


Original Article

Towards regionalization of the chondrichthyan fauna of the Southwest Atlantic: a spatial framework for conservation planning

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Biogeographic regionalization identifies natural species assemblages of a given region. In this study, the geographic distribution of chondrichthyan species richness and species assemblages for the Southwest Atlantic were identified. The geographic distribution of 103 chondrichthyans was estimated through modelling. Based on the obtained binary maps, the distribution of chondrichthyan richness was obtained at four taxonomic levels: class Chondrichthyes (chondrichthyans), subclass Holocephali (chimaeras), division Selachii (sharks), and division Batomorphi (batoids). The continental shelf off Uruguay and southern Brazil presented the highest levels of chondrichthyan richness, and a smaller peak was found in El Rincón (northern Argentina). Shark richness concentrated mainly off Lagoa dos Patos (southern Brazil). Batoid richness was maximal off Uruguay and northern Argentina, including modes in El Rincón, San Jorge Gulf, and slope of the Argentinean shelf. Classification analyses revealed the presence of a hierarchical regionalization, with three main and six minor assemblages. Main assemblages are hierarchically identifiable as provinces and minor ones as ecoregions or districts. Two of the main assemblages correspond with the Argentinean and Magellanic Provinces; the third one is identified here for the first time, the Patagonian Slope Province. This regionalization provides the basis for the design of protected area networks for conservation or management purposes.

Keywords: biogeography, chimaeras, elasmobranchs, MaxLike, rays, sharks, skates

Introduction

A fundamental objective of biogeography is the regionalization of nature, that is the elucidation of a hierarchical system that categorizes geographic areas in terms of their biota (Escalante, 2009; Morrone, 2018). From the relationships among the distribution of individual species, it is possible to identify homogeneous and continuous areas characterized by different species assemblages (Kreft and Jetz, 2010; Escalante, 2016). Identification of areas based on species assemblages has ecological relevance because natural biogeographic units are pinpointed to represent different

biological communities. Regionalization is an area of exhaustive growth, with recent development in the marine environment (Griffiths *et al.*, 2009; Kulbicki *et al.*, 2013; Costello *et al.*, 2017; Pinheiro *et al.*, 2018). In regionalization, one of the challenges is to predict how species, supraspecific taxa, or populations are distributed spatially and temporarily. However, the vast extent of distribution areas sometimes complicates the evaluation of factors that determine the habitat use by species. For this approach, species distribution models (Guisan and Zimmermann, 2000; Argáez *et al.*, 2005; Elith *et al.*, 2006; Norberg *et al.*, 2019) on a

continental or regional scale can be used to solve this problem (Mackey and Lindenmayer, 2001; Pearson and Dawson, 2003).

In the Southwest Atlantic (SWA), the current biogeographic divisions, in general, are the same as those proposed 170 years ago. In the 19th century, the first regionalization identified five provinces: (i) São Paulo (24°S to 30°S), (ii) Uruguayan, (30°S to the Río de la Plata), (iii) Río de la Plata, (iv) North Patagonian (from Río de la Plata up to 43°S), and (v) South Patagonian or Magellanic (Dana, 1853; Forbes, 1856; Woodward, 1856). During the 20th century, water masses and several faunal groups were analysed, giving an oceanographic and biogeographic framework to the region (e.g. Carcelles and Wolliamson, 1951; Guerrero and Piola, 1997; Díaz de Astarloa et al., 1999; Boschi, 2000; Menni and Stehmann, 2000). This historical legacy allowed the development of different biogeographical schemes for the SWA in the last 20 years. Longhurst (1998) identified two biophysical provinces: (i) Brazil Current Coastal Province and (ii) SWA Shelves Province. Saraceno et al. (2005), analysing physical characteristics, found a similar bioregionalization to Longhurst (1998) but incorporated a new province on slope areas, called Patagonian Shelf Break. Spalding et al. (2007), based on taxa distribution, evolutionary history, and dispersion and isolation patterns, for coastal and shelf sectors, determined a South American realm, Temperate South America, with two provinces and internal ecoregions: (i) Warm Temperate Southwestern Atlantic Province, with four ecoregions: (a) Southeastern Brazil, (b) Rio Grande, (c) Río de la Plata, and (d) Uruguay-Buenos Aires Shelf; and (ii) Magellanic Province, with four ecoregions: (a) North Patagonian gulfs, (b) Patagonian Shelf, (c) Malvinas/Falklands, and (d) Channels and Fjords of Southern Chile. Balech and Ehrlich (2008), based on hydrography and taxa distribution, recognized three provinces with internal districts: (i) Paulista Province; (ii) Argentinean Province, with two districts: (a) Uruguayan and (b) Rionegrino; and (iii) Magellanic Province with two districts (a) Chubutian and (b) South Patagonian. Recently, Briggs and Bowen (2012) proposed a realignment of the Magellanic Province based on invertebrate endemism identifying four new provinces: (i) Southern Chile, (ii) Tierra del Fuego, (iii) Southern Argentina, and (iv) Malvinas/Falkland Islands. Finally, Costello et al. (2017), based on a statistical analysis of the distribution of 65 000 species of animals and plants, divided the SWA shelf into two realms: one realm extending over the whole shelf south of Uruguay, Argentinean Realm, and another extending over the entire coast of Brazil without differentiation from the oceanic tropical Atlantic, Offshore South Atlantic Realm.

The historical biogeographic divisions above described have differences between the limits of the biogeographic units and in their internal structure. Already, the first schemes indicated a single Magellanic province south of 43°S, while to the north the biota was more subdivided (Dana, 1853; Forbes, 1856; Woodward, 1856). The region from 43°S northwards up to 23°S (Río de Janeiro, Brazil) has been known as the Argentinean Province since Cooke (1895). The Argentinean Province has usually been divided into two districts, the South Brazilian and the Bonaerensean Districts, with their limit at 34°S (López, 1963; Menni et al., 1981, 2010; Menni and Stehmann, 2000). Balech and Ehrlich (2008) indicated that the Argentinean Province extends from 42°S to 30–32°S, a much smaller extension than previous researchers, and interpreted it as an ecotone between the South Brazilian and Magellanic faunas. In the Magellanic Province, there are also differences in its limits and divisions.

While there is a general agreement to consider the Argentinean and Southern Chilean shelf as a single province (López, 1963; Menni and Stehmann, 2000; Spalding et al., 2007; Balech and Ehrlich, 2008; Cousseau et al., 2020), Briggs and Bowen (2012) divided the SWA part of the Magellanic Province into four new provinces. The proposed divisions are not based on fish distribution, as their work indicated, but on endemism levels of benthic invertebrates identified by Griffiths et al. (2009). Recently, Cousseau et al. (2020) tested the division of the Magellanic Province proposed by Briggs and Bowen (2012) and found that, based on fish distribution, there is no evidence supporting such division. Finally, the scheme of Spalding et al. (2007) agrees at the provincial level with other schemes, but its boundaries are arbitrary lines, indicative more of a geopolitical arrangement than a natural biogeographic structuring. Even though the different biogeographic schemes identify two provinces (Argentinean and Magellanic), there is no full agreement about the biogeographic regionalization of the SWA.

Chondrichthyans are an ecologically and economically significant taxon. In many cases, they have a high position in trophic networks and can be predators capable of determining species replacement of communities and control the populations of other predators (Myers et al., 2007; Heithaus et al., 2008; Ferretti et al., 2010). Furthermore, their life history, mainly their late age at maturity, makes them highly vulnerable to human activities, such as intense fishing and habitat loss (Hutchings et al., 2012). Chondrichthyans have fewer species (~1200) (Weigmann, 2016) than teleosts (~32 000) (Nelson et al., 2016), and an important amount of geo-referenced occurrences given their notoriety. They also have a diversity of shape and sizes, allowing them to occupy several ecological niches (Compagno, 1990). These characteristics make chondrichthyans an ideal taxon for models used in regionalization of the biota.

