96.6	5.6	0.0
<i>Pleuromamma robusta</i>	0.0	3.9	14.7	58.6	11.1	0.0
<i>Pleuromamma xiphias</i>	0.0	0.3	41.2	65.5	0.0	0.0
<i>Pontella patagoniensis</i>	0.0	0.0	0.0	0.0	0.0	14.9
<i>Rhincalanus cornutus</i>	0.0	0.0	32.4	0.0	0.0	0.0
<i>Rhincalanus gigas</i>	0.0	0.7	0.0	0.0	11.1	0.0
<i>Rhincalanus nasutus</i>	0.0	7.8	5.9	0.0	31.9	0.0
<i>Sapphirina angusta</i>	0.0	0.3	50.0	3.4	1.4	10.6
<i>Scolecithricella minor</i>	0.0	3.6	14.7	0.0	1.4	0.0
<i>Scolecithrix danae</i>	0.0	0.0	26.5	24.1	1.4	0.0
<i>Scottocalanus securifrons</i>	0.0	0.0	17.6	0.0	0.0	0.0
<i>Subeucalanus longiceps</i>	0.0	7.5	41.2	6.9	72.2	0.0
<i>Subeucalanus pileatus</i>	0.0	4.6	32.4	0.0	0.0	87.2
<i>Temora stylifera</i>	0.0	0.3	41.2	0.0	0.0	80.9
<i>Triconia conifera</i>	3.9	2.3	38.2	0.0	0.0	4.3
<i>Undeuchaeta plumosa</i>	0.0	0.0	8.8	20.7	0.0	0.0
<i>Undinula vulgaris</i>	0.0	0.0	20.6	0.0	0.0	4.3
<i>Urocorycaeus lautus</i>	0.0	0.0	17.6	0.0	0.0	0.0
TOTAL NUMBER OF SPECIES	22	58	74	30	36	37

Table 3: Occurrence percentage of copepod species by sampling stations at each ecoregion. The six ecoregions are based on cluster analysis and nonmetric multidimensional scaling analysis (MDS), on copepod species presence/absence. The significance of the groups defined was tested performing a similarity profile (SIMPROF) permutation test. Grayed background indicates the indicator species of each ecoregion, as identified by the SIMPER analysis. The more frequent a species is within a group, the more it will contribute to the intragroup similarity.

Table 4: Effects of temperature (T) and salinity (S) on the copepods' composition of the ecoregions. A distance-based linear model (DISTLM) analysis was developed based on temperature and salinity climatological data from the World Ocean Atlas, and the resemblance matrix based on copepods' presence/absence. DISTLM produced a final model including both temperature and salinity, explaining 16% of the variation ($R^2 = 0.16$).

Marginal test			
Environmental variable	Pseudo-F	P	Explained Variation (%)
T	50.15	0.001	9.51
S	36.44	0.001	7.09

Overall best solutions			
Environmental variable	AIC	R^2	Explained Variation (%)
T + S	3783.2	0.157	16
T	3815.2	0.095	9
S	3827.8	0.071	7

Table 5: Indicator species for each ecoregion. The percentage contribution to the average similarity within each ecoregion, the mean length range of species, the reported inshore/offshore distribution, and water masses/regions inhabited are indicated. Information was taken from Bradford-Grieve et al. (1999), and updated following Cepeda et al. (2018) and Razouls et al. (2019).

Indicator Species	Contribution to similarity (%)	Length range (mm)	Inshore/offshore distribution	Latitudinal distribution
Coastal Ecoregion				
<i>Paracalanusparvus</i>	25.75	0.70-1.30	Coastal, middle shelf	Tropical, subtropical and warm temperate, wide distribution
<i>Acartia(Acanthacartia) tonsa</i>	18.82	0.90-1.50	Estuarine and, coastal	Tropical, subtropical and warm temperate, wide distribution
<i>Oithona nana</i>	11.32	0.44-0.72	Estuarine, coastal	Tropical, subtropical, and warm temperate, wide distribution
<i>Labidocerafluviatilis</i>	10.15	2.40-2.50	Estuarine and coastal ¹	Tropical, subtropical and warm temperate
<i>Ditricorycaeusamazonicus</i>	8.65	0.84-1.04	Coastal	Tropical, S America
<i>Euterpinaacutifrons</i>	7.74	0.50-0.75	Estuarine and coastal	Tropical, subtropical and warm temperate, wide distribution
<i>Ctenocalanusvanus</i>	6.69	0.92-1.26	Coastal, shelf and oceanic	Subantarctic and cold temperate, wide distribution
Shelf Ecoregion				
<i>Oithonasimilisaff. helgolandica</i>	25.36	0.67-0.96	Coastal, shelf and oceanic	Wide distribution
<i>Drepanopusforcipatus</i>	16.79	1.66-2.74	Coastal, shelf and oceanic	Antarctic, subantarctic, SW Atlantic and SE Pacific
<i>Calanusaustralis</i>	15.03	2.60-3.59	Inner and middle shelf	SW Atlantic, SE Atlantic? SE Pacific?
<i>Clausocalanusbrevipes</i>	8.14	1.12-1.62	Shelf and oceanic	Antarctic, subantarctic and cold temperate, wide distribution
<i>Ctenocalanusvanus</i>	7.72	0.92-1.26	Coastal, shelf and oceanic	Subantarctic and cold temperate, wide distribution
<i>Oithonaatlantica</i>	6.64	0.82-1.43	Middle and outer shelf	Wide distribution
<i>Calanussimillimus</i>	6.24	2.62-3.80	Middle shelf, outer shelf and oceanic	Antarctic, subantarctic, cold temperate, Southern Hemisphere
Northern Shelf Break Ecoregion				
<i>Oithonaatlantica</i>	9.17	0.82-1.43	Middle and outer shelf	Wide distribution
<i>Mecynoceraclausi</i>	8.64	0.92-1.21	Oceanic	Tropical, subtropical and temperate, wide distribution
<i>Centropagesbrachiatus</i>	7.29	1.58-2.30	Shelf	Wide distribution south of 35°N ²
<i>Pleuromammagracilis</i>	4.81	1.60-2.15	Oceanic	Tropical and subtropical, wide distribution
<i>Acartia(Acartia) danae</i>	4.32	0.72-1.34	Oceanic	Wide distribution excepting the Arctic Ocean
<i>Euchaeta marina</i>	4.31	2.88-3.64	Oceanic	Tropical, subtropical and temperate, wide distribution
<i>Sapphirinaangusta</i>	4.10	2.50-7.60	Oceanic	Tropical, subtropical,

