



Research papers

Distribution of planktonic cnidarians in response to South Atlantic Central Water intrusion in the South Brazilian Bight

Miodeli Nogueira Júnior ^{a,*}, Frederico P. Brandini ^b, Juan C.U. Codina ^a^a Programa de Pós-Graduação em Zoologia, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná 81531-980, Brazil^b Instituto Oceanográfico, Universidade de São Paulo, Praça do Oceanográfico 191, Cidade Universitária, São Paulo, SP 05508-120, Brazil

ARTICLE INFO

Article history:

Received 21 January 2013

Received in revised form

26 February 2014

Accepted 28 February 2014

Available online 18 March 2014

Keywords:

Medusae

Siphonophores

South Atlantic Central Water

Oceanic bottom intrusion

ABSTRACT

Five oceanographic cruises were made between November 2005 and June 2006, sampling a cross-shelf transect off the South Brazilian Bight (SBB; 26°46'S) to follow the seasonal development of the South Atlantic Central Water (SACW) intrusion over the shelf and its influence on the assemblage of planktonic cnidarians. An onshore wind-driven bottom intrusion of the SACW was clearly perceptible, reaching the coast in January. From March onward, the SACW influence was gradually displaced seaward due to wind and tidal mixing. By late June the SACW influence was offshore and the inshore was dominated by low-salinity waters (< 34.5). The abundance, distribution, and general taxonomic composition of both medusae and siphonophores were strongly influenced by the onshore intrusion of the SACW. An inshore-offshore gradient was clear. The Canonical Correspondence Analysis suggested that coastal species – dominated by *Liriope tetraphylla*, actinula larvae and *Muggiaeae kochi* – were mostly related to food availability and a vertically mixed environment inshore, and their abundance and extent were reduced during intrusion periods. In contrast, species with offshore affinities tended to increase their abundance and distribution during intrusion periods, and were mostly related to the presence of thermal stratification and a deep chlorophyll maximum layer. Most of these offshore species, such as *Aglaura hemistoma*, *Rhopalonema velatum* and many calyptophorans, are associated with the warm upper layer. However, high concentrations of large (> 20 mm in diameter) *Solmaris corona* were observed exclusively in cold waters, suggesting this medusa is a SACW indicator.

© 2014 Elsevier Ltd. All rights reserved.

1. Introduction

Wind-driven bottom intrusions of oceanic water over the continental shelf are a typical oceanographic feature of western boundary current systems, which fertilize these ecosystems periodically, sustaining high phytoplankton production that may propagate up the food chain (Brandini, 1990; Lohrenz and Castro, 2006; Longhurst, 2006). The South Brazilian Bight (SBB) is a typical western boundary current ecosystem with a wide shelf, up to 200 km, where three water masses determine the predominant environmental conditions (Matsuura, 1986; Castro et al., 1987, 2006a, 2006b): (i) the less-saline Coastal Water (CW), (ii) the warm (> 20 °C), saline, and oligotrophic Tropical Water (TW), and (iii) the deep, cold (< 18 °C) and nutrient-rich South Atlantic Central Water (SACW). The configuration of these water masses is regulated by the seasonal wind pattern and the dynamics of the Brazil Current (BC) flowing over the shelf break. The TW and

SACW are typically located in the outer shelf (> 100 m). During summer, the prevailing northeast winds cause Ekman transport of surface waters offshore, with a consequent onshore bottom intrusion of the SACW, which may be enhanced by cyclonic eddies and meandering of the BC along the continental slope (Matsuura, 1986; Brandini, 1990; Castro and Miranda, 1998; Castro et al., 2006a, 2006b).

These mesoscale oceanic intrusions cause striking alterations in the pelagic environment over the SBB shelf, with important biological consequences; most of the phytoplankton production away from the continental runoff is dependent on input of nutrients from these intrusions (Brandini, 1990; Gaeta and Brandini, 2006); during the intrusions copepod biomass and production are enhanced (Miyashita et al., 2009). Planktonic cnidarians are primarily carnivorous, preying on zooplankton and/or ichthyoplankton at high rates, and commonly impacting fish stocks through competition or direct predation (Mackie et al., 1987; Mills, 1995; Pagès et al., 2001). Therefore, their importance to the community structure and energy transfer in the pelagic realm may be generally assumed to be high. They are distributed according to water masses and food availability (e.g., Mackie et al., 1987; Pagès and Gili, 1991, 1992). Mesoscale advective processes also influence their assemblages (Gili et al., 1991; Pagès, 1992; Pagès and Gili, 1992).

* Corresponding author. Present address: Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, Cidade Universitária, João Pessoa, Paraíba 58051-900, Brazil. Tel.: +55 83 32167770.

