

Spatial patterns in the diversity of sharks, rays, and chimaeras (Chondrichthyes) in the Southwest Atlantic

Luis O. Lucifora · Verónica B. García · Roberto C. Menni · Boris Worm

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Abstract Knowing how the diversity of sharks, rays and chimaeras (Chondrichthyes) is distributed helps us to design strategies to conserve these highly-vulnerable predators and their habitats. Here, we analyzed the spatial distribution of chondrichthyan species richness in the Southwest Atlantic (34–56°S), and its relationship with environmental variables and marine fronts, by using a dataset obtained before the major development of industrial trawling fisheries. We also explored the relationship between richness and reported catches of chondrichthyans from commercial, demersal fisheries. Generalized linear models were used to assess the relationship of species richness with environmental variables; with marine fronts and with commercial catches. Species richness increased towards the north, particularly close inshore and on the outer shelf, with cells of highest richness found north of 48°S. Dissolved oxygen was related negatively with richness; depth, latitude and longitude were also related with richness, but to a lesser extent. Chondrichthyan diversity hotspots, i.e. cells with richness higher than the 90% percentile of the richness distribution, were more likely to occur on marine fronts than elsewhere. High chondrichthyan catches were significantly associated to hotspots, but low-catch areas were not related to coldspots, i.e. cells with less than the 10% percentile of the richness distribution. Areas of high richness of chondrichthyans coincide with high levels of catches and are used by other species of high conservation concern. Given the importance of these areas to multiple species in the Southwest Atlantic, any conservation strategy based on a network of protected areas should include marine fronts.

L. O. Lucifora (✉)

Centro de Investigaciones del Bosque Atlántico (CeIBA), Instituto de Biología Subtropical—Iguazú, Universidad Nacional de Misiones, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Casilla de Correo 9, N3370AVQ Puerto Iguazú, Misiones, Argentina
e-mail: luis.lucifora@gmail.com

V. B. García · B. Worm

Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, NS B3H 4J1, Canada

R. C. Menni

Departamento Científico Zoología Vertebrados, Museo de La Plata, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Paseo del Bosque s/n, B1900FWA La Plata, Argentina

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Introduction

Designing protected area-based conservation strategies for a taxonomic group requires basic knowledge of spatial patterns of biodiversity (Primack 2006). When based on taxa that are found in a wide variety of ecosystems, that are sensitive to human impacts, and that have important ecological functions, spatial biodiversity patterns could be particularly useful to identify areas of high conservation value, not only for a particular group, but also for the entire ecosystem.

Chondrichthyans are widespread predators, vulnerable to human impact, capable of influencing ecosystem functioning by determining the species turnover of benthic communities (e.g. vanBlaricom 1982; Thrush et al. 1991; Jiménez 1997; Peterson et al. 2001), and of controlling populations of other predators directly (e.g. Lucas and Stobo 2000; Myers et al. 2007) and indirectly (e.g. Acevedo-Gutiérrez 2002; Heithaus and Dill 2002). Overexploitation has affected multiple chondrichthyan populations worldwide (e.g. Brander 1981; Casey and Myers 1998; Graham et al. 2001; Baum et al. 2003; Devine et al. 2006; Robbins et al. 2006), producing declines of up to 99% in several populations (Baum and Myers 2004; Otway et al. 2004; Ferretti et al. 2008) with the potential to alter significantly marine ecosystems (Heithaus et al. 2007; Myers et al. 2007).

Large-scale patterns of fish diversity have been related to a number of environmental factors. Species richness and density of open-ocean predatory fish increase with oxygen content and are maximal at temperatures of around 21–24°C (Worm et al. 2005; Boyce et al. 2008). Species richness of both groundfish and skates (Rajidae) in the Gulf of Alaska peaks close to the continental slope and at intermediate depths (Mueter and Norcross 2002; Stevenson et al. 2008). Also, high diversity of open-ocean top predators, like tunas, billfishes and sharks, is related to areas of high biological activity, such as marine fronts (Worm et al. 2003). These areas, formed by the confluence of different water masses, have enormous biological productivity, as a result of the input of nutrients to sunlit waters by means of turbulent mixing (Acha et al. 2004). As a consequence, these areas provide optimal habitat for feeding and reproduction for many different species (e.g. Sims and Quayle 1998; Etnoyer et al. 2004; Ferraroli et al. 2004; Polovina et al. 2004; Royer et al. 2004).

