

# Effects of fishing and climate variability on spatio-temporal dynamics of demersal chondrichthyans in the Río de la Plata, SW Atlantic

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**ABSTRACT:** The structure of marine communities is affected by both fishing and climate variability. The Argentinean–Uruguayan Common Fishing Zone (AUCFZ) comprising the Río de la Plata and its oceanic front (SW Atlantic, 34° 30' to 39° 30' S) has a high environmental variability. Intensive trawling activity results in the bycatch of many chondrichthyan species. Using generalized linear mixed models, we analyzed the effects of commercial fishing effort, sea surface thermal anomalies (SSTA) and depth on the spatio-temporal dynamics of chondrichthyan species richness and total number of individuals in 3 zones of the AUCFZ between 1984 and 2009. Species richness increased with fishing effort in warmer years in the northern zone but displayed the opposite trend in the river and southern zones. While the total number of individuals decreased in the coldest years and at greater depths in the northern zone, these 2 variables had opposite effects in the southern zone. Depth had a stronger effect on both chondrichthyan species richness and the total number of individuals than the other 2 explanatory variables. While SSTA and depth had statistically significant effects on species richness and the total number of individuals, commercial fishing effort was significantly related only with species richness. The spatial variability of both response variables was greater than their temporal variation during the study period. These findings contribute to a greater understanding of the spatio-temporal dynamics of demersal chondrichthyans in the AUCFZ and are of relevance to the long-term sustainable management of chondrichthyans in this area and elsewhere.

**KEY WORDS:** Species richness · Abundance · Trawling hours · Sea temperature

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## INTRODUCTION

Overfishing and climate variability are two of the main processes affecting the spatio-temporal dynamics of marine fish communities (Hiddink & ter Hofstede 2008). Fishing may affect the dynamics of both fish populations and communities through the selective removal of large-bodied individuals, resulting in a shift in body size spectra of target species (Dulvy et al. 2000, ter Hofstede & Rijnsdorp 2011) and through the bycatch of non-targeted species (Field et al. 2009).

Bottom trawls can have strong effects on habitat structure that may indirectly affect benthic fish species (Jennings & Kaiser 1998). On the other hand, climatic variability affects both primary productivity and the efficiency of energy transfer through bottom-up effects impacting the spatial distribution and abundance of species at higher trophic levels (Rijnsdorp et al. 2009). These changes have been demonstrated in the North Atlantic (Hiddink & ter Hofstede 2008, ter Hofstede & Rijnsdorp 2011) and in Southeastern Australia (Last & White 2011). While the relative impor-

tance of environmental factors varies regionally, changes in sea surface temperature have important effects on marine communities worldwide (Rijnsdorp et al. 2009). For instance, mean annual sea surface temperature was demonstrated to be the best predictor for the latitudinal gradient in benthic fish species richness in the Atlantic Ocean (Macpherson 2002).

The joint effects of climate variability and fishing activities on the structure and dynamics of fish populations and communities are difficult to quantify because both often interact with other environmental drivers (ter Hofstede & Rijnsdorp 2011). As a result, their effects are often region-specific and may vary widely depending on species and community characteristics and regional variation in environmental conditions (Brander 2010). In addition, fish populations and communities often become more sensitive to climate variability after being subjected to intense harvesting (Planque et al. 2010).

Demersal chondrichthyans are often caught incidentally by fisheries that target other species, and tend to be discarded because of their low commercial value (Petersen et al. 2008). Diminishing catch volumes (Stevens et al. 2000) and sharp declines and/or extinction of several chondrichthyan species have been documented worldwide (Ferretti et al. 2010 and references therein). Two main underlying reasons for these declines are that most chondrichthyan species are generally top predators, and that they typically have a 'slow life history' (Stevens et al. 2000) characterized by a slow growth rate, late maturity, low annual fecundity, large adult body size and large size at birth. These features result in low resilience and make chondrichthyan populations particularly vulnerable to intense fishing pressure (Frisk et al. 2005). Several chondrichthyan species have been categorized as near threatened, threatened (vulnerable, endangered, critically endangered) or extinct, at both global and regional scales (IUCN 2013). Field et al. (2009) analyzed the global distribution of threatened chondrichthyan populations from least (vulnerable) to most threatened (critically endangered), showing that the Southwest Atlantic along the coasts of southern Brazil, Uruguay and Argentina was among the most critical regions.

This study was conducted in the Argentinean–Uruguayan Common Fishing Zone (AUCFZ) in the SW Atlantic (34° 30' to 39° 30' S, 52° 00' to 59° 00' W; see Fig. 1), comprising the Río de la Plata and its oceanic front. The area is a region of intensive trawling activity, resulting in the capture of several species of chondrichthyans (Paesch & Domingo 2003). Landings of these species have declined from the 'fishing

down marine food web' process within the AUCFZ (Jaureguizar & Milessi 2008). The abundance and distribution of demersal fish assemblages (including both bony fishes and chondrichthyans) in the AUCFZ and adjacent marine waters are affected by the spatio-temporal variability of environmental conditions (Jaureguizar et al. 2006, Lorenzo et al. 2011). The variation in sea temperature with respect to latitude is the main variable explaining the spatial distribution of chondrichthyans across the southwestern Atlantic Ocean (Menni et al. 2010). However, the impact of fishing on chondrichthyans in the study area remains poorly understood. In this paper, we use long-term catch data (1984 to 2009) of chondrichthyan species collected by research vessels to examine the combined effect of industrial fishing effort and climatic variability on the spatio-temporal dynamics of species richness and abundance of demersal chondrichthyans.

## MATERIALS AND METHODS

### Study area

The study area referred to as AUCFZ covers 35.848 n mile<sup>2</sup> and includes the outer region of the Río de la Plata and its adjacent inner continental shelf, the Atlantic Uruguayan coast (depth <50 m) and the outer continental shelf (50 to 250 m) between the latitudes of 34° 30' and 39° 30' S (Fig. 1). The dynamic mixing of freshwater from the Río de la Plata with subtropical waters of the Brazil current and cold waters of the Malvinas/Falkland current generates high spatio-temporal variability in hydrographic parameters and primary productivity in the study area (Acha et al. 2004). The latter is manifested in frontal systems with peaks in primary production related to the spatial dynamics of nutrients from the Río de la Plata and the seasonal latitudinal shifts (northward in winter and spring and southward in summer and autumn) of the confluence between the Brazil and Malvinas/Falklands currents (Ortega & Martínez 2007). Based on the spatial variability in environmental parameters and their associated fish assemblages (Norbis 1993, Jaureguizar et al. 2006, Lorenzo et al. 2011), we divided the study area into 3 zones: (1) the River Zone (RZ), including the outer region of the Río de la Plata and its adjacent inner continental shelf; (2) the Northern Zone (NZ), covering the Atlantic Uruguayan coast (depth <50 m) and the outer continental shelf between 34° 30' and 37° 00' S; and (3) the Southern Zone (SZ), comprising the outer continental shelf from 37° 00' to 39° 30' S (Fig. 1).

