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Biological, physical and chemical properties at the Subtropical Shelf Front Zone in the SW Atlantic Continental Shelf

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ABSTRACT

The physical aspects of the Subtropical Shelf Front (STSF) for the Southwest Atlantic Continental Shelf were previously described. However, only scarce data on the biology of the front is available in the literature. The main goal of this paper is to describe the physical, chemical and biological properties of the STSF found in winter 2003 and summer 2004. A cross-section was established at the historically determined location of the STSF. Nine stations were sampled in winter and seven in summer. Each section included a series of conductivity-temperature-depth (CTD) stations where water samples from selected depths were filtered for nutrient determination. Surface samples were taken for chlorophyll a (Chl-a) determination and plankton net tows carried out above and below the pycnocline. Results revealed that winter was marked by an inner-shelf salinity front and that the STSF was located on the mid-shelf. The low salinity waters in the inner-shelf indicated a strong influence of freshwater, with high silicate (72 μ M), suspended matter (45 mg l⁻¹), phosphate (2.70 μ M) and low nitrate (1.0 μ M) levels. Total dissolved nitrogen was relatively high (22.98 µM), probably due to the elevated levels of organic compound contribution close to the continental margin. Surface Chl-a concentration decreased from coastal well-mixed waters, where values up to 8.0 mg m^{-3} were registered, to offshore waters. Towards the open ocean, high subsurface nutrients values were observed, probably associated to South Atlantic Central Waters (SACW). Zooplankton and ichthyoplankton abundance followed the same trend; three different groups associated to the inner-, mid- and outer-shelf region were identified. During summer, diluted waters extended over the shelf to join the STSF in the upper layer; the concentration of inorganic nutrients decreased in shallow waters; however, high values were observed between 40 and 60 m and in deep offshore waters. Surface Chl-a ranged 0.07–1.5 mg m⁻³; winter levels were higher. Three groups of zoo and ichthyoplankton, separated by the STSF, were also identified. Results of the study performed suggest that the influence of freshwater was stronger during winter and that abundance distribution of Chl-a, copepods and ichthyoplankton was related to the Plata Plume Waters (PPW), rather than to the presence of the STSF. During summer, when the presence of freshwater decreases, plankton interactions seem to take place in the STSF.

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1. Introduction

Fronts are a clear example of the complicated biophysical interaction processes that occur in the ocean (Owen, 1981; Le Fèvre, 1986). The understanding of those processes constitutes an

* Corresponding author. E-mail address: docjhm@furg.br (J.H. Muelbert). important challenge since both, demersal and pelagic fisheries involve frontal systems (Olson, 2002).

As regards pelagic environments, discernment of water masses distribution, currents, upwellings and fronts is essential to interprete plankton distribution patterns (Boltovskoy, 1999). In the Southwest Atlantic, in particular, the abundant marine fronts cover different space and time scales (Acha et al., 2004). It is agreed that abundance of phytoplankton biomass and enhanced activity at high trophic levels are features distinctive to fronts

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(Le Fèvre, 1986; Largier, 1993; Mann and Lazier, 1996). Winds, tides, freshwater discharges and oceanic currents are the forcing factors that influence distribution and production patterns in those systems (Acha et al., 2004).

Albardão, in the South Brazilian coast, is a region of extreme importance to local fisheries (Haimovici, 1997; Castello et al., 1997a). The area is enriched by the contribution of the Río de la Plata river runoff and, to a lesser extent, by the Patos/Mirim Lagoons Complex. As described by Piola et al. (2008), the Río de la Plata river discharges approximately $23,000 \, \text{m}^3 \, \text{s}^{-1}$ of freshwater into the western South Atlantic thus inducing a large scale buoyant plume that extends beyond 1000 km from the estuary in winter and spreads along the coasts of Argentina, Uruguay and Brazil; lateral mixing with other water masses forms the so-called Coastal Waters (CW) (Möller et al., 2008) or Plata Plume Waters (PPW) (Piola et al., 2008). Interaction with Subantarctic Shelf Waters (SASW) transported by the Patagonian current and with Tropical and Subtropical (Central) Waters (STCW) from the Brazil current influence nutrients concentration (Fillmann, 1990; Ciotti et al., 1995) and biological productivity (Teixeira et al., 1973; Ciotti et al., 1995). As a result, mean annual primary production can reach up to $160 \text{ g C m}^{-2} \text{ year}^{-1}$ (Castello et al., 1997b). The PPW fertilizes the southern Brazilian shelf area making of it one of the most important fisheries zones of Brazil (Castello et al., 1990). The influence of the PPW varies along the year. In response to variations in the along-shore wind stress the plume presents large northeast penetrations and retractions along the continental shelf in late fall-winter and late spring-summer, respectively (Piola et al., 2005).

Piola et al. (2000) showed that in such a complex region extension of the Brazil/Malvinas confluence over the shelf defines a thermo-haline subsurface front, called the Subtropical Shelf Front (STSF), between Subtropical and Subantarctic Shelf Waters. The front is located near the 50 m isobath, at 32°S, and extends southwards towards the shelf-break close to 36°S. The front, covered by a low salinity surface layer generated by the discharge of the Río de la Plata river and the Patos Lagoon is not evident on the surface. Its biology and contribution to the productivity of the region is still poorly known; the information available shows that the copepods communities in the area present the highest species turnover (Berasategui et al., 2006). The seasonal plume variations in the area may induce a strong impact on the shelf ecosystem (Ciotti et al., 1995; Castello et al., 1990; Muelbert and Sinque, 1996; Sunyé and Servain, 1998). The importance of the STSF on the biology of the region deserves further research.

In the Austral winter 2003 and summer 2004 two multidisciplinary surveys of the continental shelf and slope between Mar del Plata, Argentina (38°S) and Itajaí, Brazil (26°S) were conducted (see Piola et al., 2008). The fieldwork design included two transects in the Albardão region, one during a large runoff penetration of the PPW (winter) and another in a plume retraction (summer). The aim of this paper was to characterize the oceanography of the STSF and the chemical and biological properties during said conditions.