The Southwest Atlantic continental shelf—one of the largest in the world—is characterized by large-scale oceanographic complexity (Acha et al. 2004) and heavy fishing effort (Tyedmers et al. 2005; Campagna et al. 2006a). Two main oceanographic currents—the tropical Brazil Current and the subpolar Malvinas/Falkland Current—influence the region and, acting together with continental-shelf water masses and freshwater discharges, form three main systems: a coastal system of homogeneous waters mixed by tidal and wind forces, a shelf-water system with a seasonal thermocline, and an offshore Malvinas/Falkland system with colder and more saline waters (Esteves et al. 2000). These systems are separated by a large number of marine fronts, formed by estuarine discharges, tidal currents and mixing of shelf and open-ocean waters (Esteves et al. 2000; Acha et al. 2004). The fronts serve as reproductive grounds for several fish and squid species that provide the basis of trawl fisheries in the area (Brunetti et al. 1998; Bezzi et al. 2004; Jaureguizar et al. 2008) and are also feeding grounds of several species of high conservation concern and high ecotourism value (Acha et al. 2004; Xavier et al. 2004; Campagna et al. 2006b).

Conservation status of the Southwest Atlantic ecosystem is a cause of concern among conservationists and fishery biologists. Declines of chondrichthyan and bony-fish populations (Carozza et al. 2004; Cordo 2004; Massa et al. 2004; Wöhler et al. 2004), and the collapse of the most important commercial species, the Argentine hake *Merluccius hubbsi* (Aubone et al. 2004; Bezzi et al. 2004; Cañete 2006), were already observed by 1999. Emerging currently as one of the highest in the world (Tyedmers et al. 2005), the industrial fishing effort in the area increased by 108% between 1990 and 1995 (Campagna et al. 2006a). Most of this effort (85%), corresponds to demersal trawling (Cousseau and Perrotta 2000), one of the most damaging and unselective fishing practices (Kaiser et al. 2002; Thrush and Dayton 2002; Crowder et al. 2008). At the ecosystem level, overfishing produced a non-random impact on the trophic web where populations were impacted sequentially from the upper to the lower trophic levels between 1991 and 2003 (Jaureguizar and Milessi 2008).

In this paper, we aimed to analyze patterns of chondrichthyan diversity in the Southwest Atlantic, particularly for demersal and benthic species, which are the most vulnerable to trawling. We used a dataset taken well before the major development of industrial trawling fisheries in the area (Campagna et al. 2006a), providing a good estimate of the baseline chondrichthyan diversity in the Southwest Atlantic. Specifically, we wanted to determine (1) how chondrichthyan diversity is distributed, (2) what are the main environmental variables affecting chondrichthyan diversity, (3) what is the relationship between marine fronts and chondrichthyan diversity, and (4) what is the relationship between reported chondrichthyan catches and chondrichthyan diversity.

Materials and methods

Data sources

The data used to estimate species richness and to identify hotspots of diversity were collected from 456 trawls conducted during four bottom-trawl research cruises performed during 4 June to 3 August 1966, 11 January to 16 March 1968, 1 January to 26 February 1971, and 7 May to 27 June 1978 by the fishery research vessel 'Walther Herwig' of the Institute for Sea Fisheries, Germany, (Fig. 1). During 1966, the vessel conducted 104 trawls on the Southwest Atlantic shelf along the Uruguayan coast and slope, and on the Argentinean shelf and slope to north of Islas Malvinas/Falkland Islands, from 35°04'S to 50°10'S. During 1968, nine trawls were conducted on the Uruguayan shelf. In 1971, the 171 trawls conducted covered almost all the Argentine shelf and slope from 44°00'S to 56°25'S. In 1978, 172 trawls were conducted that covered the area from 40°02'S to 54°31'S, off Patagonia. Overall, 1379 occurrences of chondrichthyans were recorded in the four cruises.

