

Zooplankton and ichthyoplankton distribution on the southern Brazilian shelf: an overview

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SUMMARY: The southern Brazilian coast is the major fishery ground for the Brazilian sardine (*Sardinella brasiliensis*), a species responsible for up to 40% of marine fish catches in the region. Fish spawning and recruitment are locally influenced by seasonal advection of nutrient-rich waters from both inshore and offshore sources. Plankton communities are otherwise controlled by regenerative processes related to the oligotrophic nature of the Tropical Water from the Brazil Current. As recorded in other continental margins, zooplankton species diversity increases towards outer shelf and open ocean waters. Peaks of zooplankton biomass and ichthyoplankton abundance are frequent on the inner shelf, either at upwelling sites or off large estuarine systems. However, meandering features of the Brazil Current provide an additional mechanism of upward motion of the cold and nutrient-rich South Atlantic Central Water, increasing phyto- and zooplankton biomass and production on mid- and outer shelves. Cold neritic waters originating off Argentina, and subtropical waters from the Subtropical Convergence exert a strong seasonal influence on zooplankton and ichthyoplankton distribution towards more southern areas. This brief review highlights the need for further experimental studies on zooplankton life cycle strategies in order to understand the major processes controlling food web dynamics in this shelf ecosystem.

Keywords: zooplankton, ichthyoplankton, distribution, biomass, water masses, upwelling, continental shelf, south-western Atlantic Ocean.

RESUMEN: INFLUENCIA DE LOS PROCESOS FÍSICOS EN LA DISTRIBUCIÓN DEL ZOOPLANCTON E ICTIOPLANCTON: UNA REVISIÓN DE LOS ESTUDIOS REALIZADOS EN LA COSTA SUR DE BRASIL. – La costa sur de Brasil representa la principal zona de pesca de la sardina brasileña (*Sardinella brasiliensis*), especie responsable de más del 40% de las capturas de especies marinas de la región. El desove y el reclutamiento están influenciados localmente por la advección estacional de aguas ricas en nutrientes procedentes tanto de fuentes costeras como oceánicas. Por otro lado, las comunidades planctónicas son controladas por procesos regenerativos asociados a la naturaleza oligotrófica del Agua Tropical procedente de la Corriente de Brasil. Como se ha observado para otros márgenes continentales, la diversidad de especies del zooplancton aumenta hacia las aguas de la plataforma externa y de océano abierto. Máximos en la biomasa de zooplancton y la abundancia de ictioplancton son frecuentes en la plataforma interna, tanto en afloramientos como en grandes sistemas estuáricos. No obstante, la formación de meandros en la Corriente de Brasil proporciona un mecanismo adicional para la ascensión de las aguas frías y ricas en nutrientes del Atlántico Sur Central, aumentando la biomasa fito- y zooplanctónica y la producción en la plataforma media y externa. Las aguas neríticas frías procedentes del estuario de La Plata y las aguas subtropicales de la Convergencia Subtropical ejercen una fuerte influencia en la distribución del zooplancton e ictioplancton hacia las regiones de más al sur. La presente revisión pone de relieve la necesidad de investigaciones más completas de las estrategias de los ciclos de vida del zooplancton con el objetivo de entender los procesos principales que controlan la dinámica de las redes tróficas en este ecosistema costero.

Palabras clave: zooplancton, ictioplancton, distribución, biomasa, masas de agua, afloramiento, plataforma continental, Atlántico Suroeste.

INTRODUCTION

The southern Brazil shelf ecosystem accounts for over half of the country's marine fisheries yield (Matsuura, 1996; Odebrecht and Garcia, 1997). Among the locally exploited pelagic species, the Brazilian sardine (*Sardinella brasiliensis*) used to contribute up to 40% of total landings of marine fish, with annual catches ranging from 75,721 to 228,037 tons for the 1968 to 1986 period (Matsuura, 1996). However, fishery yields for this species have decreased dramatically in the last 20 years – not surpassing 120,000 tons per year – and catches below or around 35,000 tons per year have been the norm since 1999 (Cergole *et al.*, 2005; FAO, 2003). This is due to over-exploitation of stocks (Cergole *et al.*, 2005), and because of climate change and oceanographic anomalies that have led to recruitment failures (Matsuura, 1999).

Fish spawning and recruitment in this oligotrophic region depend strongly on seasonal advection of nutrient-rich waters from both inshore and offshore sources, which affects the availability of planktonic food for the larvae (Matsuura *et al.*, 1992). Physical processes such as oceanic fronts and eddies have been intensively studied because of their implications to biological processes, including the variability of zooplankton and ichthyoplankton stocks (Iles and Sinclair, 1982; Nakata, 1989; McGowen, 1993; Sabatés and Olivar, 1996; Grioche *et al.*, 1999). Such biological variability is, in turn, of utmost importance for the recruitment of economically important fish such as *Sardinella brasiliensis*.

Research into zooplankton and ichthyoplankton taxonomy and ecology has been carried out on the southern Brazilian coast since the late nineteenth century when international oceanographic expeditions such as the Challenger and Terra Nova sporadically collected samples in the region (Brandini *et al.*, 1997). During the last 30 years a reasonable knowledge of zooplankton and ichthyoplankton mesoscale distribution in relation to major circulation systems has been gained (Katsuragawa *et al.*, 2006; Lopes *et al.*, 2005). However, access to the information available for the region is rather difficult for the international oceanographic community because many important papers and reports were published in local, non-indexed journals with Portuguese as the dominant language, or remain as unpublished theses and dissertations (Brandini *et*

al., 1997). This paper intends to fill part of this gap by presenting a brief overview of the effects of major circulation processes on the distribution of zooplankton and ichthyoplankton assemblages of the area.

THE REGIONAL PHYSICAL ENVIRONMENT AND FERTILIZATION MECHANISMS

The southern Brazilian coast can be divided into two latitudinal areas according to their hydrographic features: (i) the Southern Brazilian Bight (SBB) located between Cape Frio and Cape Santa Marta (roughly 22°00'S 28°30'S), and (ii) the Southern Subtropical Shelf (SSS) from Cape Santa Marta towards the border with Uruguay, but extending until the La Plata estuary (~ 28°30'S 35°00'S) (Fig. 1). The major contrast between these two areas comes from the stronger influence of cold coastal waters (CCW) derived from the La Plata outflow on the SSS compared to northern latitudes (Fig. 1). In addition, the oceanic domain off the SSS is affected by seasonal changes in the latitudinal position of the northern border of the Subtropical Convergence (STC), which is derived from the confluence of the major boundary currents in the Southwest Atlantic:



FIG. 1. – The Brazilian shelf and its two southernmost areas: the Southern Brazilian Bight (SBB) and the Southern Subtropical Shelf (SSS). Symbols: sSEC (southern branch of the South Equatorial Current), BC (Brazil Current), CCW (Cold Coastal Water), FC (Falkland Current = Malvinas Current), STC (Subtropical Current). Adapted from Castro Filho and Miranda (1998).