E-mail address: miodeli@gmail.com (M. Nogueira Júnior).

Therefore, SACW bottom intrusions and associated biological changes in the SBB environment are expected to be followed by changes in the cnidarian fauna.

The large (> 30 mm) hydromedusae *Olindias sambaquiensis* and *Rhacostoma atlanticum* may reach high biomasses over the shelf during intrusion periods (Mianzan and Guerrero, 2000). However, understanding the distributional patterns of planktonic cnidarians in relation to the hydrographic regime is challenging because of the limited knowledge of the ecology of the group. Apart from the study by Mianzan and Guerrero (2000), who used large mesh sizes (1 mm in the code end) and therefore focused on larger species, it has been more than two decades since the last published oceanographic-oriented field studies on planktonic cnidarians were carried out on the continental shelf off the SBB. Most of these studies had poor spatial or seasonal coverage relevant to the scale of the seasonal SACW intrusion, i.e., were limited to a few cruises and/or shallow waters, and their samples were not stratified (Vannucci, 1957, 1963; Moreira, 1973; Abreu and Nogueira, 1989; Cordeiro and Montú, 1991; Nogueira and Oliveira, 1991).

Most zooplankton investigations in Brazilian shelf systems have focused on herbivorous copepods because of their high abundance and direct link to fishery food webs (Brandini et al., 1997; Lopes et al., 2006). In addition, the body fragility and poor preservation of these organisms lead to difficulties in precise identification, which may have prevented further studies on cnidarians in the SBB. At the best, this group was included in the general term "hydromedusae" or "siphonophores" in tabular lists of plankton collections. In this study we attempt to increase the knowledge of coupling the planktonic cnidarians abundance and composition and the hydrographic dynamics in the SBB. We sampled across the shelf through the seasonal cycle to address the following questions: (i) how summer intrusions of the SACW influence the taxonomic composition, abundance and distribution of medusae and siphonophores, and (ii) how the dominant cnidarian species are related to the physical and biological environment.

2. Material and methods

2.1. Field surveys and laboratory analyses

Between November 2005 and June 2006, five oceanographic cruises were conducted with the support of the R.V. "Soloncy Moura" along a cross-shelf transect off Itajaí, Santa Catarina State, Brazil ($26^{\circ}46'S$; 10–12 November 2005; 16–18 January 2006; 14–16 March 2006; 19–21 April 2006 and 20–22 June 2006). During these cruises, 15 stations positioned between the 20- and 140-m isobaths were sampled (Fig. 1). At each station, vertical profiles of temperature and salinity were obtained with an InterOcean Systems CTD coupled S4P current meter, and of chlorophyll with a Biospherical Instruments PNF-300 Profiling Natural Fluorometer System. In November 2005 salinity was not measured due to technical failures of the equipment, and the temperature was obtained from the PNF sensor. Wind data were provided by the Centro de Informações Ambientais e de Hidrometeorologia de Santa Catarina (EPAGRI/CIRAM), located in Itajaí, near the transect. Temperature stratification (TSI) and chlorophyll heterogeneity (CHI; Richardson, 2005) indices were calculated for each station.

Zooplankton was sampled with vertical hauls using a WP2 net (200 µm mesh) with a closing mechanism. A total of 123 hauls were made. At the inner-shelf stations (< 50 m) a single haul was made, from near the bottom to the surface. Between the isobaths of 50 and 90 m, two depth strata were sampled, through the upper mixed layer above the thermocline (UML), and through the bottom

layer below the thermocline (BL). Offshore from the 90-m isobath, three depth strata were sampled: the UML, the BL, and an intermediate stratum encompassing the thermocline and its associated deep chlorophyll maximum layer. All organisms were transferred to polyethylene bottles and fixed with a 4% formaldehyde solution.

In laboratory, whole samples were analyzed under a stereomicroscope and all specimens were identified (mainly following Bouillon, 1999 and Bouillon et al., 2004), and counted. Based on the length (m) of the haul, the opening of the net and assuming 100% filtering efficiency of the net, abundances were standardized as numbers of individuals per 10 m^{-3} for medusae and numbers of colonies per 10 m^{-3} for siphonophores. For calycophorans, the number of anterior nectophores was used for estimating the polygastric stage abundance, and eudoxid bracts were enumerated for the eudoxid stage abundance (e.g., Hosia and Bamstedt, 2007; Hosia et al., 2008). For physonects, numbers of pneumatophores were used; when these were not available the numbers of colonies were roughly estimated by dividing the number of nectophores by 10 (Pugh, 1984). The abundances of other zooplankton groups, potential prey for the cnidarians, were calculated from 1/4 to 1/32 aliquots, until at least 300 individuals were counted.