2. Materials and methods

The NICOP-La Plata cruises were carried out on board of R/V *A.R.A Puerto Deseado*, between 20 August and 2 September 2003, and R/V *N.Oc. Antares*, between 1 and 19 February 2004. Two cross-shelf sections in the SW Atlantic Continental shelf were performed during winter 2003 and summer 2004 (Fig. 1). In each section, a Sea Bird Electronics model 911 Plus CTD fitted with a turbidity sensor was used. For additional description on the sampling strategy refer to Piola et al. (2008).

Water samples were collected to determine dissolved oxygen, nutrients, chlorophyll a (Chl-a) and suspended particulate matter (SPM) levels. A General Oceanics 1015 (winter) and SBE 23 (summer) rossette, both with 51 Niskin bottles were used. As described in Grasshoff et al. (1983), dissolved oxygen was determined using the Winkler method with a Mettler DL 21 automatic titrator. Nutrients samples were filtered with a Whatman GF/F membrane and stored in polyethylene bottles, prewashed with HCl 1:1, rinsed with distilled water, then with filtrated water sample and frozen for further analysis. Filters were stored at -20 °C in the dark for posterior analysis of suspended material. Following the recommendation in Grasshoff et al. (1983), nitrate was determined using an AutoAnalyzer II-Bran-Luebbe[®] and silicate and phosphate with a Genesys spectrophotometer-Bauch&Lomb®. As described by Strickland and Parsons (1968), SPM and suspended organic matter (SOM) were analyzed gravimetrically.

Biological sampling included collection of zooplankton and Chl-*a* on the surface and at selected depths. Seawater was filtered onto GF/F filters kept frozen at -20 °C until laboratory analysis. In the laboratory, filters were left for 24 h in the freezer in a 90% acetone solution to extract pigments. The Chl-*a* concentration was measured in a fluorometer (Turner Designs TD-700) using the non-acidification technique (Welschmeyer, 1994). The fluorometer was previously calibrated with a Sigma[®] Chl-*a* standard.

A Motoda net 60 cm mouth diameter and $300\,\mu$ m mesh size mounted on a closing mechanism structure was used to study zooplankton distribution (see Wiebe and Benfield, 2003 for description). The net was equipped with a digital flowmeter. Tows were horizontal and lasted 10 min; samples were taken below and above the halocline.

Copepods were selected as one of the target groups because they are among the most numerous multicelled organisms on Earth (Mauchline, 1998) that consume large amounts of microplankton; in turn, they are eaten by fish and other predators thereby transferring energy and carbon to higher trophic levels (Runge, 1988; Howlett, 1998); they represent one of the keystone trophic links in aquatic ecosystems (Turner et al., 1984). The Copepoda class is well represented in terms of species richness in all aquatic environments and, in the study region, it is one of the richest and taxonomically best-known groups (Bradford-Grieve et al., 1999). Copepods were identified under a compound microscope to the lowest possible taxonomic level following descriptions by Ramírez (1966a, b, 1969), Björnberg (1981) and Bradford-Grieve et al. (1999).

Ichthyoplankton was studied to identify the importance of the front in fishes early life history (spawning and/or nursery grounds). Fish larvae were identified under a compound microscope to the lowest possible taxonomic level following the descriptions by Weiss (1981), Fahay (1983) and Richards (2005). Due to uncertainties in specific identifications, only *Engraulis anchoita* and *Trichiurus lepturus* eggs were identified; the remaining fish eggs were analyzed as a single group.

2.1. Data analysis

Copepods and ichthyoplankton communities distribution patterns were investigated using a combination of clustering and ordination analysis to check adequacy and mutual consistency of both representations (Clarke and Warwick, 2001). Bray–Curtis similarities (Bray and Curtis, 1957) were calculated and stations classified into assemblages using groups average similarities. Raw data (individuals m^{-3} for copepods and individuals $100 m^{-3}$ for ichthyoplankton) were transformed using the $\log_{10}(x+1)$ function to allow the less abundant species to exert



Fig. 1. Distribution of stations along the two transects occupied during winter 2003 and summer 2004 in the SW Atlantic Continental Shelf (isobath in meters).

some influence on similarities calculation (Clarke and Warwick, 1994). A samples ordination analysis with multi-dimensional scaling (MDS) (Clarke and Warwick, 2001) was also performed to display the biological relations among stations. The analysis was performed to study seasonal changes in the communities composition; then separately for winter and summer as a complimentary method to the cluster analysis.

3. Results

3.1. Austral winter

3.1.1. Hydrography

Properties distribution across the shelf off Albardão showed a thermal and a salinity front. The thermal one was the STSF located in the outer-shelf between stations 44 and 43, at water depths ranging 60–90 m (Fig. 2a and b). The STSF separated the inner-shelf Subantarctic Shelf Waters (SASW; cool-low salinity waters) present only at station 44 from the outer Subtropical Shelf Waters

(STSW) (warm-high salinity waters) identified at station 43 and the upper layer of station 42. Further offshore Tropical Waters (TW) were present at the subsurface of stations 41 and 40. Temperature (Fig. 2a) across the 100 km inner-shelf band was totally homogeneous in the range of 1 °C. The salinity front was observed at station 46 and separated the inner PPW from the outer SASW. The density section indicated weakening of stratification in offshore direction and density compensation on the T and S gradients across the STSF (Fig. 2c).

3.1.2. The nutrient field

The highest concentrations of organic and suspended matter were associated to the PPW (station 46) (Fig. 2e and f). In subsurface an important phosphate $(2.70 \,\mu\text{M})$ (Fig. 2j) and remarkably high silicate $(50 \,\mu\text{M})$ concentrations were found (Fig. 2k); nitrate was markedly low ($\sim 1 \,\mu\text{M}$) (Fig. 2i). Bottom waters closest to the coast revealed high values of organic $(18.0 \,\text{mg} \,\text{l}^{-1})$ and suspended matter (44.80 mg l⁻¹) (Fig. 2e and f) associated to high turbidity levels (Fig. 2d) and relatively high



Fig. 2. Winter 2003 the onshore–offshore transect in the SW Atlantic Continental Shelf. Vertical distribution of temperature (a), salinity (b), potential density (c), turbidity (d), suspended organic matter (e), suspended particulate matter (f), dissolved oxygen (g), surface Chl-*a* (h), nitrate (i), phosphate (j), silicate (k), copepods abundance (l), copepod assemblages (m), fish larvae abundance (n) fish larvae assemblages (o) and fish eggs abundance (p). Dash and solid lines on figures (l–p) are salinity and temperature isolines at the front and the thermocline, respectively.

phosphate (0.96 μ M) (Fig. 2j). With distance from the coast, an important reduction of terrestrial input was observed. The high values of nutrients present in deep waters could be linked to the influence of the SACW. At station 42 phosphate reached 1.4 μ M and nitrate 25 μ M at 60 m depth (Fig. 2i and j); no silicate concentration enhancement was seen; the values measured hovered 5 μ M (Fig. 2k).

