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ORIGINAL ARTICLE

Seasonal mesoscale shifts of demersal nekton assemblages in the subtropical South-western Atlantic

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ABSTRACT

The present study shows a hitherto undocumented pattern of mesoscale seasonal shifts of teleost fish and cephalopod assemblages along the shelf and upper slope of southern Brazil. Through multivariate techniques we discerned four consistent groups: coastal, warm shelf, cold shelf and upper-slope assemblages. The warm shelf and the upper-slope assemblages were present year round, whereas the cold shelf assemblage occurred almost exclusively in the cold season, and the coastal assemblage expanded toward the south in the warm season. The coastal and shelf nekton fauna was dominated by juveniles and adults of the sciaenid fishes *Macrodon ancylodon*, *Cynoscion guatucupa*, *Micropogonias furnieri*, *Umbrina canosai* and *Paralonchurus brasiliensis*, the cutlassfish *Trichiurus lepturus* and the hake *Merluccius hubbsi*. The upper-slope assemblage was more diversified and included *Polyprion americanus*, *Urophycis mystacea*, the squid *Illex argentinus* and macrourids. Similar to other subtropical Atlantic ecosystems, the dominance of sciaenids is related to the large areas of sand and mud bottoms, and the low salinity due to the high freshwater runoff of the La Plata River and Patos Lagoon. The choice of seasonal or spatial closures or the planning of marine protected areas may benefit from a greater understanding of the seasonal spatial shifts of the fish assemblages.

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Introduction

Understanding shifts and changes in species composition of faunal communities is important for defining their home range and habitat use, which entails important consequences for fisheries and conservation management (Woodroffe & Ginsberg 1998; Sale et al. 2005). Movements of entire species groups (e.g. assemblages, communities, associations) are expected to occur in response to changes in environmental conditions, among which temperature is the most frequently cited dynamic factor (Longhurst & Pauly 1987).

In the present study, the term 'assemblage' is used to define a group of species (or size ranges of species) with a similar distribution pattern in both space and time and that are abundant in the same places (Pianka 1974). Demersal assemblages have been studied worldwide; however, they mostly focus on spatial patterns (Moranta et al. 1998), inter-annual variation including effects of climate change (Southward et al. 2004; Dulvy et al. 2008) and fishery impacts (Zwanenburg 2000; Daan et al. 2005). Seasonal movements of communities or assemblages are less well documented and most of them are associated with the estuarine–marine gradient (Garcia et al. 2004; Jaureguizar et al. 2006).

The southern extreme of Brazil (29°–34°S) is particularly suitable to identify and describe displacements of entire assemblages affected by seasonal hydrographic shifts since it is influenced by the subtropical convergence, which involves the Brazil Current and the seasonal input of colder waters from southern regions (Peterson & Stramma 1991). This is among the country's most productive marine regions and yields a significant part of the demersal and pelagic fish landings (Haimovici 1998; Haimovici et al. 2006). The demersal fish fauna of this region is well known; bottom-trawl surveys in the late 1960s and early 1970s have revealed more than 200 species of bony fishes in over 100 families (Menezes et al. 2003). Furthermore, a large data set was obtained in the 1980s with large commercial bottom trawls (Haimovici et al. 1994, 1996).

In this paper we used classification and ordination techniques to identify nektonic assemblages and to

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The supplementary material for this article (Table SI) is available at http://dx.doi.org/10.1080/17451000.2016.1217025.

relate their displacements to the main oceanographic features in the region, namely the seasonal spatial displacements of shelf and upper-slope fronts. The identification of the assemblages may contribute to fishery management and conservation. Moreover, we compare the different dominant taxa of the region with those from other tropical and subtropical environments described by Longhurst & Pauly (1987) and Lowe-McConnell (1987).

Materials and methods

The study area

The Southern Brazilian shelf, between 30°30′S and 34°35′S, has a width of approximately 140 km, and less than 50 km in the northern part. The shelf break lies at depths from 150 m to 185 m. The dominant sediments vary gradually from sand on the inner shelf to mud with silts, clay and biodetrites on the outer shelf and mud on the upper slope (Martins et al. 1972).

The surface circulation of the south-western Atlantic Ocean along northern Argentina and southern Brazil is characterized by the opposing flows of the Brazil and Malvinas Currents on the one hand, and the runoff of the La Plata River on the other (Piola et al. 2000; Moller et al. 2008). The confluence zone between the two currents is called the Subtropical Convergence, an oceanographic feature of high mesoscale variability. It oscillates seasonally along a latitudinal gradient between 30° and 46°S, with an alternate southward displacement of the warm and more salty Brazil Current on the one hand and a northward penetration of the Malvinas Current on the other (Peterson & Stramma 1991). The seasonal variation of water temperature and stratification over the shelf is strong in summer and weak or non-existent in winter (Castro & Miranda 1998). These changes result in a displacement of the Shelf Subtropical Front (SSTF) perpendicular to the coastline, separating the nutrient-rich, colder and less salty waters resulting from the mixture with Subantarctic Shelf Waters along the Argentinean shelf from the Rio de la Plata waters. The SSTF reaches up to 30°S in winter and retreats southward to around 34°S during the warm months (Piola et al. 2000; Moller et al. 2008). A wind-induced intrusion of the nutrient-rich South Atlantic Central Water over the shelf break and outer shelf occurs mainly in spring and summer, when north-east winds are dominant (Garcia & Garcia 2008).

Data collection

The study was carried out on the shelf and upper slope of southern Brazil between Solidão (30°42′S) and Chuí (34°33′S) (Figure 1). It is based on the species composition from 289 hauls taken during eight demersal trawl cruises by the RV *Atlântico Sul*, distributed across equidistant transects perpendicular to the coastline at pre-established depths (i.e. 10, 20, 40, 60, 80, 120, 180, 250, 350, 450 and 600 m).

During the April and September 1981 surveys, a net with a relatively small vertical opening and a 52.9 m ground-rope designed for the commercial fishing of hake (*Merluccius hubbsi* Marini, 1933) was used. During the January 1982 and April, August and November 1983 cruises, a net with a larger vertical opening and a 49.3 m ground-rope was used. In August 1986 and April 1987, the hauls on the upper slope were performed with a 23.4 m ground-rope net with 40 cm-diameter metallic bobbins. The codend, stretched between opposite knots, had a mesh size of 40–50 mm and was covered by a second codend of the same mesh size. The trawling speed was around 5.5 km/h (3 knots). The hauls were usually one hour long and were performed during daytime, beginning after sunrise and finishing before sunset. Bottom temperatures were recorded with inversion thermometers or bathythermographs after each haul. A more detailed description of the sampling design and catches is given by Haimovici et al. (1994, 1996).

