Biodiversity and Conservation

VOLUME 19 NUMBER 3 2010
ISSN 0960-3115 CODEN BONSEU

Editor-in-Chief: David L. Hawksworth

Springer

ORIGINAL PAPER

Marine biodiversity at the community level: zoogeography of sharks, skates, rays and chimaeras in the southwestern Atlantic

Roberto C. Menni · Andrés J. Jaureguizar · Matthias F. W. Stehmann · Luis O. Lucifora

Abstract For more than a century, two major zoogeographic provinces have been proposed for the southwestern Atlantic: a warm water Argentinean Province from Rio de Janeiro (23°S, Brazil) to Valdés Peninsula (42°S, Argentina), and a cold water Magellanic Province from Valdés Peninsula to Cape Horn. This zoogeographic scheme has been recognized so far using data covering only parts of the whole geographic area. Here, we test the validity of this scheme by analyzing the distribution of sharks, skates, rays and chimaeras, using data from research cruises covering the entire area. We used cluster, similarity and dissimilarity analyses to identify species assemblages, and canonical correspondence analysis to identify the main environmental variables affecting the composition of the assemblages. The distribution of chondrichthyan assemblages strongly supports the current zoogeographic scheme and identifies a previously unknown and distinctive deep water zoogeographic unit off southern Brazil. Both, the Argentinean and Magellanic Provinces had extensive internal structure, with four and three subareas identified in each of them, respectively. These subareas correspond, with slight differences, to previously proposed zoogeographical districts within the Argentinean Province and

R. C. Menni
Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Museo de La Plata, Paseo del Bosque s/n, B1900FWA, La Plata, Buenos Aires, Argentina

A. J. Jaureguizar
Comisión de Investigaciones Científicas, Instituto Nacional de Investigación y Desarrollo Pesquero, B7602HSA, Mar del Plata, Buenos Aires, Argentina

M. F. W. Stehmann
Ichthys Consultant, 22459 Hamburg, Germany

L. O. Lucifora
Department of Biology, Dalhousie University, 1355 Oxford St., Halifax, NS B3H 4J1, Canada

L. O. Lucifora (✉)
CONICET, Centro de Investigaciones Ecológicas Subtropicales, Centro de Investigaciones del Bosque Atlántico, Casilla de Correo 9, N3370AVQ, Puerto Iguazú, Misiones, Argentina
e-mail: luis.lucifora@gmail.com

confirm ecological differences within the Magellanic Province. Species composition had the highest correlation with depth and bottom water temperature. Since the distribution of anthropogenic disturbances in the region is uneven, different assemblages can be subjected to different impacts. Our results provide an objective basis to establish priority areas for the conservation of chondrichthyans in the southwestern Atlantic.

Keywords Chondrichthyes · Elasmobranch communities · Biodiversity · Southwestern Atlantic · Chondrichthyan conservation

Introduction

The zoogeographic scheme of the eastern South American shelf off southern Brazil, Uruguay and Argentina, one of the largest continental shelves of the world, includes two provinces, the Magellanic Province (Woodward 1856) and the Argentinean Province (Cooke 1895). The Magellanic Province ranges from Cape Horn to about Valdés Peninsula over the Patagonian shelf following northward along the edge of the shelf and on the slope. The Argentinean Zoogeographic Province ranges from Rio de Janeiro to Valdés Peninsula (Woodward 1856; Cooke 1895; Doello Jurado 1938; Balech 1964; López 1964; Krefft 1968; Briggs 1974; Palma et al. 2004) (Fig. 1).

The ichthyofauna living in these two large areas is well known from information obtained by large foreign expeditions and local research since the early twentieth Century (Norman 1937; Krefft 1968; Ringuelet 1984; Menni 1981; Menni and López 1984; Menni and Stehmann 2000). At large scales, the distribution of both chondrichthyan and teleostean fish assemblages closely agree with that of other animals, such as molluscs, crustaceans and asteroid echinoderms (Cooke 1895; Carcelles 1950; Bernasconi 1964; Boschi 2000). Less extended assemblages correspond to districts within the provinces or particular communities (Menni and Gosztonyi 1982; Menni and López 1984; Angelescu and Prenski 1987; Díaz de Astarloa et al. 1999; Jaureguizar et al. 2006).

The limits between the Argentinean and Magellanic provinces and the structure within them have been so far studied only with data sets comprising parts of the whole area, which is susceptible to edge effects. Here, we analyze an extensive database on specific composition and distribution of chondrichthyans gathered by the German fishery research vessels 'Walther Herwig' during cruises in 1966, 1968, 1971 and 1978. We use the database in a standardized way throughout the region to test the validity of the current zoogeographic scheme of the southwestern Atlantic. We predict that, if the whole zoogeographic scheme is valid, the organization of chondrichthyan assemblages will agree with previous knowledge of community organization in the area. The presence of defined assemblages of both chondrichthyans and teleost fishes was shown for the western Atlantic off Argentina by Menni and Gosztonyi (1982), Menni and López (1984) and Angelescu and Prenski (1987). We conjecture that similar assemblages will be identified again off Argentina and along the Uruguayan and Brazilian coasts.

In addition to testing the validity of the current zoogeographic scheme of the southwestern Atlantic, we also aim to identify the spatial distribution of chondrichthyan assemblages in order to contribute basic information needed for the conservation of chondrichthyan fishes. Important areas for conservation can be better designed based on the boundaries of biological communities rather than, for example, on an important area for a single species' life cycle (Groves et al. 2002; Primack 2006); in this way, a whole functioning ecosystem can be protected.
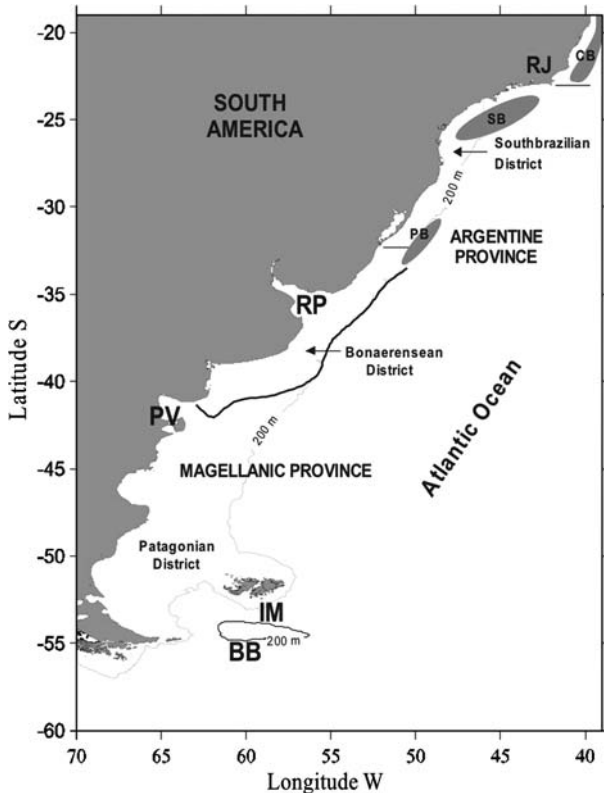
Fig. 1 Current zoogeographic divisions of the western Atlantic off Brazil, Uruguay and Argentina (modified from Lopez 1963). *Dark grey areas* show the location of gas and oil fields discovered off southern Brazil. *RJ* Rio de Janeiro, *RP* Río de la Plata, *PV* Valdés Peninsula, *IM* Islas Malvinas, *BB* Burdwood Bank, *CB* Campos Basin, *SB* Santos Basin, *PB* Pelotas Basin

In this paper, we (1) test the validity of the currently accepted zoogeographic scheme of the southwestern Atlantic using, for the first time, a dataset that covers the whole study area, and (2) identify the structure of lower level zoogeographic divisions.

Material and methods

Four scientific cruises with the fishery research vessels 'Walther Herwig' from the Institute for Sea Fisheries, Hamburg, Germany, were carried out during 1966, 1968, 1971 and 1978 (Fig. 2) fishing with commercial size bottom trawl nets. The cruises covered the southwestern Atlantic from 22°20′S (off Rio de Janeiro, Brazil) to 54°52′S (off Isla de los Estados, Argentina) between 25 and 1,560 m depth. The first cruise (WH cr. 1966) was conducted from 4 June to 3 August 1966 (winter), the second (WH cr. 1968) from 11 January to 16 March 1968 (summer), the third (WH cr. 1971) from 31 December to 26 February 1971 (summer) and the fourth (WH cr. 1978) from 7 May to 27 June 1978 (autumn–winter, first leg of three). In spite of bearing the same name, the ship used during the WH cr. 1978 was a larger and more powerful vessel, operating a larger net.