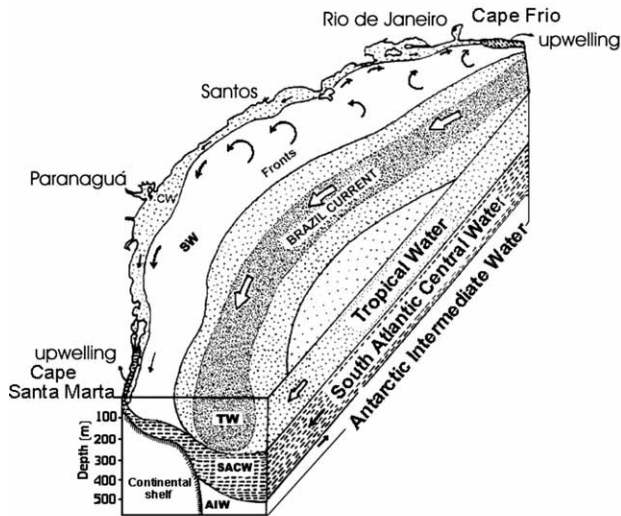


FIG. 2. – Major circulation patterns and water masses on the southern Brazilian shelf. TW: Tropical Water; SACW: South Atlantic Central Water; SW: Shelf Water; CW: Coastal Water; AIW: Antarctic Intermediate Water. From Ribeiro (1996).

the Brazil and Falklands (=Malvinas) currents (Castro Filho and Miranda, 1998).

Three different water masses characterize the neritic region of the SBB (Fig. 2). The warm Tropical Water (TW) carried by the Brazil Current flows southwards near the shelf break in the upper 200 m depth layer with temperature higher than 20°C and salinity higher than 36.40 (Castro Filho and Miranda, 1998). The cool South Atlantic Central Water (SACW), with temperature and salinity maxima below 20°C and 36.40 respectively is also transported southwards along the continental slope between 200 and 500 m by the lower layer of the Brazil Current. Coastal Water (CW) results from mixing of shelf water (with both TW and SACW influences) with waters of continental origin, and is characterized by lower salinities (Castro Filho and Miranda, 1998; Silveira *et al.*, 2000). Finally, Antarctic Intermediate Water (AIW) flows northwards below the SACW layer in offshore areas.

The SBB and the SSS can be divided into three major bathymetric regions according to the prevailing oceanographic conditions: the inner, mid- and outer shelf. The inner shelf, where the CW is the main component, is distinguished from the mid-shelf by a bottom thermal front. The mean position of the thermal front changes seasonally: it is closer to the coast during summer (between 10 to 20 km from the coast), and further offshore during winter (between 40 to 50 km from the coast). During summer, when a seasonal and shallow thermocline

occurs, a two-layered system is formed on the mid-shelf: below the thermocline waters derived from SACW intrusions prevail, while the upper layer is dominated by CW or by CW/TW mixtures. Mid-shelf waters are separated from those of the outer shelf by a strong salinity front located between 80 and 120 km from the coast. High salinity waters from the TW are present in the surface layer, whereas in the bottom layer there is a strong influence of the SACW (Castro Filho and Miranda, 1998).

Except for the mouth of some estuarine systems, oligotrophic conditions prevail off the SBB due to TW predominance in upper layers. Oceanic stocks of nutrients are trapped below in the South Atlantic Central Water (SACW) thanks to the physical stability of permanent thermoclines. Nutrient levels within the euphotic zone are therefore low and usually controlled by regenerative processes (Metzler *et al.*, 1997) that keep rates of organic production below 0.1 g C m⁻² d⁻¹ (Brandini *et al.*, 1997; Gaeta and Brandini, 2006). Different physical mechanisms may be responsible for inputs of new nutrients into the euphotic zone along the SBB and on the SSS. Variations in shelf topography, wind patterns and hydrographic regime provide various opportunities of upward motions of the SACW at different time and spatial scales (Fig. 3).

Fertilization by oceanic nutrients in the SBB is the most important process in terms of geographic magnitude. Under the stress of northeast winds during summer seasons, surface shelf waters are pushed offshore following the Ekman transport, and are counteracted by onshore bottom intrusions of the SACW. This brings new nutrients shoreward, thus increasing their concentrations at lower euphotic layers. Consequently, deep chlorophyll maximum layers (DCML) are formed at subsurface levels, usually dominated by diatoms (Brandini *et al.*, 1989; Odebrecht and Djurfeldt, 1996; Gaeta and Brandini, 2006), leading to an increase in net production between 25 and 100 m isobaths during spring and summer (October to March).

Cyclonic eddies ("vortex" in Fig. 3) of the Brazil Current are common mesoscale processes on the mid- and outer shelf throughout the year (Kampel *et al.*, 2000), increasing net production up to 2.4 g C m⁻² d⁻¹ in neritic domains (Gaeta *et al.*, 1999). Shelf-break upwelling of the SACW is enhanced by these eddies, inducing the formation of DCML along the shelf-break (Mesquita *et al.*, 1993; Brandini *et al.*, 1989). Gaeta and Brandini (2006) estimated the con-