This study aims to generate a regionalization of chondrichthyan fauna of the SWA as a framework for the development of conservation programmes and sustainable use. Our specific aims are (i) to determine geographic distribution patterns of chondrichthyan richness; (ii) to identify chondrichthyan species assemblage areas; and (iii) to test the current biogeographical scheme of the SWA, with the most complete distribution data used so far in the region, objectively derived from species distribution modelling.

Material and methods

Study area

The study area covers the SWA from 25°S (off Isla Comprida, São Paulo, Brazil) to 57°S (in the northern part of the Drake Passage) between 0 and 2500 m depth. We selected the bottom depth up to 2500 m because this lower limit is close to the limit of chondrichthyan distribution (Priede et al., 2006). Also, from this depth to the coastline, it was possible to obtain a continuous study area that includes the continental shelf and slope (Figure 1). The SWA continental shelf can be divided into Subantarctic, with a northward cold water flow, and Subtropical, with a southward flow of warm water (Matano et al., 2010; Franco et al., 2018). The oceanic circulation over the SWA shelf is influenced by large tidal amplitudes, substantial freshwater discharges, high wind speeds, and—most importantly—its proximity to two of the largest western boundary currents: the Brazil and Malvinas currents (Matano et al., 2010). Climatic, topographic,

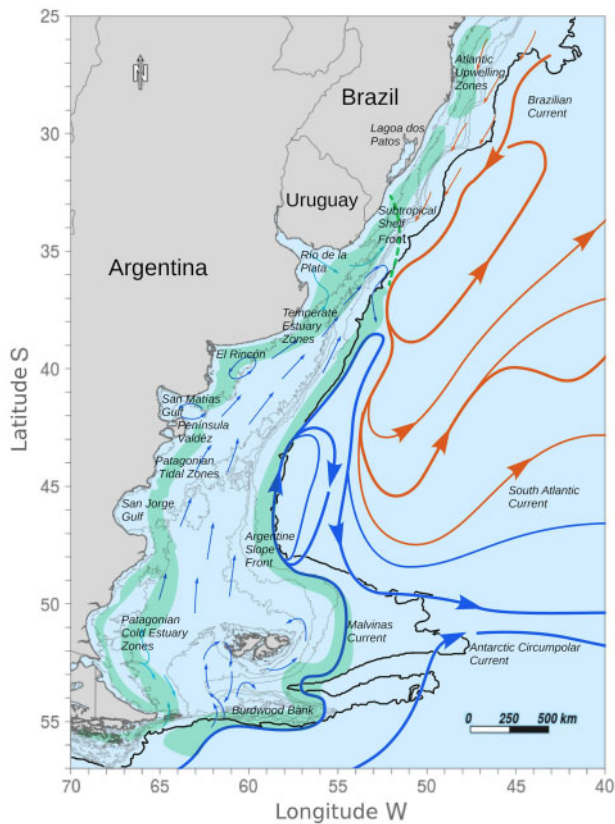


Figure 1. Study area in the Southwest Atlantic, geographic references, circulation patterns, and marine fronts. Adapted from Acha *et al.* (2004), Matano *et al.* (2010), Falabella *et al.* (2013), and Franco *et al.* (2018). Blue, red, and green arrows indicate cold-temperate water, warm-temperate water, and freshwater discharges areas or water of lower salinity, respectively. Green shaded areas indicate marine fronts. Grey lines indicate the 50, 100, 200, 500, and 1000 m isobaths, and the black solid line indicates the 2500 m isobath that limits the study area.

and oceanographic characteristics determine important physical-chemical gradients that show relative seasonal predictability and allow to identify a series of oceanographic regimes denominated marine fronts (Acha *et al.*, 2004). Particular ecological processes occur in these areas, resulting in high biological production that affects pelagic and benthic organisms of all trophic levels. The SWA is characterized by six front zones (Acha *et al.*, 2004) (Figure 1).

Data sources

An intensive search of geo-referenced data was carried out. Occurrence records were obtained from ichthyological collections, published records in the scientific literature, books, technical reports, unpublished records from research surveys, online repositories [Global Biodiversity Information Facility (GBIF), Ocean Biogeographic Information System (OBIS)], photos, and videos. For each species, we determined an occurrence whenever we had accurate geo-referencing data. Location was taken directly from coordinates when they were available or digitized from maps using XYscan software (Ullrich, 2002). Some records (e.g. photos or videos), whose locations were given by geographic names, were geo-referenced and included only when their

locations could be assigned to a specific place that was very small (i.e. <0.001%) in comparison with the study area (e.g. Bahía Blanca, Falsa, y Verde, Buenos Aires, Argentina). Occurrences from GBIF and OBIS were taken into account solely for easily identifiable species, to minimize misidentifications, e.g. records of *Atlantoraja castelnaui* were taken from these databases, but records of *Squatina* spp. were not. We inspected all data to remove duplicates (records with same coordinates). To determine the species that occur in the study area, we followed the lists of Menezes *et al.* (2003), Menni and Lucifora (2007), Gomes (2010), and Nion *et al.* (2016).

Environmental data were selected from two sources: bathymetry data were obtained from MARSPEC (Sbrocco and Barber, 2013) and mean chlorophyll, mean sea surface temperature, mean salinity, and mean dissolved oxygen covering 6 years (2005–2010) were obtained from Bio-ORACLE (Tyberghein *et al.*, 2012). All predictor layers contained high-resolution data of 5 min degree latitude by 5 min degree longitude (5 arcmins or 9.2 km).

Species distribution modelling and species richness

First, we estimated the geographic distribution of each species fitting MaxLike models (Royle *et al.*, 2012). This modelling approach combines presence-only data with environmental predictors to estimate the probability of occurrence of a species (Fitzpatrick *et al.*, 2013; Lucifora *et al.*, 2016). MaxLike uses all background data of the study area to estimate the probability of occurrence of a species. It accomplishes this by maximizing the likelihood conditioned on the probability of observing a cell given the species is present. In all models, we included quadratic and cubic terms for each environmental predictor to account for potential non-linear effects (Royle *et al.*, 2012). Before fitting models, all predictors were standardized as recommended by Royle *et al.* (2012). Also, we inspected the relationships between each pair of environmental predictors to avoid multicollinearity. Variable pairs that had a correlation coefficient of $>(\pm)0.5$ were not included together in the same model (Lucifora *et al.*, 2015). For each species, we fitted models where the response variable was geographical occurrences (latitude and longitude) and explanatory variables were environmental predictors. Initially, 64 combinations of environmental predictors were considered. The best combination of explanatory variables was selected by minimizing the Akaike information criterion for the 64 proposed combinations (Johnson and Omland, 2004). Once the best combination was selected, a sequential selection of the explanatory variables was made until all possible combinations of the best model were tested. Therefore, a simpler model could be obtained under the same predictors. MaxLike modelling was conducted using the *maxlike* package version 0.1.5 (Royle *et al.*, 2012) in R version 3.4.2 (R Core Team, 2016). In some species, the probability of occurrence evidenced over-representation due to the accumulation of occurrences in one or more areas. To get a more balanced dataset, we drew a random subsample (without replacement) with the *sperrorest* package (Brenning, 2012). Each over-represented area was resampled 10 times, generating a total of ten datasets. We selected the best model using one of the new datasets, chosen randomly. Next, we reran the best model for each dataset. The mean of the ten runs of the best model was our final estimation of the geographic distribution. Finally, from the probability occurrence map, we obtained a binary (presence-absence) map by applying a threshold to the probability of

occurrence. The threshold applied maximized the sum of sensitivity and specificity (Liu *et al.*, 2013).