Fig. 2 Stations sampled during the Walther Herwig cruises 1966, 1968, 1971 and 1978 on the western Atlantic off Brazil, Uruguay and Argentina. *RJ* Rio de Janeiro, *RP* Río de la Plata, *PV* Valdés Peninsula, *IM* Islas Malvinas, *BB* Burdwood Bank
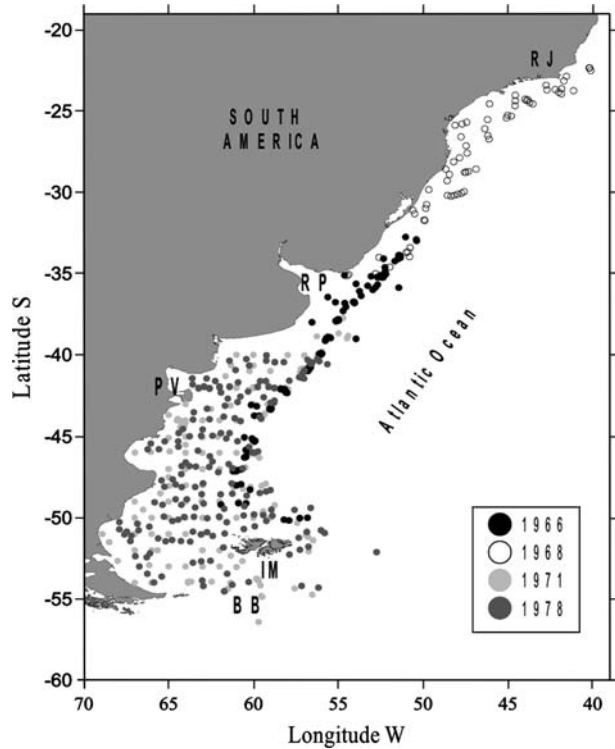
The WH cr. 1966 sampled the southwestern Atlantic on the shelf along the Uruguayan coast and slope, and on the Argentinean shelf and slope to north of Islas Malvinas. Fifty-three stations were fished on the shelf and 52 stations at depths between 200 and 1,200 m from $35°04'$S to $50°10'$S. The WH cr. 1968 was performed from the mouth of the Rio de la Plata along the Uruguayan and Brazilian coasts from $35°08'$S to $22°20'$S and from $40°11'$W to $54°29'$W with 38 stations on the shelf and 27 at deeper waters, with bottom water temperatures ranging from 3.28 to 21.77°C and within a depth range from 25 to 1,200 m. The WH cr. 1971 covered almost all the Argentinean shelf and slope in Magellanic waters from $44°00'$S to $56°25'$S, with 116 stations on the shelf and 61 stations at deeper waters to 1,200 m. The WH cr. 1978, first leg, covered the area from $40°02'$S to $54°31'$S, sampling 135 stations at shelf depths and 40 stations down the slope to 1,500 m.

A standard commercial 42.67 m bottom trawl net (WH cr. 1966, 1968, 1971) and a 60.96 m bottom trawl net (WH cr. 1978) were used during the surveys equipped with a codend of 20 mm mesh size.

Presence–absence by sampling station was used to obtain a grouping of stations based on species composition (chondrichthyan assemblage areas), using a similar approach as Menni and López (1984), Mahon et al. (1998) and Jaureguizar et al. (2003). The spatial trend or change in the chondrichthyan assemblage areas was examined with a cluster analysis using the Bray-Curtis similarity index and average grouping as cluster mode (Clarke and Warwick 2001).

Following Mahon et al. (1998) and Jaureguizar et al. (2003), an affinity index was devised to limit each species to a single group of stations (chondrichthyan assemblage areas) in which it has the highest standardized presence. The affinity index is (Pg/Nsg)/(Pt/Nst)

where Pg is the number of sampling stations with presence of the species of the group, Nsg the number of total sampling stations in the group, Pt the number of sampling stations with presence of the species in the study area, and Nst the number of total sampling stations in the study area. The species affinity, when it has the highest standardized presence in each group of stations (chondrichthyan assemblage areas) was labeled as 'exclusive' (present only in the group) or 'common' (present in more than one group).

Similarity percentage analysis (SIMPER) was used to identify species responsible for each area similarity and dissimilarity among different areas. Species within each assemblage area were defined as 'typical' if they contributed to the top 90% of average similarity within the assemblage area, or as 'discriminators' if they contributed to the top 90% of dissimilarity between assemblage areas with a low ratio of average dissimilarity to its standard deviation. This procedure uses the standard deviation of the Bray-Curtis dissimilarity matrix attributed to a species for all species pairs, and compares that with the average contribution of a species to the dissimilarity. It also allowed us to quantify the average contribution by species, as the measure of dissimilarity among different assemblages (Clarke and Warwick 2001).

The BIO-ENV procedure (Clarke and Warwick 2001) and Canonical Correspondence Analysis (CCA) (CANOCO version 4.02) were used to estimate the influence of latitude, longitude and depth on the spatial distribution of chondrichthyan assemblage areas for all cruises. The same procedures were used to assess the influence of bottom water temperature, salinity, latitude, longitude and depth for the WH cr. 1978 because temperature and salinity data were available for this cruise only. The BIO-ENV procedure selects the abiotic variables that maximize the correlation rank (ρ) between the biotic and abiotic (dis)similarity matrices (Bray-Curtis for biota and Euclidean distance for environmental variables). Their rank was compared through a Spearman coefficient (ρ) that lies in the range ± 1 with the extreme values corresponding to the cases when the two sets of ranks are in complete opposition or complete agreement. The CCA is a direct analysis that selects the linear combination of environmental variables that maximizes the dispersion of the species scores. The distribution species scores are restricted to be a linear combination of measured environmental variables, and the correlation of the environmental variables with the first two axes is termed intra-set correlation. The ordination output shows patterns that are directly related to the environmental conditions being examined. The significance test was based on a Monte Carlo permutation test (103 permutations) for the sum of all eigenvalues and the significance of relationships between gradients and the individual environment variables were evaluated using a *t*-test.

Results

Main zoogeographic divisions

During the four cruises, 8,120 specimens of 59 chondrichthyan species were sampled from 521 stations (Fig. 2). The number of species in each cruise was 41, 33, 25 and 28, respectively. Only five species were common to all cruises, namely *Mustelus schmitti*, *Squalus* sp. cf. *S. cubensis*, *Atlantoraja cyclophora*, *Sympterygia bonapartii* and *Myliobatis freminvillei*.