Environmental data were taken from four sources. Data on depth were provided with the original samples. Data on mean annual bottom temperature (°C), mean annual bottom salinity, mean annual bottom dissolved oxygen content (ml/l), and mean annual surface nitrate, phosphate, and silicate concentration (all in $\mu\text{mol/l}$) were taken from the World Ocean Atlas with a resolution of one degree latitude by one degree longitude (Locarnini et al. 2006; Antonov et al. 2006; García et al. 2006a, b). Bottom rugosity was estimated as the standard deviation of bottom depth for each 1-degree-square cell. For each cell, 3600 bottom-depth values were taken from the Global Topography website (Smith and Sandwell 1997) and the standard deviation calculated; cells with smooth bottoms had low standard

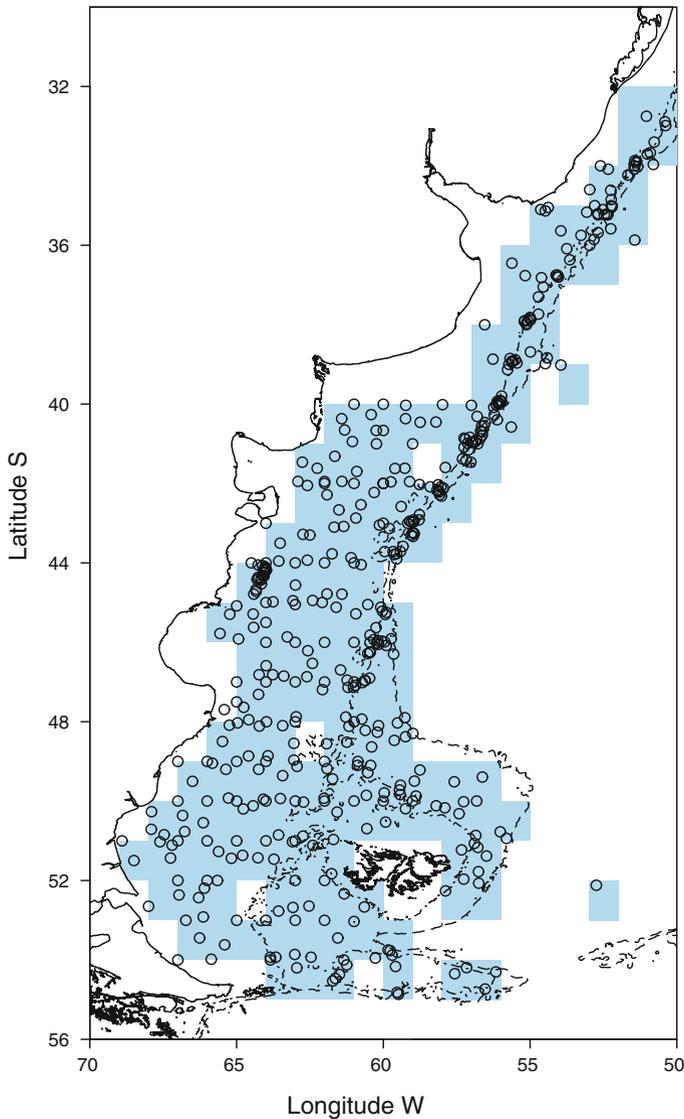


Fig. 1 Map of the Southwest Atlantic ocean showing trawl stations used to estimate species richness of sharks, rays and chimaeras (Chondrichthyes) (*open circles*) and the grid of one degree square used in the analyses. *Broken lines* are the 200 and 1,000-m isobaths

deviations and cells with a more complex bathymetry had a higher standard deviation in bottom depth. Finally, data on geographic locations of marine fronts in the Southwest Atlantic were taken from Acha et al. (2004).

Data on chondrichthyan catches used to identify cells with the highest catches were taken from official Argentine statistics, as reported by Massa et al. (2004). These data consist of cumulative catches of chondrichthyans, in metric tonnes, reported by fishing vessels to fishing authorities between 1994 and 1999 at a resolution of 1-degree-square

cell. These data represent a minimum value of actual catches since discards are not included in the reports, the data did not include the catches of the Uruguayan fleet (which also operates as far south as 40°S), and there is no control of the accuracy of the reporting but there are no incentives to overreporting (as is the case when individual transferable catch quotas are about to be set).