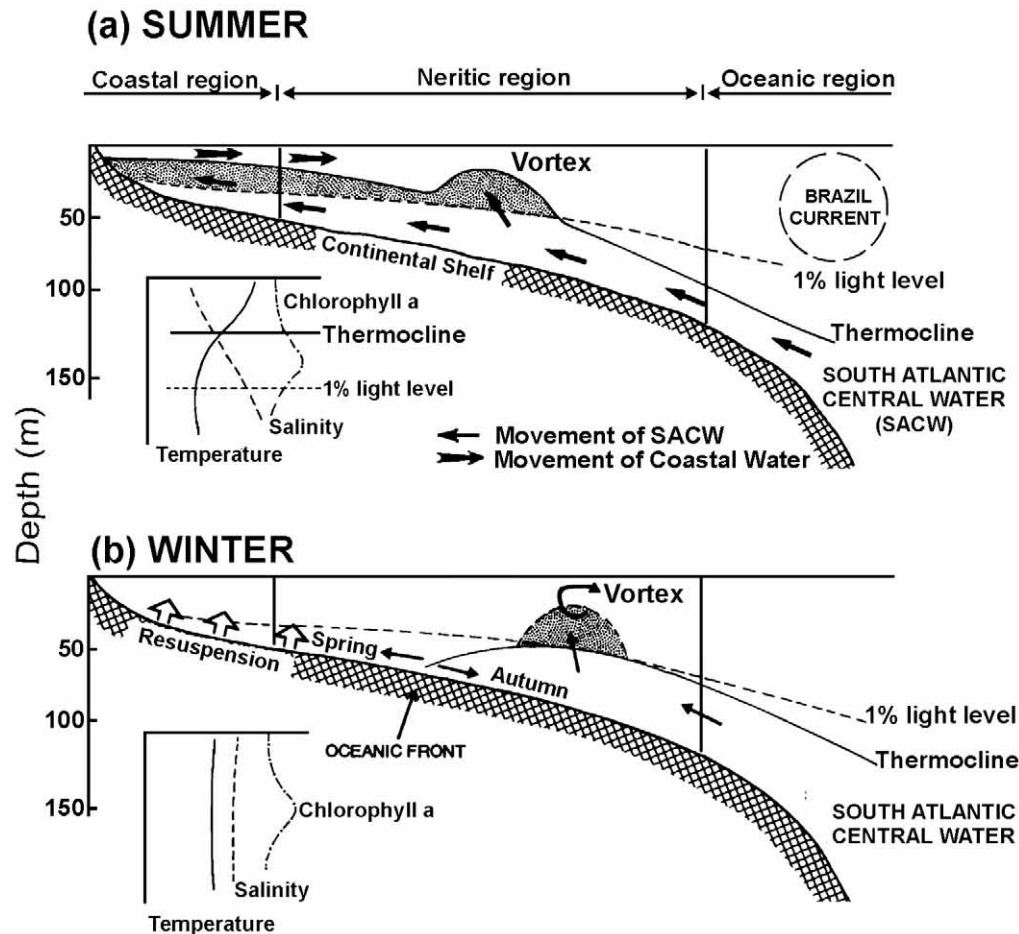


FIG. 3. – Seasonal contrasts in shelf processes off the southern Brazilian coast. Bottom intrusions of the South Atlantic Central Water (SACW) are more frequent during summer, and surface upwelling may occur at certain areas. Cold waters derived from shelf-break upwelling may also be driven towards the coast by bottom intrusions. As surface waters are dominated by Tropical Water (TW) and its mixtures with CW and SACW, a seasonal thermocline develops during summer. During winter the SACW retreats offshore and only occasionally penetrates onto the shelf. Shelf-break eddies and meanders (“Vortex” on FIGure) are more geographically confined and do not exert a strong influence on the oceanic fertilization of mid- and inner shelves. However, sediment resuspension may be a major nutrient supply to the water column in shallower areas during winter. From Matsuura (1996).

tribution of eddies along the shelf break for the annual net production of the SBB as being of the same order of magnitude as the oceanic intrusions of the SACW into the mid- and inner shelf. During summer, eddy-derived waters are pushed towards the inner shelf with SACW intrusions, but during winter eddies are short-lived and geographically restricted (Fig. 3).

Internal waves are another important mechanism of nutrient enhancement in the lower euphotic layers in the SBB (Brandini, 2006). Johannessen (1968) has reported internal waves in the SBB moving up to 20 meters on the 16°C isotherm towards the euphotic zone. Therefore, it is reasonable to associate chlorophyll enhancements at the levels of the DCML with upward motions of nutriclines. Sediment resuspension also plays an important role in nutrient export to the euphotic zone in shallower

areas, especially during wintertime when turbulence caused by wind stress is stronger throughout the water column compared to summer (Fig. 3).

On the southernmost shelf (SSS) the same physical processes take place with the persistence of the northeast winds in summer. However, south-eastern winds prevailing in winter are responsible for mass fertilization of inner and mid-shelves with new nutrients, mainly nitrate and silicate, by pushing further north the continental discharge of the La Plata river and, to a lesser extent, the Patos Lagoon Estuary, forming the Subtropical Shelf Front (Piola *et al.*, 2000). Primary production and chlorophyll stock in winter are indeed enhanced at these latitudes compared to summer rates at the same positions (Brandini, 1990). For this reason the algal production on the SSS is high all year round. In summer, plankton production is enhanced at the subsur-

face by oceanic nutrients from the SACW by the physical mechanisms described above, whereas in winter the shelf system is mainly supported by land sources of nutrients from the Argentinean shelf.

ZOOPLANKTON AND ICHTHYOPLANKTON COMPOSITION

A typical inshore-offshore gradient in zooplankton diversity occurs in the regional shelf ecosystem due to differences in the pelagic food web structure between mesotrophic coastal waters and oligotrophic waters of the Brazil Current. However, physical processes described above including SACW intrusions into both the SBB and the SSS, advection of cold coastal waters during winter on the SSS, and mesoscale eddies and fronts derived from the meandering of the Brazil Current complicate this pattern. An outline of major species groups and their relation to prevailing water masses has been provided by several studies on zooplankton distribution in the study area, and a brief account is given below.

As found in other coastal ecosystems of the world, copepods are the most abundant and diversified metazoan taxa (Björnberg, 1963, 1981). Due to the tropical influence of the Brazil Current, up to 150-200 pelagic species may be found in a typical transect survey over the shelf (e.g., Vega-Perez, 1993; Montú *et al.*, 1998; Lopes *et al.*, 1999). Small copepods (<2 mm in total length) belonging to the genera *Paracalanus*, *Temora*, *Clausocalanus*, *Oithona*, *Oncaea* and *Corycaeus* are the most ubiquitous species in CW and in mixtures of CW and TW. Some abundant species such as *Parvocalanus crassirostris*, *Labidocera fluviatilis*, *Acartia lilljeborgi* and *Euterpina acutifrons* are restricted to estuaries and the inner shelf, disappearing under the influence of oceanic waters (Sartori and Lopes, 2000). *Acartia tonsa* belongs to this “true” coastal group but only towards more southern areas close to the Patos Lagoon system; north of Cape Santa Marta this species seems to be restricted to meso- and polyhaline waters inside estuaries (Lopes *et al.*, 1986, 1998).