Cluster analysis of distribution, considering stations according to their specific composition for the four cruises pooled, resulted in 10 groups defining three different areas
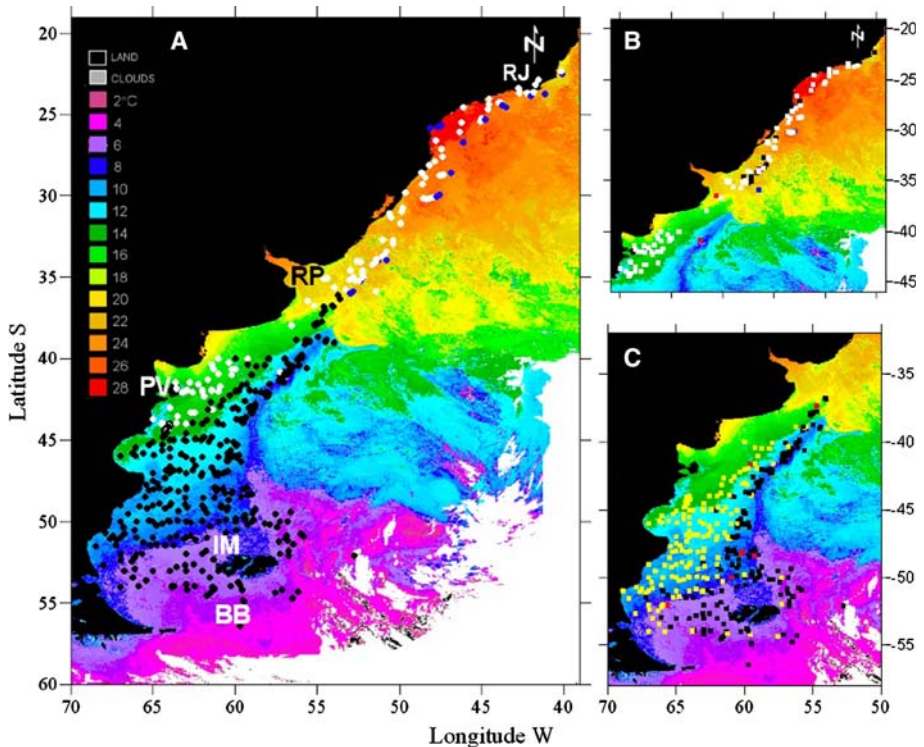
Fig. 3 Main areas resulting from a cluster analysis of a Bray-Curtis presence–absence matrix of species by stations. Stations are plotted over a Sea Surface Temperature composite image (NOAA-14, February–March 1999). Surface temperature is displayed. **a** Deep water Brazilian fauna (main Area 1, *blue circles*), Magellanic fauna (main Area 2, *black circles*), Western Temperate South Atlantic Province (main Area 3, *white circles*). **b** Subareas within main Area 3: Subarea 3.1 (*blue circles*), Subarea 3.2 (*red circles*), Subarea 3.3 (*black circles*), Subarea 3.4 (*white circles*). **c** Subareas within main Area 2: Subarea 2.1 (*yellow circles*), Subarea 2.2 (*black circles*), Subarea 2.3 (*red circles*). *RJ* Rio de Janeiro, *RP* Río de la Plata, *PV* Valdés Peninsula, *IM* Islas Malvinas, *BB* Burdwood Bank. A color version of this figure is available in the online version of Biodiversity and Conservation

(Fig. 3a; Table 1). The three main areas (Areas 1, 2 and 3, see below) match very precisely the current zoogeographic scheme of the southwestern Atlantic.

All areas are clearly defined by their different species composition, with three main areas (1, 2 and 3) including the bulk of species. Expressed as dissimilarity in percentage based on SIMPER analysis, the species composition of Area 1 differs from Areas 2 and 3 by 99.63 and 100%, respectively, whereas Areas 2 and 3 differ from each other by 95.6%. The remaining areas included scarce species and provide interesting species-specific information. Area 5 is composed of only two species (the skates *Bathyraja multispinis* and *B. papilionifera*) and Areas 4 and 6–10 by a single species each, namely *Dasyatis centroura* (which also occurs scarcely in Area 3), *Harriotta raleighana*, *Benthobatis kreffti*, *Dipturus leptocaudus*, *Carcharhinus obscurus* and *Alopias vulpinus*, respectively (Table 1).

Area 1 is composed mainly of slope stations along the Brazilian and Uruguayan coasts (Fig. 3a) southward to 36°S between 25 and 1,200 m depth (85% on the slope). The chondrichthyan fauna of this area consists of 13 species of which nine are exclusive species (i.e. they are only present in this single area), namely the skates *Amblyraja frerichsi*,

Table 1 Affinity of species to main Area 1–10 identified by cluster analysis (Bray-Curtis similarity index on presence–absence of species by stations)

Species	Main areas									
	1	2	3	4	5	6	7	8	9	10
Amblyraja frerichsi	24.81									
Bathyraja schroederi	24.81									
Dasyastis americana	24.81									
Rhinobatos percellens	24.81									
Rajella sadowskyii	24.81									
Torpedo nobiliana	24.81									
Etmopterus gracilispinnis	24.81									
Etmopterus lucifer	24.81									
Gurgesiella dorsalifera	24.81									
Etmopterus bigelowi	22.9		0.35							
Rhizoprionodon porosus	12.4		2.31							
Rioraja agassizi	9.3		2.88							
Narcine brasiliensis	6.2		3.46							
Bathyraja griseocauda		1.37								
Bathyraja scaphiops		1.37								
Amblyraja doellojuradoi		1.37								
Bathyraja albomaculata		1.37								
Bathyraja macloviana		1.37								
Bathyraja magellanica		1.37								
Dipturus trachydermus		1.37								
Lamna nasus		1.37								
Pristis sp.		1.37								
Schroederichthys bivius		1.37								
Bathyraja brachyurops		1.36	0.03							
Zearaja flavirostris		1.35	0.06							
Squalus acanthias		1.20	0.58							
Squalus mitsukurii		0.91	1.54							
Callorhinchus callorhynchus		0.70	2.27							
Sympterygia bonapartii		0.64	2.47							
Discopyge tschudii		0.58	2.65							
Squalus cf. *S. cubensis*		0.58	2.66							
Mustelus schmitti		0.26	3.75							
Carcharhinus signatus		0.14	4.13							
Myliobatis goodei		0.10	4.27							
Musteus canis		0.04	4.49							
Atlantoraja castelnaui			4.61							
Atlantoraja cyclophora			4.61							
Atlantoraja platana			4.61							
Carcharhinus plumbeus			4.61							
Dasyatis sayi			4.61							
Gymnura altavela			4.61							

Table 1 continued

Species	Main areas									
	1	2	3	4	5	6	7	8	9	10
Galeorhinus galeus			4.61							
Heptranchias perlo			4.61							
Myliobatis freminvillei			4.61							
Notorynchus cepedianus			4.61							
Rhinobatos horkelii			4.61							
S. cf. *S. besnardi*			4.61							
S. haeckeli			4.61							
Squaliolus laticaudus			4.61							
Sphyna lewini			4.61							
Schroederichthys sp.			4.61							
Dasyatis centroura				260.5						
Bathyraja multispinis					37.21					
Bathyraja papilionifera					173.67					
Benthobatis kreffti						521				
Harriotta raleighana							521			
Dipturus leptocaudus								521		
Carcharhinus obscurus									521	
Alopias vulpinus										521

The species preference to each area was considered 'exclusive' (species present only in a single area) or 'common' (present in more than one area)

Bathyraja schroederi, *Rajella sadowskii*, and *Gurgesiella dorsalifera*, the rays *Dasyatis americana*, *Rhinobatos percellens* and *Torpedo nobiliana*, and the sharks *Etmopterus gracilispinis* and *E. lucifer*. The remaining four species (the sharks *E. bigelowi*, *Rhizoprionodon porosus*, the skate *Rioraja agassizi* and the ray *Narcine brasiliensis*) are common, occurring also in Area 3. Internal average similarity of the area is 22.22% with the two species of *Etmopterus* and *Rajella sadowskii* contributing the top 88.38% of its similarity (Table 2). All the typical species (i.e. contributing to the top 90% of similarity), except *A. frerichsi,* discriminate the area (i.e. account for the top 90% of dissimilarity with other areas) (Table 3).

Area 2 covers all the Argentinean shelf and slope from Cape Horn northward to Valdés Peninsula (i.e. off Patagonia), from where it extends north to latitude 36°S (about the latitude of the Río de la Plata mouth) but excludes waters less than 80 m in depth (Fig. 3a). Its chondrichthyan fauna comprises 22 species of which 10 are exclusive and three are common, occurring also in Area 3 (Table 1). Internal average similarity is 22.92%, with *Zearaja flavirostris*, *Bathyraja brachyurops*, *Schroederichthys bivius*, *B. griseocauda*, *Amblyraja doellojuradoi*, *B. albomaculata*, *Squalus acanthias*, *B. magellanica*, *B. macloviana*, *B. scaphiops*, *Squalus* sp. cf. *S. cubensis*, *Callorhinchus callorhynchus*, *Discopyge tschudii*, *B. multispinis*, *Sympterygia bonapartii* and *Mustelus schmitti*, in decreasing order, accounting for 99.99% of its average similarity (Table 2).