SPM was high throughout the water column (Fig. 2f), particularly at stations near the coast. As a result of the intense interaction between sediments and the turbulent shelf waters, a maximum of organic and inorganic matter in shallow areas was found. The contribution of de Río de la Plata river discharge to silicate enrichment was proved by the high levels observed in low salinity PPW (Fig. 2k). The low salinity values (<31) were

Table 1

Copepods identified in the winter and summer cruises (in bold characters species common to both seasons)

Copepods	Winter			Summer		
	Inshore	Frontal	Offshore	Inshore	Frontal	Offshore
Acartia negligens						
Acartia tonsa						
Calocalanus pavo						
Centropages brachiatus						
Ctenocalanus citer						
Diaixis helenae						
Drepanopus forcipatus						
Eucalanus hyalinus						
Subeucalanus pileatus						
Eucalanus sewelli						
Euchirella amoens						
Euterpina acutifrons						
Labidocera fluviatilis						
Miracia efferata						
Neocalanus robustior						
Oithona sp. (1)						
Oithona sp. (2)						
Paracalanus parvus						
Rhincalanus nasutus						
Scolecithrix danae						
Calanoides carinatus						
Mecynocera clausi						
Nanocalanus minor						
Sapphirina angusta						
Subeucalanus pileatus						
Centropages furcatus						
Centropages velificatus						
Clausocalanus parapergens						
Corycaeus sp.						
Corycaeus (Corycaeus) speciosus						
Ctenocalanus vanus						
Euchaeta marina						
Gaetanus tenuispinus						
Labidocera acutifrons						
Oithona atlantica						
Oithona plumifera						
Oithona similis						
Oncaea sp.						
Sapphirina ovatolanceolata-gamma						
Iemora stylifera						
Unainula vulgaris	10	0	21	10	12	15
number of species	10	8	21	10	12	15

associated to low temperature ($\sim 11 \,^{\circ}$ C) and confirmed the important input from terrestrial sources and the displacement of waters over the inner-shelf. Dissolved oxygen values, relatively high (>6.00 ml l⁻¹), increased towards the coast, situation probably linked to an increase of biological production as shown by the high Chl-*a* concentration found near the coast (Fig. 2h).

3.1.3. Surface chlorophyll a and turbidity

Concentration of surface Chl-*a* decreased steadily from high in the coast (8 mg m^{-3}) to 0.43 mg m⁻³ in offshore waters (Fig. 2h). The N:P ratio that ranged, in general, <2.5 and close to 1 near the coast indicated a reduction of nitrogen for phytoplankton of surface waters along the transect. The slight increase of Chl-*a* observed at station 42 was associated to the high levels of subsurface nutrients found (Fig. 2i and j). In the mid-shelf the decrease in Chl-*a* concentration matched with a simultaneous change in salinity and turbidity (stations 45 and 44). At the offshore stations (43 and 40) the slight changes in Chl-*a* were associated to the thermohaline properties rather than to optical ones.

3.1.4. Copepod assemblages and abundance

Twenty-five copepod species were identified (Table 1). Density decreased from coastal to offshore waters (Fig. 2l), with 560 ind. m^{-3} and a peak at the bottom of station 45 (1730 ind. m^{-3}). The highest density observed in the inshore stations (46 and 44) corresponded to the coastal salinity front described above (Fig. 2b and 2l). Eastward of the STSF abundance drop coincided with the presence of subtropical and tropical water masses. The most abundant copepod species was *Ctenocalanus citer* (40–1180 ind. m^{-3}) followed by *Calanoides carinatus* (1.4–530 ind. m^{-3}).

Using the cluster analysis three assemblages were determined at the 50% similarity level. The spatial distribution of the groups allowed to recognize inshore, frontal and offshore groups (Figs. 2m and 3C). The inshore one corresponded to stations where the highest abundance was observed and that coincided with the PPW. The frontal assemblage was related to the STSF and the offshore group was present in the warmest STSW.

The inshore group (average similarity 77%, SIMPER analysis) and the frontal one (average similarity 71%) clustered stations characterized by *C. citer* and *C. carinatus*. The offshore group (average similarity 68%) was typified by *C. citer*, *Paracalanus parvus*



Fig. 3. MDS stations ordination-using data of numerical density. (A) winter versus summer for copepods, (B) winter versus summer for fish larvae, (C) copepods winter, (D) fish larvae winter, (E) copepods summer and (F) fish larvae summer.

and *Mecynocera clausi* (Table 3) that were also the main discriminating species among groups. The offshore stations presented higher abundance of *P. parvus* and *M. clausi* than the inshore and frontal groups (Table 3).

3.1.5. Ichthyoplankton

Fish larvae were classified into 19 species or taxonomic categories (Table 2). Mean abundance was 260 ind. m^{-3} with a peak at the bottom of station 45 (1603 ind. $100 m^{-3}$) located between the plume front and the STSF (Fig. 2n). A high level was also observed on the surface of station 44 (515 ind. $100 m^{-3}$) located in the STSF (Fig. 2n). The most abundant fish larva was *E. anchoita* with density ranging 10–1600 ind. $100 m^{-3}$, followed by *Merluccius hubbsi* (1–13 ind. $100 m^{-3}$). Species of the offshore assemblage showed lower density; *Symbolophorus* sp. and *Gonostoma atlanticum* that reached 9 and 10 ind. $100 m^{-3}$ were the most abundant. Mean fish eggs density was 250 ind. m^{-3} . A peak of 1180 ind. m^{-3} , associated to the coastal salinity front, was recorded at the coastal stations (Fig. 2b and p). Most of them (*ca.* 98%) were identified as *E. anchoita*.