				temperate, wide distribution SW Atlantic 20°S-47°S
<i>Calanoidescarinatus</i>	3.87	2.25-2.85	Inner and middle shelf	
<i>Eucalanuselongatuselongatus</i>	3.79	5.658	Shelf, oceanic ²	Tropical, subtropical and temperate, wide distribution
<i>Nannocalanusminor</i>	3.60	1.20-2.25	Oceanic	Wide distribution excepting the Arctic Ocean
<i>Calanusaustralis</i>	2.81	2.60-3.59	Inner and middle shelf	SW Atlantic, SE Atlantic? SE Pacific?
<i>Lucicutiaflavicornis</i>	2.76	1.30-2.00	Oceanic	Tropical, subtropical and temperate, wide distribution
Northern Offshore Ecoregion				
<i>Pleuromammagracilis</i>	24.50	1.60-2.15	Oceanic	Tropical and subtropical, wide distribution
<i>Metridialucenslucens</i>	17.83	1.62-2.93	Oceanic	Wide distribution
<i>Neocalanusgracilis</i>	15.54	2.30-4.00	Oceanic	Wide distribution excepting arctic and antarctic regions
<i>Pleuromammamaxiphias</i>	9.88	4.00-4.90	Oceanic	Wide distribution excepting the Arctic ocean
<i>Pleuromammaabdominalis</i>	9.22	2.40-3.70	Oceanic	Wide distribution excepting arctic and antarctic regions
<i>Pleuromamma robusta</i>	7.43	3.00-4.30	Oceanic	Wide distribution
<i>Euchaetaacuta</i>	4.80	3.36-4.28	Oceanic	Wide distribution excepting arctic and antarctic regions
<i>Neocalanustonsus</i>	3.90	3.30-4.40	Oceanic	Antarctic, subantarctic and cold temperate
Southern Offshore Ecoregion				
<i>Calanussimillimus</i>	33.79	2.65-3.80	Middle shelf, outer shelf and oceanic	Antarctic, subantarctic, cold temperate, Southern Hemisphere
<i>Subeucalanuslongiceps</i>	23.92	4.20-4.90	oceanic	Antarctic, subantarctic and cold temperate
<i>Metridialucenslucens</i>	8.49	1.62-2.93	Oceanic	Wide distribution
<i>Clausocalanuslaticeps</i>	7.43	1.01-1.67	Oceanic	Antarctic, subantarctic and cold temperate
<i>Clausocalanusbrevipes</i>	6.21	1.12-1.62	Shelf and oceanic	Antarctic, subantarctic and cold temperate, wide distribution
<i>Aetideusarmatus</i>	4.50	1.30-2.00	Oceanic	Wide distribution excepting the Arctic ocean
<i>Oithonaatlantica</i>	4.04	0.82-1.43	Middle and outer shelf	Wide distribution
<i>Neocalanustonsus</i>	3.71	3.30-4.40	Oceanic	Antarctic, subantarctic and cold temperate, wide distribution
Summer Northern Shelf Ecoregion				
<i>Subeucalanuspileatus</i>	30.45	1.80-2.50	Oceanic	Tropical, subtropical and temperate, wide distribution
<i>Temorastylifera</i>	24.44	1.60-1.85	Coastal, oceanic	Tropical, subtropical and temperate, wide distribution
<i>Centropagesvelificatus</i>	21.03	1.725	Estuarine, coastal ¹	Tropical and subtropical South America

<i>Labidocerafluviatilis</i>	8.97	2.40-2.50	Estuarine and coastal ¹	Tropical, subtropical and warm temperate
<i>Calanoidescarinatus</i>	6.36	2.25-2.85	Inner and middle shelf	SW Atlantic 20°S-47°S

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Table 6: Average dissimilarity (%) between groups of stations conforming the ecoregions. SIMPER pair-wise tests reveal that all the ecoregions were clearly distinct, with percentages of dissimilarity in pairwise comparisons higher than 80%.

	Coastal	Shelf	Summer Northern Shelf	Northern Shelfbreak	Northern Offshore	Southern Offshore
Coastal	---					
Shelf	84.6	---				
Summer NS	86.1	92.3	---			
Northern SB	90.6	85.8	87.7	---		
Northern Off.	98.9	95.4	98.9	83.3	---	
Southern Off.	97.2	82.1	97.5	88.6	87.1	---

Highlights

- Ecoregions based on copepod assemblages are associated with water mass characteristics
- Marine fronts match the boundaries of the ecoregions
- Ecoregions match the biogeographic provinces of the southwestern South Atlantic

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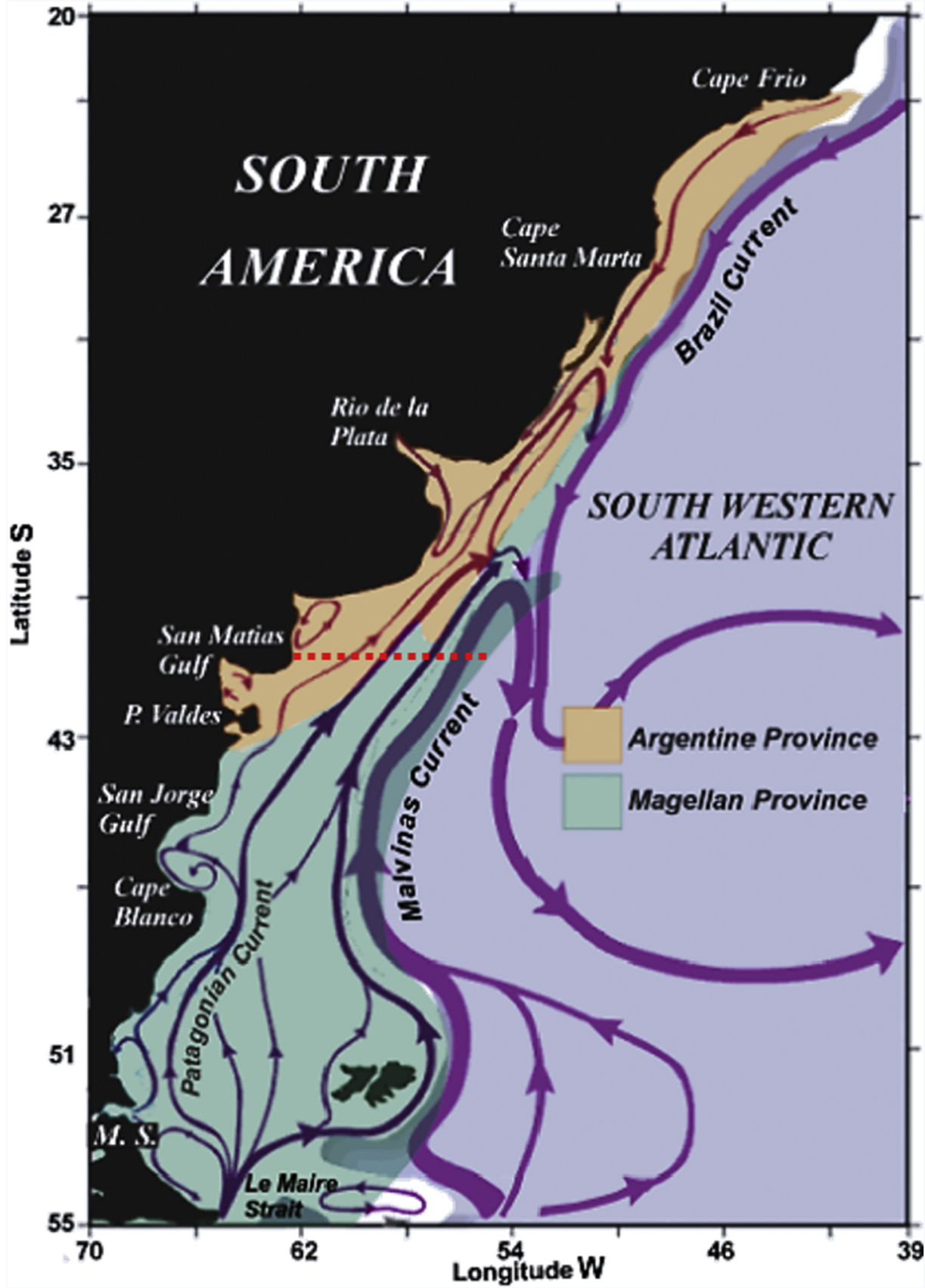