Data processing

After every haul, the catch was classified; 141 bony fish and five cephalopod species or genera were identified, and their total number and weight were recorded. The total length (TL) of a random sample of every taxon was also recorded (Haimovici et al. 1994, 1996). Relative abundance was calculated as catch per unit effort (CPUE kg/h) and standardized to the ground-rope size of the nets used in the initial shelf cruises. For the assemblage analysis, we selected the taxa that accounted for 95% of the total catch weight in each of the eight cruises, or, alternatively, 95% of the total catch in any of the depth strata. This resulted in a total of 47 species (Table SI, supplementary material).

The assemblage analysis did not include epipelagic and mesopelagic species from the families Molidae, Myctophidae and Scombridae, nor highly migratory pelagic, neritic taxa that are only occasionally caught by bottom trawls, such as *Pomatomus saltatrix* (Linnaeus, 1766) and *Mugil* sp. Nets with large metallic bobbins on the ground-rope, as used on the outer shelf and upper slope, certainly undersampled benthic species, such as flatfishes and octopuses. However, nets without bobbins, which had formerly been used for commercial fishing on the upper slope,

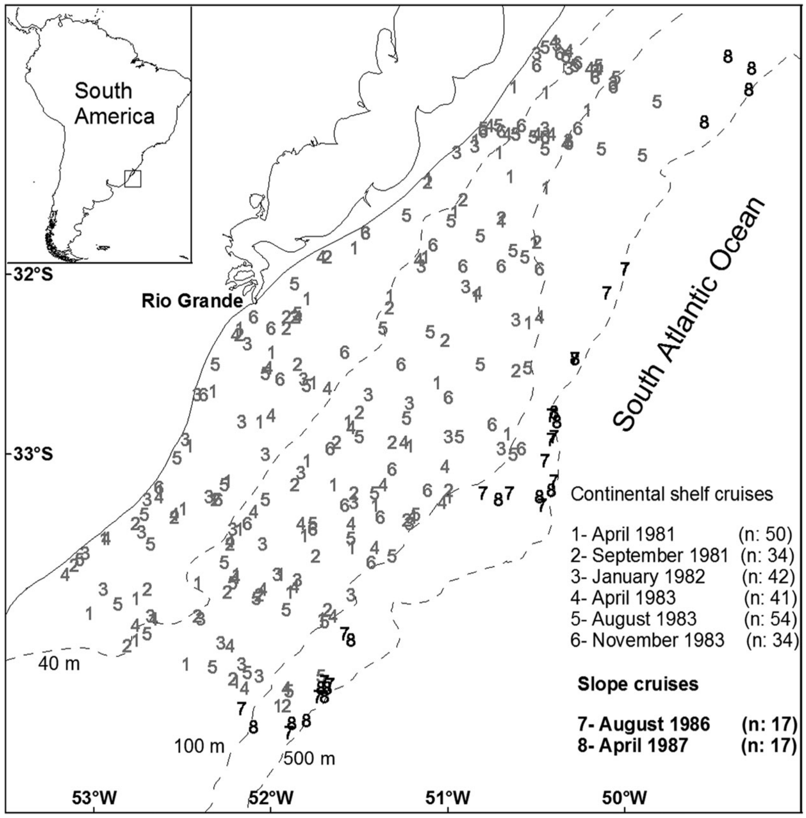

Figure 1. The study area and the positions of the bottom trawl collection sites on the continental shelf (n: 255; 1981–1983) and upper slope (n: 34, 1986–1987).

also produced a low abundance (Perez et al. 2009), and therefore these were not included either.

To take into account intraspecific size variation, each of the seven most abundant species were split into two categories: smaller and larger than the mean length at first maturity established in previous life-history studies: *Cynoscion guatucupa* (Cuvier, 1830) (TL 250 mm, Vieira & Haimovici 1997), *Micropogonias furnieri* (Desmarest, 1823) (TL 250 mm, Vazzoler 1975), *Macrodon ancylodon* (Bloch & Schneider, 1801) (TL 250 mm, Juras & Yamaguti 1989), *Urophycis brasiliensis* (Kaup, 1858) (TL 250 mm, Haimovici et al. 1996), *Merluccius hubbsi* (TL 300 mm, Haimovici et al. 1993), *Umbrina canosai* Berg, 1895 (TL 200 mm, Haimovici & Cousin 1989) and *Trichiurus lepturus* Linnaeus, 1758 (TL 700 mm, Martins & Haimovici 2000). This resulted in a total of 54 categories.

Data analysis

Because of their high mobility and different individual migratory patterns, bony fish and cephalopods are not easy to group in assemblages. The evaluation of the consistency of the resulting assemblages was approached in several ways: (1) by analysing the coherence between the results of the classification and ordination techniques used to characterize the assemblages; (2) by relating the formed groups with gradients of two of the most influential environmental variables in the distribution of nektonic organisms: bottom temperature and depth (Roel 1987; Bianchi 1992a, 1992b; Martins & Haimovici 1997); and (3) by checking the maps for the spatial and temporal consistency of the groups of hauls corresponding to each assemblage.

As a first step, we used a hierarchical cluster analysis (Ward's clustering method). We calculated the relative Euclidean distances using the catch rates (kg/h) of 54 species or categories in each haul, expressed as $\ln(x+1)$. The Ward's clustering method is distinct from other methods because it uses an analysis of variance approach to calculate the distances between clusters, which makes it very efficient (Ward 1963).

To examine the consistency of this classification, catch rates (kg/h) of species in each haul, expressed as $\ln(x+1)$, were analysed with a detrended correspondence analysis (DCA) (Hill & Gauch 1980), a method developed specifically for ecological analyses and indicated for situations in which the data to be analysed are restricted to species abundances of different samples. The correlation between logarithmized temperature and depth was tested with Pearson's R correlation coefficients (McCune & Mefford 1999).