The TW is characterized by high biological diversity, with several indicator species being easily recognized (e.g., *Clausocalanus furcatus*, *Acartia danae*, *Acrocalanus longicornis*, *Undinula vulgaris*, *Euchaeta marina*). Cold-water species occurring below the permanent thermocline in the oceanic domain (e.g., *Haloptilus longicornis*, *H. ornatus*, *H.*

fertilis, *Lucicutia gaussae* and *Centropages violaceus*) often appear on the shelf during the early upwelling phase (Lopes *et al.*, 2006). Among them, only *Calanoides carinatus* and *Ctenocalanus vanus* are able to persist in coastal areas during later upwelling and early downwelling stages when water temperature rises above 20°C (Valentin, 1989). Together with coastal species, such as *Paracalanus quasimodo* and *Temora turbinata*, they probably represent the major metazoan consumers of phytoplankton and microzooplankton assemblages in upwelling areas such as Cape Frio (Lopes *et al.*, 1999). Other examples of zooplankton taxa associated with upwelling events on the southern Brazilian coast are the hydromedusae *Rhacostoma atlantica* and *Olindias sambaquiensis* (Mianzan and Guerreiro, 2001), the appendicularian *Fritillaria pellucida* (Campos, 2000), the chaetognaths *Sagitta maxima* and *Krohnitta subtilis* (Liang, 1998), the pteropod *Hyalocylis striata* (Resgalla and Montú, 1994), the euphausiids *Euphausia americana*, *E. recurva* and *Stylocheiron* spp. (Lansac-Tôha, 1981; Muxagata, 1999), and the “cladocerans” *Penilia avirostris* and *Pleopis polyphemoides* (Valentin, 1983). The latter are also found in coastal and estuarine waters as well as in mixtures of CW, TW, and SACW (Lopes *et al.*, 2006). Salps are quite a diversified and abundant group in the shelf ecosystem, with 26 species recorded so far (Lopes *et al.*, 2006). *Thalia democratica* is the dominant species in warm waters influenced by the Brazil Current. Although not as abundant as *T. democratica*, doliolids (*Doliolum nationalis* and *Dolioletta gegenbauri*) are also frequent close to the coast (under CW influence), and towards the outer shelf (under TW influence). Large-sized thaliaceans of the genera *Doliolina*, *Ihleia*, and *Salpa* may occur in association with SACW intrusions (Lopes *et al.*, 2006).

The ichthyoplankton species composition has been analyzed in detail by studies of larval fish assemblages. For example, Itagaki (1999) found three main larval groups inhabiting SBB waters down to the 100 m isobath, which were assigned to coastal, neritic and oceanic assemblages. A transitional group containing coastal and neritic species was also identified. For some taxonomic categories the assemblage composition reflected the adult distribution pattern and reproductive strategies. The coastal assemblage, obviously influenced by CW, included larvae of *Harengula jaguana*, *Synodus foetens*, *Chloroscombrus chrysurus*, *Oligoplites* spp., *Sphyræna guachancho*, *Etropus crossotus*,

Gymnachirus sp., *Symphurus kyaropterygium*, and other larvae of the following families: Gerreidae, Sciaenidae, Mugilidae, Blenniidae and Gobiidae. Among this group there were some species typically abundant in estuarine or low saline waters, such as *H. jaguana* and the carangids *C. chrysurus* and *Oligoplites*. The neritic assemblage, influenced by SACW intrusions, included fish larvae with a wide ranging distribution over the continental shelf such as *Engraulis anchoita*, *Bregmaceros cantori*, *Trichiurus lepturus*, *Auxis* sp., *Bothus ocellatus*, and those of the families Ophidiidae, Triglidae, and Serranidae. The oceanic assemblage was characterized by the predominance of mesopelagic taxa associated with TW including *Maurolicus stehmanni*, *Pollichthys maui*, *Diaphus dumerelli*, Paralepididae and Nomeidae. A transitional larval group included species found in both coastal and neritic assemblages such as *Sardinella brasiliensis*, *Euthynnus alletteratus*, *Etropus longimanus*, *Syacium papillosum*, *Symphurus trewavasae* and *S. jenynsi*. Larvae of Engraulidae and Clupeidae, especially *Engraulis anchoita*, *Sardinella brasiliensis* and *Harengula jaguana*, represented up to 60% of the ichthyoplankton standing-stock in inner and intermediate shelf areas (<100 m depth; Katsuragawa *et al.*, 2006).

INFLUENCE OF PHYSICAL PROCESSES ON ZOOPLANKTON AND ICHTHYOPLANKTON MESOSCALE DISTRIBUTION

Zooplankton biomass and ichthyoplankton abundance are usually high in coastal areas under the influence of brackish water outflow from large embayments or lagoonal systems including the Guanabara and Paranaguá bays, the Cananéia-Iguape estuarine system and the Patos Lagoon estuary (Vannucci and Almeida Prado, 1959; Vannucci, 1962; Moreira, 1976; Björnberg, 1981; Muxagata, 1999). Biomass maxima due to coastal zooplanktonic species are restricted to a rather narrow band influenced by CW, decreasing towards the outer shelf regardless of the season (Navas-Pereira, 1973; Hubold and Gurgel, 1978; Hubold, 1980; Bonecker *et al.*, 1990; Muxagata, 1999; Resgalla *et al.*, 2001).

High zooplankton and ichthyoplankton stocks in inshore waters are otherwise associated with SACW upwelling, especially in the vicinities of Cape Frio, towards the southwest off Guanabara Bay (Rio de Janeiro) and Ubatuba, and off Cape Santa Marta

(Matsuura *et al.*, 1980; Valentin, 1989; Muxagata, 1999). Zooplankton dry weight during the productive upwelling phase may be higher than 200 mg m⁻³, while under downwelling conditions in summer or during non-upwelling seasons biomass values below 50 mg m⁻³ are the rule (Valentin and Moreira, 1978; Monteiro-Ribas, 1988; Muxagata, 1999).

Temporal changes in spawning activity of fishes in relation to SACW intrusions are suggested by variability in total egg abundance, as observed during the course of seasonal cruises carried out in 1976 (Fig. 4). During January (mid-summer) about half of the stations had low egg densities (<50 eggs m⁻²) and seven (5.2%) high-density stations with more than 400 eggs m⁻² were observed. The amount of low-density stations increased to 88.0% during May (mid-fall), when only one station (0.7%) with high egg density was found. A recovery trend was observed in the subsequent cruises, as the index of high-density stations rose to 6.4% during late winter and early spring, and reached the maximum spawning activity in late spring and early summer, when 20.3% of stations had high egg density. During summer, peak egg densities were mainly located in coastal areas shallower than 100 m at the low-temperature (<20°C) upwelling sites of Cape Frio, Rio de Janeiro and Cape Santa Marta, and also off large estuarine systems such as Paranaguá and Cananéia-Iguape where subsurface temperatures were above 22°C.