Figure 1

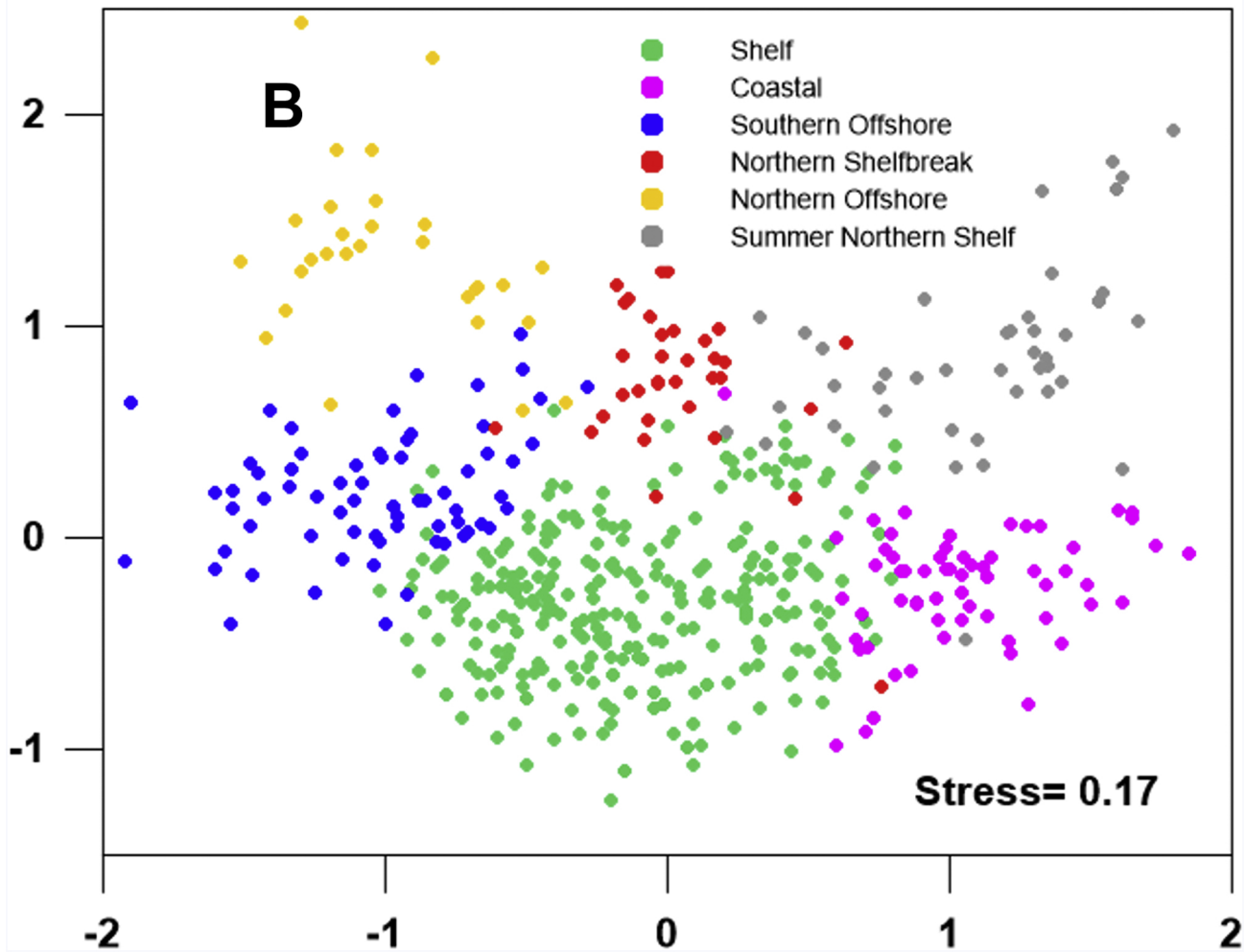
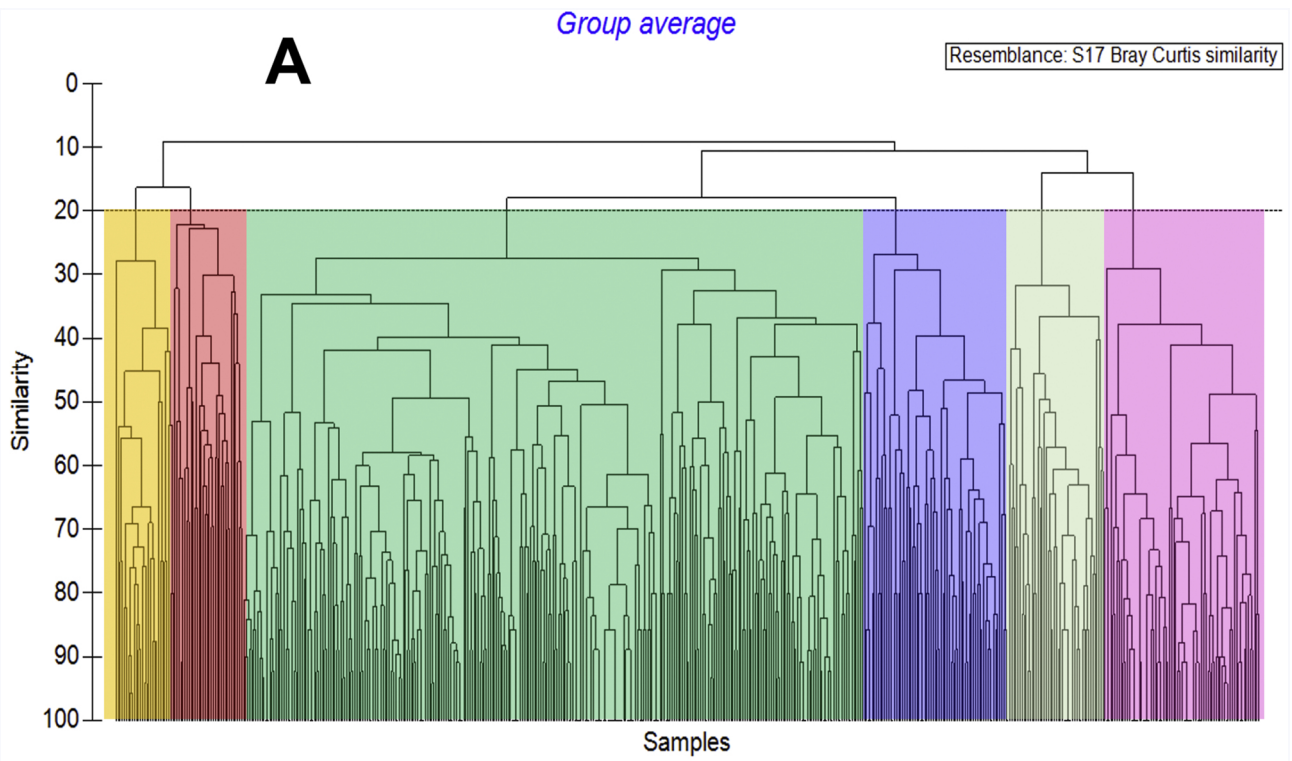