Discriminating species for each assemblage determined by the ordination and cluster analysis were identified with the indicator species analysis (Dufrene & Legendre 1997). This method uses information on abundance of species and produces indicator values (indices) for each species in each group. Species for which over 50% of their biomass index was found in a single assemblage were considered 'characteristic' for that assemblage; similarly, a threshold of 80% of their biomass index was used to identify 'indicator species'.

Results

Temperature patterns over the shelf

The bottom-water temperature distribution observed on the six cruises on the continental shelf are shown in Figure 2. In the two early autumn cruises (April 1981 and April 1983), bottom-water temperatures on the shelf were mostly above 20°C, except from the deeper areas where they were as low as 18°C. In the winter cruises (September 1981 and August 1983), typical winter oceanographic conditions prevailed, with bottom-water temperatures below 15°C on the inner shelf. In August 1983, the Shelf Subtropical Front was clearly discernible between 31°S and 33°S. In the summer cruise of January 1982 and the spring cruise of November 1983, transitional characteristics were observed, with a predominance of bottom waters from 18°C to 22°C on the inner shelf and between 14°C and 17°C on the outer shelf (Haimovici et al. 1996). On the outer shelf and upper slope cruises of August 1986 and April 1987, there was a strongly decreasing temperature gradient from 19°C at 100 m to 6.2°C at 490 m (Haimovici et al. 1994).

Definition of assemblages

The identification of the assemblages was not straightforward. It was begun by running a Cluster Anaysis that showed eight clusters (G1 to G8) (Figure 3a).

In parallel, a Detrended Correspondence Analysis, with depth, temperature and the relative abundance

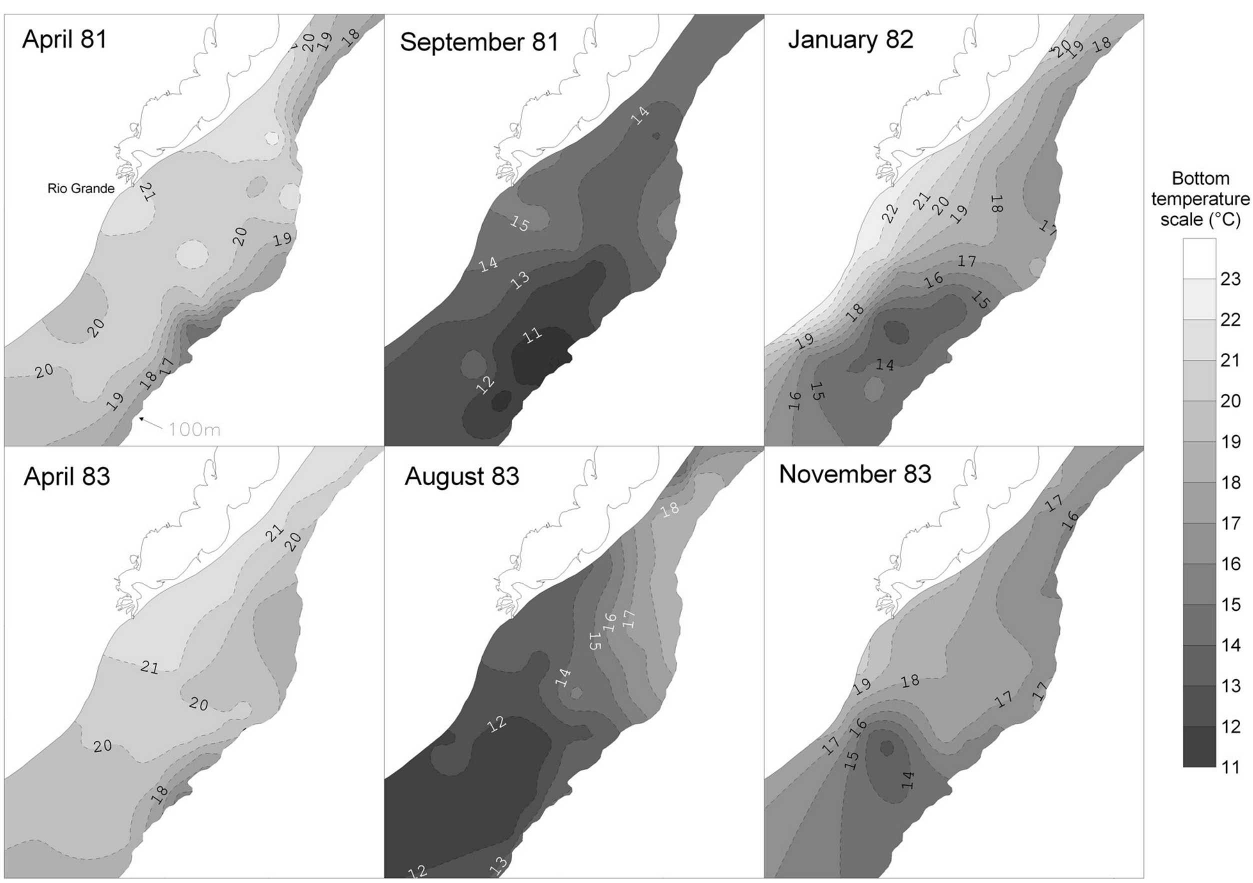

Figure 2. Bottom isotherms from the six demersal trawl cruises on the continental shelf off southern Brazil.