Geographic distribution patterns of species richness were determined by adding up the occurrences of all species per pixels, based on binary maps. Maps of species richness were created for four groups: (i) class Chondrichthyes (chondrichthyans), with 103 species; (ii) subclass Holocephali (chimaeras), with 2 species; (iii) division Selachii (sharks), with 51 species; and (iv) division Batomorphi (batoids), with 50 species.

Identification of assemblages

Classification analyses were performed to identify chondrichthyan species assemblages. We computed pairwise distances between pixels, based on the binary data of species distribution. We used the beta diversity distance measure because it reflects the variation in species composition among sites (Baselga *et al.*, 2012). The multivariate structure of the distance matrix was built using the *betapart* package (Baselga *et al.*, 2012). Hierarchical clustering analysis using the beta diversity distance matrix was performed with the *vegan* package (Clarke and Warwick, 2001; Oksanen *et al.*, 2019). The different clustering algorithms used by the *vegan* package were evaluated using the co-phenetic correlation coefficient (Sokal and Rohlf, 1962). This coefficient represents a direct measure of how much of the original information is retained in the dendrogram (Kreft and Jetz, 2010). According to the co-phenetic correlation coefficient, the best clustering algorithm was the unweighted pair group method with arithmetic mean. The appropriate number of clusters or assemblage areas was determined using 21 indexes. This approach enables to simultaneously evaluate several clustering schemes and helps determining objectively the most appropriate number of clusters for the data set of interest. The indexes were: “CH”, “Doubt”, “pseudo t2”, “index C”, “Beale”, “criterion of cubic clustering”, “Davies and Bauldin”, “Hartigan”, “Ratkowsky and Lance”, “Scott and Symons”, “Marriot”, “Ball and Hall”, “Covariance Matrix Trace”, “Dispersion Matrix Trace”, “Friedman and Rubin”, “Rubin”, “Krzanowski and Lai”, “Index D”, “Dunn”, “SD”, and “SDbw” (Charrad *et al.*, 2014). We used the *NbClust* package to calculate these indexes (Charrad *et al.*, 2014). According to the majority rule and analysing the dendrogram, we selected the optimal number of clusters or assemblage areas.

To identify and quantify the contribution of each species to the differentiation of assemblage areas, a similarity percentage analysis (SIMPER) was performed with the *vegan* package (Oksanen *et al.*, 2019). Given that the large number of pixels covered by the study area (total pixels = 40 823) required long computing times, we selected a random sample of 2000 pixels with 500 permutations to conduct this analysis. Species were defined as “common”, if they contributed to the assemblage area up to 80% of the similarity, and “discriminant”, if they contributed 80% or more of the dissimilarity between assemblage areas.

Results

Richness distribution patterns

In the study area, 134 chondrichthyan species, belonging to 12 orders and 31 families, were documented. Geographic distribution was modelled for 103 chondrichthyan species. The remaining 31 species were not considered because of incorrect locations, scant occurrences, or low spatial coverage of occurrences with far distances between them. The chondrichthyan species list, the

bibliographic references for species occurrences, the number of occurrences by species, the best MaxLike model, and maps of probability of occurrence and presence–absence (binary) of each species are shown in [Supplementary Material](#).

The continental shelf off southern Brazil and, partially, off Uruguay, between 29°S and 36°S, from the coastline up to 200 m depth, was the region with the highest richness of chondrichthyans (Figure 2). Towards the north, high richness was found along the coast decreasing towards the slope. Southward of 36°S, a secondary richness peak extended up to the San Jorge Gulf, with an increase in species number in the El Rincón region (Figure 1). On the rest of the Argentinean shelf, chondrichthyan richness was very low, with a slightly higher concentration on the middle shelf than in the area southward of the San Jorge Gulf up to 55°S, and decreasing towards the continental slope.

Chimaeras were poorly represented in the region with only two species. One of them, *Callorhynchus callorhynchus*, was distributed on the continental shelf off Argentina and Uruguay; the other one, *Hydrolagus matallanasi*, was restricted to the slope off Brazil (Figure 2).

Sharks had a very high number of species between 29°S and 36°S, from the coastline to 200 m depth (Figure 2). This region corresponded mainly to the southern part of the Brazilian shelf. Northward of 29°S, a high richness area extended along the coastline, decreasing on the rest of the Brazilian shelf. On the other hand, southward of 36°S, shark richness decreased considerably between the coast and 100 m depth, up to the San Jorge Gulf (Figure 1). On the rest of the Argentinean shelf, shark richness was very low (Figure 2).

Batoids had a very high species richness on the continental shelf off northern Argentina, Uruguay, and southern Brazil (Figure 2). Most species were found mainly between 32°S and 38°S, at depths of <200 m. Northwards from Lagoa dos Patos (Figure 1), batoid richness decreased sharply throughout the Brazilian shelf. South of 38°S, in Argentinean waters, there was a broad region between the coast and middle shelf up to 47°S with high richness that included two areas with secondary peaks: El Rincón and San Jorge Gulf (Figure 1). Also, high batoid richness was found along the 200 m isobath and slope up to 50°S. Finally, batoid richness was low south of the San Jorge Gulf on the Argentinean shelf, between coastal waters and 100 m depth, including the Burdwood Bank (Figure 1). Eastwards from the Malvinas/Falkland Islands at depths >500 m depth, richness was very low (Figure 2).

Chondrichthyan assemblage areas

Based on geographic species distribution, a hierarchical structure was found that allows regionalization of the SWA for chondrichthyan fauna. This biogeographic scheme (main areas containing minor areas) is represented by the regional divisions of species assemblage areas. The 21 indexes used for determining the optimal number of clusters allowed us to identify this hierarchical structure. Eight indexes identified 3 clusters, 5 identified 7 clusters, and the remaining 7 showed optimal values of 2, 4, 9, and 12 clusters. Considering the optimal values for most indexes and dendrogram analysis, we determined the presence of three main assemblage areas with a beta dissimilarity level of 0.845 (Figure 3). Internally, main assemblage areas were structured in six smaller assemblage areas with a beta dissimilarity level of 0.517 (Figure 3). The proposed hierarchy is consistent with