In all our analyses, the sample unit was a cell of one degree latitude by one degree longitude. In each cell, we counted the number of occurrences of any chondrichthyan irrespective of its species identity, and the number of species present. We used these data in rate models (Faraway 2006), in which the number of species was a function of the chondrichthyan occurrences, and of covariates of interest.

Spatial pattern and determinants of chondrichthyan biodiversity

To estimate the number of chondrichthyan species per cell, we used generalized linear models (GLM) (Venables and Ripley 2002). Generalized additive models (GAM) were fitted preliminary to take into account possible nonlinear relationships (Wood 2006). If nonlinear relationships were found with GAMs, appropriate terms (e.g. quadratic) were added to the GLM. The number of species (NS) was the response variable, and latitude (La), longitude (Lo), depth (D), bottom rugosity (R), temperature (T), salinity (S), oxygen content (O), and concentration of phosphates (P), nitrates (N) and silicates (Si) were treated as explanatory variables. Explanatory variables were not included together in the same model if a correlation was detected among them. For the best model, variance inflation factors (VIF) were calculated to test for the occurrence of multicollinearity, with VIF values higher than 10 indicating multicollinearity (Kutner et al. 2004). The number of chondrichthyan occurrences (Oc) was included as a quadratic offset term because the relationship between NS and Oc was curvilinear.

The models were specified to have a Poisson distribution because the response variable was a count and a log link because the response variable took only positive values.

We selected the best hypothesis explaining NS using a multiple-hypothesis model-selection approach (Anderson et al. 2000; Franklin et al. 2001; Johnson and Omland 2004). In this approach, models are equated to hypotheses, and the hypothesis that best describes the data is selected using Information Theory, as the model with the lowest Akaike Information Criterion (AIC) (Anderson et al. 2000; Franklin et al. 2001; Johnson and Omland 2004). A stepwise backward selection procedure based on minimization of AIC was performed. In this procedure, for each full model containing a combination of explanatory variables that were not correlated, sequential deletion of explanatory variables was conducted until all the possible combinations were tested. The best hypothesis was chosen as the model with the lowest AIC. The magnitude of the effect of each explanatory variable on the response variable was measured by the coefficients of the explanatory variables in the best model. If the explanatory variable was continuous, then the coefficient was interpreted as a slope because it gives the rate of change of the response variable along the explanatory variable's range of values. If the explanatory variable was discrete (i.e. it was a factor), then the coefficient was interpreted as an intercept. This intercept measures how many times above (if positive) or below (if negative) the response variable was located with respect to response variable's cases having the alternative state(s) of the explanatory factor.

To test whether areas of high diversity were associated to marine fronts, we built GLMs with environmental variables for each cell as before, plus a factor identifying if the cell contained a marine front or not (F), as explanatory variables. The response variable in this

model was a binary factor identifying if the cell was an area of high diversity (i.e. hotspots, *HS*)—defined as cells with diversity values higher than the 90% percentile of *NS* (Roberts et al. 2002)—or not.

The model was specified to have a binomial distribution because the response variable had only two possible values, and a logit link. The best model explaining *HS* was also selected using Information Theory.

In an analogous way, we defined areas of low diversity (i.e. coldspots, *CS*), as those cells with diversity values lower than the 10% percentile of *NS*. We investigated the relationship between coldspots and marine fronts in the same way as with hotspots.

Relationship between diversity and fishery catches

To determine if fishery catches were related to areas of high or low diversity, we built GLMs with environmental variables, plus a factor identifying if a cell was a hotspot or not (*HS*). The response variable was a binary factor identifying if a cell had high reported chondrichthyan catch or not. Cells with high chondrichthyan catches (*HC*) were those with catches higher than the 90% percentile of the reported catches.