Using the cluster analysis three assemblages were determined at the 50% similarity level. The spatial distribution of the groups showed an inshore-frontal assemblage and an offshore group (Fig. 2o). The former occupied most of the section, from the innermost station to the offshore boundary of the STSF. The latter was located farther east (Fig. 2o). The MDS analysis (Fig. 3D) revealed that the offshore group was less coherent than the inshore–frontal one (average similarity 62%, SIMPER analysis), characterized by higher density of *E. anchoita* and *M. hubbsi*. The offshore group (average similarity 37%) showed a heterogeneous composition; Myctophidae and *G. atlanticum* were the discriminating species (Table 3).

3.2. Austral summer

3.2.1. Hydrography

During summer, the temperature structure was characterized by a strong thermocline (Fig. 4a). Coastal Waters were slightly fresher (S < 34) than waters offshore (Fig. 4b); density showed stratification determined mainly by temperature (Fig. 4c). A weak coastal front, defined by salinity, was observed between stations 49 and 50 (50 km off the coast). A strong salinity front was located farther offshore, between stations 51 and 52. The SASW was present only at station 50 with salinity ranging 33.4–33.7 where a weak subsurface TW intrusion was observed. The STSW occupied the upper layer of stations 51 and 52 that showed, also, subsurface

Table 2

Fish larvae clusters identified in winter and summer (in bold characters Engraulis anchoita, the only species common to both seasons)

Fish larvae	Winter		Summer	Summer		
	Inshore-frontal	Offshore	Inshore	Frontal	Offshore	
Ceratoscopelus sp.						
Coryphoenoides sp.						
Gonostoma atlanticum						
Helicolenus dactylopterus						
Hygophum reinhardtii						
Lampadena sp.						
Lampanyctinae						
Lampanycius Mortuogius hubboi						
Macrouridae						
Maurolicus stahmanni						
Melanostomiatidae						
Myctophidae						
NN1						
Notoscopelus resplendens						
Paralepedidae						
Symbolophorus sp.						
Urophycis mystaceus						
Engraulis anchoita						
Auxis sp.						
Balistes sp.						
Benthosema sp.						
Bregmaceros atlanticus						
Citharichthys a						
Citharichthys b						
Cynoscion sp.						
Etropus sp.						
Gobiidae						
Leptocephalus larvae						
Trichiurus lepturus						
Micropogonias jurnieri						
INNO Ophictus gamasi						
Pomatomus saltatriy						
Paralonchurus brasiliensis						
Penrilus paru						
Pleuronectiforms						
Scorpaenidae						
Symphurus sp.						
Synodus sp.						
Number of taxons	7	16	18	12	3	

TW intrusion although deeper and stronger than that at station 50. The bottom layer of the three stations defined a 70 km wide per 20 m deep core of SASW-STSW mixture (Piola et al., 2008) that flows, probably, along the Pozo de Fango (a Río de la Plata river paleochannel 60–70 m deep) located 80 km from the coast that overflows eastward to the shelf-break (Fig. 4b).

3.2.2. The nutrient field

The organic matter was homogeneously distributed over the continental shelf with values that ranged from 7 to $8 \text{ mg} \text{ l}^{-1}$. Higher values were restricted to the surface offshore waters, with average values of $13 \text{ mg} \text{ l}^{-1}$ (Fig. 4e). The suspended matter showed a bimodal distribution that increased close to the shore $(24 \text{ mg} \text{ l}^{-1})$ and in offshore subsurface waters $(50 \text{ mg} \text{ l}^{-1})$ (Fig. 4f).

The concentration of inorganic nutrients in shallow waters was low. High values were observed only near the bottom. Nitrate and phosphate were high at station 51, with 4 and $0.6 \,\mu$ M, respectively (Fig. 4i and j). The high concentration of nitrate indicated a marine input of nutrients.

3.2.3. Surface chlorophyll a and turbidity

Surface Chl-*a* was in the range of $0.07-1.5 \text{ mg m}^{-3}$, values lower than in winter that were associated to the PPW close to the coast (Fig. 4h). Turbidity on the shelf, linked to an increased of SPM and organic suspended matter, was high only at coastal stations (Fig. 4d, f and e). An increase of SPM and organic matter was also observed on subsurface waters far from the coast.

3.2.4. Copepod assemblages and abundance

Twenty-one copepod species were identified (Table 1). Mean density was 370-7200 ind. m⁻³. The highest, found inshore and above the thermocline, decreased offshore (Fig. 41). The *Oncaea* spp. and *Clausocalanus parapergens* were the most abundant copepods with density ranging 2974 and 2812 ind. m⁻³, respectively.

Using the cluster analysis three assemblages were determined at the 50% similarity level. The spatial distribution showed the formation of inshore, frontal and offshore groups (Fig. 4m). The first assemblage occupied the water column of the innermost station and the bottom layer of station 51. The location of the

Table 3

SIMPER ("similarity percentages" analysis) results to compare the inshore, frontal and offshore groups defined in the multivariate analysis