Figure 2

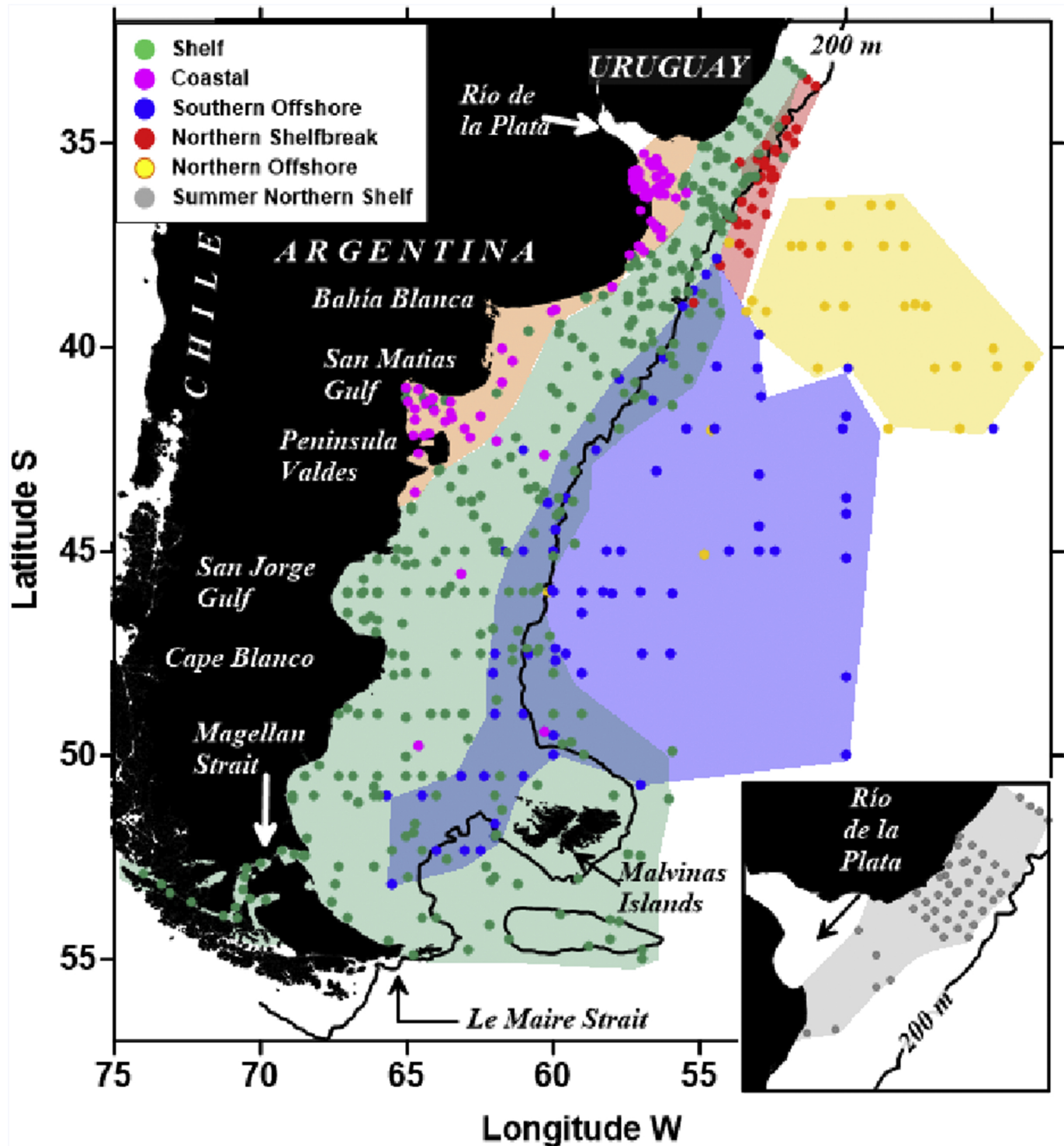


Figure 3

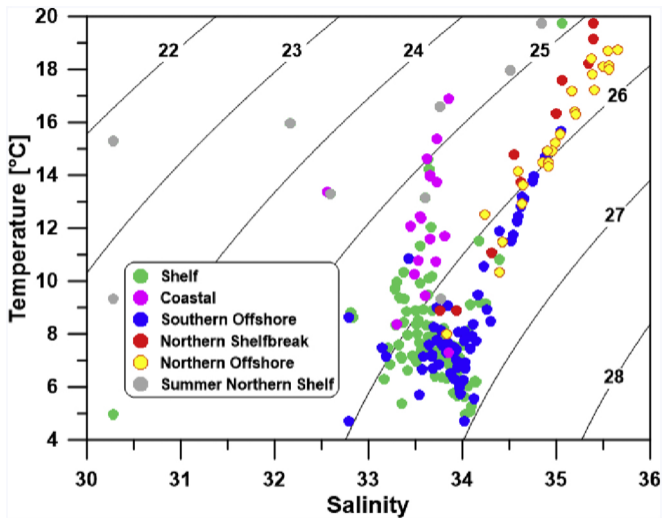


Figure 4