The seasonal pattern mentioned above reflects to a great extent the situation observed for the Brazilian sardine. For instance, Matsuura (1983, 1996) found an index of positive stations for *Sardinella brasiliensis* eggs of 14.3% in January, then a total absence of eggs in the two subsequent cruises (May and September/October), and again 12.9% of positive stations in December. *Engraulis anchoita* seems to perform a different strategy, maintaining high spawning activity even during the cold season, as observed by Nakatani (1982), who found the following indexes of positive stations: 19.4% in January, 18.1% in May, 45.8% in September/October, and 20.1% in December. Peak egg densities of *E. anchoita* occurred in September/October (average of 32.2 eggs m⁻²). Spach (1990) and Matsuura *et al.*, (1992) found similar results for the same species, during a survey carried out from 1985 to 1987 off São Paulo (23°S-24°S). According to Spach (1990) *S. brasiliensis* and *Harengula jaguana* spawn in summer, with secondary peaks in spring and fall, and their eggs are

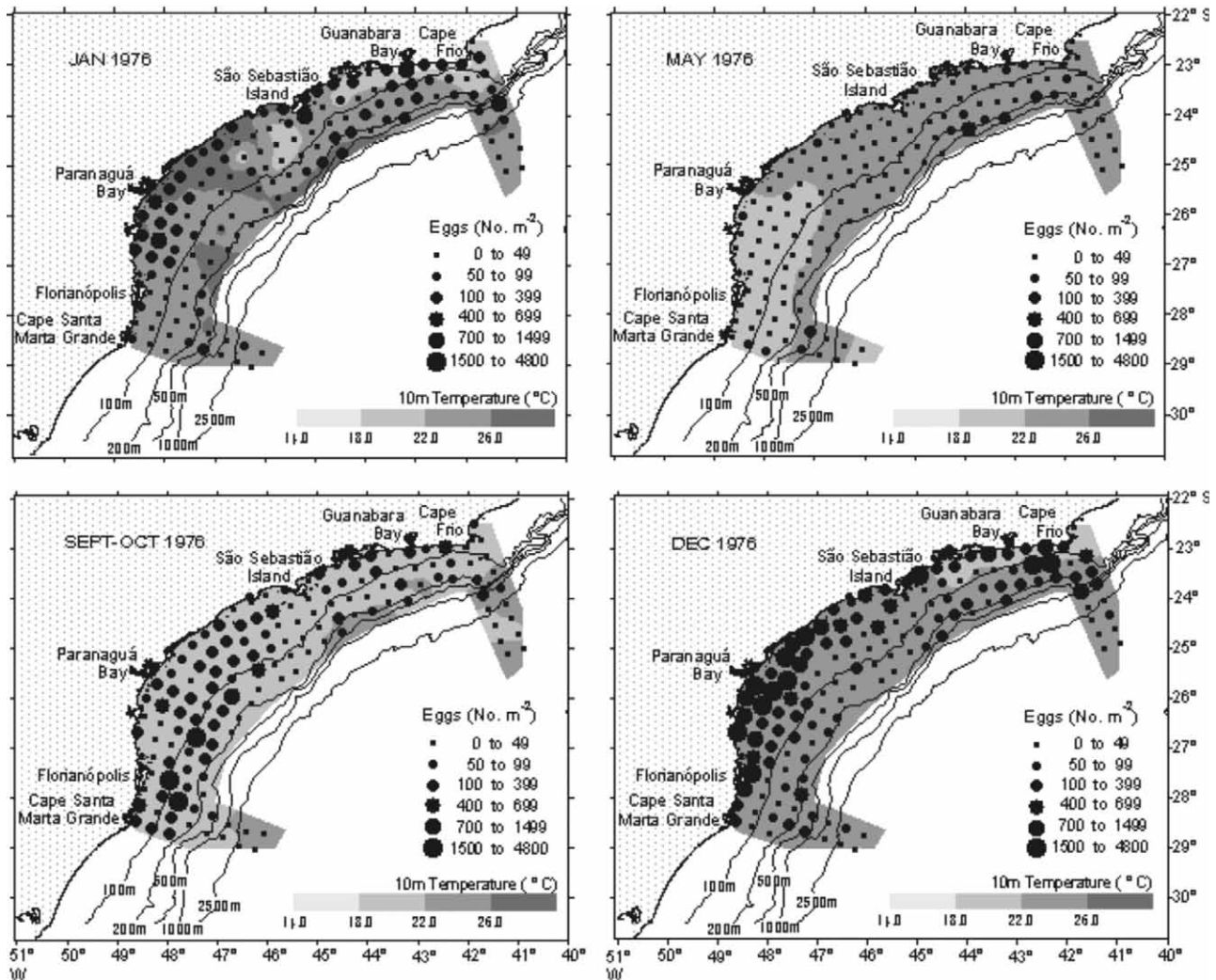


FIG. 4. – Cross-shelf and seasonal variability of fish egg abundance in the SBB during 1976. Samples were collected from 200 m to the surface, or close to the bottom to the surface when stations were shallower than 200 m, by oblique tows of a Bongo net with a 500 μ m mesh size. A temperature contour at 10 m depth is shown in order to identify major upwelling areas close to the coast. Original data from Matsuura (1978).

mostly confined to shallow (<50m) shelf waters during this season, predominantly distributed above the thermocline. In this case, the enrichment due to the presence of SACW and the retention of larvae within the favourable coastal habitat may be of fundamental importance for larval survival and recruitment success. Spawning of *Engraulis anchoita*, on the other hand, occurs all over the shelf, and does not show a clear seasonal pattern as that observed for sardines. In summary, two major spawning patterns are observed in the south-eastern Brazilian Bight: 1) higher spawning activity in summer or earlier, between late spring and summer, observed for sardines, *Trachurus lathami* (Katsuragawa and Matsuura, 1992) and some scombrids (Matsuura and Sato, 1981); 2) a second group exhibiting a year-round spawning pattern on the entire continental

shelf, including *Engraulis anchoita* and *Maurolicus stehmanni* (Ribeiro, 1996).