The model was specified to have a binomial distribution because the response variable took only two possible values, and a logit link. The best model explaining *HC* was also selected using Information Theory. A similar model was used to investigate the relationship between areas of low catches (*LC*)—i.e. those with catches lower than the 10% percentile of reported catches—and coldspots. The model was identical to the one for high catches, but with *LC* instead of *HC* as a response variable, and *CS* instead of *HS* as a predictor.

In all cases, the Moran's *I* index of spatial autocorrelation (Moran 1950) was calculated on the residuals of the best models to test for possible spatial autocorrelation not accounted for by the models. Moran's *I* values higher than two or lower than -2 indicated significant spatial autocorrelation. Moran's *I* indices for all models were very close to zero, indicating no spatial autocorrelation (Table 1). All statistical procedures were conducted using the statistical software R, version 2.6.2 (R Development Core Team 2008).

Results

Chondrichthyan species richness increased towards the north, particularly close inshore and on the outer shelf (Fig. 2a). Diversity peaked north of 48°S and hotspots—cells containing 10 or more species—were all located north of this latitude (Fig. 3a). South of 48°S, chondrichthyan diversity was generally low, with 6–8 species per cell, excepting four cells with 8–10 species (Fig. 2b). Coldspots—cells containing less than two species per cell—were located south of 45°S, except two coldspots located just off the continental slope (Fig. 3a).

Chondrichthyan diversity was related to oxygen content, mean depth, latitude, and longitude (Table 1, model 1). For each term of the best model, VIF values were all lower than 10: 1.30 for oxygen content, 7.31 for mean depth, 6.28 for squared depth, 2.59 for latitude and 2.88 for longitude, indicating that there was no multicollinearity. Dissolved oxygen content and depth emerged as the main environmental factors determining chondrichthyan diversity. Dissolved oxygen content was negatively related to species richness (Fig. 2). Depth had a curvilinear relationship with diversity: it was high at shallow inshore areas and at deep offshore areas (Fig. 2a). All other variables tested—bottom rugosity,

Table 1 Models explaining diversity patterns of chondrichthyan diversity in the Southwest Atlantic

Model	AIC	w	w ₁ /w ₂	w ₁ /w _{worst}	Moran's I
1 $NS \sim 4.612 (0.742) - 0.001 (0.0005) D + 8.9 e^{-7} (4.6e^{-7}) D2 - 0.103 (0.064) O - 0.026 (0.011) La + 0.047 (0.015) Lo$	512.50	0.57	1.33	112.17	-0.078
2 $HS \sim -12.934 (6.575) - 1.714 (0.738) NF + 1.798 (0.743) O + 0.559 (0.187) La - 0.42 (0.188) Lo$	74.01	0.56	2.43	2.77	-0.028
3 $CS \sim -9.851 (2.661) + 0.915 (0.550) NF + 0.0073 (0.0031) D - 3.8e^{-6} (2.8e^{-6}) D^2 - 0.131 (0.052) La$	115.59	0.53	1.34	6.79	-0.031
4 $HC \sim 12.765 (10.602) + 2.019 (1.384) HS - 1.598 (1.000) O - 1.431 (0.513) La + 1.03 (0.426) Lo$	48.46	0.55	1.51	6.58	-0.034
5 $LC \sim -11.575 (3.655) + 0.004 (0.002) D - 1.148 (0.536) O - 0.393 (0.075) La$	95.87	0.66	2.20	15.04	0.196

For each model, parameters, standard errors (*in brackets*), Akaike's Information Criterion (AIC), Akaike weight (*w*), the ratio between the best model's Akaike weight and the second best model's (*w₁/w₂*), the ratio of the best model's Akaike weight to the worst model (*w₁/w_{worst}*), and Moran's *I* index of spatial autocorrelation on the residuals are given. Model 1 has a Poisson distribution and a log link, models 2 to 5 have a binomial distribution and a logit link

NS number of species, *D* depth, *O* dissolved oxygen content (ml/l), *La* Latitude, *Lo* Longitude, *HS* factor identifying if a cell is a hotspot or not, *NF* absence of front (parameter is relative to the presence of a front), *CS* factor identifying if a cell is a coldspot or not, *HC* factor identifying if a cell contains a mean annual reported chondrichthyan catch >280.67 metric tonnes (high catch) or not, *LC* factor identifying if a cell contains no annual reported chondrichthyan catch

annual mean bottom temperature, annual mean bottom salinity, and annual mean concentration of nutrients (phosphates, nitrates, and silicates)—were not retained in the best model.