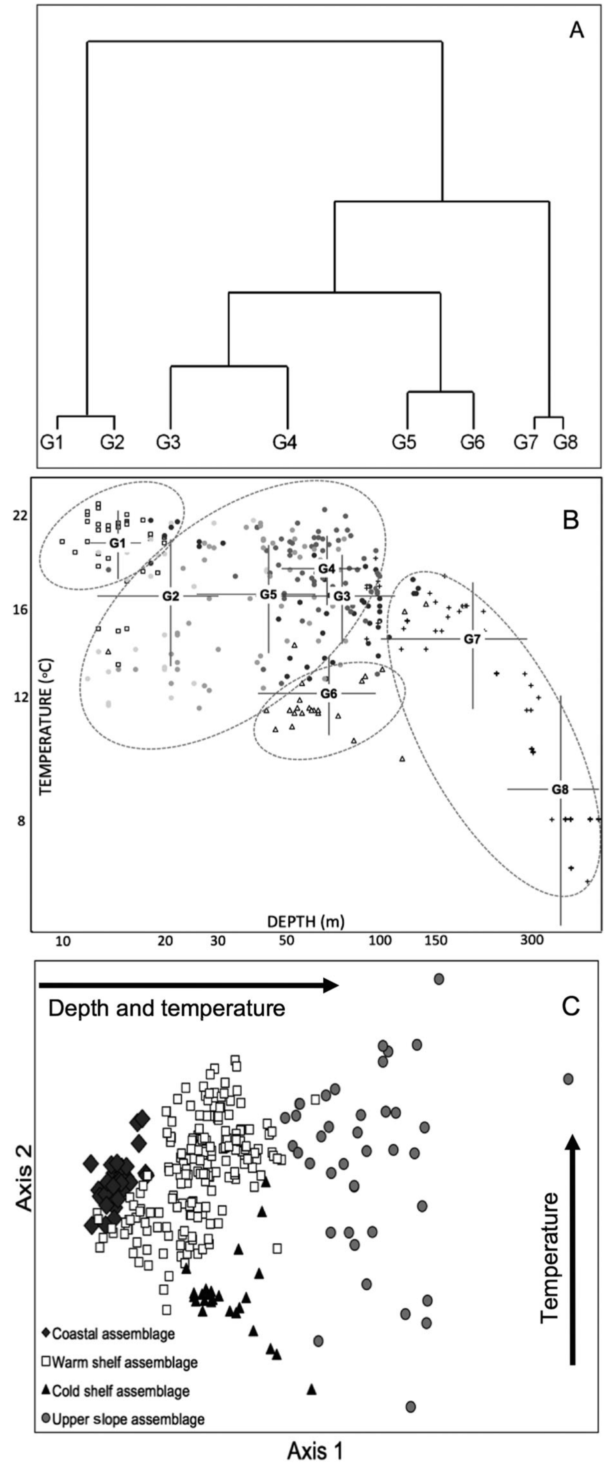

Figure 3. Simplified dendrogram with the groups of hauls formed by Ward's cluster analysis (A), plot of the each haul (squares, circles, triangles and crosses) and mean and standard deviation of depth and temperature of the groups formed by the cluster analysis (axis X and Y in logarithmic scale) (B) and plots of scores of the detrended correspondence analysis (DCA) along the two main axes; the hauls are grouped in accordance with the four assemblages defined by the cluster analysis (C).

of the 54 categories of fish as data, showed that Axis 1 was strongly correlated with depth (*R*: 0.91) and partly with temperature (*R*: −0.526), while axis 2 was moderately correlated with temperature (*R*: −0.416).

The depth and bottom temperature of each of the 289 hauls and the mean depth and bottom temperature (and confidence interval corresponding to each) of the eight clusters were plotted (Figure 3b). It was observed that G1 corresponds to shallow coastal waters in all seasons, G2 to G5 to intermediate shelf waters, and G6 corresponds to colder shelf waters only in the cold season. The G7 and G8 groups correspond to outer shelf and upper slope respectively in both seasons.

The distribution of the 289 hauls with respect to their scores on the first two axes of the DCA show that the four groups based on their temperature and depth can be discriminated (Figure 3c). The spatial representation of the hauls pertaining to these groups on the two winter cruises (Figure 4a) and the late spring to early autumn cruises (Figure 4b) reveals a consistent pattern of spatial distribution in different seasons. Moreover, the characteristic and indicator species show little overlap between the four defined groups. Therefore, four assemblages are proposed and hereafter called 'coastal assemblage', 'warm shelf assemblage', 'cold shelf assemblage' and 'upper-slope assemblage'. In the following section, we provide a brief description of each assemblage (based on the results from Table I).

Description of assemblages

Coastal assemblage

Occupying the narrow depth band between 0 m and 20 m associated with bottom water temperatures >18°C; in winter, however, it was present only in the northern part (Figure 4a, b). Indicator species was dominated by five sciaenid species: juvenile and adult *Macrodon ancylodon*, juvenile *Micropogonias furnieri*, *Pogonias cromis* (Linnaeus, 1766), *Menticirrhus litoralis* (Holbrook, 1847) and *Paralonchurus brasiliensis* (Steindachner, 1875).

Warm shelf assemblage

Present all year round on the entire inner shelf at depths from 20 m to 100 m, expanding to shallower waters in winter, mostly at bottom water temperatures between 15°C and 20°C (Figure 4a). The indicator species of this assemblage included the two sciaenids *Ctenosciaena gracilicirrhus* (Metzelaar, 1919) and