Area 3 corresponds to the shelf and slope from off Rio de Janeiro to slightly south of Valdés Peninsula, with depths from 25 to 1,200 m (Fig. 3a). Of the 32 species in the area, 25 show affinity for it and 16 are exclusive (Table 1). The internal similarity of the area is

Table 2 Species contribution to similarity of the main Areas 1, 2 and 3 (SIMPER analysis)

Species	Av. Sim.	Sim./SD	Cum. %.
Main Area 1 (average similarity: 22.22%)			
E. bigelowi	16.38	0.65	73.74
R. sadowskii	2.38	0.17	84.45
E. gracilispinnis	0.87	0.12	88.38
E. lucifer	0.87	0.12	92.31
G. dorsalifera	0.75	0.12	95.67
R. agassizi	0.61	0.11	98.43
A. frerichsi	0.19	0.07	99.29
R. porosus	0.16	0.07	100
Main Area 2 (average similarity: 22.92%)			
Z. flavirostris	5.81	0.44	25.36
B. brachyurops	3.59	0.35	41.03
S. bivius	2.95	0.3	53.90
B. griseocauda	2.66	0.26	65.51
A. doellojuradoi	1.94	0.21	73.96
B. albomaculata	1.91	0.24	82.30
S. acanthias	1.22	0.21	87.64
B. magellanica	0.81	0.16	91.18
B. macloviana	0.68	0.15	94.16
B. scaphiops	0.56	0.13	96.61
S. cf. *S. cubensis*	0.48	0.14	98.69
C. callorhynchus	0.19	0.09	99.51
D. tschudii	0.05	0.05	99.74
B. multispinis	0.03	0.03	99.86
S. bonapartii	0.03	0.03	99.95
M. schmitti	0.02	0.02	99.99
Main Area 3 (average similarity: 26.47%)			
S. cf. *S. cubensis*	13.6	0.66	51.37
M. canis	3.64	0.3	65.13
M. schmitti	2.1	0.36	73.07
C. callorhynchus	1.79	0.31	79.85
A. cyclophora	1.55	0.21	85.69
D. tschudii	0.93	0.24	89.20
M. goodei	0.88	0.21	92.51
C. signatus	0.68	0.13	95.09
S. bonapartii	0.28	0.13	96.14
M. freminvillei	0.25	0.12	97.08
C. plumbeus	0.21	0.08	97.89
G. galeus	0.21	0.11	98.67
S. acanthias	0.17	0.10	99.33
A. platana	0.05	0.04	99.52
D. sayi	0.02	0.04	99.62
R. agassizi	0.02	0.04	99.71

Table 2 continued

Species	Av. Sim.	Sim./SD	Cum. %.
N. cepedianus	0.02	0.03	99.76
G. altavela	0.01	0.03	99.82
H. perlo	0.01	0.02	99.87
S. laticaudus	0.01	0.01	99.91
S. cf. *S. besnardi*	0.01	0.01	99.94
N. brasiliensis	0.01	0.02	99.96
Z. flavirostris	0	0.01	99.97
A. castelnaui	0	0.01	99.98
S. lewini	0	0.01	99.99
R. porosus	0	0.01	100.00

Average similarity of each area is indicated. For each species, its average presence (Av. Pres.) and the ratio average presence over standard deviation (Av. Pres./SD) is provided, and its contribution in cumulative percentage to area similarity (Cum. %). In each area, only a relatively few abundant species accounted for most of the internal similarity

26.47%, with *Squalus* sp. cf. *S. cubensis*, *Mustelus canis*, *M. schmitti*, *Callorhinchus callorhynchus*, *Atlantoraja cyclophora* and *Discopyge tschudii* accounting for the top 89.20% of its average similarity (Table 2). This area is discriminated by *Squalus* sp. cf. *S. cubensis*, *M. canis*, *M. schmitti*, *A. cyclophora*, *C. callorhynchus*, *Carcharhinus signatus*, *Myliobatis goodei*, *D. tschudii*, *C. plumbeus* and *S. bonapartii* (Table 3).

Internal structure of the main zoogeographic divisions

Two areas (2 and 3) were found to have substantial internal differentiation.

Area 2 is composed by three subareas displaying a high dissimilarity (2.1–2.2 = 88.1%, 2.1–2.3 = 87.6%, 2.2–2.3 = 92.97%) (Fig. 3c).

Subarea 2.1 covers most of the Argentinean shelf within Area 2 and some stations around Islas Malvinas and on the Burdwood Bank (Fig. 3c). It includes 19 species of which eight are exclusive and 11 are common (Table 4). Subarea 2.1 has an internal similarity of 36.94%, and is discriminated by *Schroederichthys bivius*, *Zearaja flavirostris*, *Squalus acanthias*, and *Bathyraja magellanica*.

Subarea 2.2 covers deeper waters eastward of Subarea 2.1, along the slope and around Islas Malvinas (Fig. 3c). It includes 16 species of which five are exclusive species (the skates *Amblyraja doellojuradoi*, *B. scaphiops*, *B. papilionifera* and *Dipturus trachydermus*, and the pelagic shark *Lamna nasus*) (Table 4). *Amblyraja doellojuradoi*, *Bathyraja griseocauda*, *B. brachyurops* and *B. albomaculata* are discriminating species for this subarea.

Subarea 2.3 corresponds to a few stations in deep water north of Islas Malvinas (Fig. 3c). This subarea includes *Schroederichthys bivius* (widely distributed within the Magellanic Province), *Bathyraja albomaculata*, *Squalus* sp. cf. *S. cubensis* and *B. macloviana*; all of them occur in the three subareas, but the latter two species prefer Subarea 2.3. *Bathyraja macloviana* and *Squalus* sp. cf. *S. cubensis* are discriminating species for Subarea 2.3.

Four subareas can be identified within Area 3 (Fig. 3b; Table 5). Subareas 3.1 and 3.2 are probably relatively occasional associations.

	Main Area 1	Main Area 2	Main Area 3
Table 3 Discriminator species (columns) (SIMPER analysis) of the main Areas 1, 2 and 3			
Main Area 1		Z. flavirostris	S. cf. S. cubensis
		B. brachuyrops	M. canis
		S. bivius	M. schmitti
		B. griseocauda	A. cyclophora
		A. doellojuradoi	C. callorhynchus
		B. albomaculata	C. signatus
		S. acanthias	M. goodei
		B. magellanica	D. tschudii
		B. macloviana	C. plumbeus
		B. scahiops	S. bonapartii
Main Area 2	E. bigelowi		S. cf. S. cubensis
	R. sadowskii		M. canis
	E. gracilispinnis		M. schmitti
	E. lucifer		A. cyclophora
	G. dorsalifera		C. callorhynchus
	R. agassizi		C. signatus
	R. porosus		M. goodei
			D. tschudii
			C. plumbeus
			S. bonapartii
Main Area 3	E. bigelowi	Z. flavirostris	
	R. sadowskii	B. brachuyrops	
	E. gracilispinnis	S. bivius	
	E. lucifer	B. griseocauda	
	G. dorsalifera	A. doellojuradoi	
	R. agassizi	B. albomaculata	
	R. porosus	S. acanthias	
		B. magellanica	
		B. macloviana	
		B. scahiops	

Species for each pair-wise comparison in the matrix are discriminator for the area at the top of the column

Subarea 3.1 includes four species, of which *Schroederichthys* sp. appears to be a rare species, whereas *Zearaja flavirostris* and *Callorhinchus callorhynchus* are Magellanic species also reaching northern latitudes. This fact accounts for their loose associations with other subareas. *Carcharhinus signatus*, which is common off northeastern Brazil, also occurs in this subarea.

Subarea 3.2 includes two stations where *Callorhinchus callorhynchus* (a species from the inner shelf mixed fauna in northern Patagonia) and *Myliobatis goodei* (which is a common Bonaerensean species) appeared with the much more abundant *Bathyraja brachyurops* (a wide ranging Magellanic species).

Subarea 3.3 is a well defined assemblage consisting of many species clearly associated to warm waters, including one species (*Sphyrna lewini*) which does not occur south of the latitude of the Río de la Plata mouth. It includes 13 species. A single species, *Dasyatis*

Table 4 Affinity of species to subareas within main Area 2 (Magellanic)

Species	Subareas		
	2.1	2.2	2.3
C. signatus	2.2		
D. tschudii	2.2		
M. canis	2.2		
M. goodei	2.2		
M. schmitti	2.2		
Pristis sp.	2.2		
S. *mitsukurii*	2.2		
S. *bonapartii*	2.2		
S. *acanthias*	2.2	0.1	
B. magellanica	1.4	0.7	
C. callorhynchus	2.1	0.1	
Z. flavirostris	1.4	0.7	
S. bivius	2.0	0.1	0.5
A. doellojuradoi	0.0	1.9	
B. brachyurops	0.8	1.3	
B. griseocauda	0.1	1.8	
B. multispinis	0.3	1.6	
B. scaphiops	0.0	1.9	
B. papilionifera		1.9	
D. trachydermus		1.9	
L. nasus		1.9	
B. albomaculata	0.2	1.7	0.6
S. cf. *cubensis*	1.8	0.2	2.0
B. macloviana	1.0	0.8	6.4

The species preference to each subarea was considered 'exclusive' (species present only in a single subarea) or 'common' (present in more than one subarea). Subareas 2.1 and 2.2 corresponds to different depths associations within the Magellanic Province. Subarea 2.3 is a more occasional association

centroura, occasionally occurring off Argentina, is exclusive of the subarea, whereas the rest of species were common (i.e. occurring also in Subarea 3.4), but nine of them with higher affinity to this subarea.