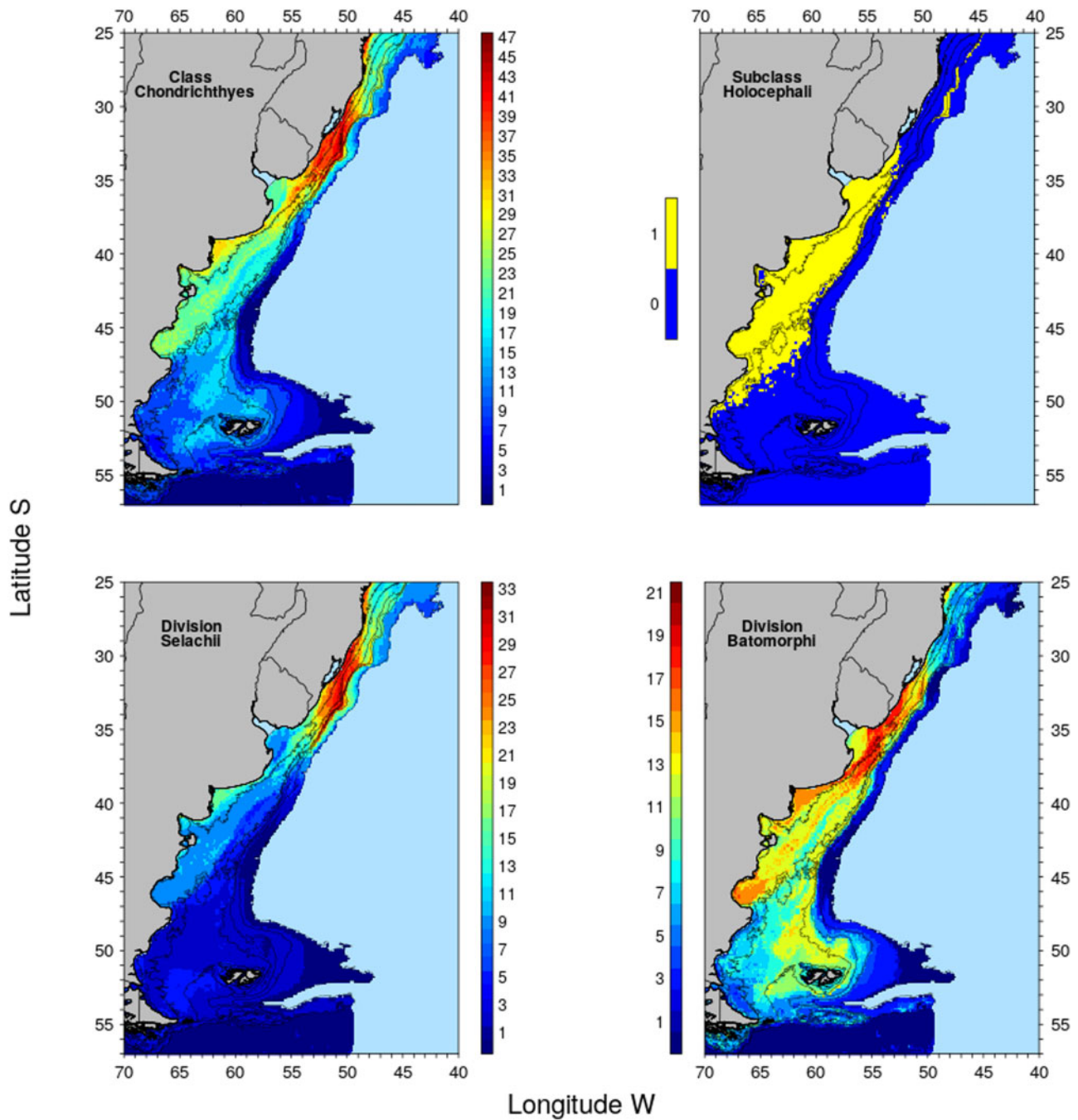


Figure 2. Distribution of species richness for the class Chondrichthyes (chondrichthyans), the subclass Holocephali (chimaeras), the division Selachii (sharks), and the division Batomorphi (batoids) in the Southwest Atlantic. The colour bars indicate the number of species. Grey lines indicate the 50, 100, 200, 500, and 1000 m isobaths. The bathymetric limit of the study area is marked by the 2500 m isobath.

biogeographic units defined as provinces, containing districts or ecoregions (Spalding *et al.*, 2007; Griffiths *et al.*, 2009; Kreft and Jetz, 2010; Morrone, 2018). Here, we use ecoregion as a synonym for district. The biogeographic provinces identified (main assemblage areas) corresponded to (i) Argentinean, (ii) Patagonian Slope, and (iii) Magellanic. Ecoregions (minor assemblage areas) were, in the Argentinean Province: (i) South Brazilian, (ii) South Brazilian Deep-Sea, (iii) Bonaerensean, and (iv) Patagonian Shelf Break. In the Patagonian Slope Province, ecoregions were (v) Southern Patagonian Slope and (vi) Northern Patagonian Slope.

Finally, no ecoregional subdivisions were detected for the Magellanic Province.

Provinces (main assemblage areas)

The Argentinean Province ranged from 25°S to 36°S, from the coastline to 2500 m depth. Southward of 36°S, this area split into two branches. The western branch narrowed following the 50 m isobath to include the North Patagonian gulfs (San Matías, San José, and Nuevo) (Figure 1). The eastern branch was located

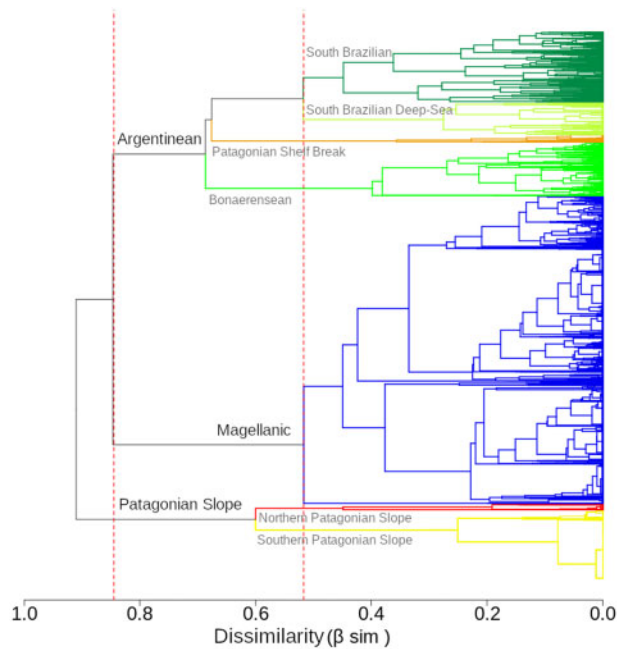


Figure 3. Dendrogram results from the UPGMA hierarchical algorithm on a set of 2000 pixels of chondrichthyan species from the Southwest Atlantic, based on a similarity matrix with the β similarity index. Names on branches correspond to provinces (black) and ecoregions (grey) identified. Dashed lines mark the dissimilarity levels differencing provinces and ecoregions. UPGMA, unweighted pair group method with arithmetic mean.

from 1000 to 2500 m up to 39°S, continuing southwards narrowing over the 1000 m depth up to 49°S (Figure 4).

The Patagonian Slope Province was the smallest and most geographically restricted assemblage. It ranged from 41°S to 57°S, in two separated areas on the slope between 500 and 2500 m depth. The area with maximum longitudinal extension was located east of the Malvinas/Falkland Islands, between 46°S and 55°S. Northward of 46°S it was discontinued, ending in a second area between 1000 and 2500 m depth, ranging from 39°S to 41°S (Figure 4).

The Magellanic Province covered almost the whole Argentinean shelf south of the Río de la Plata (Figure 1). From 36°S to 42°S, it was located offshore, between 50 and 1000 m depth. Southward of 42°S, it covered the whole shelf, from the coastline to 500 m depth, including the Malvinas/Falkland Islands, the Burdwood Bank, and the southern waters of Tierra del Fuego (Figure 4).

Ecoregions (minor assemblage areas)

The Argentinean Province contained four ecoregions (Figure 4). The South Brazilian ecoregion ranged from 25°S to ~39°S. From its northernmost point to 31°S, it extended from the coastline to 200 m depth; south of 31°S, it veered eastward going progressively offshore and reaching the 2500 m isobath. The South Brazilian Deep-Sea ecoregion corresponded to the deep-water and offshore assemblage off Brazil, extending from 200 to 2500 m depth, between 25°S and 31°S. The Bonaerensean ecoregion stretched from the mouth of the Lagoa dos Patos (Figure 1) to 35°S, along a narrow coastal strip, and south of 35°S it ranged to 43°S, just