Eleven out of 13 identified hotspots were located in cells making part of a marine front (Fig. 3a; Table 1, model 2). The probability of a cell to contain a hotspot was 2.89 times higher if the cell had a marine front than if it had not. The probability of the occurrence of a coldspot in a given cell was 1.44 times higher if the cell did not contain a marine front, than if it had one.

Like hotspots, high-catch areas—those having a mean annual reported catch of chondrichthyans higher than 280.67 metric tonnes—were all located in the northern half of the study area (Fig. 3b). Although the relationship was weak, high-catch areas were significantly more likely to occur in a hotspot cell than in a non-hotspot cell (1.02 times). On the contrary, low-catch areas—cells containing no reported catch of chondrichthyans—were widespread and did not have a relationship with coldspots (Fig. 2; Table 1, model 5).

Discussion

Our results show that (1) diversity of chondrichthyans in the Southwest Atlantic is heterogeneously distributed, (2) oxygen content is negatively correlated to chondrichthyan species richness, (3) marine fronts contain the areas with the highest chondrichthyan

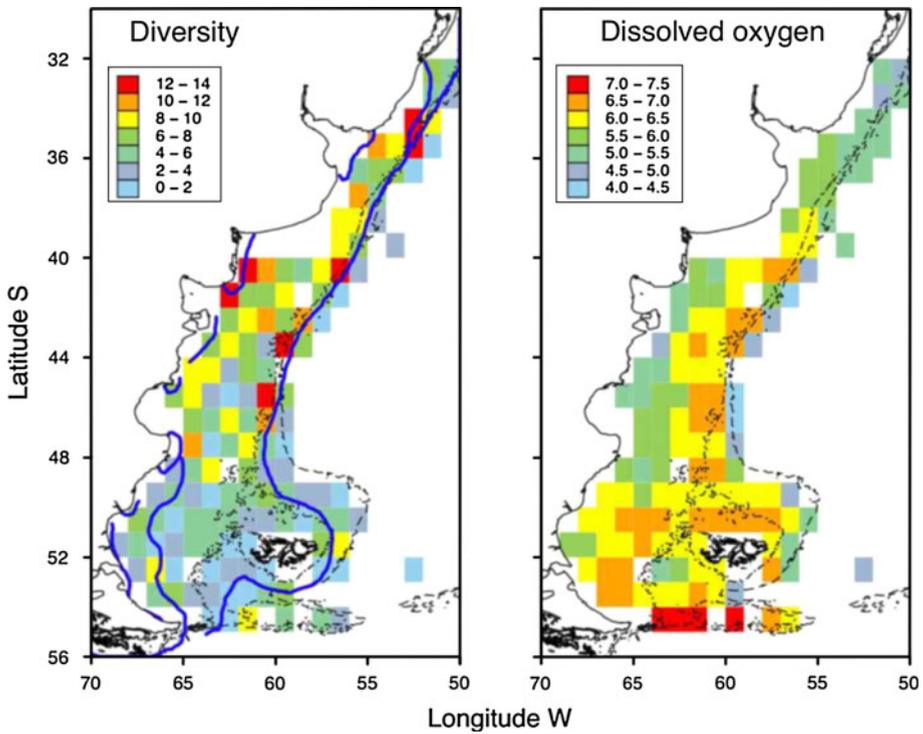


Fig. 2 Maps of the Southwest Atlantic Ocean showing estimated mean diversity (number of species) of sharks, rays and chimaeras (Chondrichthyes) and mean annual dissolved oxygen content (ml/l). *Broken lines* are the 200 and 1,000-m isobaths, the *bold lines* are the location of marine fronts (areas of mixing of different water masses) after Acha et al. (2004)

diversity (hotspots), and (4) the highest reported catches of chondrichthyans overlap with hotspots of chondrichthyan diversity.