Subarea 3.4 is a well defined assemblage. It consists of 30 species of which half are exclusive. This subarea extends through nearly all the latitudinal range of Area 3 (Fig. 3b).

Influence of environmental factors

Considering all cruises for longitude, latitude and mean depth, we found that the combination of latitude and depth showed the highest correlation coefficient (0.483) (BIO-ENV), followed by latitude (0.388), longitude (0.378) and depth (0.319). For WH cr. 78, environmental data were available for nearly all stations, allowing an examination of the relative importance of abiotic factors in the species composition of assemblages. Depth and bottom water temperature have the highest correlation values with specific composition, 0.473 and 0.437, respectively. Lower coefficients were obtained for salinity, latitude and longitude. The coefficient for the depth-salinity pair was 0.475 and for depth-temperature

Table 5 Affinity of species to main Area 3 (Western Temperate South Atlantic Province) and its subareas

Species	Sub areas			
	3.1	3.2	3.3	3.4
Schroederichthys sp.	22.6			
C. signatus	6.6		0.8	0.7
Z. flavirostris	11.3			0.6
C. callorhynchus	0.6	1.6		1.2
B. brachyurops		56.5		
M. goodei		4.5		1.2
D. centroura			7.1	
D. sayi			1.4	1.0
A. platana			5.7	0.3
C. plumbeus			3.5	0.6
G. altavela			3.5	0.6
R. porosus			3.5	0.6
Scyliorhinus sp.			3.5	0.6
S. lewini			3.5	0.6
M. canis			2.6	0.8
S. bonapartii			0.5	1.2
S. cf. *S. cubensis*			0.2	1.2
M. schmitti			0.2	1.2
A. castelnaui				1.3
A. cyclophora				1.3
D. tschudii				1.3
E. bigelowi				1.3
G. galeus				1.3
H. perlo				1.3
M. freminvillei				1.3
N. brasiliensis				1.3
N. cepedianus				1.3
R. agassizi				1.3
R. horkelii				1.3
S. acanthias				1.3
S. haeckeli				1.3
S. laticaudus				1.3
S. mitsukurii				1.3

The species preference to each area was considered 'exclusive' (species present only in a single area) or 'common' (present in more than one area). Subareas 3.3 and 3.4 correspond respectively to the South Brazilian and Bonaerensean Districts within the Western Temperate South Atlantic Province. Subareas 3.1 and 3.2 are more occasional associations

was 0.469. The CCA ordination diagram shows that the gradient represented by the first two axes is the most important in the spatial segregation between the Magellanic and Argentinean chondrichthyan faunas (Fig. 4). These axes explain 84.3% of the variance of the species–environment relationship, the first axis explaining 60.5%. Temperature and latitude are significantly related to the first axis, and depth and longitude are related to the second one. The variance explained by the whole ordination, as well as the first axis, was significant ($P = 0.01$). The permutation Monte Carlo test was also significant ($n = 199$, $P = 0.01$ for both tests).
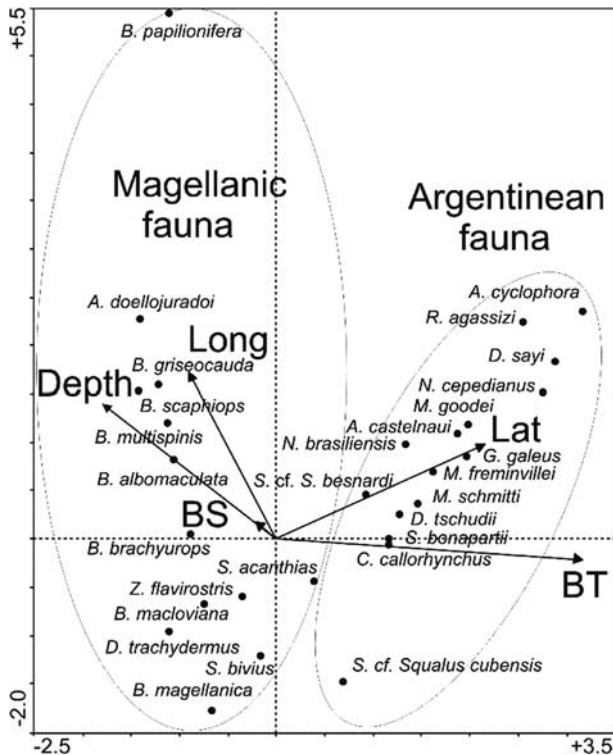
Fig. 4 CCA ordination diagram showing the spatial distribution of chondrichthyan fauna in the western South Atlantic and environmental variables (bottom temperature, BT; bottom salinity, BS; Depth; Lat, latitude; Long, longitude)

Discussion

Validity of the current zoogeographic scheme of the southwestern Atlantic

The results of this study confirm the two main zoogeographic divisions of the southwestern Atlantic, the Argentinean and Magellanic provinces, and identify for the first time several other assemblages. The geographic limits and species composition of the Argentinean and Magellanic provinces coincide well with previous works that identified the same assemblages using more restricted datasets (Balech 1964; López 1964; Krefft 1968; Briggs 1974).

The Brazilian deep water fauna (Area 1) has not been recognized before as a zoogeographic unit, despite its large geographic extension. Our identification of a distinctive Brazilian deep water fauna is confirmed by the recent discovery of several deep water species so far not known to occur off S Brazil (Soto 2001a; Soto and Mincarone 2001) and even new deep water chondrichthyan species in that area (Gomes and Paragó 2001; Soto 2001b, c; Soto and Vooren 2004).

Potential limitations of our analyses are seasonal effects and differences in fishing gear between cruises. The "Walther Herwig" cruises covered neither the whole study area in a single season nor each area in different seasons in a regular design, which would be a serious logistic problem in a large scale exploration such as this, comprising an area that

spans over 4,000 km in the N–S axis. This obligated us to assume that, at such a large scale, seasonal effects are less important than biogeographic differences. Differences in size in both ships and gear were not considered a limitation, because we used only presence-absence data, which are less affected than abundance data by those differences (Fraser et al. 2008).

The Argentinean Zoogeographic Province

Main Area 3 corresponds to a shelf fauna which extends from Rio de Janeiro to slightly south of Valdés Peninsula. This area is for the first time derived from a dataset covering its whole latitudinal range, and sustains the so-called Argentinean Zoogeographic Province (Balech 1964; López 1964), and the more restricted Eastern South American Region (Briggs 1974). It shows the continuous distribution of the warm temperate fauna along the southern coast of Brazil, Uruguay and northern Argentina. In spite of the geographic extension of the area, 15 species were exclusive. Very recently the name Patagonian was used for this region (Musick et al. 2004). We consider the use of this term inadequate because Patagonian is practically a synonym of Magellanic in all systems proposed before, as well as in a wider geographic use. Ringuelet (1955) provides a long list of specialists in diverse groups who agreed with this statement (e.g. Dollo 1904; Lahille 1913; Regan 1914; Waite 1916) and treated historical aspects extensively. Instead, we suggest Temperate Western South Atlantic Province (or South American Eastern Province as in Briggs (1974)), which do not refer to any particular country.

Menni and Stehmann (2000) showed the agreement between provinces and districts proposed for the area and the distribution of batoids. They recognized two Magellanic species groups, an Argentinean Province species group and deep water Brazilian and northern Brazilian groups.