2.2. Statistical analysis

With the software CANOCO 4.5, a canonical correspondence analysis (CCA) was used to evaluate associations between the most abundant cnidarian species and the environmental characteristics. This method offers an integrated description of the relationship between the species and the explanatory variables measured (Ter Braack, 1986; Palmer, 1993; McCune, 1997). It essentially maximizes the dispersion of the species (and samples) along axes that represent linear combinations of the environmental variables (Ter Braack, 1986). Both abiotic and biological environmental parameters were included as possible explanatory variables: mean temperature and chlorophyll in the different strata sampled; distance from the coast; TSI; CHI; integrated chlorophyll; and abundance of copepods, cladocerans, decapod larvae, ostracods, and polychaetes. Before the analysis, explanatory variables were centered (mean=0) and standardized (SD=1) to express them on the same scale, and species data were square-root transformed. A Monte Carlo randomization procedure, a routine available in the CANOCO software, was used to test if each of the explanatory variables might significantly ($p < 0.05$ after 999 runs) clarify a fraction of the observed variation. Only significant variables were included in the model.

3. Results

3.1. Environmental dynamics

Seasonal shifts in the oceanographic conditions over the shelf due to the summer bottom intrusion of the cold SACW and the winter overturn of the water column in the nearshore could be clearly perceived throughout the study period (Fig. 2). The shoreward limit of the intrusion can be determined by the bottom insertion of the deep thermal front (DTF, sensu Castro et al., 1987). Areas shallower than the DTF remain vertically mixed due to tidal circulation, whereas the side located outward of the front is constantly stratified (Castro et al., 2006a, 2006b). In November, the DTF was positioned over the 80 m isobath, reaching the inner shelf by January when NE winds predominated (Fig. 2). Temperature ranged from < 16 °C in bottom layers dominated by the SACW to > 26 °C in the UML (Fig. 2). Salinity ranged from 33 near the coast to > 37 offshore in the upper layers dominated by TW. In January the halocline was well defined in the upper 30 m of the

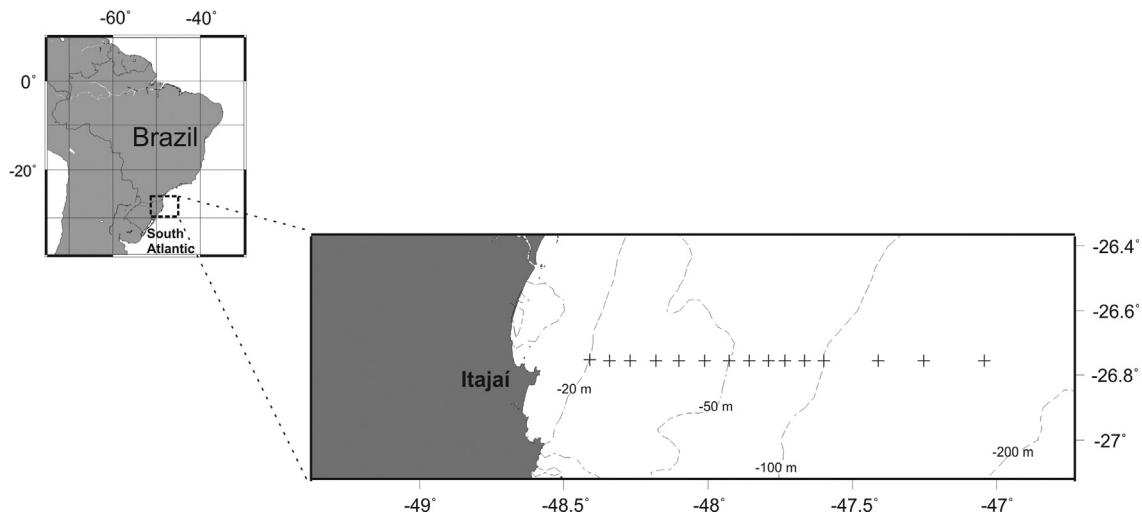


Fig. 1. Map of the cross-shelf transect sampled between November 2005 and June 2006, showing the sampling stations (crosses) and the location off Brazil.