Diversity of demersal and benthic chondrichthyans in the Southwestern Atlantic is related negatively with diluted bottom oxygen concentration. Worm et al. (2005) found a positive relationship between open ocean pelagic predatory fish diversity (including chondrichthyans) and oxygen concentration at 100 m deep. Therefore, there is an opposite trend between diversity and oxygen concentration in the pelagic and demersal/benthic habitat. This difference can be explained by several causes. First, the mean annual bottom oxygen concentrations observed in the Southwest Atlantic—a minimum of 4 ml O₂/l (i.e. 5.716 mg O₂/l)—are above the minimum requirements for aerobic metabolism in most marine taxa—a 90% percentile of 4.59 mg O₂/l of the median lethal concentration (Vaquer-Sunyer and Duarte 2008). In this way, a positive relationship between oxygen content and diversity is not expected, since oxygen content appears not to be a limiting factor. Second, most of the species on which our diversity estimates are based are demersal or benthic ectothermic species, whose oxygen requirements are lower than those of pelagic and endothermic species (Carlson et al. 2004). The difference in metabolic rate between demersal and pelagic species may explain why the relationship between diluted oxygen and chondrichthyan diversity is not positive, as is the case among open-ocean fishes (Worm et al. 2005). Finally, oxygen content is usually negatively correlated to levels of biological activity (Zamorano et al. 2007), since a high abundance of aerobic benthic

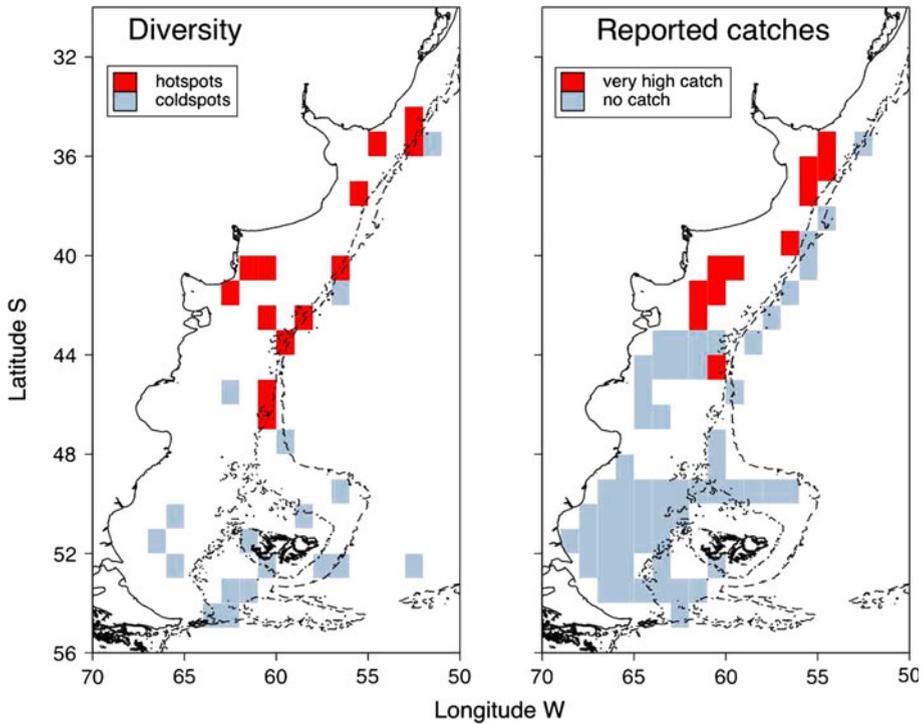


Fig. 3 Maps of the Southwest Atlantic ocean showing hotspots (cells with more than 10 species) and coldspots (cells with less than two species) of sharks, rays and chimaeras (Chondrichthyes), and areas with the highest reported catches (>280.67 metric tonnes) and no reported catches of Chondrichthyes. Broken lines are the 200 and 1000-m isobaths

organisms can deplete the oxygen concentration. If chondrichthyan diversity is positively associated to areas of high abundance of benthic prey, a negative correlation between oxygen content and diversity would be observed.