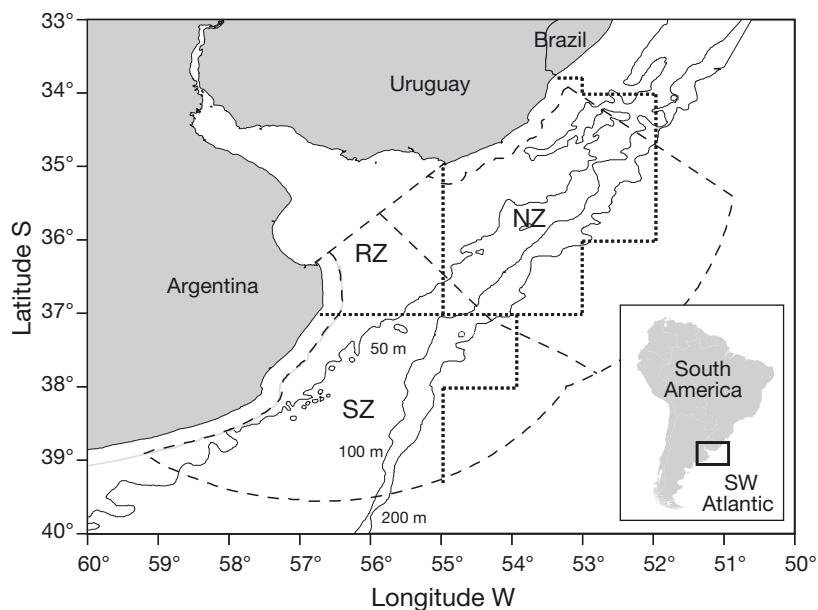


Fig. 1. Study area showing the boundaries of the 3 zones (RZ = River Zone, NZ = Northern Zone, SZ = Southern Zone), represented by dotted lines. Dashed lines indicate the limits of the Argentinean-Uruguayan Common Fishing Zone

#### Research cruise data

We obtained catch data from 62 bottom trawl research cruises conducted in distinct seasons between 1984 and 2009 by the RV 'Aldebarán' (operated by Dirección Nacional de Recursos Acuáticos, DINARA, Uruguay). Among these 62 cruises, 24 were coastal (depths <50 m) and 38 were in the outer continental shelf (depths between 50 and 250 m; Fig. 1). Trawl stations (hauls) were selected using a stratified random sample design, and each trawl consisted of a 30 min tow during daylight at a speed of approximately 3 knots. A high-opening 'Engel' type bottom trawl with an 80 mm (stretched mesh) cod-end and 24 m horizontal mouth opening was used. The geographic coordinates, depth and total number of individuals of each chondrichthyan species were recorded for each haul. The research cruises were unevenly distributed over time and space during the study period, whereby the Río de la Plata and inner continental shelf were more frequently sampled in spring and the outer continental shelf in autumn (see Table S1 in the Supplement at [www.int-res.com/articles/suppl/m508p187\\_supp.pdf](http://www.int-res.com/articles/suppl/m508p187_supp.pdf)). For analysis, the 3912 total bottom trawls were assigned to 26 geographic degree cells (cells of 1° latitude by 1° longitude; Fig. S1) for each season and year (hereafter instances).

#### Fishing effort data

As an indicator of fishing effort (equivalent to fishing pressure), we used total monthly trawl hours from the Uruguayan trawling fleet for each of the 26 degree cells in the AUCFZ obtained from fisheries statistics of DINARA for the study period. The trawling coastal commercial fleet targets 2 sciaenid species, the white-mouth croaker *Micropogonias furnieri* and the striped weakfish *Cynoscion guatucupa* in the Río de la Plata and the inner continental shelf (<50 m depths) (Norbis et al. 2006), while the trawling industrial fishing fleet operates in the outer continental shelf, targeting hake *Merluccius hubbsi* (Galli et al. 2013). All chondrichthyan species are caught as bycatch by the commercial fleets. These 2 fishing fleets are comprised of vessels with average dimensions of 23 and 44 m in length, 124 and 608 gross registered tons, and 409 and 1529 HP, respectively (MGAP-DINARA 2010).

#### Sea surface thermal anomalies

We obtained summer (January to March), autumn (April to June), winter (July to September) and spring (October to December) sea surface temperatures (SST, mean values) for each year from [http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn\\_Smith/OIv2/.monthly/.sst](http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_Smith/OIv2/.monthly/.sst) at a resolution of 0.5° (Reynolds et al. 2002). We calculated sea surface thermal anomalies (SSTA) for each degree cell, season and year by subtracting the mean value between 1984 and 2009 from the SST value at each instance (average surface isotherms by season are provided in Fig. S2).

#### Data analysis

We studied the spatio-temporal dynamics of species richness ( $S$ ) and total abundance ( $N$ ) for the 714 instances for which data was available. Both response variables were analyzed in relation to explanatory variables using generalized linear mixed models (GLMM, Zuur et al. 2009). These models used the Gaussian and Poisson distributions with identity and log links for the total number of individuals and spe-

cies, respectively. All GLMMs incorporated fishing effort, SSTA, depth and zones (North, River and South) as fixed effects, and 2 crossed (i.e. uncorrelated) random effects: the geographic degree, reflecting spatial variation, and season nested within year, denoting the structure of the temporal variation for each response variable. The paucity and unbalanced nature of the sampling design (Table S1) prevented us from jointly considering the spatial and temporal variability in the data. We used the number of hauls in each geographic degree as a weighted variable in all analyses to account for differences in sampling effort among the 714 instances (instances came from the assignment of total hauls to geographic degree for each season and year, see Fig. S3). All analyses started with the same initial model containing all pairwise interactions relevant for the objectives of this research, namely the variation in fishing effort, SSTA and depth among zones, and the main effects of each explanatory variable. All explanatory variables were centered and standardized to facilitate the interpretation of their relative importance. Starting with full models, fixed effects were reduced by sequentially deleting the least significant term in a model and comparing successive steps in model simplification with Akaike's information criterion (AIC; deleting a term whenever  $\Delta\text{AIC} > 2$ ) until arriving at the most parsimonious model that fit the data. All models were subjected to a residual analysis to determine the fulfilment of model assumptions for GLMM (Zuur et al. 2009). Because the appropriate number of degrees of freedom in assessing the statistical significance of GLMM remains controversial, we assessed the statistical significance of the fixed effects for the total number of individuals with estimates of highest posterior density intervals, which are the Bayesian equivalent of confidence intervals, calculated at the 95% level with Markov chain Monte Carlo sampling with 10000 samples (Baayen et al. 2008). For each response variable, we used random effects coefficients (Zuur et al. 2009) to characterize the spatial (among degree cells) and temporal (seasons within years, among years) variation of  $N$  and  $S$ . These coefficients indicated the magnitude and sign of the variation of  $N$  and  $S$  from average values predicted by fixed effects. The ratios between the coefficients and standard errors of random effects are analogous to a  $t$ -test and were used as an indicator for the relative importance of the spatial and temporal variation of the data, using the criterion that the absolute value of the ratio be greater than 2. We calculated the marginal and conditional  $R^2$  GLMM (Nakagawa & Schielzeth 2013) to evaluate the goodness-of-fit of the fitted model where the marginal

and conditional  $R^2$  are the percent deviance explained solely by fixed factors ( $R^2_c$ ), and by both fixed and random effects ( $R^2_m$ ). All GLMMs were analyzed with the libraries lme4 (Bates et al. 2011) and languageR (Baayen et al. 2008) using the program R, ver. 2.15.1 (R Development Core Team 2012).