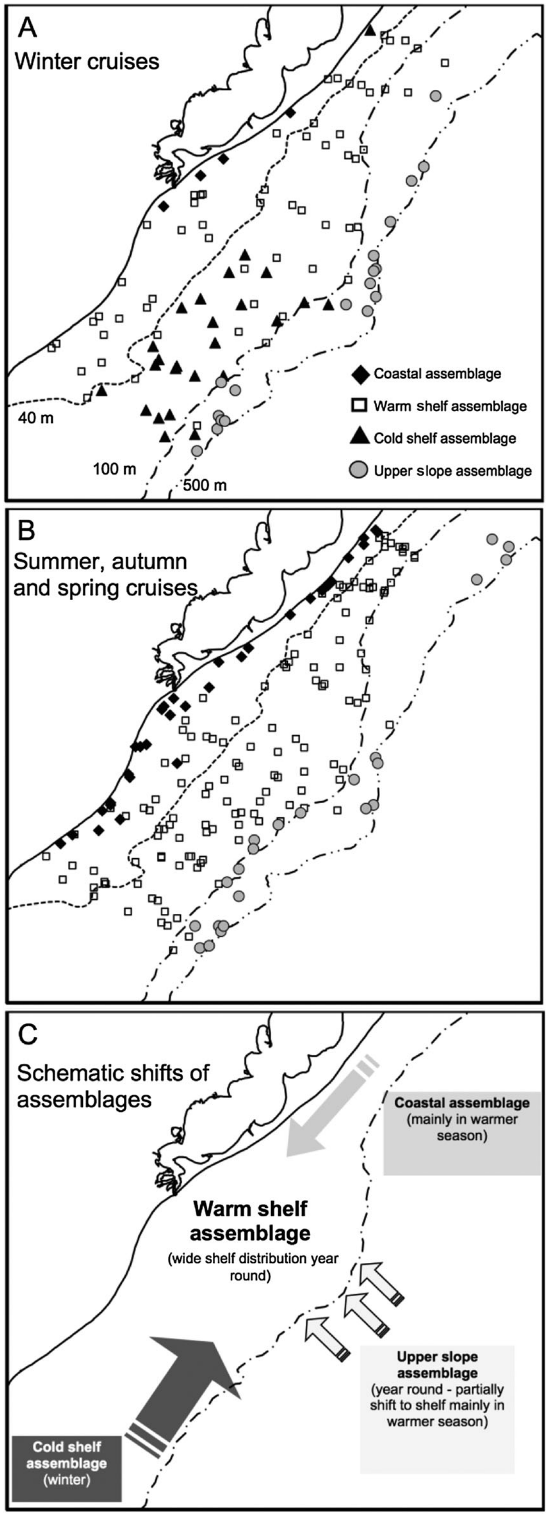

Figure 4. Spatial distribution of the assemblages (as defined by the cluster analysis) on the shelf and upper slope of southern Brazil during the winter cruises (A) and the summer, autumn and spring cruises (B). Schematic representation of seasonal shifts of assemblages (C).

Cynoscion jamaicensis (Vaillant & Bocourt, 1883), the triglid *Prionotus punctatus* (Bloch, 1793), and juveniles of the trichiurid *Trichiurus lepturus*.

Cold shelf assemblage

Present exclusively in winter on the southern half of the shelf between 40 m and 80 m depth and at bottom temperatures <15°C (Figure 4a). Indicator species were the two sciaenids *Cynoscion guatucupa* (Cuvier, 1830) (adults) and *Umbrina canosai* Berg, 1895 (adults and juveniles), the gadiform *Merluccius hubbsi*, and two small neritic species associated with productive cold waters: the engraulid *Engraulis anchoita* Hubs & Marini, 1935 and the carangid *Trachurus lathami* Nichols, 1920.

Upper-slope assemblage

Present all year round, occupying the entire region at depths deeper than 100 m and bottom temperatures <17°C, as well as at shallower depths during the warm season (Figure 4b). Fifteen indicator species were found. The most abundant species was the wreckfish *Polyprion americanus* (Bloch & Schneider, 1801); moreover, there were the ommastrephid squid *Illex argentinus* (Castellanos, 1960), the hake *Urophycis mystacea* Miranda Ribeiro, 1903, and the macrurids *Coelorinchus marinii* Hubbs, 1934 and *Malacocephalus occidentalis* Goode & Bean, 1885 (Table I). This assemblage was less clearly delimited, probably due to its wide depth range and the small number of hauls along specific demersal habitats, such as the deep-water corals, along the shelf break.

Some abundant species, such as *M. furnieri*, *C. guatucupa* and *T. lepturus*, had wide distribution ranges and were characteristic but not indicators of assemblages (Table I). Some species were abundant in more than one assemblage; for example *M. furnieri* was abundant in both the coastal and the warm shelf assemblage, and *U. canosai* and *C. guatucupa* were abundant in the warm shelf, cold shelf and upper-slope assemblages (Table II).

The general pattern of the seasonal displacement of the assemblages is shown in Figure 4c. The warm shelf assemblage is dominant year round on the inner shelf. In winter, the cold shelf assemblage migrates from the south to the southern half of the study area at between 50 and 100 m depth, while the coastal assemblage retracts to the north. During the warm months, the coastal and warm water assemblages occupy almost the entire inner shelf, and the upper-slope assemblage intrudes from the north into the southern part of the inner shelf.

Discussion

In the present study, we show that in southern Brazil, the spatial distribution pattern of demersal nektonic

Table I. Percentage of total biomass and of the biomass in each of the four assemblages of indicator (in bold) and characteristic species (in grey).

		Percentage of biomass in each assemblage			
Species	% total biomass	Coastal	Warm shelf	Cold shelf	Upper slope
Pogonias cromis (Linnaeus, 1766)	*0.2*	100			
Macrodon ancylodon (Bloch & Schneider, 1801) (**juveniles**)	*1.1*	93	7		
Paralonchurus brasiliensis (Steindachner, 1875)	*2.6*	93	7		
Menticirrhus littoralis (Holbrook, 1847)	*0.1*	89	10	1	
Macrodon ancylodon (Bloch & Schneider, 1801) **(adults)**	*3.7*	89	11		
Micropogonias furnieri (Desmarest, 1823) **(juveniles)**	*0.2*	82	18		
Urophycis brasiliensis (Kaup, 1858) (adults)	*0.7*	**68**	21	12	
Urophycis brasiliensis (juveniles)	*0.2*	**68**	29	1	3
Balistes capriscus Gmelin, 1789	*0.7*	**59**	39		2
Ctenosciaena gracilicirrhus (Metzelaar, 1919)	*3.8*		100		
Cynoscion jamaicensis (Vaillant & Bocourt, 1883)	*1.8*		100		
Prionotus punctatus (Bloch, 1793)	*2.7*		88	2	9
Trichiurus lepturus Linnaeus, 1758 **(juveniles)**	*1.1*	13	83		3
Astroscopus sexpinosus (Steindachner, 1876)	*<0.1*	21	**79**		
Netuma sp.	*0.3*	27	**72**		1
Peprilus paru (Linnaeus, 1758)	*0.8*	37	**63**		
Porichthys porosissimus (Cuvier, 1829)	*0.9*	1	**59**	31	9
Menticirrhus americanus (Linnaeus, 1758)	*<0.1*	42	**58**		
Trichiurus lepturus (adults)	***7.3***	23	**54**	10	13
Micropogonias furnieri (adults)	***7.9***	44	**50**	6	
Merluccius hubbsi Marini, 1933 **(adults)**	*5.4*			100	
Engraulis anchoita Hubbs & Marini, 1935	*0.3*		1	99	
Cynoscion guatucupa (Cuvier, 1830) **(adults)**	*9.9*		10	89	
Trachurus lathami Nichols, 1920	*1.2*		4	88	8
Umbrina canosai Berg, 1895 (**adults**)	*8.5*		15	85	
***Merluccius hubbsi* (juveniles)**	*0.8*		6	82	11
***Umbrina canosai* (juveniles)**	*5.8*		19	81	
Percophis brasiliensis Quoy & Gaimard, 1825	*0.1*		25	**74**	
Pagrus pagrus (Linnaeus, 1758)	*0.2*		3	**74**	23
Thyrsitops lepidopoides (Cuvier, 1832)	*0.1*		3	**71**	25
Cynoscion guatucupa (juveniles)	***26.2***		38	**61**	
Nemadactylus bergi (Norman, 1937)	*0.1*		8	**58**	34
Doryteuthis sanpaulensis (Brakoniecki, 1984)	*0.5*	7	24	**54**	15
***Peristedion* sp.**	*<0.1*				100
Coelorinchus marinii Hubbs, 1934	*<0.1*				100
Priacanthus arenatus Cuvier, 1829	*0.1*				100
Helicolenus lahillei Norman, 1937	*0.2*				100
Parasudis truculenta (Goode & Bean, 1896)	*<0.1*				100
Polymixia lowei Günther, 1859	*<0.1*				100
Antigonia capros Lowe, 1843	*0.1*				100
Scomber japonicus Houttuyn, 1782	*0.4*				100
Ariomma bondi Fowler, 1930	*<0.1*				100
Polyprion americanus (Bloch & Schneider, 1801)	*0.5*			1	99
Evoxymetopon taeniatus Gill, 1863	*<0.1*		1		99
Malacocephalus occidentalis Goode & Bean, 1885	*<0.1*		1		99
Synagrops spinosus Schultz, 1940	*0.1*		8		92
Illex argentinus (Castellanos, 1960)	*0.1*		5	8	87
Urophycis mystacea Miranda Ribeiro, 1903	*0.2*		4	13	83
Prionotus nudigula Ginsberg, 1950	*<0.1*		23	6	**70**
Genypterus brasiliensis Regan, 1903	*0.1*		1	34	**64**
Lophius gastrophysus Miranda Ribeiro, 1915	*0.1*		39	1	**60**
Zenopsis conchifer (Lowe, 1852)	*0.1*		4	39	**57**
Conger orbignianus Valenciennes, 1837	*0.6*	31	20	49	
Mullus argentinae Hubbs & Marini, 1933	*0.3*		48	18	34