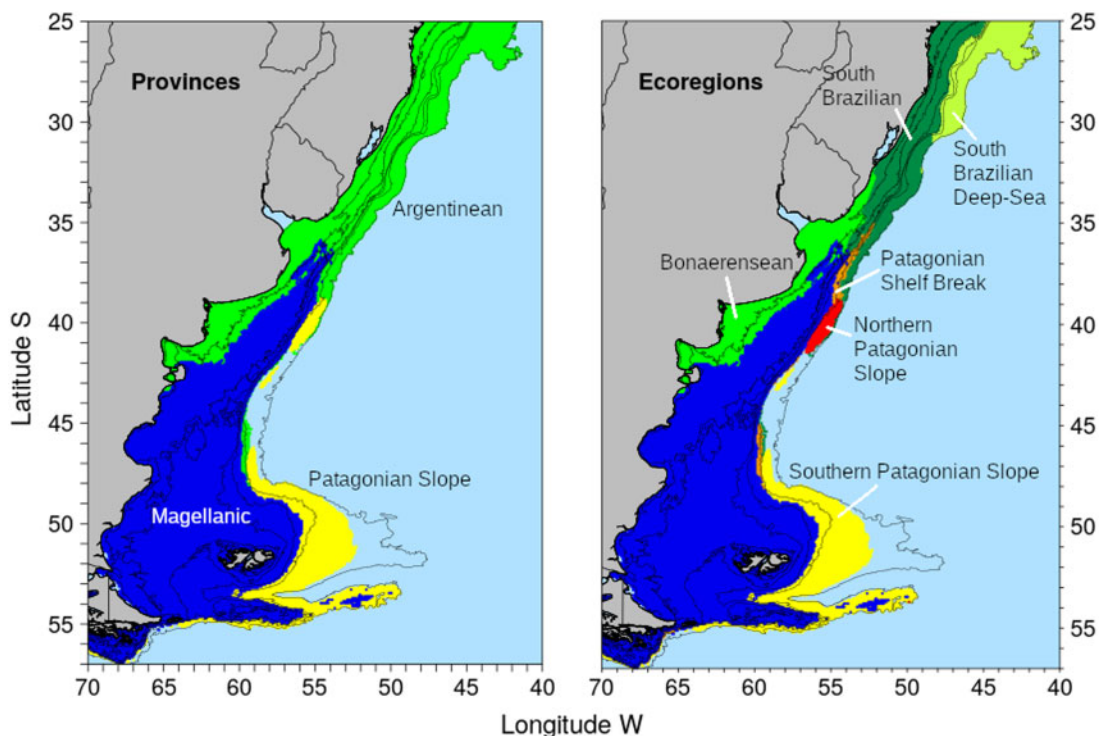


Figure 4. Biogeographic provinces and ecoregions of the Southwest Atlantic identified by the UPGMA hierarchical algorithm on a set of 2000 pixels of chondrichthyan species based on the similarity matrix with the β similarity index. Grey lines indicate the 50, 100, 200, 500, 1000, and 2500 m isobaths. UPGMA, unweighted pair group method with arithmetic mean.

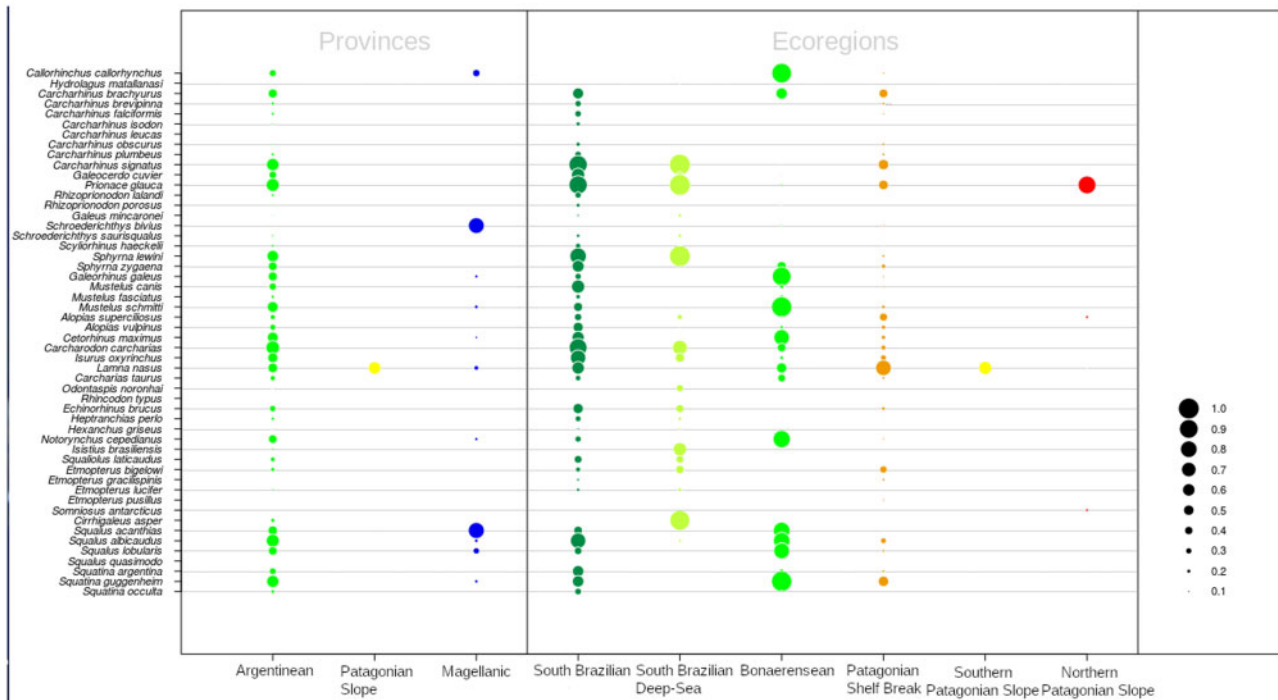


Figure 5. Relative percentage contribution of species of sharks (division Selachii), and chimaeras (subclass Holocephali) on the dissimilarity of provinces and ecoregions of the Southwest Atlantic, according to the SIMPER analysis. In black, a scale of percentages and bubble sizes is shown for reference.

north of Valdés Peninsula (Figure 1), and extended in bathymetry from the coastline to 50 m depth. The Patagonian Shelf Break was the smallest ecoregion. It was restricted to the upper slope in two sections, one between 35°S and 39°S and a very narrow longitudinally south of 41°S to 49°S (Figure 4).

The Patagonian Slope Province was split into two ecoregions, namely the Southern and the Northern Patagonian Slope ecoregions. The first one ranged between 46°S and 55°S from 500 to 2500 m depth, east of the Malvinas/Falkland Islands. The latter was located on the slope from 1000 to 2500 m depth, between 38°S and 42°S (Figure 4).

The Magellanic Province did not present any internal divisions at the level of dissimilarity determined by the optimal number of clusters.

Biogeographic identities and species contribution

Provinces (main assemblage areas)

The dissimilarity percentages obtained with SIMPER among provinces were as follows: the Argentinian Province differed from the Patagonian Slope and Magellanic provinces by 96.56 and 89.19%, respectively, and the Patagonian Slope Province from the Magellanic Province by 92.47%. Figures 5 and 6 show the average contribution of each species to the differentiation of provinces.

The Argentinian Province included a great number of species. The “common” species corresponded to 19 sharks and 11 batoids. The “discriminant” species corresponded to one holocephalan, *C. callorhynchus*, six sharks, and three batoids (Table 1). The richness of “common” and “discriminant” species was very high regarding the total species considered. The species richness of the

Argentinian Province represented 50% of the sharks, 27% of the batoids, and 38.8% of the total modelled chondrichthyans.

The Patagonian Slope Province had a considerable lower number of species than the Argentinian Province. “Common” species corresponded to the shark *Lamna nasus* and three batoids. The only “discriminant” species was the skate *Amblyraja doellojuradoi* (Table 1). The richness of “common” and “discriminant” species was very low with only four batoids, 8% of the total modelled and a single shark. “Discriminant” and “common” species of the Patagonian Slope Province represented 5% of the total number of modelled chondrichthyans.

Lastly, the Magellanic Province was represented by an important number of batoids, belonging to the families Arhynchobatidae and Rajidae, two sharks, and one holocephalan. “Common” species were represented by two sharks and 12 batoids. “Discriminant” species corresponded to the holocephalan *C. callorhynchus* and the skate *Dipturus trachyderma* (Table 1). The richness of “common” and “discriminant” species in the Magellanic Province represented 4% of sharks, 25% of batoids, and 16% of all modelled chondrichthyans.