## RESULTS

The fishing effort of the commercial fleet measured by the total trawling hours per geographic degree per year was heterogeneous across both time and space in the AUCFZ. While fishing effort declined from 2000 onwards in the NZ, it increased in the RZ until 2002, with an overall declining trend thereafter (except in 2006, when the effort was anomalously high); and increased in the SZ until 2004, but declined thereafter (Fig. 2). While the majority of fishing effort was concentrated in 2 degree cells, it tended to increase with latitude and depth in the NZ and SZ

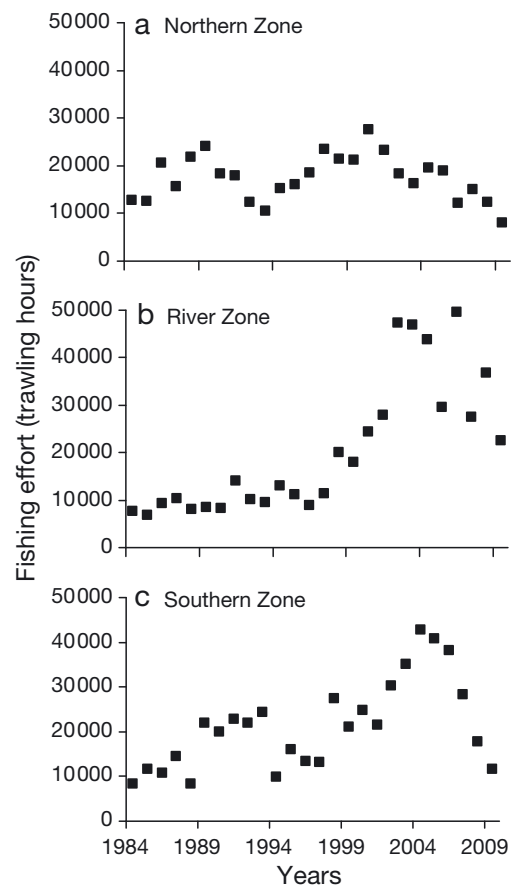


Fig. 2. Annual variation in fishing effort (represented as the total number of trawling hours by the Uruguayan commercial fishing fleet) per year in the (a) Northern, (b) River and (c) Southern Zones for the period between 1984 and 2009

(Fig. 3). SST was on average higher in the NZ than in the SZ and increased from 1996 to 2009 in the RZ (Fig. 4a). SSTA values were positive from 1996 onwards in the RZ, and from 1998 onwards in both the NZ (except 1999) and SZ (except 2003), indicating a sustained warming trend over time in the study area (Fig. 4b).

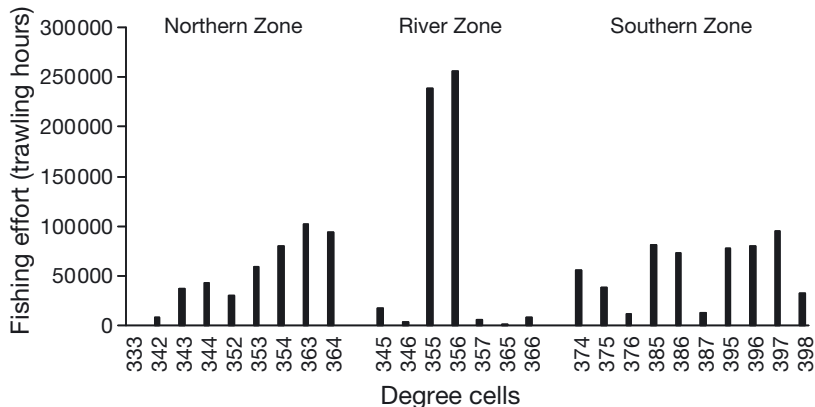


Fig. 3. Spatial variation in fishing effort (represented as the total number of trawling hours by the Uruguayan commercial fishing fleet) per degree cell ( $1^\circ$  latitude by  $1^\circ$  longitude; see Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m508p187\\_supp.pdf](http://www.int-res.com/articles/suppl/m508p187_supp.pdf) for the locations of the cells) in the Northern, River and Southern Zones for the period between 1984 and 2009

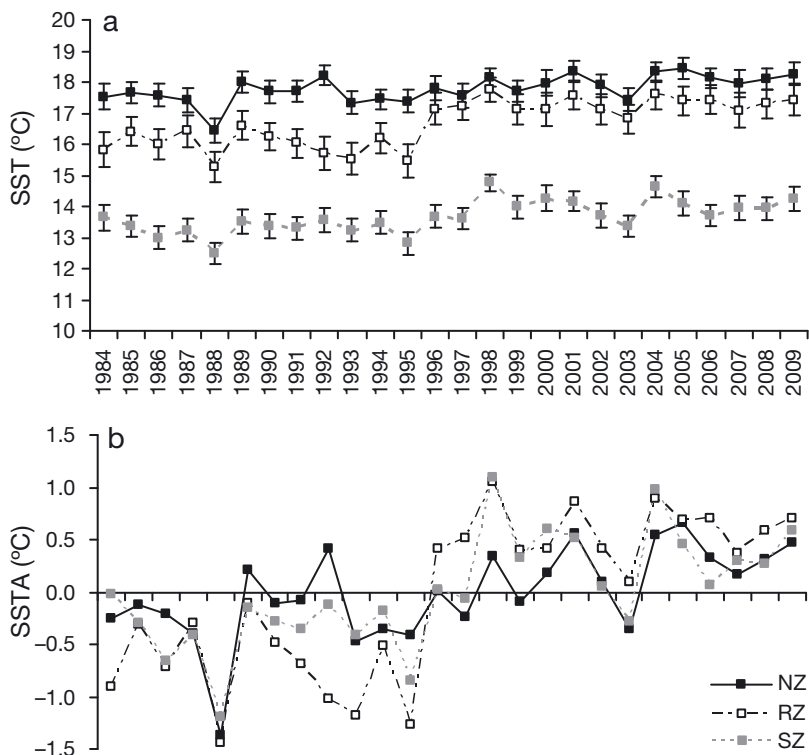


Fig. 4. Average (a) sea surface temperature (SST, standard error is represented by the vertical bars) and (b) sea surface thermal anomalies (SSTA) in the Northern (NZ), River (RZ) and Southern (SZ) Zones for the period between 1984 and 2009