■ 80–100% of the biomass in assemblage (indicator).
■ 50–80% of the biomass in assemblage (characteristic).

assemblages is associated with the bathymetry and bottom water temperature, which, on the shelf, displays seasonal oscillations. Regardless of depth, temperature had a strong influence, as shown by the seasonal displacement of the shelf assemblage due to the northward shift of the Shelf Subtropical Front in winter and, to a lesser degree, due to the position of the western boundary of the Subtropical Convergence. Temperature also affected the composition of the assemblages due to the tolerance limits of important species, for example *Trichiurus lepturus*, which has been shown to occur only at over 11°C bottom temperatures (Martins & Haimovici 1997).

Longhurst & Pauly (1987) and Lowe-McConnell (1987) analysed the distribution of the demersal fish fauna from tropical to subtropical regions in the

Table II. Proportion of biomass (kg/h) of the more abundant species of the different assemblages.

	Assemblages			
Species	Coastal	Warm shelf	Cold shelf	Upper slope
Macrodon ancylodon (adults)	29%	2%	–	–
Macrodon ancylodon (juveniles)	10%	<1%	–	–
Paralonchurus brasiliensis	23%	1%	–	–
Micropogonias furnieri (adults)	15%	10%	<1%	–
Micropogonias furnieri (juveniles)	1%	<1%	–	–
Trichiurus lepturus (adults)	7%	10%	<1%	9%
Trichiurus lepturus (juveniles)	1%	4%	–	<1%
Cynoscion guatucupa (adults)	<1%	7%	22%	3%
Cynoscion guatucupa (juveniles)	<1%	33%	20%	6%
Umbrina canosai (adults)	<1%	7%	15%	<1%
Umbrina canosai (juveniles)	<1%	6%	9%	11%
Merluccius hubbsi (adults)	–	<1%	23%	3%
Merluccius hubbsi (juveniles)	–	<1%	2%	3%
Others	12%	18%	8%	64%

Western and Eastern Atlantic. They found that communities from different environments are dominated by different groups, such as sciaenids, sparids, gadiforms and deep-water fishes. The shelf of southern Brazil, influenced alternately by tropical and temperate water masses over the bottom, fits this pattern to a certain extent. The main differences between the assemblage composition may be attributed to the vertical distribution of water masses. In the Western Atlantic, the shelf water column is generally well mixed and more influenced by river discharge, making the waters relatively less saline and favouring the dominance of sciaenids. In the Eastern Atlantic the water column is stratified, allowing the dominance of colder water masses over the bottom, favouring the dominance of sparids and gadiforms.

Communities of sciaenids are present in tropical to warm and temperate environments over sandy and muddy bottoms in brackish, estuarine and low-salinity coastal regions, as seen in the eastern Atlantic (Bianchi 1992a, 1992b), tropical western Atlantic (Lowe-McConnell 1962), warm subtropical Atlantic (Rocha & Rossi-Wongtschowski 1998) and estuarine and coastal waters in the temperate Atlantic (Prenski & Sanchez 1986; Jaureguizar et al. 2006). The subtropical low-salinity and relatively turbid waters over the shelf of southern Brazil, which is mostly covered by sand and mud and influenced by the runoff from La Plata River and Patos Lagoon, is especially suitable for sciaenids. The Sciaenidae was the most species-rich and abundant family in the present study and species or size ranges of the most abundant species were indicators or characteristic of different assemblages.

By comparison with the Eastern Atlantic, the sparid community in southern Brazil is reduced both in diversity and abundance. The only relatively abundant species is *Pagrus pagrus* (Linnaeus, 1758), which occurs on the edge of the shelf on old corals and other hard bottoms (Haimovici et al. 2004). Before overfishing in the 1970s, it also occurred on the inner shelf on biodetritic banks and patches of rubble on the shelf (Haimovici et al. 1989).

Gadiforms are important on the wide Argentinean and Uruguayan shelf and upper slope at depths down to 50 m (Prenski & Sanchez 1986). In the present study, gadiforms were mainly represented by *Urophycis brasiliensis* on the inner shelf, *Merluccius hubbsi* on the outer shelf and upper slope, and *Genypterus brasiliensis* Regan, 1903 and *Urophycis mystacea* on the upper slope. This distribution in deeper waters may be explained by the relatively warmer waters in southern Brazil in comparison with other southern areas.