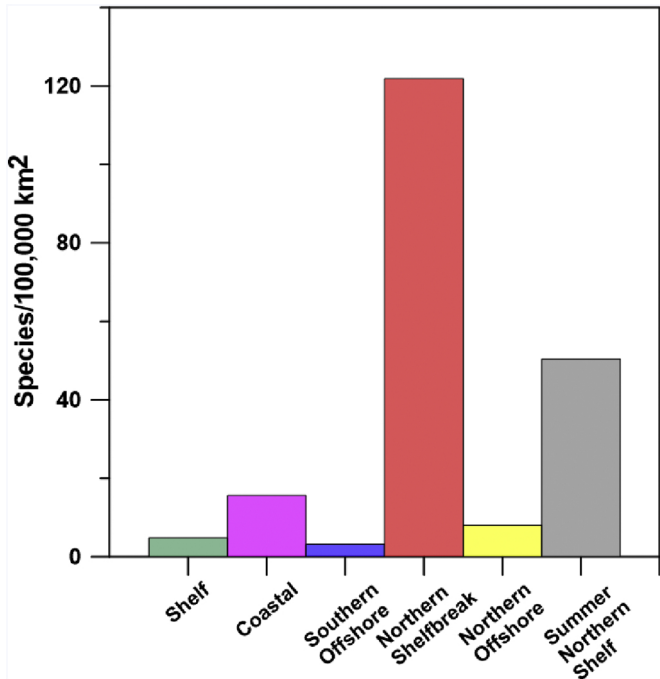


Figure 5

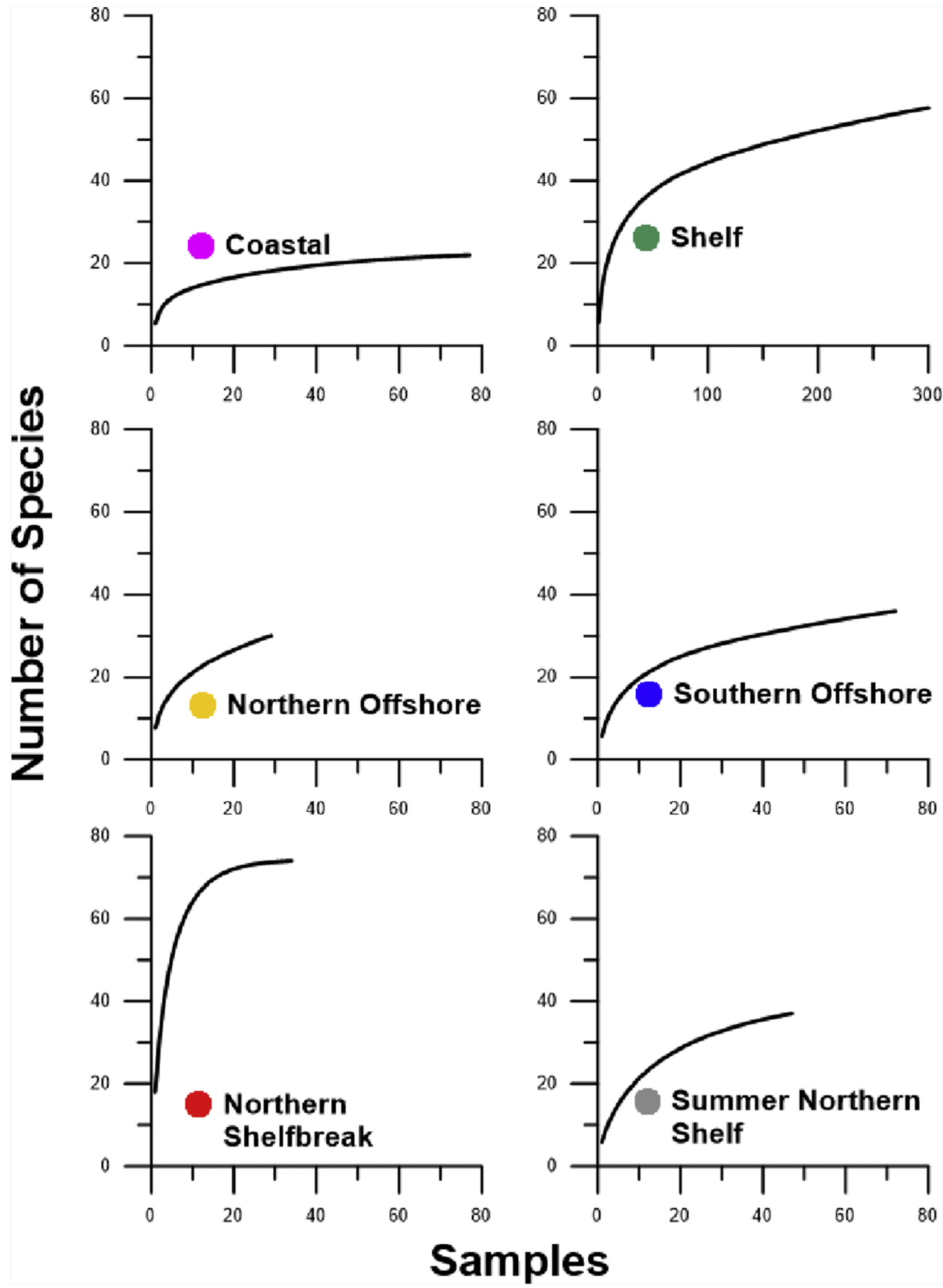


Figure 6