Ecoregions (minor assemblage areas)

The dissimilarity percentage among ecoregions was as follows: the South Brazilian ecoregion differed from the South Brazilian Deep-Sea, Bonaerensean, and Patagonian Shelf Break ecoregions, by 71.64, 67.36, and 77.48%, respectively; the South Brazilian Deep-Sea ecoregion differed from the Bonaerensean ecoregion by 95.75% and from the Patagonian Shelf Break ecoregion by 82.10%; and the Bonaerensean and Patagonian Shelf Break ecoregions differed by 87.10%. Within the Patagonian Slope Province, the Southern and Northern ecoregions differed by 81.71%.

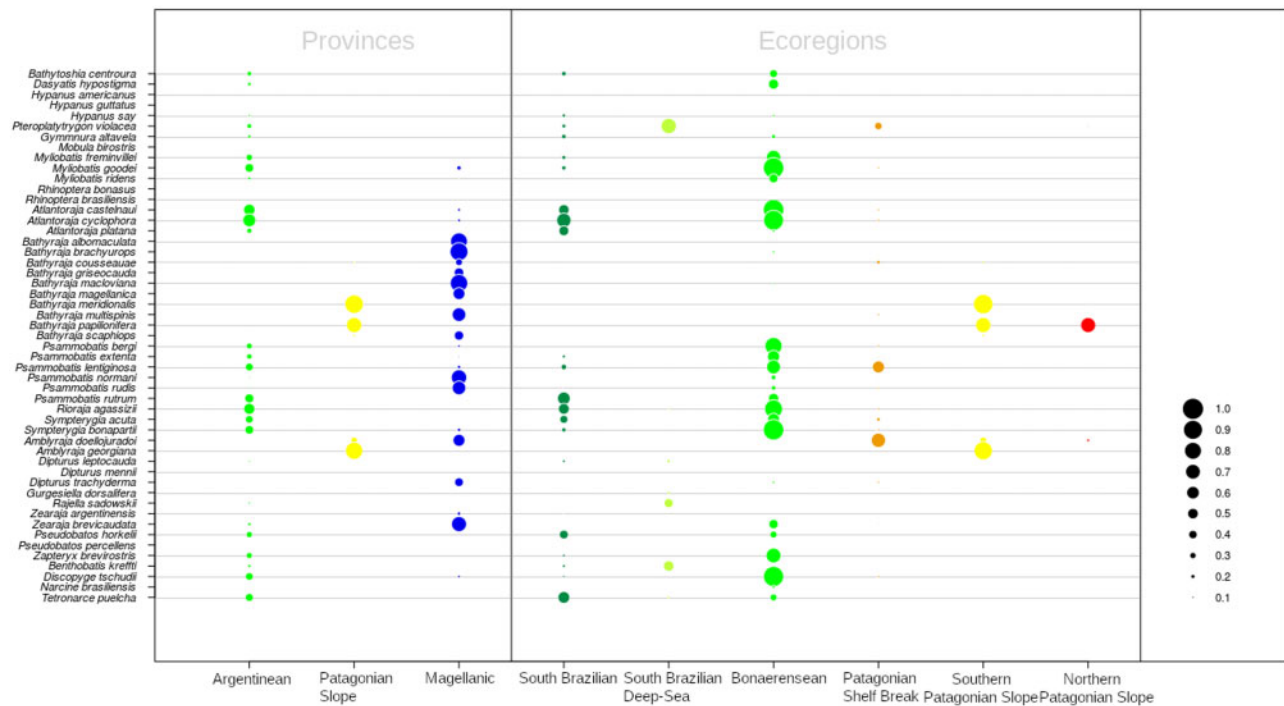


Figure 6. Relative percentage contribution of species of batoids (division Batomorphi) on the dissimilarity of provinces and ecoregions of the Southwest Atlantic, according to the SIMPER analysis. In black, a scale of percentages and bubble sizes is shown for reference.

Table 1. List of “common” and “discriminant” (*) species for each of the biogeographic provinces identified in the Southwest Atlantic.

Argentinean		Patagonian Slope	Magellanic
Chimaeras	<i>Cirrhigaleus asper</i>	Sharks	Chimaeras
<i>Callorhynchus callorynchus*</i>	<i>Squalus acanthias</i>	<i>Lamna nasus</i>	<i>Callorhynchus callorynchus*</i>
Sharks	<i>Squalus albicaudus</i>	Batoids	Sharks
<i>Carcharhinus brachyurus</i>	<i>Squalus lobularis</i>	<i>Bathyrhaja meridionalis</i>	<i>Schroederichthys bivius</i>
<i>Carcharhinus signatus</i>	<i>Squatina argentina*</i>	<i>Bathyrhaja papilionifera</i>	<i>Squalus acanthias</i>
<i>Galeocerdo cuvier</i>	<i>Squatina guggenheim</i>	<i>Amblyraja doellojuradoi*</i>	Batoids
<i>Prionace glauca</i>	Batoids	<i>Amblyraja georgiana</i>	<i>Bathyrhaja albomaculata</i>
<i>Sphyrna lewini</i>	<i>Pteroplatytrygon violacea</i>		<i>Bathyrhaja brachyurops</i>
<i>Sphyrna zygaena</i>	<i>Myliobatis freminvillei*</i>		<i>Bathyrhaja cousseauae</i>
<i>Galeorhinus galeus</i>	<i>Myliobatis goodei</i>		<i>Bathyrhaja griseocauda</i>
<i>Mustelus canis</i>	<i>Atlantoraja castelnaui</i>		<i>Bathyrhaja macloviana</i>
<i>Mustelus schmitti</i>	<i>Atlantoraja cyclophora</i>		<i>Bathyrhaja magellanica</i>
<i>Alopias superciliosus</i>	<i>Psammobatis bergi</i>		<i>Bathyrhaja multispinis</i>
<i>Cetorhinus maximus</i>	<i>Psammobatis lentiginosa</i>		<i>Bathyrhaja scaphiops</i>
<i>Carcharodon carcharias</i>	<i>Psammobatis rutrum</i>		<i>Psammobatis normani</i>
<i>Isurus oxyrinchus</i>	<i>Rioraja agassizi</i>		<i>Psammobatis rudis</i>
<i>Lamna nasus*</i>	<i>Sympterygia acuta*</i>		<i>Amblyraja doellojuradoi</i>
<i>Echinorhinus brucus</i>	<i>Sympterygia bonapartii</i>		<i>Dipturus trachyderma*</i>
<i>Notorynchus cepedianus</i>	<i>Zapteryx brevirostris*</i>		<i>Zearaja brevicaudata</i>
<i>Isistius brasiliensis*</i>	<i>Discopyge tschudii</i>		
<i>Squaliolus laticaudus*</i>	<i>Tetronarce puelcha</i>		
<i>Etmopterus bigelowi*</i>			

“Common” species are those contributing to the assemblage area up to 80% of the similarity, and discriminant ones contributed 80% or more of the “dissimilarity” between assemblage areas.

Figures 5 and 6 show the average contribution of each species to the ecoregion differentiation.

The South Brazilian ecoregion had a large number of species. “Common” species corresponded to 27 sharks and 8 batoids. “Discriminant” species corresponded to six sharks and the skate

Psammobatis lentiginosa (Table 2). In the South Brazilian Deep-Sea ecoregion, the “common” species corresponded to nine sharks and three batoids, while the “discriminant” species corresponded exclusively to six sharks (Table 2). In the Bonaerensean ecoregion, “common” species were the holoccephalan C.

Table 2. List of “common” and “discriminant” (*) species for the ecoregions identified within the Argentinean Province.