Contribution to similarity (%)		Contribution to dissimilarity (%)				
		Inshore vs frontal	Inshore vs offshore	Frontal vs offshore		
Copepods winter Inshore group (average similarity 76.99%) Ctenocalanus citer Calanoides carinatus	43.41 38.41	16.04 24.64	14.15 23.61	9.81 17.46		
Frontal group (average similarity 71.01%)						
Ctenocalanus citer Calanoides carinatus Paracalanus parvus	57.79 30.67 7.32	16.04 24.64 11.71	14.15 23.61 9.44	9.81 17.46 17.97		
Offshore group (average similarity 67.89%) Ctenocalanus citer Paracalanus parvus Mecynocera clausi Oithona sp. (1)	33.90 20.09 14.12 10.03	16.04 11.71 -	14.15 9.44 8.64 7.95	9.81 17.97 14.29 10.62		
Copepods summer Inshore group (average similarity 72.33%) Ctenocalanus vanus Centropages furcatus Temora stylifera	20.80 19.75 19.28	14.23 7.07 -	13.57 13.01 8.00	- 8.76 8.71		
Frontal group (average similarity 62.60%) Clausocalanus parapergens Corycaeus sp. Temora stylifera	20.59 19.25 17.09	13.9 - -	12.96 - 8.00	- - 8.71		
Offshore group (average similarity 60.87%) Clausocalanus parapergens Corycaeus sp. Oithona atlantica	31.62 15.57 12.86	13.9 - -	12.96 _ _	- - 7.78		
Fish larvae winter Inshore–frontal group (average similarity 62.22%) Engraulis anchoita Merluccius hubbsi Offshore group (average similarity 36.65%) Myctophidae Gonostoma atlanticum Hygophum reinhardtii	80.28 18.09 34.29 30.74 16.34		Inshore–frontal vs offshore 21.17 8.73 9.84 12.37 6.70	2		
Fish larvae summer Inshore group (average similarity 41.47%) Engraulis anchoita Etropus sp. Trichiurus lepturus	44.82 24.18 22.00	12.08 9.12 11.05	20.28 12.7 11.65	7.29 - 7.49		
Frontal group (average similarity 15.72%) Balistes sp. Pleuronectiforms Bregmaceros atlanticus	32.35 25.53 25.53	4.66 7.91 9.15		11.57 12.27 14.75		
Offshore group (average similarity 43.29%) Synodus sp.	100.0	-	8.60	13.97		

Typical species (those contributing more than 90% to the average similarity for each group) and discriminating species (those contributing more than 90% to the average dissimilarity between groups) are listed.

frontal assemblage matched with the upper layer of the salinity front in stations 51 and 52. The offshore group was located in a region stratified both in temperature and salinity (station 53 and bottom layer of station 52; Fig. 4m). The MDS analysis (Fig. 3E) showed coherence with clustering and revealed that the bottom of station 52 occupied an intermediate position between the frontal and the offshore assemblages.

The inshore (average similarity 72%, SIMPER analysis), the frontal (average similarity 63%) and the offshore (average similarity 61%) groups were characterized by three species each (Table 3). The main discriminating species among groups were *C. parapergens, Ctenocalanus vanus* and *Centropages furcatus* (Table 3).

3.2.5. Ichthyoplankton

Fish larvae were classified into 24 species or taxonomic categories (Table 2). Mean abundance was 18 ind. 100 m^{-3} . The most abundant species density ranged 0.6–28.7 ind. 100 m^{-3} (*T. lepturus*) and 0.7–24.1 ind. 100 m^{-3} (*Bregmaceros atlanticus*). Abundance was equally distributed from coastal to offshore waters and above and below the thermocline (Fig. 4n). The highest density of fish eggs was recorded in the entire water column of the inshore station and above the thermocline of stations 51 and 52 (Fig. 4p). Mean abundance was 15 ind. 100 m^{-3} . A high proportion of eggs (*ca.* 41%) was identified as *T. lepturus*.

Using the cluster analysis three assemblages were determined at the 50% similarity level. The spatial distribution allowed to



Fig. 4. Summer 2004 onshore–offshore transect in the SW Atlantic Continental Shelf. Vertical distribution of temperature (a), salinity (b), potential density (c), turbidity (d), suspended organic matter (e), suspended particulate matter (f), dissolved oxygen (g), surface Chl-*a* (h), phosphate (i), nitrate (j), silicate (k), copepods abundance (l), copepod assemblages (m), fish larvae abundance (n) fish larvae assemblages (o) and fish eggs abundance (p). Dash and solid lines on figures (l–p) are salinity and temperature isolines at the front and the thermocline, respectively.

identify inshore, frontal and offshore groups (Fig. 40). The first assemblage occupied the entire water column of the innermost station and the upper layer of station 51; no clear relation with the water masses distribution was found. The location of the frontal assemblage matched with the salinity front at stations 51 and 52. The offshore group was located in a region stratified both in

temperature and salinity (station 53, Fig. 40). The MDS analysis (Fig. 3F) showed coherence with clustering and revealed that, due to the biological composition of the bottom at station 51, the frontal group was the weakest.

Fish larvae summer groups were heterogeneous in their composition. The inshore group (average similarity 42%) was

discriminated by *E. anchoita*, the frontal group (average similarity 16%) by *B. atlanticus* and the offshore one by *Synodus* sp. (Table 3).

4. Discussion

The region showed a high variability level in physical, chemical and biological properties at seasonal and spatial scales. During summer and winter the highest copepod abundance was found on the shelf, at depths below 60 m; the oceanic region showed very low abundance. Although the spatial pattern was similar in both seasons, the numerical density during summer was one order of magnitude higher than that of winter. Copepods, fish eggs and larvae showed the same spatial pattern and a different seasonal one. Abundance was higher close to the coast and reached its maximum in winter.

Seasonal changes in copepods communities were more evident than those of fish larvae (compare Fig. 3A and B). The number of species in each season was similar (25 in winter and 21 in summer); almost all the species found during winter were absent in summer; only five were common to both season (Table 3). In some cases replacement occurred in co-generic species such as C. vanus and C. citer, dominant in summer and winter, respectively. C. vanus corresponded to cold Coastal Waters of Argentina; C. citer was reported for coastal tropical upwellings (see Björnberg, 1981, p. 595). Labidocera acutifrons, an oceanic species that inhabits Brazilian warm waters was replaced by Labidocera fluviatilis, a neritic one typical of temperate-cold waters found only during winter. Abundance of species common to both seasons showed high differences. In the whole transect Subeucalanus pileatus, a thermophyle copepod from the Brazilian continental shelf was abundant in summer and scarce in winter. C. carinatus, a species linked to cold waters was more abundant in winter. The species is also abundant in eastern and western upwelling areas of the South Atlantic (Irigoien et al., 2005; Valentin, 1984; Valentin et al., 1987).

As regards fish larvae, *E. anchoita*, the only species common to both seasons, showed low abundance in summer. *M. hubbsi* is abundant in the uruguayan and argentinian continental shelf (Cousseau and Perrota, 1998). Its presence in Coastal Waters during winter is an indicator of the influence of waters of southern origin over the coast. The presence of the STSF in summer separated the inshore from the offshore group. Inshore waters were occupied by larvae from fish known to spawn in the coastal region, among which *Micropogonias furnieri* and other Sciaenidae (Sinque and Muelbert, 1997). The frontal group contained a mixture of larvae of coastal origin such as *T. lepturus* (Sinque and Muelbert, 1997) and fish of oceanic provenance such as *B. atlanticus* (Matsuura et al., 1993).