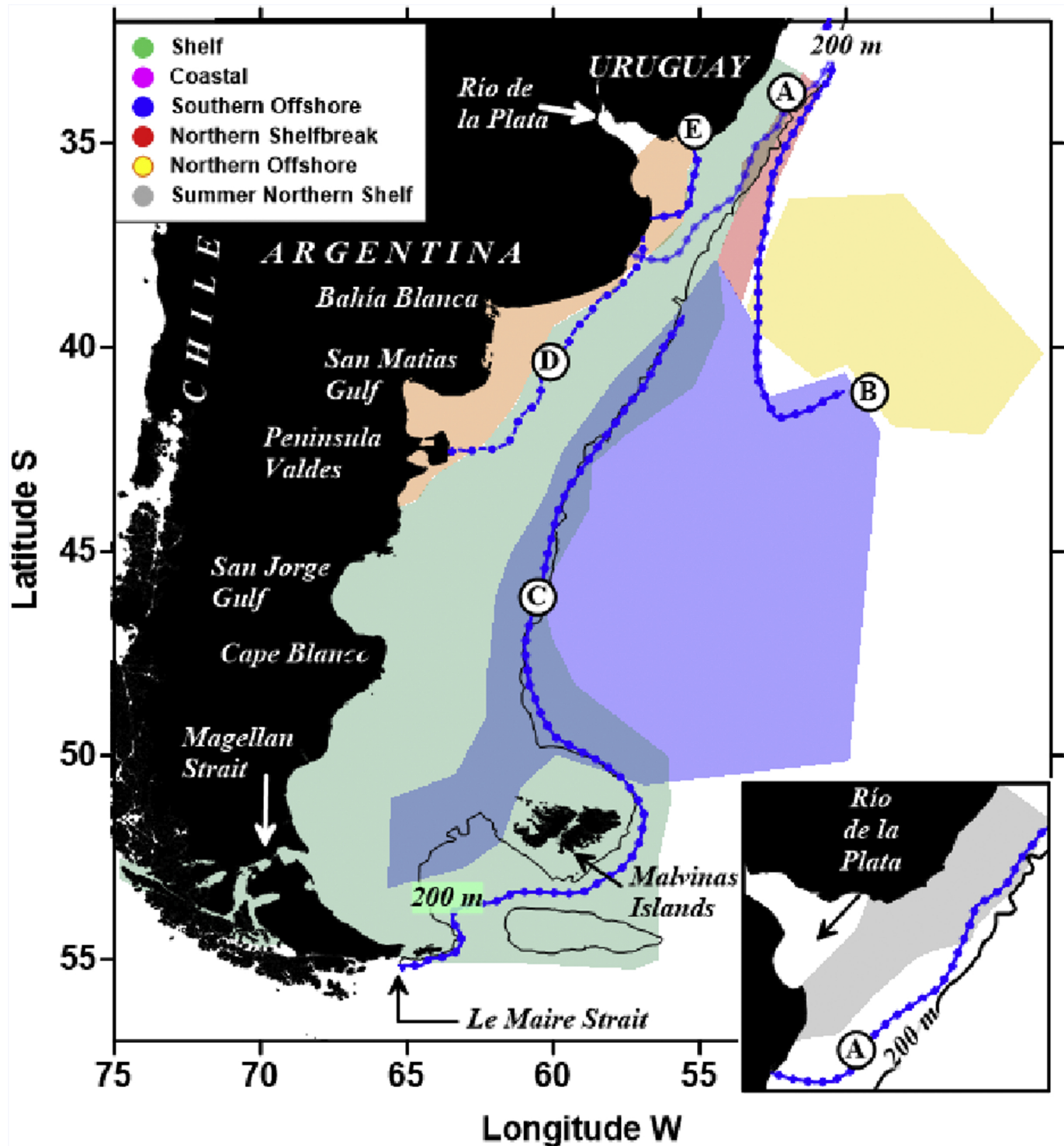


Figure 7

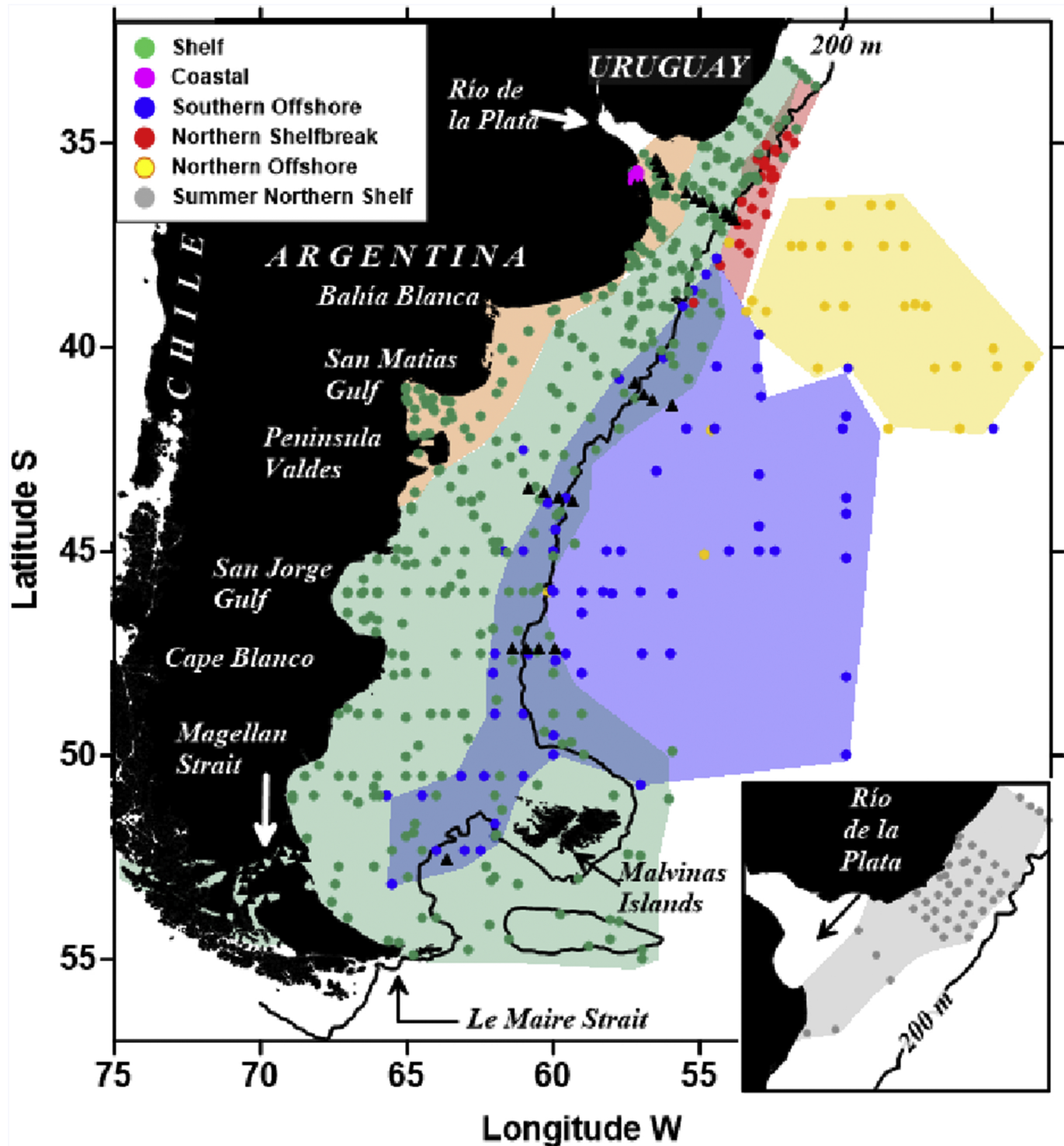


Figure 8

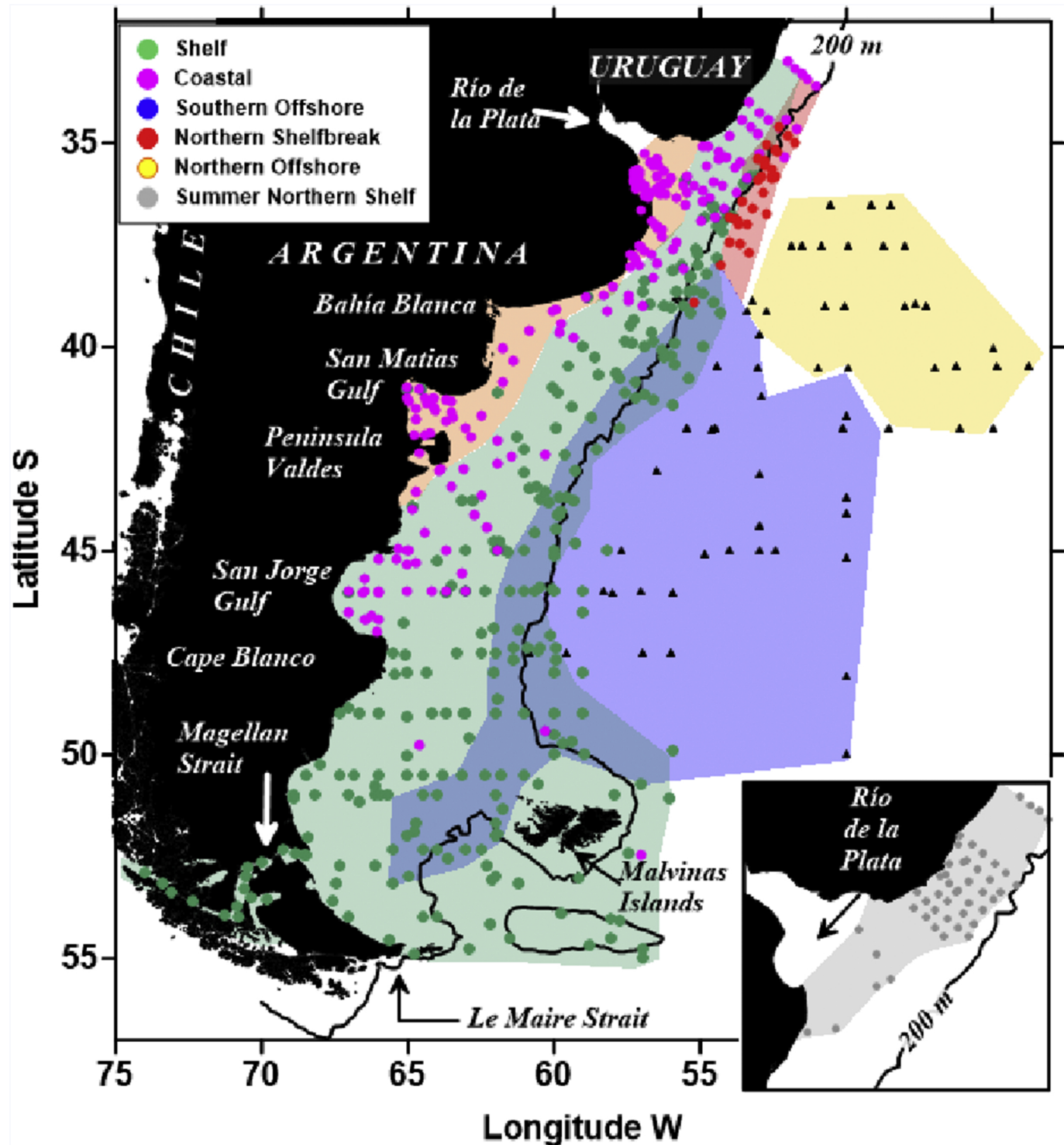