Thirty-five chondrichthyan taxa were registered during the study period, 31 of which were identified to species level (Table 1). Twenty-two of these species have been categorized by the IUCN as critically endangered (1), endangered (5) vulnerable (12), near threatened (3) or least concern (1) (Table 1). Some species typical of the NZ were also found in

the RZ but with a lower occurrence; other species were dominant in the SZ and yet others were largely restricted to the outer continental shelf of both northern and southern zones (Table 1).  $S$  increased with fishing effort during warmer years in the NZ but showed opposite trends in the RZ and SZ (Table 2), whereas it increased with depth across the study area (Table 2). According to the magnitude of estimated coefficients, depth (0.146, the same for the 3 zones) had a higher relative importance in explaining average  $S$  than fishing effort and SSTA (NZ = 0.051 and 0.034, RZ =  $-0.042$  and  $-0.040$ , SZ =  $-0.003$  and  $-0.046$ , respectively) in the 3 zones (obtained from Table 2). Spatial variation in  $S$  was higher (among degree cells, 58.4% of the variance of random effects) than temporal variation in  $S$  (29.6% among years and 12.6% among seasons within years). In the final model, the deviance explained by fixed effects ( $R^2_m = 0.15$ ) was 4 times smaller than the variance explained by both fixed and random effects ( $R^2_c = 0.65$ ). There were relatively important deviations from average  $S$  predicted by fixed effects at almost all degree cells in each zone (Fig. 5a). There was a temporal trend in the variation in chondrichthyan  $S$ , being smaller than the average predicted value before 1989 and stable afterwards throughout the study zone (Fig. 5b). Within-year seasonal variation around the average predicted  $S$  was relatively minor and similar among seasons (Fig. 5c-f), with no temporal trend during the study period, and with the lowest values occurring between 1984 and 1989 (Fig. 5b).



Table 1. Chondrichthyan taxa recorded for the period 1984 to 2009 along with the frequency of occurrence (%) in each zone (NZ = Northern Zone, RZ = River Zone, SZ = Southern Zone) and the IUCN Red List of species conservation status: LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, DD = data deficient, (-) no data (IUCN 2013)

Family	Species	NZ	RZ	SZ	Status
Hexanchidae	<i>Notorhynchus cepedianus</i>	50	36	14	DD
Scyliorhinidae	<i>Scyliorhinus</i> spp.	44	1	56	DD
	<i>Schroederichthys biviuis</i>	44	7	49	DD
Squalidae	<i>Squalus acanthias</i>	43	5	52	VU
	<i>Squalus mitsukurii</i>	52	4	44	DD
Triakidae	<i>Galeorhinus galeus</i>	69	9	22	VU
	<i>Mustelus schmitti</i>	61	22	17	EN
Squatinae	<i>Squatina guggenheim</i>	56	21	22	VU
	<i>Squatina occulta</i>	100			EN
	<i>Squatina argentina</i>	63	4	33	EN
Rajidae	Rajidae spp.	44	12	44	-
	<i>Atlantoraja castelnaui</i>	69	23	8	EN
	<i>Atlantoraja cyclophora</i>	81	17	2	VU
	<i>Atlantoraja platana</i>	100			VU
	<i>Amblyraja doellojuradoi</i>	34		66	
	<i>Dipturus chilensis</i>	40	3	57	VU
	<i>Dipturus trachyderma</i>	54		46	VU
	<i>Rioraja agassizi</i>	65	24	11	VU
	<i>Psammobatis</i> spp.	49	6	44	DD
	<i>Sympterygia bonapartii</i>	53	23	24	DD
	<i>Sympterygia acuta</i>	53	30	17	VU
	<i>Bathyraja</i> spp.	23	3	74	-
	<i>Bathyraja albomaculata</i>	31	2	68	VU
	<i>Bathyraja brachyrops</i>	29		71	LC
	<i>Bathyraja cousseauae</i>			100	-
	<i>Bathyraja griseocauda</i>	8		92	EN
	<i>Bathyraja macloviana</i>	32	2	66	NT
<i>Bathyraja multispinis</i>	20		80	NT	
<i>Bathyraja scaphiops</i>	22		78	NT	
Narcinidae	<i>Discopyge tschudii</i>	53	13	33	VU
Torpedinidae	<i>Torpedo puelcha</i>	93		7	DD
Myliobatidae	<i>Myliobatis goodei</i>	62	35	3	-
Dasyatidae	<i>Dasyatis hypostigma</i>	80	18	2	-
Rhinobatidae	<i>Rhinobatos horkelii</i>	67	31	2	CR
	<i>Zapteryx brevirostris</i>	61	38	2	VU

A total of 299 158 chondrichthyan individuals were captured by research vessels between 1984 and 2010, of which 59, 16 and 25% were in the NZ, RZ and SZ, respectively. We found that while *N* was significantly lower in colder years and at greater depths in the NZ, the opposite effects were found in the SZ. Overall, *N* decreased in colder years and increased with depth in the RZ (Table 2). The magnitude of estimated coefficients showed that depth (NZ = -0.303, RZ = 0.749, SZ = 0.265; obtained from Table 2) also had a higher relative importance in the average number of individuals than SSTA in the 3 zones (NZ = -0.056, RZ = -0.320, SZ = 0.061) (obtained from Table 2). There was low spatial variability

(29.8%) and very low temporal variability among (0.4%) and within (2.1%) years in the average number of individuals (residual variance = 67.7%) across the study area. The deviance explained by the fixed effects ( $R^2_m = 0.33$ ) was approximately half the variance explained by the entire model ( $R^2_c = 0.55$ ). There was substantial spatial variation in the average number of chondrichthyan individuals explained by fixed effects in the 3 zones (Fig. 6a). In contrast, there was little temporal variation (except for 1984 and 1994) in *N* (Fig. 6b). Nonetheless, the within-year seasonal variation around the average number of individuals showed deviations from the average predicted value for several years (except in winter) (Fig. 6c–f).

## DISCUSSION

The main results obtained in this study were (1) depth and SSTA had statistically significant effects on *S* and *N*, but fishing effort by the commercial fleet was significantly related only with *S*; (2) depth had a stronger effect on both chondrichthyan *S* and *N* than the other explanatory variables; and (3) the spatial variability of *S* and *N* was stronger than their temporal variability across the study area for the period analyzed.