Subareas within the Argentinean Zoogeographic Province (Area 3) show that there is one group (Subarea 3.3) composed by species mainly restricted to, or more common in, south Brazilian waters, whereas Subarea 3.4 shows a more complex association of warm temperate and cold temperate species, with the former ones occurring sympatrically with species of Subarea 3.3 in lower abundance. *Dasyatis centroura*, *Atlantoraja platana*, *Gymnura altavela*, *Carcharhinus plumbeus* and *Mustelus canis* are species from Subarea 3.3 that occasionally or seasonally extend southward to off Argentina. Instead, *Rhizoprionodon porosus*, *Sphyrna lewini* and *Scyliorhinus* sp. do not occur at latitudes south of southern Uruguay.

The fish composition of Subareas 3.3 and 3.4 strongly supports the validity of the Bonaerensean and the Southern Brazilian districts of the Argentinean Zoogeographic Province (Menni 1981, 1985, 2004; Menni and López 1984; Menni and Stehmann 2000). There are indications that the southern border of the Southern Brazilian District is more near the mouth of the Río de La Plata (Briggs 1974) than to 34°S (López 1964). Several coastal species (not registered in our data base) are common in Subarea 3.3 (particularly common coastal sharks, such as *Carcharhinus limbatus*, *C. brevipinna*, and *C. acronotus*), but they are absent in Subarea 3.4, thus providing more support to the distinction between these two subareas.

The Magellanic Province

Main Area 2 corresponds to the classic Magellanic Province in the sense first used by Woodward (1856) for molluscs and later consistently used also by ichthyologists (Regan

1914; Norman 1937; Ekman 1953; Balech 1964; López 1963, 1964; Krefft 1968; Briggs 1974; Lloris and Rucabado 1991). In Argentina, the Magellanic Province includes all the southern shelf of Argentina south of about 43°S, including Islas Malvinas, the outer part of the shelf to the latitude of the Río de la Plata, the Burdwood Bank (55°S) and surrounding waters. This fauna also occupies slope depths along the continental margin to about the latitude of the Río de la Plata. As noted by Menni and Gosztonyi (1982), Menni and López (1984) and Sánchez and Mabragaña (2002), subareas of Area 2 clearly demonstrate the existence of several Magellanic depth groups. A western or transitional zone (Subarea 2.1) includes both, cold water species which often reach northern latitudes (typical examples are *Zearaja flavirostris*, *Schroederichtys bivius* and *Callorhinchus callorhynchus*), and species which are very common at the northern part of the province (all exclusive species from Subarea 2.1). All are shelf species, with the exception of *Carcharhinus signatus* (45–520 m), *Bathyraja magellanica* (32–400 m) and *Z. flavirostris* (32–1,560 m). An eastern or deep water group includes almost all species with higher affinity to Subarea 2.2, which occur also as deep as the upper slope (*B. multispinis*, 95–995 m, 2.8–7.47°C; *B. scaphiops*, 100–810 m, 2.8–7.1°C; *B. albomaculata*, 79–960 m, 2.4–8.2°C), or the lower slope (*A. doellojuradoi*, 110–1,215 m, 2.3–6.7°C; *B. brachyurops*, 25–1,560 m, 2.4–10.2°C; *B. griseocauda*, 80–1,560 m, 2.3–7.8°C; *B. papilionifera*, 660–1,040 m, 2.3–4.09°C).

Influence of environmental factors

Temperature, related to latitude, is the major variable that splits the spatial distribution of the chondrichthyan fauna along the western South Atlantic, followed by depth. Although some Magellanic and Argentinean species occur at similar depths, they were segregated by temperature. The Magellanic fauna is more restricted to low temperature, with some species segregated by depth.

Considering relationships resulting from BIO-ENV and CCA analyses, we ordered the studied species according to decreasing temperature (Table 6), which evidence the following five species groups: Shelf, Outer Shelf Eurybathic, Upper Slope, Lower Slope Eurybathic, and Lower Slope species.

The Shelf group includes species restricted to the shelf, with only *Heptranchias perlo* reaching 220 m in depth. Nearly all species belong in Area 3 (i.e. from the Argentine Province), six of which also occur in Area 2 (Magellanic), where only two are strictly Magellanic (*Schroederichthys bivius* and *Dipturus trachydermus*). Species occurring at maximum temperatures over 20°C are mainly Brazilian warm water species which are uncommon farther south. Species occurring at maximum temperatures between 13.3 and 18°C are very common at the Bonaeresean District (i.e. northern Argentine Sea and off Uruguay). Three species occurring at maximum temperatures from 6.3 to 11.7°C (*S. bivius*, *S. mitsukurii* and *D. trachydermus*) occur on the Patagonian shelf.

The Outer Shelf Eurybathic group includes species that occupy the shelf, but are also found along the upper slope, including several Magellanic species that reach nearly 1,000 m in depth. Although depth ranges are similar for all these species, they segregate according to temperature with Magellanic species not occurring over 15.8°C. Not surprisingly, species preferring high temperatures are all common in the Argentine Province, whereas the rest are Magellanic ones. *Carcharhinus signatus* appeared here with cold-water-preferring species, but it occurs within a temperature range from 14 to 26°C off northeastern Brazil (Menni et al. 1995).

There is an Upper Slope group clearly defined by depth ranges. However, there is only a single temperature record of 4.6°C for *Lamna nasus*, although this species has been

Table 6 Groups of species according decreasing maximum temperature and depth ranges from all four cruises

WH cr. 66	WH cr. 78	WH cr. 71	WH cr. 68	Depth range (m)	Temp. range (°C)
Shelf group					
D. centroura			*D. centroura*	170–200	13.28–26
R. porosus			*R. porosus*	25–75	20.56–21.6
D. sayi	*Dasyatis sayi*		*D. sayi*	40–130	16.5–21.6
G. altavela			*G. altavela*	40–170	16–21.6
C. plumbeus			*C. plumbeus*	75–200	15.6–21.6
A. platana			*A. platana*	75–120	15.5–21.6
M. schmitti	*M. schmitti*	*M. schmitti*	*M. schmitti*	30–200	7.6–21.6
M. goodei	*M. goodei*		*M. goodei*	25–100	6.4–21
	N. cepedianus	*N. cepedianus*	*N. cepe dianus*	39–50	15.5–20.84
			R. percellens	25	20.56–20.56
	N. brasiliensis		*N. brasiliensis*	25–75	9.6–20.56
R. horkelii				45	18
S. bonapartii	*S. bonapartii*	*S. bonapartii*	*S. bonapartii*	30–120	7.1–17.1
C. callorhynchus	*C. callorhynchus*	*C. callorhynchus*		25–150	5.7–17.1
M. freminvillei	*M. freminvillei*	*M. freminvillei*	*M. freminvillei*	38–170	11.29–16.6
G. galeus	*G. galeus*			38–75	8–16.5
D. tschudii	*D. tschudii*	*D. tschudii*		38–110	7.1–16.05
H. perlo			*H. perlo*	112–220	15.17–15.38
A. castelnaui	*A. castelnaui*			40–70	13.3
S. bivius	*S. bivius*	*S. bivius*		38–150	5.7–11.7
S. cf. *S. mitsukurii*	*S.* cf. *S. mitsukuri*	*S.* cf. *S. mitsukurii*		60–92	9.98–10.7
	D. trachyderma	*D. trachyderma*		185–200	5.7–6.3
			D. americana	25	
C. obscurus				125	
			S. haeckeli	130	
S. lewini				75–160	
		Pristis sp.		Surface	
Outer shelf eurybathic group					
M. canis		*M. canis*	*M. canis*	40–300	7.6–21.6
S. cf. *S. cubensis*	*S.* cf. *S. cubensis*	*S.* cf. *S. cubensis*	*S.* cf. *S. cubensis*	30–350	4.83–21.6
A. cyclophora	*A. cyclophora*	*A. cyclophora*	*A. cyclophora*	30–350	11.1–21
R. agassizi	*R. agassizi*		*R. agassizi*	25–600	14.6–21
S. acanthias	*S. acanthias*	*S. acanthias*		38–350	5.1–16.05
C. signatus		*C. signatus*	*C. signatus*	45–520	9.5–15.8
B. magellanica	*B. magellanica*	*B. magellanica*		32–400	4.61–10.2
B. macloviana	*B. macloviana*	*B. macloviana*		78–894	3–8.8
B. albomaculata	*B. albomaculata*	*B. albomaculata*		79–960	2.4–8.2
B. multispinis	*B. multispinis*			95–995	2.8–7.47
B. scaphiops	*B. scaphiops*	*B. scaphiops*		100–810	2.8–7.1
Upper slope group					
A. vulpinus				260	