Figure 9

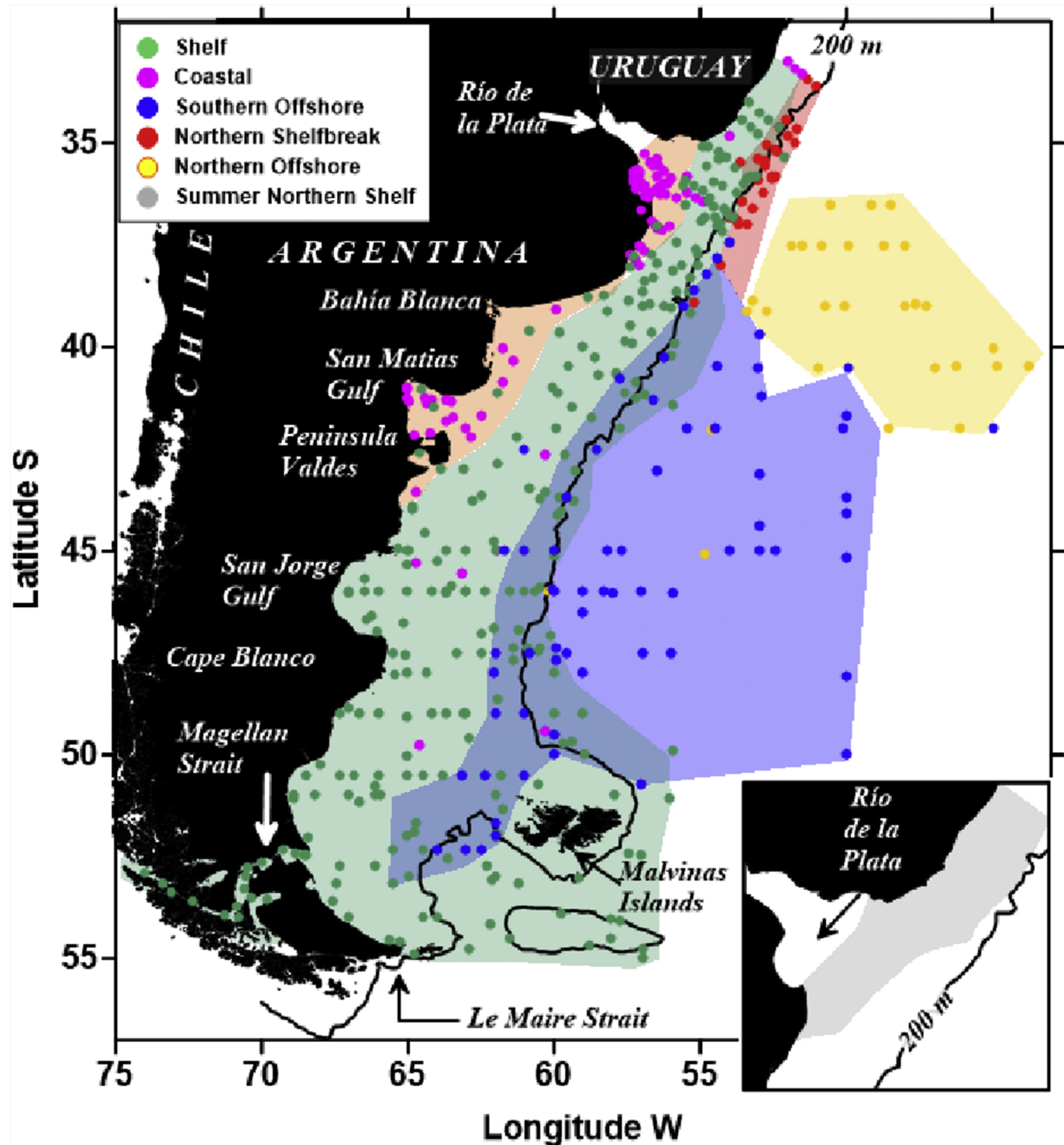


Figure 10

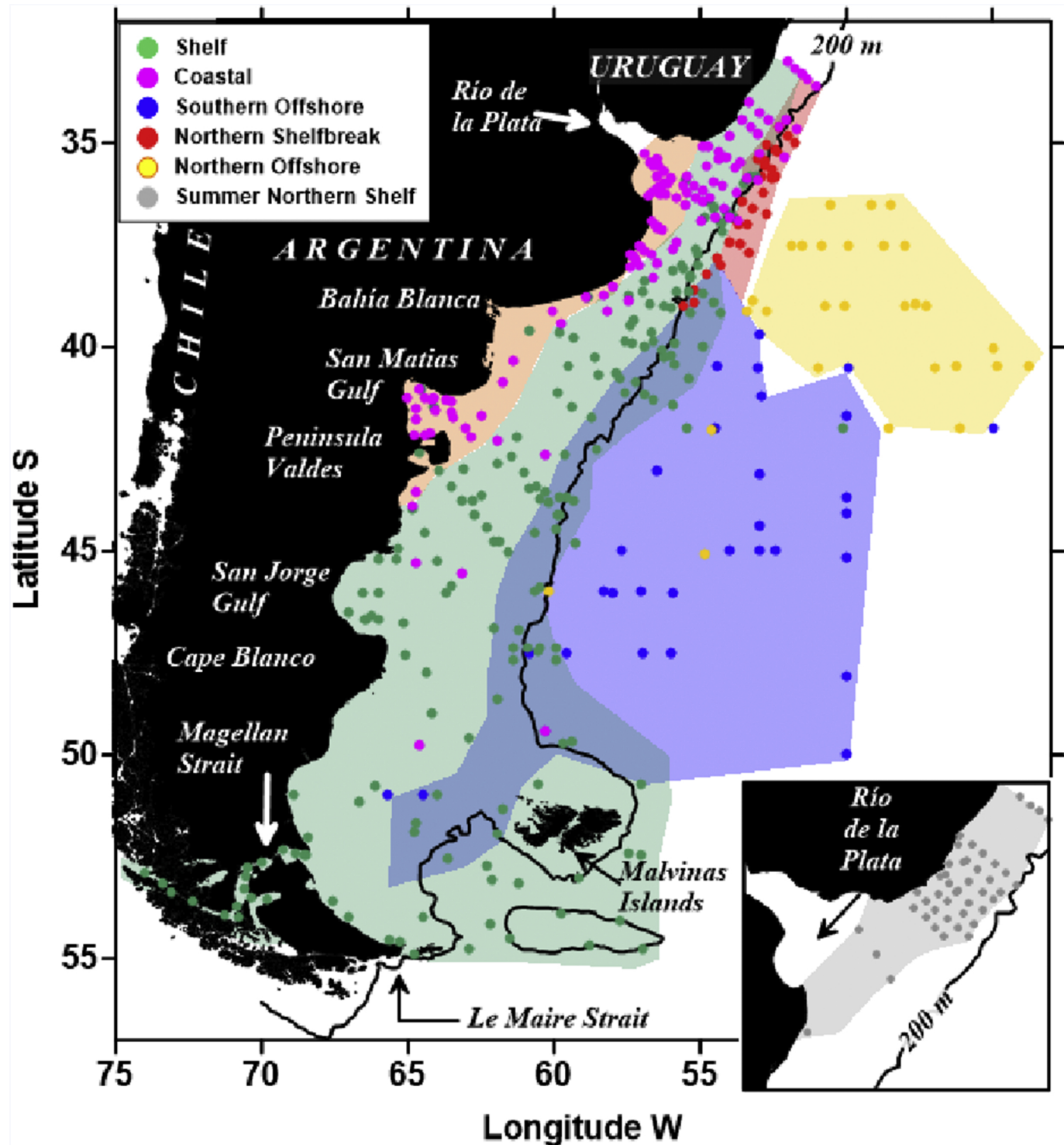