Depth was a key variable explaining the number of individuals and species richness in the entire study area. Similarly, a marked zonation in the spatial distribution of chondrichthyans off the western coast of southern Africa was governed by depth and latitude (Compagno et al. 1991). In the southwestern Atlantic, bathymetric gradients associated with water temperature, salinity and other habitat features determine the spatial distributions of many chondrichthyan species (Menni et al. 2010). In the RZ, where bottom salinity covaries with bathymetry (Acha et al. 2004), the increase in the number of chondrichthyan individuals with depth is due to increasing marine influence, which allows marine species to occupy the outer estuary (Jau-reguizar et al. 2006, Lorenzo et al. 2011). In our study,

Table 2. Results of the final generalized linear mixed models (GLMM) analyzing the effects of fishing effort of the commercial fleet (effort), sea surface temperature anomalies (SSTA) and depth of trawling events for the chondrichthyan species richness ( $S$ ) and the total number of individuals ( $N$ ) by zone. Results are shown for estimated coefficients, their standard errors (SE) and the statistical significance for the explanatory variables having fixed effects. For each response variable, the intercept reflects the mean value for the Northern Zone (NZ, taken as the group of reference); the River Zone (RZ) and Southern Zone (SZ) coefficients are the changes in the mean value of the response variable between the RZ and SZ and the group of reference (NZ). Effort, SSTA, and Depth are the slopes for the reference group (NZ); RZ  $\times$  Effort, SZ  $\times$  Effort, RZ  $\times$  SSTA, SZ  $\times$  SSTA, RZ  $\times$  Depth and SZ  $\times$  Depth reflect the changes in slopes of the fishing effort, SSTA and depth for the RZ and SZ and the slopes of the group of reference (NZ). For each response variable, these coefficients reflect the magnitude of the effect of each explanatory variable with respect to the group of reference. We then obtained the coefficients for each explanatory variable and their interactions by recalculating the magnitude of their effects for each zone (mentioned in the text). All explanatory variables were centred and standardized prior to the analyses. pMCMC is the probability of having obtained a result as or more extreme than the one estimated in the data that was estimated using the Markov chain Monte Carlo method (see 'Materials and methods: Data analysis' for details)

Fixed effects	$S$			$N$		pMCMC Pr(> t )
	Estimate	SE	Pr(> z )	Estimate	SE	
Intercept	2.232	0.155	<0.001	5.877	0.160	<0.001
RZ	-0.582	0.216	0.007	-0.574	0.330	0.082
SZ	-0.248	0.194	0.202	-0.586	0.224	0.009
Effort	0.051	0.012	<0.001	-	-	-
SSTA	0.034	0.017	0.045	-0.056	0.027	0.034
Depth	0.146	0.025	<0.001	-0.303	0.065	<0.001
RZ $\times$ Effort	-0.094	0.031	0.003	-	-	-
SZ $\times$ Effort	-0.053	0.020	0.007	-	-	-
RZ $\times$ SSTA	-0.074	0.015	<0.001	-0.264	0.029	<0.001
SZ $\times$ SSTA	-0.080	0.016	<0.001	0.117	0.032	<0.001
RZ $\times$ Depth	-	-	-	1.052	0.206	<0.001
SZ $\times$ Depth	-	-	-	0.568	0.092	<0.001

the increased number of individuals with depth in the SZ was related to the presence of several *Bathyrāja* species, whose thermal preferences were associated with greater depths (Menni et al. 2010). Conversely, the decrease in the number of individuals with depth in the NZ was explained by the fact that most chondrichthyan species characteristic of this zone typically occur at depths <200 m (Norbis 1993, Paesch 2006), probably due to thermal preferences and resource availability (Brown 1984).

The availability and species composition of the trophic resources consumed by demersal fishes varies with depth across the continental shelf (Macpherson & Duarte 1991). Chondrichthyan species are generally at the highest trophic levels (Field et al. 2009) and often consume a wide variety of prey species. Most demersal chondrichthyan species in the study area consume benthic invertebrates (polychaetes, crustaceans and mollusks) and prey oppor-

tunistically on fishes as adults (Paesch 2000). These ontogenetic shifts in diet are generally associated with changes in their bathymetric distribution as they seek prey. In addition, several chondrichthyan species recorded in this study change their bathymetric distribution during breeding, parturition and/or egg-laying (Vooren 1997).

The opposite effects of SSTA on species richness and the number of individuals in each zone were expected, and are likely related to the thermal preferences of the species that inhabit each zone. The increased species richness in warmer years and the decline in the total number of individuals in the coldest years in the NZ are consistent with each other. In this sense, there are persistent fish assemblages (comprising both bony and chondrichthyan fishes) in terms of their species composition and environmental requirements in the estuarine, coastal and shelf environments of the study area (Jaureguizar et al. 2006, Menni et al. 2010, Lorenzo et al. 2011). The chondrichthyan assemblages in the NZ (>50 m) are clearly separated from those of the SZ by the 10°C bottom isotherm (Prensky & Sánchez 1988, Norbis 1993), with species in the NZ preferring bottom temperatures of about 12 to 18°C

(Menni et al. 2010, Lorenzo et al. 2011). Sharks such as *Galeorhinus galeus*, *Mustelus schmitti* and *Squatina guggenheim*, the skates *Atlantoraja castelnaui*, *A. cyclophora*, *A. platana*, *Rioraja agassizi*, *Sympterygia bonapartii* and *S. acuta*, and other rays such as *Myliobatis goodei*, *Dasyatis hypostigma*, *Rhinobatos horkelii* and *Zapterix brevirostris* are characteristic of this northern continental shelf fish assemblage, although some have also been recorded in deeper areas of the RZ (Jaureguizar et al. 2006, Paesch 2006, Lorenzo et al. 2011). Chondrichthyan species occurring in the RZ that prefer temperature ranges of 14.2 to 20.1°C in the outer estuary were less abundant in the RZ, where increases in temperature are often associated with decreases in salinity (Lorenzo et al. 2011). In terms of chondrichthyan species composition, the main difference between the NZ and SZ was the presence of *Bathyrāja* species. Most species of *Bathyrāja* and *Amblyrāja doelloju-*