A seasonal trend similar to that observed for sardines is the usual picture in the case of zooplankton (Fig. 5), but in addition to biomass agglomerations associated with low-temperature inshore areas during summer, patches also occurred on the intermediate and outer shelves (between 100 and 200 m depth) and close to the shelf break, following an apparently recurrent pattern observed since early quantitative studies (Jacob *et al.*, 1966). These maxima probably result from cumulative growth of both coastal- and SACW-derived zooplankton taxa preying upon large phytoplankton aggregates that develop within upwelling systems associated with vortices and eddies of the Brazil Current (Gaeta, 1999). Since these fertilization mechanisms are at their

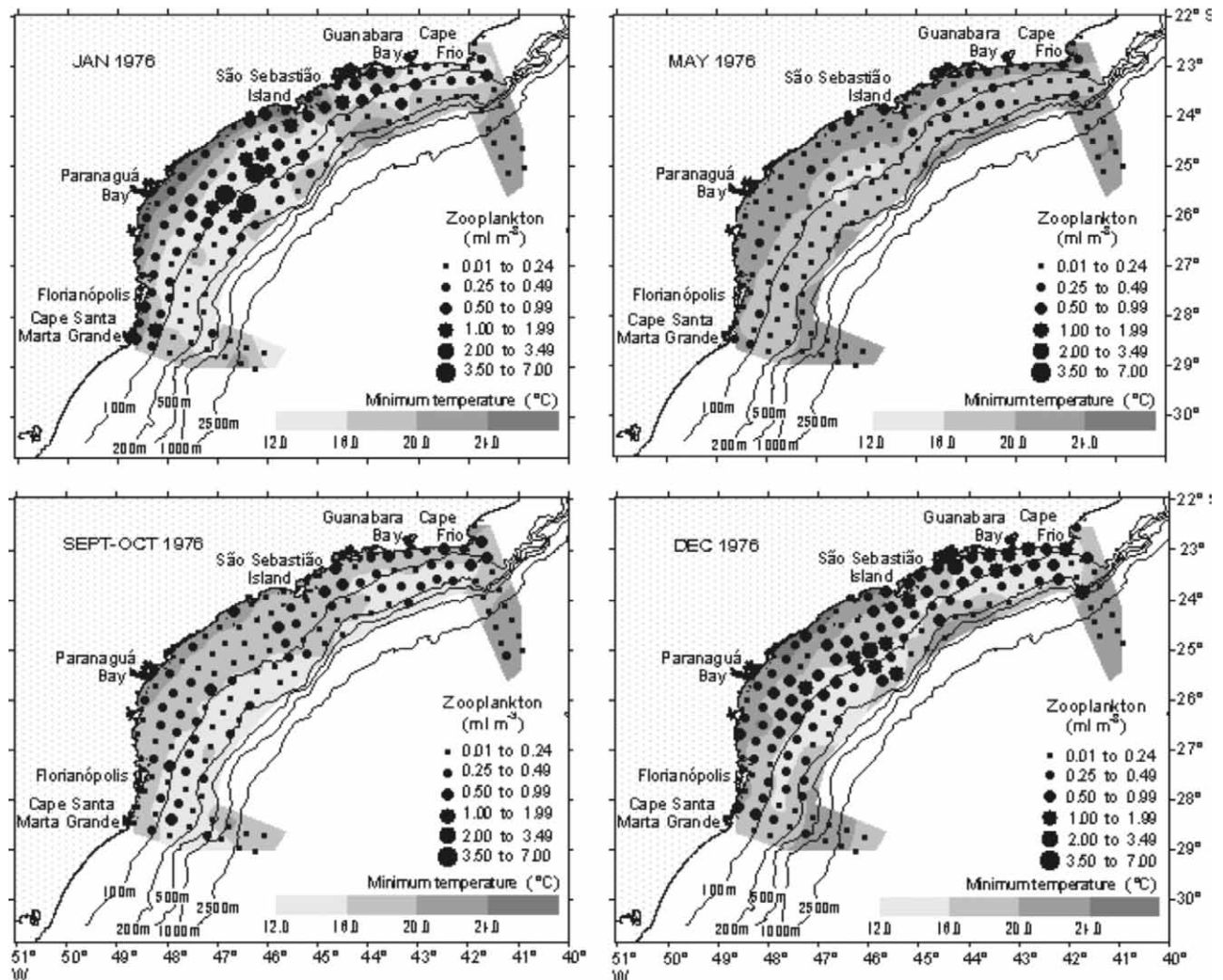


FIG. 5. – Cross-shelf and seasonal variability of zooplankton biomass in terms of displacement volume in the SBB during 1976. Samples were collected from 200 m to the surface, or close to the bottom to the surface when stations were shallower than 200 m, by oblique tows of a Bongo net with a 333 μm mesh size. Minimum temperatures within the depth layer of zooplankton sampling are shown in order to identify major SACW intrusion areas on the shelf. Original data from Matsuura (1978).

highest during late spring and summer (although not restricted to these seasons), maximum zooplankton biomass on mid- and outer shelves is consistently observed at this time of the year (Matsuura, 1978; Matsuura *et al.*, 1980).

Biomass accumulation of crustacean plankton and other non-gelatinous taxa in the SBB is indeed related to the persistence of cold waters in the range of 12 to 18°C, and salp abundance follows the same pattern (Fig. 6). Salp aggregations are quite common along the entire continental shelf and their biovolume may be as high as that of other zooplankton groups combined. When they occur in such large numbers, salps supposedly have a deleterious effect on fish foraging behaviour by affecting the food environment of dietary components of fish larvae (Matsuura *et al.*, 1980; Katsuragawa *et al.*, 1993;

Ribeiro, 1996). However, the extent of this hypothesized impact on fish spawning and recruitment still needs to be studied in detail.