Table 6 continued

WH cr. 66	WH cr. 78	WH cr. 71	WH cr. 68	Depth range (m)	Temp. range (°C)
		L. nasus		350	4.6
			B. kreffti	485	
			S. laticaudus	300–500	
			D. leptocauda	500	
			S. tenuis	520	
E. gracilispinis			*E. gracilispinis*	410–600	
			G. dorsalifera	500–800	
A. frerichsi				600–800	
			E. lucifer	800	
			T. nobiliana	800	
B. schroederi				800	
Lower slope eurybathic group					
Z. flavirostris	*Z. flavirostris*	*Z.. flavirostris*		32–1,560	2.8–11.7
B. brachyurops	*B. brachyurops*	*B. brachyurops*		25–1,560	2.4–10.2
B. griseocauda	*B. griseocauda*	*B. griseocauda*		80–1,560	2.3–7.8
A. doellojuradoi	*A. doellojuradoi*	*A. doellojuradoi*		110–1,215	2.3–6.7
E. cf. *E. bigelowi*			*E.* cf. *E. bigelowi*	300–1,200	
	B. papilionifera	*B. papilionifera*		660–1,040	2.3–4.09
			R. sadowskii	800–1,200	
Lower slope species					
			H. raleighana	1,200	

recorded in the area in waters up to 22.69°C (Lucifora and Menni 1998). Most of these species belong to the Brazilian deep water fauna.

The Lower Slope Eurybathic group is mainly composed by typical Magellanic batoid species with the exceptions of the shark *Etmopterus bigelowi* which occurs in both, the Brazilian deep water fauna and the Argentine Province, and the skate *Rajella sadowskii* from the Brazilian deep water fauna. All these species reach the upper slope in low temperature stations. However, four of them extensively distribute over the shelf, whereas *E. bigelowi*, *Bathyraja papilionifera* and *R. sadowskii* were obtained below shelf depths.

The Lower Slope group is represented by a single species, the rhinochimaerid *Harriotta raleighana*. It was captured at 1,200 m depth.

Distribution of rare species in the southwestern Atlantic

Several uncommon species were obtained during the 'Walther Herwig' cruises. The capture of the holocephalan *Harriotta raleighana* during WH cr. 1968 was the first Brazilian record of the species (Stehmann and Menni 1995). The observation of *Pristis* sp. off Argentina (Stehmann pers. obs.) during the WH cr. 1971 was the second in nearly a century, and that of *Heptranchias perlo* is the only available precise locality off Argentina at 35°57′S, 51°27′W. The intrusion to waters off Argentina of the night shark *Carcharhinus signatus*, first reported by Krefft (1968), is widely confirmed. Our material shows that this species is relatively abundant along the Uruguayan coast. The occurrence of

Atlantoraja platana in a deep area probably explains the previous scarcity of information about it (Sadowsky and Menni 1974; Menni and Stehmann 2000). The southernmost record of *Sphyrna lewini* is still that from La Paloma, Uruguay (34°39′S, Menni 1976), and the species does not occur farther south (Domingo et al. 2005). *Dasyatis centroura* occasionally reaches to about 40°33′S (Lucifora pers. obs.).

Conservation implications

The existence of three main chondrichthyan assemblages (two of them with major subdivisions) on a wide and continuous continental shelf and slope indicates that the uneven distribution of anthropogenic disturbances, such as fishing, pollution or other habitat alterations, can affect communities and species that are not represented in another, less affected part of the southwestern Atlantic. An uneven distribution of disturbances is warranted by the administrative fragmentation of the southwestern Atlantic: four management authorities are involved in the area (Argentina, Brazil, Islas Malvinas (Falkland Islands) and Uruguay), each of them with its own agendas and priorities. For example, the recently discovered oil fields in deep water off south Brazil coincide with the distinct assemblage of Area 1 (the deep water Brazilian fauna) (Fig. 1). If this fauna is affected (e.g. by chemical pollution of its habitat or by physical modification of the bottom on which they live by oil exploration activities), it will not be represented anywhere else as a distinct functioning natural community. Fishing effort (mainly bottom trawling) in deep waters off S Brazil increased since 1999, resulting in an unsustainable fishing pressure on deep water species (Perez and Pezzuto 2006) that may also affect this unique assemblage. A similar situation occurs with fishing exploitation off N Argentina and Uruguay. The highest chondrichthyan catches in Argentinean waters are taken in an area that coincides almost exactly with the whole extent of the Bonaerensean District of the Argentinean Province (Subarea 3.4, between 34°S and 42°S) in Argentinean and Uruguayan waters (Massa et al. 2004), indicating that the entire chondrichthyan assemblage of the Bonaerensean District can be affected by overfishing. As this is coupled with heavy overfishing off southern Brazil affecting the whole chondrichthyan assemblage (Vooren and Klippel 2005; Velasco et al. 2007), the entire Argentinean Province (Area 3) may be at serious risk of being severely affected as a functioning ecological system.

The results presented here provide a framework for ecosystem management and conservation of the southwest Atlantic. We propose that, in order to conserve chondrichthyan assemblages and functioning ecosystems, conservation plans in the Southwest Atlantic should aim to conserve representative units of each of the assemblages identified in our work. Given the uneven distribution of threats and chondrichthyan assemblages, particular areas must be identified within each assemblage to ensure that a representative network of protected or strictly regulated areas is established. These areas must be identified by objective analyses of the level of threat to, uniqueness of, and connectivity between each of them.

Conclusions

The use of cluster, similarity, dissimilarity and canonical correspondence analyses allows us to display assemblages of chondrichthyan fishes along the southwestern Atlantic from 23° to 56°S. Each assemblage occupies defined geographical areas that strongly support the consistence of the zoogeographic scheme currently used by marine biologists in South

America. Districts (i.e. subdivision of provinces) also proved to be valid. For the first time, a wide dataset is used to sustain the Argentinean Province, as it was called previously, which we propose to name the Temperate Western South Atlantic Province. A considerable restriction of species to each faunal area is observed. Evidence of a well marked subdivision of the Magellanic Province corresponding to depth is provided. Depth and bottom water temperature have the highest correlations with species composition. Groups of species show ranges of these variables strictly related to the traditional depth zonation of the sea. The uneven distribution of anthropogenic disturbances in the southwestern Atlantic may affect large parts of, or even the whole chondrichthyan assemblages, which calls for immediate action for conservation.

References

Angelescu V, Prenski LB (1987) Ecología trófica de la merluza común del Mar Argentino (Merluccidae, *Merluccius hubbsi*), Parte 2. Dinámica de la alimentación analizada sobre la base de las condiciones ambientales, la estructura y las evaluaciones de los efectivos en su área de distribución. Contrib Inst Nac Inv Desarrollo Pesq 561:1–205

Balech E (1964) Caracteres biogeográficos de la Argentina y Uruguay. Bol Inst Biol Mar Mar del Plata 7:107–112

Bernasconi I (1964) Distribución geográfica de los equinoideos y steroideos de la extremidad austral de Sudamérica. Bol Inst Biol Mar Mar del Plata 7:43–49

Boschi EE (2000) Species of decapod crustaceans and their distribution in the American marine zoogeographic provinces. Rev Invest Desarrollo Pesq 13:1–136

Briggs JC (1974) Marine zoogeography. McGraw Hill, New York

Carcelles AR (1950) Catálogo de los moluscos marinos de Patagonia. An Mus Nahuel Huapí 2:41–49

Clarke KR, Warwick RM (eds) (2001) PRIMER-E, 2nd edn. Plymouth

Cooke AH (1895) Molluscs. Cambridge natural history 3. MacMillan, London

Díaz de Astarloa JM, Aubone A, Cousseau MB (1999) Asociaciones ícticas de la plataforma costera de Uruguay y Norte de Argentina y su relación con los parámetros ambientales. Physis 57A:29–45

Doello Jurado M (1938) Nuevos datos sobre la fauna de la meseta continental de la Argentina y del Uruguay. Physis 12:279–292

Dollo L (1904) Résultats du voyage du S.Y. "Belgica" en 1897–1898–1899 sous le commandement de A. de Gerlache de Gomery. Zoologie. Buschmann, Antwerp