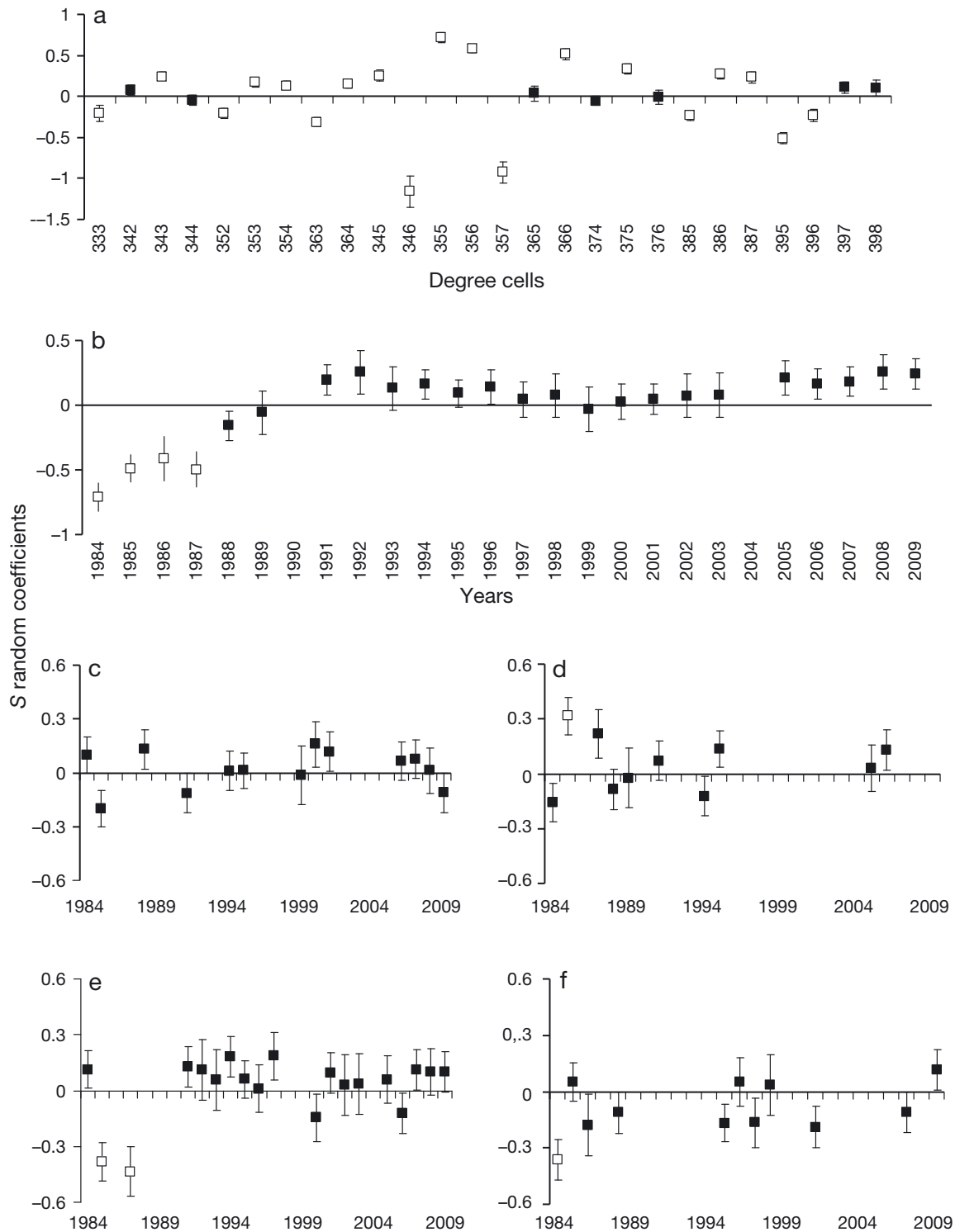


Fig. 5. Spatial and temporal variation of chondrichthyan species richness ( $S$ ) characterized by the coefficients of random effect obtained from the generalized linear mixed models. The random effect coefficients (differences between the observed and predicted mean species richness) and their standard error are shown for (a) each degree cell (see Fig. S1 in the Supplement), (b) by year and by season in years: (c) autumn, (d) winter, (e) spring and (f) summer. White squares indicate large temporal/spatial variation as quantified by the absolute value >2 of the ratio between the coefficients and standard errors of random effects. The error bars in panel (a) were too small to be shown for most cells. Note the different scales in the y-axis for panels (a), (b) and (c-f)