Upwelling off Cape Frio and other coastal areas of the SBB has a rather pulsing nature; each event usually lasts for 15 days or less, even during summer when north-eastern winds are at their maximum strength (Silva *et al.*, 1988; Gonzalez-Rodriguez, 1994). Phytoplankton responses to nitrate flux occur at the same time scales, and primary production rates of 0.5 g C m⁻² d⁻¹ are common in the area (Gonzalez-Rodriguez *et al.*, 1992). It has been argued that large zooplankters do not have a strong grazing impact on such dense but short-living phytoplankton patches because of their longer generation time compared to diatoms and other dominant microalgae (Gaeta and Brandini, 2006). Yet copepod

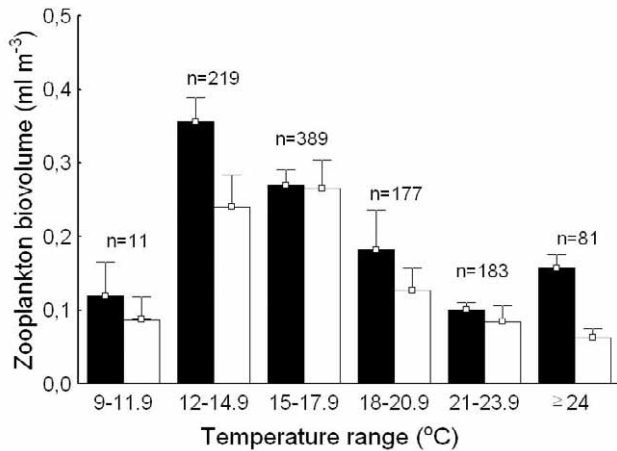


FIG. 6. – Zooplankton biovolume excluding salps (filled bars) and salp biovolume (empty bars) according to ranges of minimum temperature taken from the deepest position of Bongo net hauls (333 μ m mesh size) performed on the SBB between 1975 and 1982 (1062 stations). Filled bars account for planktonic crustaceans and other non-gelatinous taxa. Original data.

biomass accumulation off Cape Frio following the onset of upwelling can be fast, in the scale of hours (Valentin *et al.*, 1986). In addition, food web connectivity towards higher trophic levels seems to be strong in the region because the seasonal signal of the SACW intrusion regime matches the period of higher spawning activity of most nektonic populations. Short-term increases in zooplankton biomass following SACW penetration probably promotes higher survival rates during early life stages of pelagic fish such as sardines (Matsuura, 1996), carangids (Katsuragawa and Matsuura, 1992), and scombrids (Chatwin, 1997). As experimental work on zooplankton feeding and reproductive strategies is still in its infancy in the region, this hypothesis awaits validation.

SACW intrusions are also an important pathway for some fish eggs and larvae moving from oceanic to neritic regions as in the case of *Maurolicus stehmanni*, a typical mesopelagic species that can occasionally be found widespread over the shelf area (Weiss *et al.*, 1988; Ribeiro, 1996). However, Ekman transport may carry eggs and larvae offshore, and depending on the extent of such advective transport, survival and growth rates of the fish larvae could be lowered (Spach, 1990). The only evidence of offshore transport impacting other zooplankton groups in the region are not related to wind-driven circulation, but rather to tidal transport of estuarine decapod larvae towards the shelf (Veloso and Valentin, 1993; Fernandes *et al.*, 2002).

Bakun and Parrish (1990) and Bakun (1996) have discussed the remarkable similarities between

the Brazilian sardine and the California sardine stocks in terms of reproductive strategies. They analyzed the main oceanic processes that may affect the reproductive habitat of coastal pelagic fish in the SBB (wind stress, Ekman transport, wind mixing index, insolation, cloud cover and sea surface temperature). The oceanographic features in this bight, mainly influenced by the large-scale boundary flow of the Brazil Current and associated upwelling regimes, contribute to creating favourable environmental conditions for the spawning activity of the Brazilian sardine in a very similar fashion to the southern California Bight and in other eastern boundary current systems. The reproductive strategy of the Brazilian sardine appears to be in close conformity with the hypotheses that correlate the environmental effects on the reproductive success of small pelagic fishes. Peak spawning occurs during summer, when the enrichment by food particles required for first-feeding larvae (Lasker, 1975) is provided by upwelling together with more frequent periods of weak winds, which help to prevent fine-scale food particle aggregations from being destroyed by wind-induced turbulent mixing. Similar to what is observed in the southern California Bight (Parrish *et al.*, 1981), a closed gyral circulation pattern derived from the main Brazil Current flow may contribute to retaining egg and larvae in the bight, avoiding advection to offshore areas.

Reduction of SACW intrusions may lead to an increase in larval fish mortality. Oceanographic anomalies during the spawning season of 1986/87 were the main cause of the recruitment failure that occurred in the 1987 age class of the Brazilian sardine, and which led to a drastic decrease in spawning stock biomass in subsequent years (Matsuura, 1998). Low egg densities confirmed the decrease in sardine population size again in 1988 and in the spawning season of 1991/1992 (Castello *et al.*, 1991; Matsuura *et al.*, 1992; Cergole, 1995). Studies on nutritional condition of sardine larvae provided further evidence of unfavourable food availability during years of weak SACW intrusions on the continental shelf. This was the case for the 1990/91 and 1991/92 spawning seasons, when 7 to 13% of the larvae were in a weak nutritional condition as estimated by biochemical indicators (Dias, 1995) (Table 1). During summer 1994, when the SACW penetration extended only until the mid-shelf, a more dramatic scenario was depicted off São Sebastião,

TABLE 1. – Percentages of sardine and anchovy larvae in weak feeding and nutritional condition during the peak of the spawning season. Biochemical indicators used to analyze individual fish larvae were tryptic enzyme activity (feeding condition) and RNA/DNA ratio (nutritional condition). Relatively lower percentages of larvae in weak condition occurred during more pronounced summer intrusions of the SACW over the continental shelf (Summer 1992/1993). Data from Dias (1995) and Dias *et al.*, (2004).

		Feeding condition		Nutritional condition	
		N	%	N	%
CONTINENTAL SHELF					
<i>Sardinella brasiliensis</i>	summer 1990/1991	290	12.7	-	-
	summer 1991/1992	110	7.0	-	-
	summer 1992/1993	120	5.8	38	0
<i>Engraulis anchoita</i>	summer 1990/1991	413	23.0	-	-
	summer 1991/1992	433	9.7	-	-
	summer 1992/1993	175	7.4	-	-
INNER COAST					
<i>Sardinella brasiliensis</i>	summer 1994	62	33.3	39	57.9

where 33 and 58% of the larvae were in bad feeding and nutritional conditions respectively (Dias *et al.*, 2004). Moreover, during this season high percentages of dead larvae (24 to 63%) were found.

The nutritional condition of the southern anchovy larvae (*Engraulis anchoita*) off Brazil is related to SACW intrusions in a similar fashion. However, this species occurs throughout the entire year and its distribution seems to be related to other oceanographic features. Freire and Castello (2000) suggested that winter is the favourable foraging season for *E. anchoita* in southern offshore waters. During this season, probability of prey consumption increases because of fertilization effects associated with shelf-break upwelling, strong vertical stability in the water column, and high production in the coastal region. Clemmesen *et al.* (1997) found anchovy larvae in better conditions in the stratified water column, whereas Sieg (1998) suggested that in the case of this species starvation was more significant for larval fish mortality than predation. High percentages (up to 23%) of anchovy larvae in a bad feeding condition occurred in the SSB during austral summers of 1990-1991 and 1991-1992, decreasing to 7.4% in the 1992-1993 summer (Table 1) when the SACW retreated to the outer shelf.