Hotspots of chondrichthyan diversity in the southwest Atlantic are associated with marine fronts—areas of high biological activity. Marine fronts are proven attraction areas for many species of the southwest Atlantic and elsewhere. For example, the basking shark, *Cetorhinus maximus*, uses disproportionately frontal areas as feeding grounds due to increased prey abundance (Sims and Quayle 1998); porbeagles, *Lamna nasus*, aggregate along marine fronts of the Northwest Atlantic during spring, presumably to feed (Campana and Joyce 2004); the smallnose fanskate, *Sympterygia bonapartii* (Mabragaña et al. 2002); and the angular angel shark, *Squatina guggenheim* (Vögler et al. 2008) are most abundant and have nursery and feeding grounds along estuarine frontal areas. We propose that the high chondrichthyan diversity around Southwest Atlantic marine fronts is a result of an abundant supply of prey organisms (e.g. benthic invertebrates) that acts as an attractor to individual chondrichthyan species and, at the same time, allows for the coexistence of a high number of predator species. For instance, the skates *Psammodontus normani* and *P. rudis* have a similar diet when they coexist in a marine front area, but their diets differ when they coexist in non-frontal areas of the Southwest Atlantic, a result hypothesized to be caused by the relaxation of competition due to high prey abundance in marine fronts (Mabragaña and Giberto 2007).

Southwest Atlantic marine fronts are also heavily used by other species of conservation concern (Acha et al. 2004; Campagna et al. 2008), like southern elephant seals *Mirounga leonina* (Campagna et al. 1999, 2006b), wandering albatrosses *Diomedea exulans* (Xavier et al. 2004), shortfin squid *Illex argentinus*, and the Argentine hake *Merluccius hubbsi* (Chen et al. 2007; Wang et al. 2007). In this way, Southwest Atlantic marine fronts harbour high chondrichthyan diversity and, at the same time, act as valuable habitats for many other marine animals. Given the importance of these areas to multiple species in the Southwest Atlantic, any conservation strategy based on the building of a network of protected areas in this ecosystem should include areas of marine fronts.

Prospects for the Southwest Atlantic chondrichthyan diversity

Areas of high reported catches of chondrichthyan overlap significantly with hotspots of chondrichthyan diversity, suggesting that high-diversity areas are at a direct risk from industrial trawling. Supporting this argument, declines of at least 50% of the biomass estimates are already documented for several species of chondrichthyan, e.g. the elephantfish *Callorhynchus callorhynchus*, the lesser guitarfish *Zapteryx brevirostris*, the Brazilian guitarfish *Rhinobatos horkelii*, the apron ray *Discopyge tschudii*, the spiny dogfish *Squalus acanthias*, the spotback skate *Atlantoraja castelnaui*, the eyespot skate, *A. cyclophora*, and the sand skates *Psammobatis* spp. These declines coincide with a 12-fold increase in the reported fishing effort on chondrichthyan by the industrial trawling fleet between 1991 and 1998 (Massa et al. 2004).

Protecting hotspots of chondrichthyan diversity may be a cost-effective strategy to conserve many individual species at once and the communities in which they live. However, low diversity areas (i.e. coldspots) may contain species and communities not occurring in hotspots that are also in need of protection (Kareiva and Marvier 2003). As chondrichthyan diversity is heterogeneously distributed in the Southwest Atlantic, i.e. most hotspots are located north of 45°S, the design of protected areas based on diversity hotspots is only a first step towards a network of protected areas representative of all species and communities. An additional analysis of the distribution of areas containing endemic species and communities will be necessary.

Multiple chondrichthyan and bony-fish population declines (Lucifora 2003; Aubone et al. 2004; Bezzi et al. 2004; Carozza et al. 2004; Cordo 2004; Massa et al. 2004; Wöhler et al. 2004; Cañete 2006) and the occurrence of the “fishing-down-marine-food-webs” phenomenon (Pauly et al. 1998; Jaureguizar and Milessi 2008) are evidence that the whole ecosystem of the Southwest Atlantic is being seriously affected by industrial fishing. A plan considering the conservation and restoration of ecosystem properties, functions and services, while taking into account conservation at the species level is needed for the Southwest Atlantic, as opposed to the current management based exclusively on the single-population approach (Campagna et al. 2008).

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