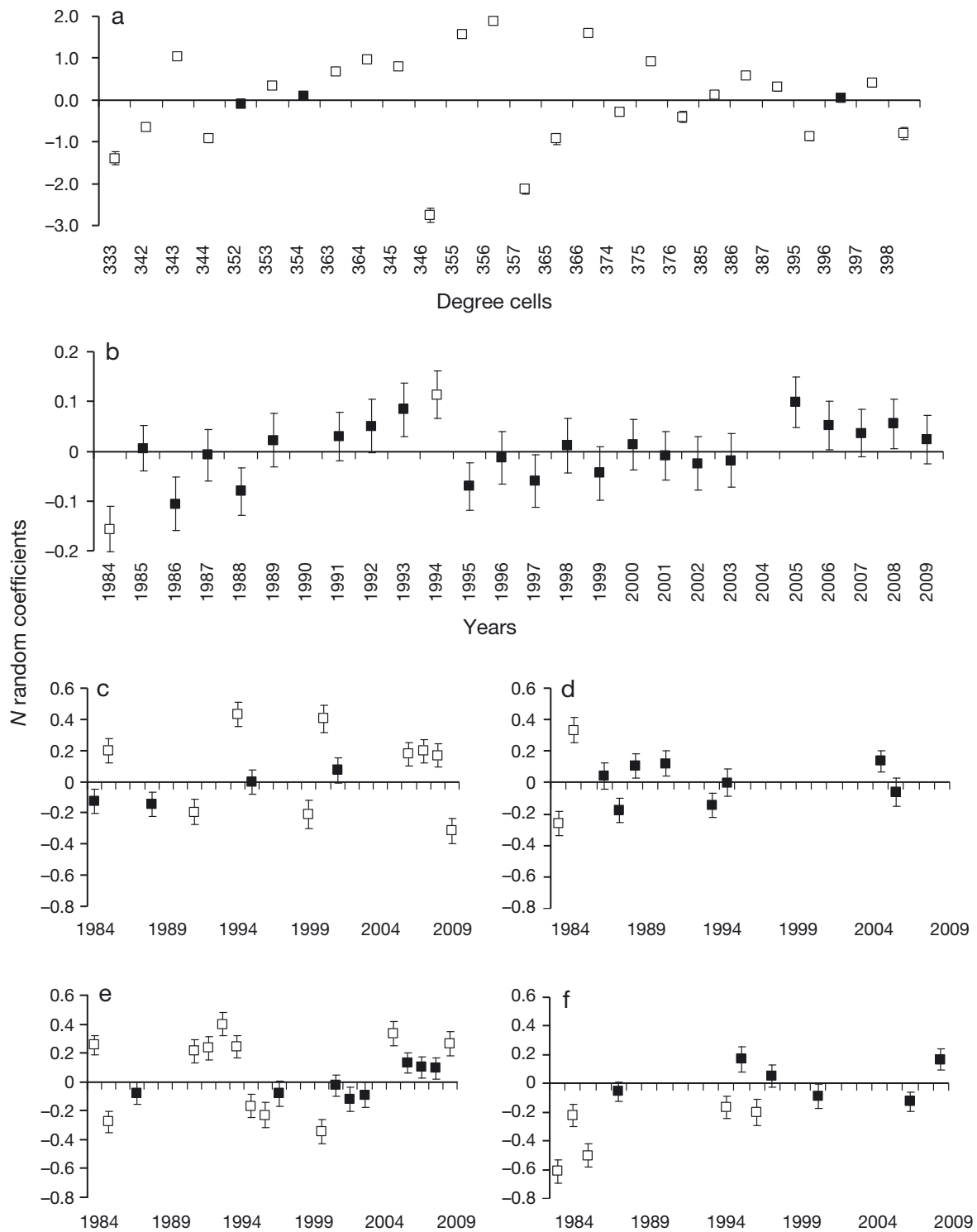


Fig. 6. Spatial and temporal variation in the total number of chondrichthyan individuals ( $N$ ) characterized by the coefficients of random effects obtained from the generalized linear mixed models. The random effect coefficients (differences between the observed and the predicted mean number of chondrichthyans) and their standard error are shown for (a) each degree cell (see Fig. S1 in the Supplement), (b) by year, and by season in each year: (c) autumn, (d) winter, (e) spring and (f) summer. White squares indicate large temporal/spatial variation as quantified by the absolute value  $> 2$  of the ratio between the coefficients and standard errors of random effects. The error bars for random effect coefficients for panel (a) were too small to be shown.

Note the different scales in the y-axis for panels (a), (b) and (c) to (f)

*radoi* are part of the Magellanic fauna that is restricted to areas with low sea temperature (Menni et al. 2010) and generally found south of 37° S. However, some taxa such as *Squalus acanthias*, *S. mitisukurii*, *Schroederichthys biviuis*, *Scyliorhinus* spp., *Dipturus chilensis* and *Discopyge tschudii* were present both in the NZ and SZ. These species were widely distributed in the outer continental shelf, where a mixing of warm temperate and cold temperate species occurs (Menni et al. 2010), related to the large, permanent frontal system formed at 36° S by the convergence of the Brazil and Malvinas/Falklands currents (Acha et al. 2004). The high chondrichthyan species diversity in the southwestern Atlantic is associated with marine frontal zones due to the higher abundance of food resources (Lucifora et al. 2012).

In general, there is little information about the impacts of climate warming on most shark and ray species anywhere in the world (Chin & Kyne 2007). Studies concerned with the effects of climate warming on marine communities in the North Atlantic that have included references to chondrichthyan species have discussed the implications for their abundance (e.g. a trend for species with cool water affinity to decline with warming) (Poulard & Blanchard 2005) and distribution (e.g. a trend to move deeper with warming) (Perry et al. 2005). However, Williams et al. (2008) found that the geographic distribution and relative abundance of chondrichthyans along the northern coast of Norway did not appear to change significantly despite an increase in average water temperature between 1992 and 2005. The effects of climate variability across the study area are rather complex because the dynamic mixing of marine currents and freshwater generates frontal zones that play a fundamental role in offering feeding and/or reproductive habitats for all fishes (Acha et al. 2004). The effects of sea temperature on total abundance and species richness could be indirect, and expressed through an impact on the abundance and spatial distribution of trophic resources and the habitat preferences of each chondrichthyan species. Despite knowing the ranges of bottom temperature and salinity preferences for most chondrichthyan species in the study area (Menni et al. 2010), the lack of continuous data for these key variables from all seasons analyzed prevented us from using this ecophysiological information to understand the effects of SSTA that we detected. Most chondrichthyan species in the study area are opportunistic predators and their diets have an ontogenetic variation (Paesch 2000). We thus find it difficult to disentangle the effects of SSTA, as

mediated by food resource abundance and habitat preferences, on total abundance and species richness of chondrichthyans in the study area.

The different effects of fishing effort on chondrichthyan species richness among the 3 zones may be a consequence of the spatially uneven distribution of the fishing effort across the study area. Although the Uruguayan industrial coastal fleet targeting white-mouth croaker *Micropogonias furnieri* and striped weakfish *Cynoscion guatucupa* operates both in the Rio de la Plata (RZ) and Atlantic coast (NZ, depth <50 m), its effort is largely concentrated in the former zone. Besides being strongly constrained by low salinity in the RZ (Jaureguizar et al. 2006, Lorenzo et al. 2011), chondrichthyan species richness is further impacted by the concentrated fishing effort of the coastal fishing fleet. The effort of the offshore fleet targeting hake *Merluccius hubbsi* was concentrated on the continental shelf and slope (50 to 400 m depth; NZ and SZ). However, in the NZ, the offshore fleet operates at depths greater than 200 m because of the seasonally banned area for young hake (Velasco et al. 2007). The annual ban on trawling between 34° 30' and 37° 30' S to protect juvenile hake could thus indirectly and partially protect many chondrichthyan species in the NZ (Oddone et al. 2007). The hake ban area in depths between 80 and 200 m could generate source-sink dynamics (Pulliam 1988) that would lead to high species richness in the NZ. Therefore, the increase of species richness with fishing effort in the NZ may be analogous to a rarefaction curve in which higher species richness would result from the protection derived from the banned hake area.

In contrast to species richness, the total number of chondrichthyan individuals was not significantly related to fishing effort. We had expected that the commercial fishing effort would negatively affect total chondrichthyan abundance obtained from fishery-independent research vessel surveys, but no such relationship was observed. Chondrichthyans were not targeted by the Uruguayan commercial fishing fleet. The capture of some species reported in this study are declared (identified at a rough level of taxonomic resolution) in Uruguayan fishery statistics (Paesch & Domingo 2003). Total landings of chondrichthyans (only sharks) by the Uruguayan commercial fleet between 1977 and 2001 ranged between 650 and 1600 t yr<sup>-1</sup> until 1993, increased from 1994 (when skate landing began) onwards reaching a maximum of around 4000 t in 1997, and subsequently declined (Paesch & Domingo 2003). However, as the 3 target species of the Uruguayan fleet (mentioned

above) accounted for more than 90% of the annual catches between 1996 and 2009 (data obtained from the web site of Comisión Técnico Mixta del Frente Marítimo, CTMFM; see Table S2 in the Supplement at [www.int-res.com/articles/suppl/m508p187\\_supp.pdf](http://www.int-res.com/articles/suppl/m508p187_supp.pdf)), chondrichthyans represented less than 7% of the catch.