Results show an almost complete replacement of planktonic species during the annual cycle. Such biological variability seemed to be driven by the high dynamics of water masses in the region caused by the seasonal expansion and reversion of the PPW along the coastal zone. In fact, in winter, the low salinity plume was over 100 km wide, two well-defined coastal fronts were easily recognizable and no thermocline was present (Fig. 2a–c). On the contrary, during summer, the coastal front was very weak, the low salinity plume weak and reduced and a strong thermocline was present. The STSF, in turn, was marked and more intrusive toward the coast.

Chl-*a* measurements were similar to the values reported for the region in austral winter and summer (Teixeira et al., 1973; Hubold 1980a,b; Ciotti et al., 1995; Odebrecht and Garcia, 1997; Carreto et al., 2003). Chl-*a* showed the lowest values during summer when the PPW influence over the Brazilian shelf is lower. Carreto et al. (1986) indicated that in the Río de la Plata estuary there is excess of silicate and phosphate and that nitrate might control phytoplankton production. Besides the inorganic nutrients input, the Río de la Plata river outflow enriches the coastal system with dissolved organic material such as vitamins, hormones, humic and fulvic acids (Carreto et al., 1986) that stimulate phytoplankton growth and explains the high Chl-*a* values found close to the coast in winter, when the PPW influence is stronger.

In summer, Chl-*a* values were very low. Far from the coast, a high concentration of nitrate in deep waters was observed. However, the strong thermocline present might prevent availability of nutrients for photosynthesis on the surface. The very low Chl-*a* values might also be the result of copepods grazing. The extremely abundant species are mainly suspension feeders, and their prey include tintinids, ciliates, copepod nauplii and phytoplankton (see Bradford-Grieve et al., 1999).

The role of fronts in the marine environment has been largely discussed and it is now accepted that they are organism production and destruction areas (Olson, 2002). In the Southwest Atlantic, the extension of the continental shelf allows the development of different mesoscale fronts. Although comparatively small, fronts play an extremely valuable role in ecological processes thus allowing high primary production through nutrients pumping, offering feeding and/or reproductive habitats for fishes, squids and birds; they also act as retention areas for benthic species larvae and promote settlement of benthic invertebrates (Acha et al., 2004). The Santa Marta Grande cape upwelling, the Río de la Plata estuarine front, the Península de Valdés tidal front and the large shelf-break front in the Argentine Sea are some regional examples. In those systems, concentration of different planktonic groups (mysids, copepods, salps, ctenophores, medusae, fish eggs and larvae, etc.) were reported (Acha et al., 1999; Acha and Macchi, 2000; Alvarez Colombo et al., 2003; Berasategui et al., 2004, 2006; Ehrlich, 2000; Marrari et al., 2004; Mianzan and Guerrero, 2000; Mianzan et al., 2001a, b; Sabatini and Alvarez Colombo, 2001; Schiariti et al., 2006). The sampling strategy adopted brought about results that do not allow to demonstrate the role the STSF plays in zooplankton concentration. Chl-a distribution, copepods and icthyoplankton abundance seemed more related to the PPW than to the presence of the STSF. It must be considered here that the region in which the front is located is already enriched by the Río de la Plata river runoff (Ciotti et al., 1995; Castello et al., 1990; Muelbert and Singue, 1996; Sunyé and Servain, 1998). The effect of the STSF was evident when the plankton community structure was analyzed. Changes in the assemblages composition can be explained by the change in water properties on both sides of the STSF clearly seen in both seasons considered. The zooplankton assemblages pattern and abundance distribution were arranged in a horizontal plane in winter and vertical in summer, both following the physical structure of the water column.

Results allow to characterize the oceanography of the Albardão area in the Southwest Atlantic in winter and summer. The role of the STSF on the plankton biota shows a seasonal, minor difference if compared to the marked seasonal control of the PPW. The dynamic interplay of the different water masses creates a region with high nutrient input, primary production and copepod and ichthyoplankton abundance. The high biological production in the Albardão region constitutes the evidence of the processes that take place there and support the important fisheries activities in the area.