South Brazilian	South Brazilian Deep-Sea	Bonaerensean	Patagonian Shelf Break
Sharks	Sharks	Chimaeras	Sharks
<i>Carcharhinus brachyurus</i>	<i>Carcharhinus signatus</i>	<i>Callorhynchus callorhynchus</i>	<i>Carcharhinus brachyurus*</i>
<i>Carcharhinus brevipinna</i>	<i>Galeocerdo cuvier*</i>	Sharks	<i>Carcharhinus signatus*</i>
<i>Carcharhinus falciformis</i>	<i>Prionace glauca</i>	<i>Carcharhinus brachyurus</i>	<i>Prionace glauca*</i>
<i>Carcharhinus obscurus*</i>	<i>Schroederichthys saurissqualus*</i>	<i>Sphyrna zygaena</i>	<i>Sphyrna zygaena*</i>
<i>Carcharhinus plumbeus</i>	<i>Sphyrna lewini</i>	<i>Galeorhinus galeus</i>	<i>Alopias superciliosus</i>
<i>Carcharhinus signatus</i>	<i>Carcharodon carcharias</i>	<i>Mustelus schmitti</i>	<i>Alopias vulpinus*</i>
<i>Galeocerdo cuvier</i>	<i>Isurus oxyrinchus</i>	<i>Cetorhinus maximus</i>	<i>Lamna nasus</i>
<i>Prionace glauca</i>	<i>Odontaspis noronhai*</i>	<i>Carcharodon carcharias*</i>	<i>Etmopterus bigelowi*</i>
<i>Rhizoprionodon lalandii</i>	<i>Echinorhinus brucus*</i>	<i>Lamna nasus*</i>	<i>Squalus albicaudus*</i>
<i>Schroederichthys saurissqualus</i>	<i>Heptranchias perlo*</i>	<i>Carcharias taurus</i>	<i>Squatina guggenheim*</i>
<i>Scyliorhinus haeckelii</i>	<i>Isistius brasiliensis</i>	Notorynchus cepedianus	Batoids
<i>Sphyrna lewini</i>	<i>Squaliolus laticaudus*</i>	<i>Squalus acanthias</i>	<i>Pteroplatytrygon violacea*</i>
<i>Sphyrna zygaena</i>	<i>Etmopterus bigelowi</i>	<i>Squalus albicaudus</i>	<i>Bathyraja cousseauae</i>
<i>Galeorhinus galeus*</i>	<i>Etmopterus lucifer*</i>	<i>Squalus lobularis</i>	<i>Bathyraja multispinis*</i>
<i>Mustelus canis</i>	<i>Cirrhigaleus asper</i>	<i>Squatina guggenheim</i>	<i>Psammobatis lentiginosa</i>
<i>Mustelus schmitti</i>	Batoids	Batoids	<i>Amblyraja doellojuradoi</i>
<i>Alopias superciliosus</i>	<i>Pteroplatytrygon violacea</i>	<i>Bathytoshia centroura</i>	
<i>Alopias vulpinus</i>	<i>Rajella sadowskii</i>	<i>Dasyatis hypostigma</i>	
<i>Cetorhinus maximus</i>	<i>Benthobatis kreffti</i>	<i>Myliobatis goodei</i>	
<i>Carcharodon carcharias</i>		<i>Myliobatis freminvillei</i>	
<i>Isurus oxyrinchus</i>		<i>Myliobatis ridens</i>	
<i>Lamna nasus</i>		<i>Atlantoraja castelnaui</i>	
<i>Carcharias taurus*</i>		<i>Atlantoraja cyclophora</i>	
<i>Echinorhinus brucus</i>		<i>Psammobatis bergi</i>	
<i>Heptranchias perlo</i>		<i>Psammobatis extenta</i>	
<i>Notorynchus cepedianus*</i>		<i>Psammobatis lentiginosa</i>	
<i>Squaliolus laticaudus</i>		<i>Psammobatis rutrum</i>	
<i>Squalus acanthias</i>		<i>Rioraja agassizii</i>	
<i>Squalus albicaudus</i>		<i>Sympterygia acuta</i>	
<i>Squalus lobularis</i>		<i>Sympterygia bonapartii</i>	
<i>Squatina argentina</i>		<i>Zearaja brevicaudata</i>	
<i>Squatina guggenheim</i>		<i>Zapteryx brevirostris</i>	
Batoids		<i>Discopyge tschudii</i>	
<i>Atlantoraja castelnaui</i>			
<i>Atlantoraja cyclophora</i>			
<i>Atlantoraja platana</i>			
<i>Psammobatis lentiginosa*</i>			
<i>Psammobatis rutrum</i>			
<i>Rioraja agassizii</i>			
<i>Sympterygia acuta</i>			
<i>Pseudobatos horkelii</i>			
<i>Tetronarce puelcha</i>			

“Common” species are those contributing to the assemblage area up to 80% of the similarity, and discriminant ones contributed 80% or more of the “dissimilarity” between assemblage areas.

callorhynchus, 11 sharks, and 17 batoids. The “discriminant” species corresponded to two sharks, *Carcharodon carcharias* and *L. nasus* (Table 2). In the Patagonian Shelf Break ecoregion, “common” species corresponded to two sharks, *Alopias superciliosus* and *L. nasus*, and three batoids, while “discriminant” species corresponded to eight sharks and two batoids, *Pteroplatytrygon violacea* and *Bathyraja multispinis* (Table 2).

The Southern Patagonian Slope ecoregion included as “common” species the shark *L. nasus* and two skates, *Bathyraja meridionalis* and *Bathyraja papilionifera*. The skate *Amblyraja georgiana* was the only “discriminant” species (Table 3). In the Northern Patagonian Slope, *Prionace glauca* was the “discriminant” species (Table 3).

Table 3. List of “common” and “discriminant” (*) species for the ecoregions identified within the Patagonian Slope Province.

Southern Patagonian Slope	Northern Patagonian Slope
Sharks	Sharks
<i>Lamna nasus</i>	<i>Prionace glauca*</i>
Batoids	
<i>Bathyraja meridionalis</i>	
<i>Bathyraja papilionifera</i>	
<i>Amblyraja georgiana*</i>	

“Common” species are those contributing to the assemblage area up to 80% of the similarity, and discriminant ones contributed 80% or more of the “dissimilarity” between assemblage areas.

Discussion

Our analysis reveals that diversity of chondrichthyans—as a group—is heterogeneous in the SWA. The highest richness was found over the Subtropical Shelf Front, the Atlantic Upwelling Zones, and the northern area of the Temperate Estuary Zones (Figure 1). Southward of El Rincón, richness begins to decrease, is homogeneous up to the San Jorge Gulf, and then falls and it is low south of 47°S. However, significant spatial decoupling among higher taxa is observed. Sharks peak off southern Brazil and Uruguay around the area of the Subtropical Shelf Front (Figure 1), presenting a small northern mode on the Brazilian coast. Southward, over the Argentinean shelf, their richness is very low. On the other hand, batoid richness is maximal off Uruguay and northern Argentina with maximum richness on the Temperate Estuary Zones and small modes over the Patagonian Tide Zones and Argentinean Slope Front (Figure 1). Our work also confirms the natural biogeographic boundaries of the SWA found in previous works through the regionalization determined by objective methods. We confirm the presence of the Argentinean and Magellanic Provinces on the continental shelf, delineating their limits with precision. For the first time, we show the presence of a biogeographic province in the slope sector (Figure 4). Furthermore, the inner structure—ecoregions or districts—of the biogeographic provinces is determined. This regionalization is an initial step towards biogeographic ordering based on species assemblages.