The geographic ranges of most chondrichthyan species extend beyond the boundaries of the study area to the north and/or south as consequence of migration (Vooren 1997). Consequently, these fishery resources are also exploited by the fleets of Argentina (inside and outside the AUCFZ) and southern Brazil. The fishery statistics from southern Brazil showed a reduction in the catch of several species of demersal chondrichthyans between 1975 and 1997 after a large increase in the fishing effort (Villwock de Miranda & Vooren 2003). The biomass of several demersal chondrichthyans declined as the fishing effort by the Argentinean commercial fleet increased between 1991 and 1998 (Massa et al. 2004). Our analysis does not show statistically significant relationships between the total number of individuals and fishing effort. The large concentration of effort in only 2 geographic degrees (Fig. 3) and the temporal decrease of the Uruguayan fishing effort (Fig. 2) that did not target chondrichthyans may explain why we did not detect significant effects of fishing effort on the total chondrichthyan abundance despite having 25 yr of data. Given that chondrichthyans were not the target species of commercial fishing fleets, many captured individuals with no commercial value were discarded. However, capture may not necessarily imply death since several chondrichthyan species have a high post-catch survival (Braccini et al. 2012).

Little is known about how trawl fisheries have impacted chondrichthyan species at the community level in our study area. The highest reported chondrichthyan commercial catches by the Argentinean fishing fleet occurred between 34 and 41°S (including the AUCFZ; Fig. 1), and overlapped with the hotspots of chondrichthyan diversity (Lucifora et al. 2012). While the vulnerability of chondrichthyans to fishing effort has been well documented at a single species level (Field et al. 2009 and references therein), its overall effects at the community level remain poorly known, and existing studies have drawn conflicting conclusions. Several chondrichthyan species showed different responses to changes in fishing pressure in the central Mediterranean Sea (Ferretti et al. 2005) and in southern Africa (Petersen et al. 2008). In the eastern Mediterranean Sea, chondrichthyan species richness and abundance declined due

to fishing, but differential responses to fishing exploitation at the species level were found (Damalas & Vassilopoulou 2011). The reduction of trawl fishing effort was suggested to account for the recovery of chondrichthyan populations in the Cantabrian Sea (Sánchez et al. 2005); however, the current fishing levels along the northern coast of Norway do not appear to be impacting the populations of the more common chondrichthyan species (Williams et al. 2008).

Given that natural communities are generally assemblages of a few abundant species and many rarer ones, the use of aggregate metrics such as the total number of individuals may hinder the detection of individual species declines caused by increases in fishing effort. This is because declines of less abundant species due to high fishing effort might be compensated by increases of more abundant ones at the local scale, thus weakening the overall relation between the total number of chondrichthyan individuals and the fishing effort (Dulvy et al. 2000). Nevertheless, we believe that analyses of aggregate metrics such the total number of chondrichthyan individuals are worth pursuing when evaluating the overall effect of fisheries on non-targeted species. The direct effect of fishing effort on the abundance of non-targeted species largely depends on the fine-scale coincidence among the spatial distributions of the targeted and non-targeted species (Gillis 2003), but there is very little knowledge of the fine spatio-temporal distribution of chondrichthyan species in the AUCFZ. Dulvy et al. (2000) suggested that the contrasting species response to high fishing effort was related to their body size ranges. Some chondrichthyan species in the study area could be considered nearly small-bodied species that would have more recovery potential than other large-bodied species (Ward-Paige et al. 2012). The absence of a significant relationship between the total number of individuals and fishing effort could therefore be explained by species-specific responses to fishery mortality in relation to body size. These aspects will be analyzed in other studies.

We found that spatial variability in  $S$  was greater than its temporal variability (both between years and seasons within years) and that there was greater spatial variation in the RZ than in the SZ and NZ. Chondrichthyan species are mainly marine (Field et al. 2009), and thus their presence in the RZ is intermittent depending upon variability in hydrographic conditions (mainly salinity). The presence of estuarine and coastal species demonstrates the influence of the high/low freshwater discharge of the Río de la Plata

during El Niño and La Niña years (Genta et al. 1998), respectively. Chondrichthyan species assemblages in the NZ and SZ were spatially and temporally persistent, with bottom sea temperature being the main environmental factor that separated these species assemblages (Menni et al. 2010). The boundary between southern and northern species assemblages often shifts northward during the cold months and southward in warm months depending on fluctuations in the Falkland/Malvinas current (Ortega & Martínez, 2007). In addition, the number and composition of chondrichthyan species in the study area was similar to those reported by Abella et al. (1979) between 1973 and 1978, which suggests the permanence of most chondrichthyan species in the study area over time.

The spatial variability of *N* was stronger than the magnitude of its temporal variation. The geographic range of most chondrichthyan species exceeds the limits of the study area, with most species having a continuous distribution in the warm temperate Argentinean Zoogeographic Province along the coast of southern Brazil, Uruguay and northern Argentina (Menni et al. 2010). Nonetheless, the northern limits of some species belonging to the Magellanic Zoogeographic Province reach the SZ of AUCFZ (Menni et al. 2010). Species with large geographic ranges tend to have higher local abundances than species with restricted geographic ranges (Brown 1984). This same pattern was observed in the study area, where the most abundant demersal chondrichthyan species tended to be widely distributed (i.e. occurring in more than 30% of the total area) and species with either intermediate or low abundances displayed restricted geographic distribution (i.e. less than 30% of the total area) (Paesch 2006).

The within-year variation in the number of individuals showed important deviations from the average predicted value for most years, mainly during autumn and spring. This may be related to seasonal reproductive movement of many species in the study area (Vooren 1997). For instance, *M. schmitti* and *S. guggenheim* adults move to shallow waters during breeding periods (Vooren 1997, Oddone et al. 2007) and migrate to deeper waters in the continental shelf of southern Brazil after parturition (Vooren 1997). Both *Squalus* species migrate northwards in the colder months and southwards in warmer periods, following the fluctuations of Falkland/Malvinas current (Prensky & Sánchez 1988). These *Squalus* species, as well as *S. bonapartii*, *D. tschudii*, *G. galeus*, *M. schmitti* and *Notorhynchus cepedianus*, are all winter migrants in the southern Brazilian shelf and

return to reproduce in Argentine and Uruguayan waters during the summer (Vooren 1997). SSTA were mostly negative in the study area between 1984 and 1995 in the 3 zones, in agreement with Lentini et al. (2001) after El Niño events in the offshore regions of the Rio de la Plata. The winter migrants could have been more abundant during the cooler period, but the data were not analyzed by species.

Our study quantitatively examined the long-term effects of fishing effort, depth and SSTA as a proxy of climate variability on 2 aggregate metrics (total number of individuals and species richness) of the chondrichthyan community structure in a large area of the southwestern Atlantic. We are unaware of other community-level studies for chondrichthyans carried out over comparable lengths of time in the southwestern Atlantic. Large data sets typically enhance the possibility of detecting statistically significant effects (even of small magnitude) on the response variables in any statistical analysis.

In closing, given that several chondrichthyan species in the SW Atlantic have been declared 'vulnerable' or 'endangered' (IUCN 2013), future studies should aim to evaluate the amount caught, amount discarded and the fishing mortality per species by the commercial fishing fleets, as well as the climatic variability at a sufficiently small spatial resolution (i.e. degree cells), so as to assess the effects of these 2 key drivers in the context of accelerating changes in the marine environment.

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