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References

- Acha, E.M., Macchi, G.J., 2000. Spawning of Brazilian menhaden, Brevoortia aurea, in the Río de la Plata estuary off Argentina and Uruguay. Fishery Bulletin 98 (2), 227–235.
- Acha, E.M., Mianzan, H.W., Lasta, C.A., Guerrero, R.A., 1999. Estuarine spawning of the whitemouth croaker *Micropogonias furnieri* in the Río de la Plata, Argentina. Marine Freshwater Research 50 (1), 57–65.
- Acha, M., Mianzan, H., Guerrero, R., Favero, M., Bava, J., 2004. Marine fronts at the continental shelves of austral South America. Physical and ecological processes. Journal of Marine Systems 44, 83–105.
- Alvarez Colombo, G., Mianzan, H., Madirolas, A., 2003. Acoustic characterization of gelatinous plankton aggregations: four study cases from the argentine continental shelf. ICES Journal of Marine Science 60, 650–657.
- Berasategui, A.D., Acha, E.M., Fernández Araoz, N.C., 2004. Spatial patterns of ichthyoplankton assemblages in the Rio de la Plata estuary (Argentina, Uruguay). Estuarine, Coastal and Shelf Science 60, 599–610.
- Berasategui, A., Menu Marque, S., Gomez Erache, M., Ramírez, F.C., Mianzan, H.W., Acha, E.M., 2006. Copepod assemblages in a highly complex hydrographic region. Estuarine, Coastal and Shelf Science 66, 483–492.
- Björnberg, T.K.S., 1981. Copepoda. In: Boltovskoy, D. (Ed.), Atlas del Zooplancton del Atlántico Sudoccidental y métodos de trabajo con el zooplancton marino. Publicacion Especial Instituto Nacional Investigacion y Desarrollo, Pesquero, Mar del Plata, Argentina, pp. 587–679.
- Boltovskoy, D., 1999. Diversidad y biogeografia del zooplancton del Atlántico Sur. Anales de la Academia Nacional de Ciencias Exactas, Físicas y Naturales 51, 111–136.
- Bradford-Grieve, J.M., Markhaseva, E.L., Rocha, C.E.F., Abiahy, B., 1999. Copepoda. In: Boltovskoy, D. (Ed.), South Atlantic Zoplankton. Backhuys Publishers, Leiden, The Netherlands, pp. 869–1098.
- Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecological Monography 27, 325–349.
 Carreto, J.I., Negri, R.M., Benavides, H.R., 1986. Algunas características del
- Carreto, J.I., Negri, R.M., Benavides, H.R., 1986. Algunas características del florecimiento del fitoplancton en el frente del Río de la plata I: Los sistemas nutritivos. Revista Investigacion Desarrollo Pesquero 5, 7–29.
- Carreto, J., Montoya, N., Benavides, H., Guerrero, R., Carignan, M., 2003. Characterization of spring phytoplankton comunities in the Rio de la Plata maritime front, using pigment signature and cell microscopy. Marine Biology 143, 1013–1027.
- Castello, J.P., Duarte, A., Möller, O., Niencheski, F., Odebrecht, C., Weiss, G., Habiaga, R., Bellotto, V., Kitzmann, D., Souto, C., Souza, R., Ciotti, A., Fillmann, G., Schwingell, P., Bersano, J., Cirano, M., Freire, K., Lima, I., Mello, R., Monteiro, A., Resgalla, C., Soares, I., Suzuki, M., 1990. On the importance of coastal and subantartic waters for the shelf ecosystems off Rio Grande do Sul. II Simpósio de Ecossistemas da Costa Sul e Sudeste Brasileira: Estrutura, Função e Manejo, ACIESP, São Paulo, Brazil, pp. 112–119.
- Castello, J.P., Haimovici, M., Vooren, C.M., 1997a. Fisheries. In: Seeliger, U., Oderbrech, C., Castello, J.P. (Eds.), Subtropical Convergence Environments: The Coast and Sea in the Southewestern Atlantic. Springer, Berlin.
- Castello, J.P., Haimovici, M., Oderbretch, C., Vooren, C.M., 1997b. Relationships and function of coastal and marine environments: the continental shelf and slope. In: Seeliger, U., Oderbrech, C., Castello, J.P. (Eds.), Subtropical Convergence Environments: The Coastal and Sea in the Southwestern Atlantic. Springer, Berlin.
- Ciotti, A.M., Odebrecht, C., Fillmann, G., Möller Jr., O.O., 1995. Freshwater outflow and subtropical convergence influence on phytoplankton biomass on the southern Brazilian continental shelf. Continental Shelf Research 15, 1737–1756.
- Clarke, K.R., Warwick, R.M., 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Natural Environment Research Council, Plymouth, UK, pp. 1–144.

- Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, second ed. PRIMER-E, Plymouth, UK.
- Cousseau, M.B., Perrota, R.G., 1998. Peces Marinos de Argentina. Biología Distribución y Pesca. INIDEP, Mar del Plata, Argentina, 163pp.
- Ehrlich, M.D., 2000. Distribución y abundancia de huevos, larvas y juveniles de merluza (*Merluccius hubbsi*) en la Zona Común de Pesca Argentino-Uruguaya 1996–1998. Frente Maritimo 18, 31–44.
- Fahay, M.P., 1983. Guide to the early stages of marine fishes occuring in the western North Atlantic Ocean, Cape Hatteras to the Southern Scotian Shelf. Journal of the Northwest Atlantic Fisheries Society 4, 423.
- Fillmann, G., 1990. Caracterização Química das Massas de Água da Plataforma Continental do Sul do Brasil. M.Sc. Thesis, Fundação Universidade do Rio Grande, Brasil, unpublished.
- Grasshoff, K., Ehrhardt, M., Kremling, K., 1983. Methods of Seawater Analysis, second ed. Verlag Chemie, Weimnheim.
- Haimovici, M., 1997. Recursos Pesqueiros Demersais da Região Sul. Avaliação do Potencial Sustentável de Recursos Vivos da Zona Económica Exclusiva (Revizee). Fundação de Estudos do Mar, Rio de Janeiro.
- Howlett, R., 1998. Sex and the single copepod. Nature 394, 423-424.
- Hubold, G., 1980a. Hydrography and plankton off Southern Brazil and Rio de la Plata, August-November 1977. Atlantica 4, 1–22.
- Hubold, G., 1980b. Second report on Hydrography and plankton off Southern Brazil and Rio de la Plata, Autumn cruise: April–June 1978. Atlantica 4, 23–42.
- Irigoien, X., Verheye, H.M., Harris, R.P., Harbour, D., 2005. Effect of food composition and hatching success of two copepod species (*Calanoides carinatus* and *Rhincalanus nasutus*) in the Benguela upwelling system. Journal of Plankton Research 27 (8), 735–742.
- Largier, J.L., 1993. Estuarine fronts: how important are they? Estuaries 16 (1), 1–11. Le Fèvre, J., 1986. Aspects of the biology of frontal systems. Advances in Marine
- Biology 23, 163–299. Mann, K.H., Lazier, J.R.N., 1996. Dynamics of Marine Ecosystems: Biological– Physical Interactions in the Oceans. Blackwell Scientific Publications.
- Marrari, M., Viñas, M.D., Martos, P., Hernandez, D., 2004. Spatial patterns of mesozooplankton distribution in the Southwestern Atlantic Ocean (34–41°S) during austral spring: relationship with the hydrographic conditions. ICES Journal of Marine Science 61, 667–679.
- Matsuura, Y., de Silva, G.A.C., Katsuragawa, M., Suzuki, K., 1993. Distribution and abundance of two species of codlet (Teleostei, Bregmacerotidae) larvae from the south-eastern Brazilian bight. Fisheries Oceanography 2, 82–90.
- Mauchline, J., 1998. The biology of calanoid copepods. Advances in Marine Biology 33, 1–710.
- Mianzan, H.W., Guerrero, R.A., 2000. Environmental patterns and biomass distribution of gelatinous macrozooplankton. Three study cases in the Southwestern Atlantic Ocean. Scientia Marina 64 (Suppl.1), 215–224.
- Mianzan, H.W., Lasta, C.A., Acha, E.M., Guerrero, R.A., Macchi, G.J., Bremec, C., 2001a. The Río de la Plata estuary. Argentina, Uruguay. In: Seeliger, U., Kjerfve, B. (Eds.), Ecological Studies 144: Coastal Marine Ecosystems of Latin America. Springer, Berlin, pp. 185–204.
- Mianzan, H.W., Pájaro, M., Alvarez Colombo, G., Madirolas, A., 2001b. Feeding on survival-food: gelatinous plankton as a source of food for anchovies. Hydrobiologia 451 (1–3), 45–53.
- Möller Jr., O.O., Piola, A.R., Freitas, A.C., Campos, E.J.D., 2008. The effects of river discharge and seasonal winds on the shelf off Southeastern South America. Continental Shelf Research, this issue, doi:10.1016/j.csr.2008.03.012.
- Muelbert, J.H., Sinque, C., 1996. Distribution of bluefish (*Pomatomus saltatrix*) larvae along the continental shelf off southern Brazil. Marine and Freshwater Research 47, 311–314.
- Odebrecht, C., Garcia, V.M.T., 1997. Coastal and marine environmental and their biota: Phytoplakton. In: Seeliger, U., Odebrecht, C., Castello, J.P. (Eds.), Subtropical Convergence Environments. The Coast and Sea in the Southwestern Atlantic. Springer, Berlin Heidelberg, p. 308.
- Olson, D.B., 2002. Biophysical dynamics of ocean fronts. In: The Sea, Biological-Physical Interactions in the Sea, vol. 12. John Wiley and Sons.
- Owen, R.W., 1981. Fronts and eddies in the sea: mechanisms, interactions and biological effects. In: Longhurst, A.R. (Ed.), Analysis of Marine Ecosystems. Academic Press, Orlando, FL, pp. 197–233.
- Piola, A.R., Campos, E.J.D., Möller Jr., O.O., Charo, M., Martinez, C.M., 2000. Subtropical shelf front off eastern South America. Journal of Geophysical Research 105 (C3), 6566–6578.
- Piola, A.R., Matano, R.P., Palma, E.D., Möller, O.O., Campos, E.J.D., 2005. The influence of the Plata River discharge on the western South Atlantic shelf. Geophysical Research Letters 32, L01603.
- Piola, A.R., Möller Jr., O.O., Guerrero, R.A., Campos, E.J.D., 2008. Variability of the Subtropical Shelf front off eastern South America: winter 2003 and summer 2004. Continental Shelf Research, this issue, doi:10.1016/j.csr.2008.03.013.
- Ramírez, F.C., 1966a. Copépodos calanoideos marinos del área de Mar del Plata, con la descripción de Pontella marplatensis, n. sp. Boletin del Instituto de Biologia Marina 11, 1–24.
- Ramírez, F.C., 1966b. Copépodos ciclopoidos y harpacticoidos del plancton de Mar del Plata. Revista Physis 26 (72), 285–292.
- Ramírez, F.C., 1969. Copépodos plantónicos del sector Bonaerense del Atlántico Suroccidental. Series Contribuciones del Instituto de Biologia Marina 98, 116.
- Richards, W.J., 2005. Early Stages of Atlantic Fishes. An Identification Guide for the Western Central North Atlantic. CRC Press, Boca Raton, FL, USA.