Geographical features such as islands may also influence the oceanic current systems and contribute to retention or dispersive mechanisms for fish egg and larvae. Results of a small-scale study around the São Sebastião island in the southeast coast (Katsuragawa *et al.*, 2006) showed a tendency of fish larvae to concentrate at a particular portion of the study area, coinciding with an increase in nutrient and plankton concentration. Brazilian sardine larvae could have more survival capability due to better

feeding and nutritional condition at this specific area (Dias *et al.*, 2004). The oceanographic structure, including the local current system flowing from southwest to northeast (thus in the opposite direction from the main flow of the Brazil Current), as well as the presence of the island, act together to favour larval and food retention. In addition, SACW intrusions and continental run-off may provide further nutrient inputs to the area (Gianesella-Galvão *et al.*, 1997). This situation may contribute to raising optimal conditions for larval development, leading to a high reproductive success of local fish populations.

As mentioned earlier, the SSS is influenced strongly by the dynamics of the Subtropical Confluence, by the freshwater contribution from Patos Lagoon and La Plata River, and by wind action over the ocean surface (Castello and Möller, 1977; Lima *et al.*, 1996; Garcia, 1997). The importance of these processes to the distribution and abundance of zooplankton and early life stages of fish have been demonstrated by many studies, e.g., Matsuura and Kitahara (1995), Muelbert and Sinque (1996), and Sieg (1998).

Contrasting with the observed high primary production and chlorophyll concentration on the SSS during summer, zooplankton biomass due to copepods and other crustacean plankton is usually low along the entire shelf at this time of the year, except in areas under the direct influence of the continental drainage of Patos Lagoon. Such distribution pattern might be related to negative impacts associated with salp outbreaks in summer (Meneghetti, 1973; Navas-Pereira, 1973; Hubold 1980). On the other hand, high zooplankton biovolumes contributed by copepods and—to a lesser extent—by euphausiids occur during winter and spring on offshore areas

affected by the Subtropical Convergence, and also towards inshore areas under the influence of cold coastal waters advected from the Argentinean shelf (Montú *et al.*, 1998).

Nearshore waters of the SSS are strongly influenced by continental runoff and have low salinity values. This region is dominated by estuarine and coastal species of zooplankton and fish larvae (Montú *et al.*, 1998; Sinque and Muelbert, 1998). Dominant fish larvae in low-temperature waters of the intermediate shelf belong to the anchovy *Engraulis anchoita*. Larval fish diversity increases towards the shelf break (~200 km from the coast) where high-salinity Tropical Waters (TW) from the Brazil Current (BC) dominate. The importance of water column stability, larval transport and retention, as well as enrichment processes for selecting the reproductive habitat of *Engraulis anchoita* was discussed by Lima and Castello (1995).

Several fish species in southern Brazil are dependent on the Patos Lagoon as a nursery ground, especially *Micropogonias furnieri*, *Lycengraulis grossidens*, *Brevoortia pectinata* and *Mugil* spp. (Muelbert and Weiss, 1991; Sinque and Muelbert, 1998). The transport of fish eggs and larvae is related to variations in local circulation patterns of coastal currents (Muelbert and Weiss, 1991; Vieira and Scalabrin, 1991). Most of this variability is determined by the dynamics of freshwater outflow from the lagoon and wind-induced penetration of seawater into the estuary (Costa *et al.*, 1988). Busoli (2001) has demonstrated that when freshwater outflow increases, recirculation cells provide a mechanism for concentration and retention of anchovy eggs and larvae. During periods of low freshwater influence, shelf circulation is predominantly northwards and the area becomes unfavourable for larval retention. Recent evidences suggest that anomalous periods of freshwater outflow, linked to ENSO events, have a profound effect on the diversity of young fish in the Patos Lagoon estuary (Garcia *et al.*, 2001).

CONCLUDING REMARKS

Zooplankton investigations conducted in the study area have provided a notion on how water mass distribution affects species composition and density patterns along relatively coarse temporal and mesoscale gradients (coast-ocean, north-south,

summer-winter, etc.). Detailed information on physical-biological coupling is still lacking because zooplankton sampling strategies failed to cover spatial and temporal scales relevant to key physical processes such as SACW intrusions, shelf-break upwelling associated with eddies and meanders of the Brazil Current, and CCW advection towards northern areas. In addition to implementing more refined sampling methods, there is an urgent need for experimental work on dominant zooplanktonic species in order to estimate basic process rates such as ingestion, egestion, growth, and mortality in the study area (Lopes *et al.*, 2005). These measurements are critical in order to understand food web dynamics, including the relationships between fish spawning and planktonic food availability.

The influence of oceanographic processes on larval fish development, distribution, abundance, dietary composition, and preferred spawning periods has been reasonably well investigated in the case of pelagic species such as sardines, anchovies, scombrids and carangids. However, similar studies with other species must be encouraged. Studies on the interaction between physical processes and ichthyoplankton are important in order to obtain more information on ecological and oceanographic aspects of the early life history of fish and a more adequate understanding of the variability of recruitment of fishery resources (Castello and Haimovici, 1991; Heath, 1992).

Eddies and frontal processes are regarded as important mechanisms for retention and concentration of zooplankton and fish larvae towards the shelf (Lima and Castello, 1995). However, there is still very little knowledge about transport processes along the shelf break in this region. Understanding the mechanisms and degree of interchange between neritic and oceanic domains should help to clarify the dynamics of plankton communities and recruitment to fishery stocks of pelagic species.

ACKNOWLEDGEMENTS

We thank M. L. Zani Teixeira and K. Suzuki for their continuous technical assistance during the course of our studies, and particularly in the preparation of this manuscript. Dr. M. Pilar Olivar (Institut de Ciències del Mar - CSIC) and two anonymous reviewers gave many useful suggestions that helped to improve the initial version of the text.

Authors RML and JHM acknowledge the Brazilian funding agency CNPq for financial support (grants 308055/2004-7 and 305969/2003-0 respectively).

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Scient. ed: M.P. Olivar

Received October 6, 2004. Accepted September 14, 2005.