Figure 11

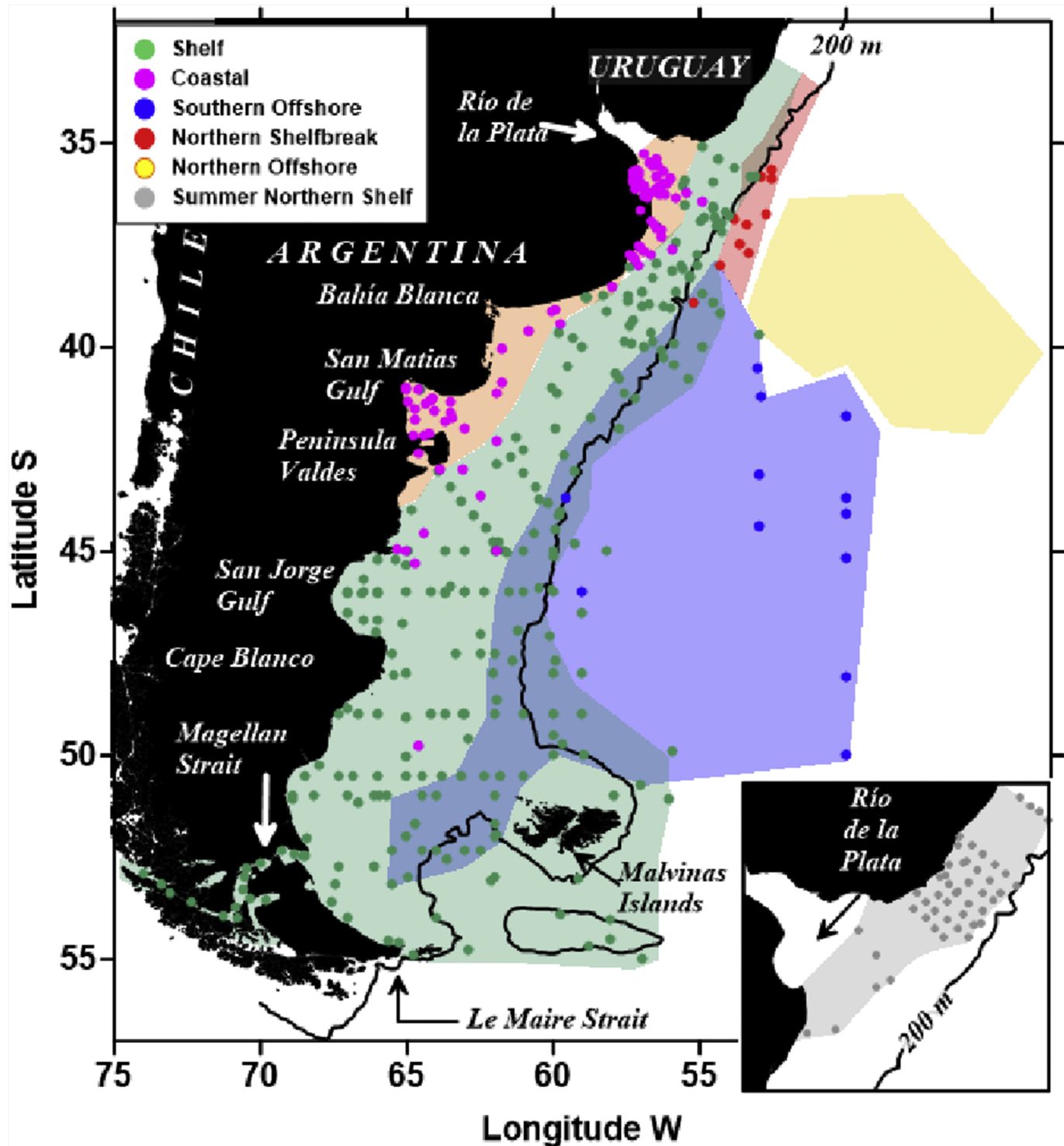


Figure 12

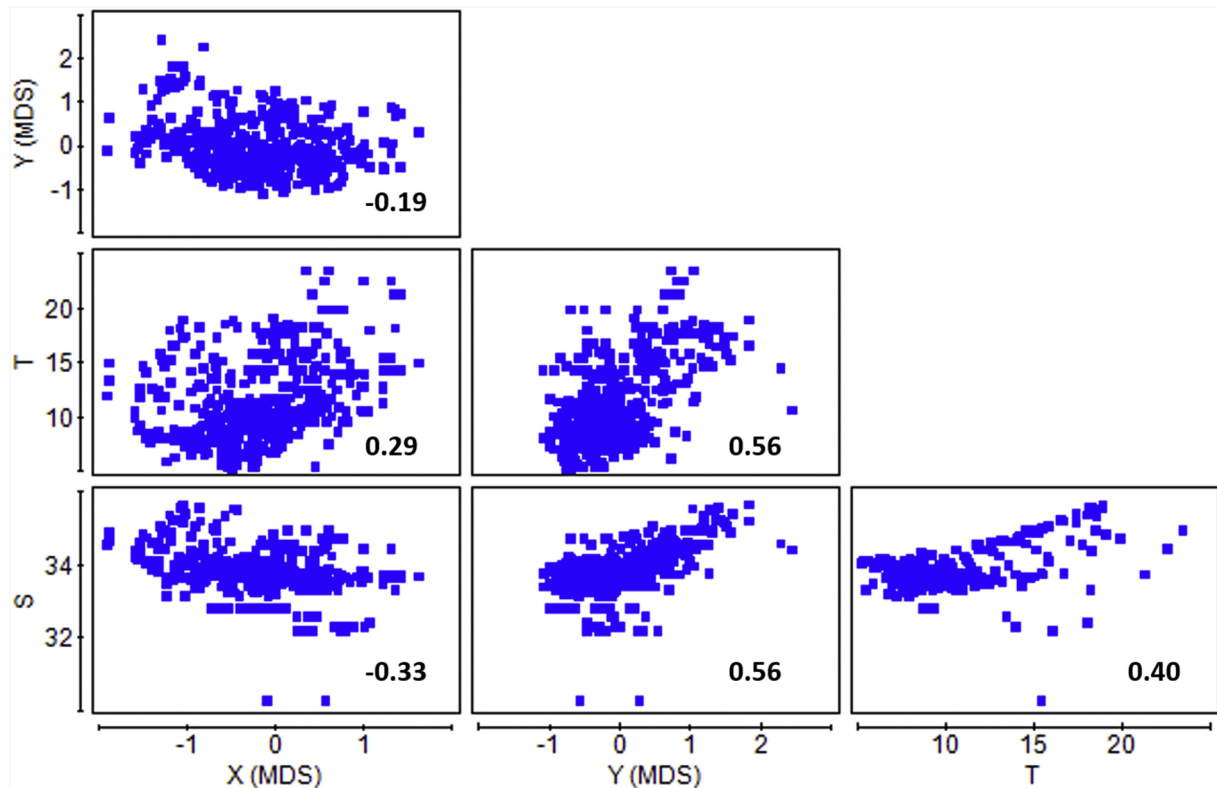


Figure 13