Domingo A, Menni RC, Forselledo R (2005) Bycatch of the pelagic ray *Dasyatis violacea* in Uruguayan longline fisheries and aspects of distribution in the southwestern Atlantic. Sci Mar 69:161–166

Ekman S (1953) Zoogeography of the sea. Sidgwick and Jackson Ltd, London

Fraser HM, Greenstreet SPR, Fryer RJ, Piet GJ (2008) Mapping spatial variation in demersal fish species diversity and composition in the North Sea: accounting for species- and size-related catchability in survey trawls. ICES J Mar Sci 65:531–538

Gomes UL, Paragó C (2001) Espécie nova de rajídeo (Chondrichthyes, Rajiformes) do Atlântico sul occidental. Bol Mus Nac Rio de Janeiro 448:1–10

Groves CR, Jensen DB, Valutis LL, Redford KH, Shaffer ML, Scott JM, Baumgartner JV, Higgins JV, Beck MW, Anderson MG (2002) Planning for biodiversity conservation: putting conservation science into practice. Bioscience 52:499–512

Jaureguizar AJ, Menni RC, Bremec C, Mianzan H, Lasta C (2003) Fish assemblage and environmental pattern in the Rio de la Plata estuary. Estuar Coast Shelf Sci 56:921–933

Jaureguizar AJ, Menni RC, Lasta C, Guerrero R (2006) Fish assemblages of the northern Argentinean coastal system: spatial patterns and their temporal variations. Fish Oceanogr 15:326–344

Krefft G (1968) Neue and erstmalig nachgewiesene Knorpelfische aus dem Archibenthal des Südwestlantiks, einschiesslich einer Diskussion einiger *Etmopterus* – Arten südlicher Meere. Arch Fischwiss 19:1–42

Lahille F (1913) Nota sobre un pez de Arica (*Agonus chilensis*). Rev Chilena Hist Nat 17:179–191

Lloris D, Rucabado J (1991) Ictiofauna del canal Beagle (Tierra del Fuego), aspectos ecológicos y análisis biogeográfico. Publ Espec Inst Esp Oceanogr 8:1–182

López RB (1963) Problemas de la distribución geográfica de los peces marinos sudamericanos. Rev Mus Arg Cienc Nat 1:109–135

López RB (1964) Problemas de la distribución geográfica de los peces marinos sudamericanos. Bol Inst Biol Mar Mar del Plata 7:57–63

Lucifora LO, Menni RC (1998) First record of a porbeagle shark, *Lamna nasus*, in brackish waters of Mar Chiquita lagoon, Argentina. Cybium 22:87–88

Mahon R, Brown SK, Zwanenburg KCT, Atkinson DB, Buja KR, Claflin L, Howell GD, Monaco ME, O'Boyle RN, Sinclair M (1998) Assemblages and biogeography of demersal fishes of the east coast of North America. Can J Fish Aquat Sci 55:1704–1738

Massa AM, Lucifora LO, Hozbor NM (2004) Condrictios de las regiones costeras bonaerense y uruguaya. In: Sánchez RP, Bezzi SI (eds) El Mar Argentino y sus recursos pesqueros, tomo 4. INIDEP, Mar del Plata

Menni RC (1976) Presencia de *Sphyrna lewini* (Griffith and Smith, 1834) en el Uruguay (Chondrichthyes, Sphyrnidae). Stud Neotrop Fauna Environ 11:199–203

Menni RC (1981) Sobre la distribución de los peces marinos de la Argentina. In: Symposia VI Jornadas Argentinas de Zoología, Ramos Americana, La Plata

Menni RC (1985) Distribución y biología de *Squalus acanthias*, *Mustelus schmitti y Galeorhinus vitaminicus* en el Mar Argentino en Agosto-Setiembre de 1978 (Chondrichthyes). Rev Mus La Plata, Nueva Serie, Zool 13:151–207

Menni RC (2004) Zoogeografía de los peces marinos de la Argentina. In: Montero R, Autino A (eds) Sistemática y filogenia de los Vertebrados de la Argentina. Universidad Nacional de Tucumán, San Miguel de Tucumán

Menni RC, Gosztonyi AE (1982) Benthic and semi demersal fish associations in the Argentine Sea. Stud Neotrop Fauna Environ 17:1–29

Menni RC, López HL (1984) Distributional patterns of Argentine marine fishes. Physis 42A:71–85

Menni RC, Stehmann MFW (2000) Distribution, environment and biology of batoid fishes off Argentina, Uruguay and Brazil. A review. Rev Mus Argent Cienc Nat 2:69–109

Menni RC, Hazin FHV, Lessa RP (1995) Occurrence of the night shark *Carcharhinus signatus* and the pelagic stingray *Dasyatis violacea* off northeastern Brazil. Neotropica 41:105–110

Musick JA, Harbin MM, Compagno LJV (2004) Historical zoogeography of the Selachii. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton

Norman JR (1937) Coast fishes, part II. The Patagonian region. Discov Rep 16:1–150

Palma ED, Matano RP, Piola AR (2004) A numerical study of the Southwestern Atlantic shelf circulation: barotropic response to tidal and wind forcing. J Geophys Res 109:1–17

Perez JAA, Pezzuto PR (2006) A pesca de arrasto de talude do sudeste e sul do Brasil: tendências da frota nacional entre 2001 e 2003. Bol Inst Pesca São Paulo 32:127–150

Primack RB (2006) Essentials of conservation biology, 4th edn. Sinauer, Sunderland

Regan CT (1914) British Antarctic ("Terra Nova") expedition, 1910. Nat Hist Rep Fish Zool 1:1–54

Ringuelet RA (1955) Ubicación zoogeográfica de las Islas Malvinas. Rev Mus Univ La Plata (Nueva Serie) Zool 6:419–464

Ringuelet RA (1984) Breve reseña histórica de la ictiología argentina y uruguaya. In: Menni RC, Ringuelet RA, Arámburu RH (eds) Peces marinos de la Argentina y Uruguay. Reseña histórica, clave de familias, géneros y especies. Catálogo crítico. Hemisferio Sur, Buenos Aires

Sadowsky V, Menni RC (1974) Sobre Raja platana Günther, 1880 (Chondrichthyes, Rajidae). Physis 33:413–439

Sánchez MF, Mabragaña E (2002) Características biológicas de algunas rayas de la región sudpatagónica. Inf Téc INIDEP 48:1–15

Soto JMR (2001a) First record of southern lantern shark, *Etmopterus granulosus* (Günther, 1880) (Squaliformes, Dalatiidae), in Brazilian coast. Mare Magnum 1:7–10

Soto JMR (2001b) *Schroederichthys saurisqualus* sp. nov. (Carcharhiniformes, Scyliorhinidae), a new species of catshark from southern Brazil, with further data on *Schroederichthys* species. Mare Magnum 1:37–50

Soto JMR (2001c) *Galeus mincaronei* sp. nov. (Carcharhiniformes, Scyliorhinidae), a new species of sawtail catshark from southern Brazil. Mare Magnum 1:11–18

Soto JMR, Mincarone MM (2001) First record of kitefin shark, *Dalatias licha* (Bonnaterre, 1788) (Squaliformes, Dalatiidae), in the South Atlantic. Mare Magnum 1:23–26

Soto JMR, Vooren CM (2004) *Hydrolagus matallanasi* sp. nov. (Holocephali, Chimaeridae) a new species of rabbitfish from southern Brazil. Zootaxa 687:1–10

Stehmann M, Menni RC (1995) Condrictios y ambientes frente al Sur de Brasil y Norte de Uruguay, 1968. In: Resumos, VII Reunião do Grupo de Trabalho sobre Pesca e Pesquisa de Tubarões no Brasil, Universidade de Rio Grande

Velasco G, Araújo JN, Castello JP, Oddone MC (2007) Exploring MSY strategies for elasmobranch fishes in an ecosystem perspective. Pan-Am J Aquat Sci 2:163–178

Vooren CM, Klippel S (2005) Diretrizes para a conservação de espécies ameaçadas de elasmobrânquios. In: Vooren CM, Klippel S (eds) Ações para a conservação de tubarões e raias no sul do Brasil. Igaré, Porto Alegre

Waite ER (1916) Fishes. Australasian Antarctic Expedition 1911–1914. Sci Rep Australas Antarct Exped 3:1–92

Woodward SP (1856) A manual of the Mollusca. John Weale, London