The deep-water community contained several species with a wide distribution in both the eastern and western Atlantic (Roel 1987; Bianchi 1992a, 1992b; Haimovici et al. 1994). This pattern may be explained by their evolutionary stability, which has allowed them to disperse in similar habitats across the entire South Atlantic basin (Briggs 1974).

Although demersal nekton consists of species with certain habits and dependence on benthic environments (Walrond 2012), the present study reveals a hitherto undocumented pattern of seasonal mesoscale shifts of entire groups of nektonic species that live near or on the sea floor. These shifts may be described by three different processes: (1) the progress of the cold shelf assemblage at intermediate depth of the shelf at scales of hundreds of kilometres can be associated with the cold season and the northward displacement of the Shelf Subtropical Front (Moller et al. 2008); (2) the southward expansion and distribution of the coastal and warm shelf assemblages in the warm season; and (3) the coastward influence of the upper-slope assemblage on the shelf during spring and summer is caused by the intrusion of the South Atlantic Central Water over the shelf break (Garcia & Garcia 2008).

There are several abundant and ubiquitous species such as the sciaenids *Micropogonias furnieri*, *Umbrina canosai* and *Cynoscion guatucupa*, and the trichiurid *T. lepturus* in this area. They can be considered 'resident' or structural components of the demersal shelf nektonic fauna of Southern Brazil (*sensu* Castello et al. 1997). However, some of these species, e.g. *M. furnieri*, as juveniles are important components of the coastal assemblage and the adults are characteristic of the warm shelf assemblage.

The shifts of entire assemblages in Southern Brazil may occur as a consequence of feeding dispersions as the optimal temperature conditions expand to a larger area. Alternatively, this process can be amplified by seasonal reproductive migrations of important species (Haimovici et al. 1989; Haimovici & Umpierre 1996; Martins & Haimovici 1997).

Seasonal shifts of individual fish populations and of the assemblages represent a challenge for the creation and maintenance of marine protected areas in soft-bottom shelf areas in which oceanographic processes strongly influence the marine nekton. In these regions, the potential impact of fishery on biodiversity may be underestimated, since part of the fauna often occupies larger areas than predicted (Palumbi 2004). For fisheries management, the identification of the assemblages and their seasonal displacement may be helpful to evaluate the impact of single species seasonal or spatial closures on the whole nektonic fauna. For example, in Southern Brazil, fishing on the warm shelf assemblage in summer results in large catches of juveniles of the most important target species for the demersal local fishery.

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References

Bianchi G. 1992a. Demersal assemblages of the continental shelf and upper slope off Angola. Marine Ecology Progress Series 81:101–20. doi:10.3354/meps081101

Bianchi G. 1992b. Study of the demersal assemblages of the continental shelf and upper slope off Congo and Gabon, based on the trawl surveys of the RV 'Dr Fridtjof Nansen'. Marine Ecology Progress Series 85:9–23. doi:10.3354/meps085009

Briggs JC. 1974. Marine Zoogeography. New York: McGraw-Hill. 480 pages.

Castello JP, Haimovici M, Odebrecht C, Vooren CM. 1997. Relationships and function of coastal and marine environments: the continental shelf and slope. In: Seeliger U, Odebrecht C, Castello JP, editors. Subtropical Convergence Environments: The Coast and Sea in the Southwestern Atlantic. Berlin: Springer, p 171–78.

Castro BM, Miranda LB. 1998. Physical oceanography of the western Atlantic Continental shelf located between 4°N and 34°S, coastal segment (4°W). The Sea 11:209–51.

Daan N, Gislason H, Pope JG, Rice JC. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? ICES Journal of Marine Science 62:177–88. doi:10.1016/j.icesjms.2004.08.020

Dufrene M, Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345–66.

Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR. 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. Journal of Applied Ecology 45:1029–39. doi:10.1111/j.1365-2664.2008.01488.x

Garcia AM, Vieira JP, Winemiller KO, Grimm AM. 2004. Comparison of the 1982–1983 and 1997–1998 El Niño effects on the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil). Estuaries 27:905–14. doi:10.1007/BF02803417

Garcia CAE, Garcia VMT. 2008. Variability of chlorophyll-*a* from ocean color images in the La Plata continental shelf region. Continental Shelf Research 28:1568–78. doi:10.1016/j.csr.2007.08.010

Haimovici M. 1998. Present state and perspectives for the southern Brazil shelf demersal fisheries. Fisheries Management and Ecology 5(4):277–89. doi:10.1046/j.1365-2400.1998.540277.x

Haimovici M, Cousin JCB. 1989. Reproductive biology of the castanha *Umbrina canosai* (Pisces, Sciaenidae) in Southern Brazil. Revista Brasileira de Biologia 49(2):523–37.

Haimovici M, Umpierre RG. 1996. Variaciones estacionales en la estructura poblacional y cambios de crecimiento de la corvina *Micropogonias furnieri* (Desmarest, 1823) en el extremo sur de Brasil. Atlântica 18:179–202.

Haimovici M, Pereira SD, Vieira PC. 1989. La pesca demersal en el sur de Brasil en el período 1975–1985. Frente Maritimo 5:151–63.

Haimovici M, Martins AS, Teixeira RL. 1993. Distribuición, alimentación y observaciones sobre la reproducción de la merluza *Merluccius hubbsi* en el sur de Brasil. Frente Maritimo 14:81–86.

Haimovici M, Martins AS, Figueiredo JL, Vieira PC. 1994. Demersal bony fish of the outer shelf and upper slope of the southern Brazil Subtropical Convergence Ecosystem. Marine Ecology Progress Series 108:59–77. doi:10.3354/meps108059

Haimovici M, Martins AS, Vieira PC. 1996. Distribuição e abundância de teleósteos demersais sobre a plataforma continental do sul do Brasil. Revista Brasileira de Biologia 56(1):27–50.

Haimovici M, Rossi-Wongtschonski CLDB, Cergole MC, Madureira LS, Bernardes RA, Ávila-da-Silva AO. 2006. Recursos pesqueiros da região Sudeste-Sul. In: Ministério do Meio Ambiente (MMA), Secretaria de Qualidade Ambiental, Brasil. Programa REVIZEE: Avaliação do Potencial Sustentável de Recursos Vivos na Zona Econômica Exclusiva: Relatório Executivo. Brasília: MMA, p 207–42.