In all cases, chondrichthyan richness is greater on the continental shelf than beyond, which is consistent with the importance of the neritic habitat for most of the chondrichthyan species (Compagno, 1990; Lucifora et al., 2011; Dulvy et al., 2014). In general, the richness pattern found coincides with the observed for sharks previously, with a maximum on the shelf off southern Brazil and an abrupt decrease in front of the Río de la Plata (Figures 1 and 2) (Lucifora et al., 2011). On the other hand, the maximum in batoid richness is shifted southwards relative to the maximum of shark richness and had secondary peaks at high latitudes on the Patagonian shelf (Figures 1 and 2). The sharp difference in richness between sharks and batoids, on both sides of the Subtropical Shelf Front, is notorious. This front is an extension of the Brazil/Malvinas Convergence over the continental shelf and runs in a north–south direction from the intersection of the 50 m isobath with the 32°S parallel to the 200 m isobath at 36°S (Figure 1) (Piola et al., 2000). The Subtropical Shelf Front is formed by the confluence of subantarctic and subtropical waters. Our results indicate that it acts as a biogeographic barrier separating a mostly tropical shark fauna (i.e. Carcharhinidae, Sphyrnidae) to the north and a temperate batoid fauna (i.e. dominated by Arhynchobatidae and Rajidae) to the south. Previously, freshwater discharges of the Río de la Plata were postulated as a barrier to many species, supporting the hypothesis of the Río de la Plata as a biogeographic boundary (Menni et al., 2010). Although for both groups a richness decrease is observed on the mouth of the Río de la Plata, the almost exact coincidence of the shark-batoid richness discontinuity with the location of the Subtropical Shelf Front suggests a bigger role for this front than for the Río de la Plata discharge as a biogeographic barrier. Likewise, the pattern on sharks is consistent with the distribution hypothesis for ectothermic and mesothermic predators, where sharks are included (Grady et al., 2019). Grady et al.'s (2019) theory highlights the importance of energetics and metabolic

processes in species interactions (endothermy—mammals and bird—with ectothermic—sharks, tuna, billfish, large teleosts), and the consequences for global scales fauna distribution for climate change. With an increase in the average temperature of the oceans already underway, the current bioregional scheme will undergo modifications. Our results highlight the need to understand the ecological roles, habitats use, and physiology as determinants in species movement through biogeographic barriers such as confluence sectors, freshwater discharges, and depth ranges. These understandings will be fundamental in future regionalization schemes and conservation programmes.

The regions off Uruguay and southern Brazil were catalogued as priority for conservation with a high number of endemic and endangered species (Davidson and Dulvy, 2017). The richness pattern found indicates a high concentration of species in this area, coincident with the areas identified as priority (Davidson and Dulvy, 2017; Dulvy et al., 2017) and with evidence of diversity peaks in mid-latitudes (Lucifora et al., 2011; Dulvy et al., 2014; Weigmann, 2016). However, our results also indicate richness patterns and species assemblage areas beyond these limits. It is also necessary to consider the geographical spaces outside the areas of species concentration, as priorities.

A hierarchical biogeographic structure (with main assemblage areas containing minor assemblage areas) of the SWA was found based on species distribution patterns. The main assemblage areas are equivalent to biogeographic provinces, and the minor assemblage areas would correspond to ecoregions (Spalding et al., 2007; Kreft and Jetz, 2010; Morrone, 2018). These provinces and ecoregions represent the first hierarchical ichthyogeographic classification in the SWA based on quantitative estimations of geographic ranges of species.

Our results confirmed the currently accepted biogeographic scheme of the SWA. The two significant agreements that strengthen the current scheme are the spatial correspondence of the main assemblage areas found on the shelf sectors with the Argentinean and Magellanic Provinces. At lower levels, the minor assemblage areas north of 41°S correspond almost exactly with the South Brazilian and Bonaerensean districts of the Argentinean Province, previously identified by the overwhelming majority of previous works, conducted on different taxa and with different methods (e.g. López, 1963; Menni et al., 1981, 2010; Menni and Stehmann, 2000). On the other hand, our results differ from conclusions by Balech and Ehrlich (2008), who stated that the Argentinean Province was limited to the Bonaerensean ecoregion, and that it was unrelated to the South Brazilian fauna. Contrary to this view, our results identify the South Brazilian and the Bonaerensean ecoregions as belonging to a higher-order assemblage, the Argentinean Province. This is supported by 31 “common” species explaining 80% of the similarity of sites within the Argentinean Province. Also, a homogeneous Magellanic Province is recovered by our analysis. This agrees with a recent revision by Cousseau et al. (2020) indicating a lack of regional differentiation within the Magellanic Province. Likewise, the hierarchical homogeneity found here does not support the inner structuring of the Magellanic Province proposed by previous classifications (Spalding et al., 2007; Balech and Ehrlich, 2008; Menni et al., 2010).

Two major findings of this work represent deviations from the biogeographic scheme accepted for the SWA. First, the South Brazilian Deep-Sea ecoregion appears to include the deep-water Brazilian fauna of Menni et al. (2010). Besides the geographic

coincidence, some of the species contributing significantly to the similarity of sites within this area, such as *Etmopterus bigelowi*, *Etmopterus lucifer*, and *Rajella sadowskii*, are the same in this study and in Menni *et al.* (2010). However, contrary to the results of Menni *et al.* (2010), many epipelagic species are also characteristic of this ecoregion, such as *Isurus oxyrinchus*, *Sphyrna lewini*, and *P. violacea*. We believe that this difference may be due to the inclusion of pelagic species in our study, which were largely absent in Menni *et al.* (2010). We hypothesize that using modelling tools that make explicit the vertical dimension of a sample unit (i.e. a pixel) (Bentlage *et al.*, 2013; Duffy and Chown, 2017) will differentiate a deep water from an epipelagic fauna in this area. Second, the Patagonian Slope Province is recognized here for the first time as a biogeographic unit at the same level as the Argentinean and Magellanic provinces. This area also includes mainly deep-water species of a southern or even subantarctic origin, as indicated by its “common” species *B. meridionalis*, *B. papilionifera*, and *A. georgiana*. This deep-water fauna represents perhaps the northernmost extension of a truly subantarctic rather than Patagonian (i.e. Magellanic) fauna. These results agree with evidence from other taxa with distinct subantarctic assemblages on the lower continental slope as far north as off Uruguay, e.g. ascidians (Scarabino *et al.*, 2018) and pycnogonids (Scarabino *et al.*, 2019). Previously, Saraceno *et al.* (2005) identified the slope break on the Argentinean shelf as a possible oceanographic province.

The regional differentiation of the biota must be taken into account for management and conservation planning (Kreft and Jetz, 2010; Escalante, 2016). We propose that the biogeographic scheme found here, based on objective methods, can be used as a geographical framework for conservation planning in the SWA. Currently, there are three major regionalization schemes used in the SWA for conservation goals: the large marine ecosystems of the world (LME) (<http://lme.edc.uri.edu>), the Forum for the Conservation of the Patagonian Sea and Areas of Influence (Falabella *et al.*, 2013), and the marine ecoregions of the world (MEOW) (Spalding *et al.*, 2007). The LME includes relatively large areas of 200 000 km² or greater. In the study area, there are two LMEs: the South Shelf of Brazil and the Patagonian Shelf, with a boundary between them at approximately the Brazil–Uruguay border (IOC-UNESCO and UNEP, 2016). The Patagonian Sea Forum recognizes the entire marine area around the Southern Cone as a continuous ecoregion (Falabella *et al.*, 2013). The MEOW classification shares the most similarity to our findings; however, the MEOW are delineated as arbitrary lines dividing latitudinal bands defined administratively rather than biologically. None of these frameworks have been derived using an objective methodology, nor they try to identify natural associations of species, representing biological communities. For this reason, we propose that the biogeographic regionalization found here is a more accurate framework for spatial conservation planning of chondrichthyan resources in the SWA. We recommend to use this biogeographic scheme, which has been tested and validated by this and previous work for a long time. Using this regionalization for spatial planning will make possible to have conservation and management efforts adequately allocated among the different natural biogeographic units of the SWA.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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