- Runge, J.A., 1988. Should we expect a relationship between primary production and fisheries? The role of copepod dynamics as a filter of trophic variability. Hydrobiologia 167–168, 61–71.
- Sabatini, M.E., Alvarez Colombo, G.L., 2001. Seasonal pattern of zooplankton biomass in the Argentinian shelf off Southern Patagonia (45–55°S). Scientia Marina 65, 21–31.
- Schiariti, A., Berasategui, A., Giberto, D., Guerrero, R., Acha, E.M., Mianzan, H., 2006. Living in the front: *Neomysis americana* (Mysidacea) in the Río de la Plata estuary, Argentina, Uruguay. Marine Biology 149 (3), 483–489.
- Sinque, C., Muelbert, J.H., 1997. Ichthyoplankton. In: Seeliger, U., Oderbrech, C., Castello, J.P. (Eds.), Subtropical Convergence Environments: The Coastal and Sea in the Southwestern Atlantic. Springer, Berlin, pp. 120–123.
- Strickland, J.D., Parsons, T.R., 1968. A practical handbook of seawater analyses. Bulletin of the Fisheries Research Board of Canada, 293.
- Sunyé, P.S., Servain, J., 1998. Effects of seasonal variations in meteorology and oceanography on the Brazilian sardine fishery. Fisheries Oceanography 7, 89–100.
- Teixeira, C., Aidar, E., Fernandez, R.M., 1973. Relatório sobre a segunda pesquisa oceanográfica e pesqueira do Atlântico Sul entre Torres e Maldonado. Programa Rio Grande do Sul II, Technical Report GEDIP/IOUSP, 27pp.

- Turner, J.T., Tester, P.A., Conley, W.J., 1984. Zooplankton feeding ecologypredation by the marine cyclopoid copepod *Corycaeus amazonicus* F Dahl upon natural prey. Journal of Experimental Marine Biology and Ecology 84, 191–202.
- Valentin, J.L., 1984. Spatial structure of the zooplankton community in the Cabo Frio region (Brazil) influenced by coastal upwelling. Hidrobiologia 113, 183–199.
- Valentin, J.L., Monteiro Ribas, W.M., Mureb, M.A., Pessotti, E., 1987. Sur quelques zooplanctontes abondants dans l 'uppwelling de Cabo Frio (Bresil). Avano 9 (6), 1195–1216.
- Weiss, G., 1981. Ictioplancton del estuario de Lagoa dos Patos, Brasil. Ph.D. Thesis, Universidad Nacional de La Plata, Facultad de Ciencias Naturales y Museo, La Plata, Argentina.
- Welschmeyer, N.A., 1994. Fluorometric analysis of chlorophyll-a in the presence of chlorophyll-b and pheopigments. Limnology and Oceanography 39, 1985–1992.
- Wiebe, P.H., Benfield, M.C., 2003. From the Hensen net toward four-dimensional biological oceanography. Progress in Oceanography 56, 7–136.