Hill MO, Gauch Jr HG. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47–58. doi:10.1007/BF00048870

Jaureguizar AJ, Menni R, Lasta C, Guerrero R. 2006. Fish assemblages of the northern Argentine coastal system: spatial patterns and their temporal variations. Fisheries Oceanography 15(4):326–44. doi:10.1111/j.1365-2419.2006.00405.x

Juras AA, Yamaguti N. 1989. Sexual maturity and fecundity of the king weakfish *Macrodon ancylodon* (Bloch and Schneider, l801) caught in the southern coast of Brazil (Lat 29° S-32° S). Boletim do Instituto Oceanográfico de São Paulo 33(2):149–57.

Longhurst AR, Pauly D. 1987. Ecology of Tropical Oceans. New York: Academic Press. 407 pages.

Lowe-McConnell RH. 1962. The fishes of the British Guiana continental shelf, Atlantic coast of South America, with notes on their natural history. Zoological Journal of the Linnean Society 44(301):669–700. doi:10.1111/j.1096-3642.1962.tb01964.x

Lowe-McConnell RH. 1987. Ecological Studies in Tropical Fish Communities. Cambridge: Cambridge University Press. 400 pages.

Martins AS, Haimovici M. 1997. Distribution, abundance and biological interactions of the cutlassfish *Trichiurus lepturus* in the southern Brazil subtropical convergence ecosystem. Fisheries Research 30:217–27. doi:10.1016/S0165-7836(96)00566-8

Martins AS, Haimovici M. 2000. Reproduction of the cutlassfish *Trichiurus lepturus* in the southern Brazil subtropical convergence ecosystem. Scientia Marina 64:97–105. doi:10.3989/scimar.2000.64n197

Martins LR, Villwock JA, Martins IR. 1972. Estudo preliminar da distribuição faciológica da plataforma continental brasileira. Pesquisas (Porto Alegre) 1:51–56.

McCune B, Mefford MJ. 1999. PC-ORD. Multivariate Analysis of Ecological Data. Version 4.41. Gleneden Beach, OR: MjM Software. Computer program.

Menezes NA, Buckup PA, Figueiredo JL, Moura RL. 2003. Catálogo de Peixes Marinhos do Brasil. São Paulo: Museu de Zoologia da USP. 160 pages.

Möller Jr OO, Piola J, Freitas A, Campos E. 2008. The effects of river discharge and seasonal winds on the shelf off southeastern South America. Continental Shelf Research 28 (13):1607–24. doi:10.1016/j.csr.2008.03.012

Moranta J, Stefanescu C, Massutí E, Morales-Nin B, Lloris D. 1998. Fish community structure and depth-related trends on the continental slope of the Balearic Islands (Algerian basin, western Mediterranean). Marine Ecology Progress Series 171:247–59. doi:10.3354/meps171247

Palumbi SR. 2004. Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. Annual Review of Environmental Resources 29:31–68. doi:10.1146/annurev.energy.29.062403.102254

Perez JAA, Pezzuto PR, Wahrlich R, Soares ALS. 2009. Deepwater fisheries in Brazil: history, status, and perspectives. Latin American Journal of Aquatic Research 37:513–41. doi:10.3856/vol37-issue3-fulltext-18

Peterson RG, Stramma L. 1991. Upper-level circulation in the South Atlantic Ocean. Progress in Oceanography 26:1–73. doi:10.1016/0079-6611(91)90006-8

Pianka ER. 1974. Evolutionary Ecology. New York: Harper and Row. 512 pages.

Piola AR, Campos EJD, Möller Jr OO, Charo M, Martinez C. 2000. Subtropical shelf front off eastern South America. Journal of Geophysical Research: Oceans 105(3):6565–78. doi:10.1029/1999JC000300

Prenski B, Sanchez F. 1986. Estudio preliminar sobre asociaciones ícticas en la zona común de pesca argentino-uruguaya. Frente Maritimo 4:75–88.

Rocha GRA, Rossi-Wongtschowski CLDB. 1998. Demersal fish community on the inner shelf of Ubatuba, southeastern Brazil. Revista Brasileira de Oceanografia 46(2):93–109. doi:10.1590/S1413-77391998000200001

Roel BA. 1987. Demersal communities off the west coast of South Africa. In: Paine AIL, Gulland JA, Brink KH, editors. The Benguela and Comparable Ecosystems. South African Journal of Marine Science 5:575–84.

Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, et al. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology & Evolution 20(2):74–80. doi:10.1016/j.tree.2004.11.007

Southward AJ, Langmead O, Hardman-Mountford NJ, Aiken J, Boalch GT, Dando PR, et al. 2004. Long-term oceanographic and ecological research in the western English Channel. Advances in Marine Biology 47:1–105. doi:10.1016/S0065-2881(04)47001-1

Vazzoler G. 1975. Distribuição da fauna de peixes demersais e ecologia dos Sciaenidae da plataforma continental brasileira, entre as latitudes 29°21′S (Tôrres) e 34°44′S (Chuí). Boletim do Instituto Oceanográfico de São Paulo 24:85–169. doi:10.1590/S0373-55241975000100006

Vieira PC, Haimovici M. 1997. Reprodução da pescada olhuda *Cynoscion guatucupa*, sin. *C. striatus* (Sciaenidae, Teleostei) no sul do Brasil. Atlântica 19:133–44.

Walrond C. 2012. Coastal fish – fish of the open sea floor. Te Ara – The Encyclopedia of New Zealand. http://www.TeAra.govt.nz/en/coastal-fish/page-5 (accessed 16 February 2015).

Ward Jr JH. 1963. Hierarchical grouping to optimize an objective function. Journal of the American Statistical Association 58:236–44. doi:10.1080/01621459.1963.10500845

Woodroffe R, Ginsberg JR. 1998. Edge effects and the extinction of populations inside protected areas. Science 280:2126–28. doi:10.1126/science.280.5372.2126

Zwanenburg KCT. 2000. The effects of fishing on demersal fish communities of the Scotian Shelf. ICES Journal of Marine Science 57:503–09. doi:10.1006/jmsc.2000.0744