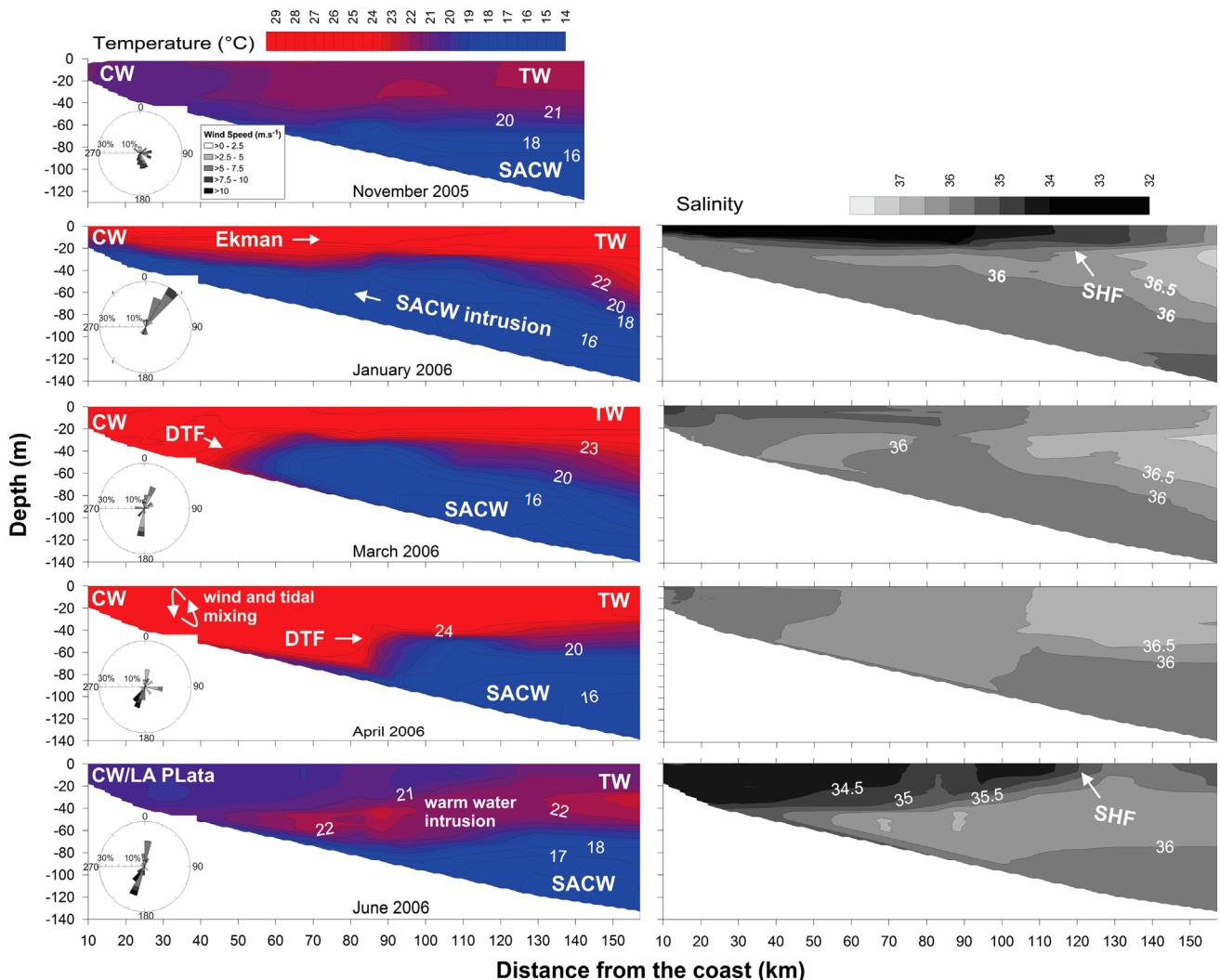


Fig. 2. Cross-shelf profiles of temperature ($^{\circ}\text{C}$), and salinity off Santa Catarina, South Brazilian Bight, between November 2005 and June 2006. Wind persistence (%) and speed (m s^{-1}) are shown in the temperature profiles (modified from Brandini et al., 2014). CW=Coastal Water; TW=Tropical Water; SACW=South Atlantic Central Water; DTF=deep thermal front (*sensu* Castro et al., 1987); SHF=surface haline front (*sensu* Castro et al., 1987).

water column until the mid-shelf, where it forms the Surface Haline Front (SHF *sensu* Castro et al., 1987) that separates coastal waters from the TW of the Brazilian Current. From March onward,

tidal and wind mixing gradually displaced the DTF seaward. By late June the SACW influence was again restricted to outside the 80 m isobath, and water with low salinity (< 34.5) dominated

inshore (Fig. 2). This probably resulted from the lateral advection of waters from the La Plata River pushed northward by the persistence of southerly winds typical of winter (Möller et al., 2008). The influence of this low-salinity water mass extended more than 100 km offshore (Fig. 2).

3.2. Planktonic cnidarian dynamics

A total of 35 medusae and 22 siphonophore taxa were found, as well as polyps, and unidentified larval forms such as actinula, bitentaculata, ephyrae, and athorybia. Among medusae, *Liriope tetraphylla* and actinula larvae dominated (46.6% and 21.6% respectively), and *L. tetraphylla* was almost always the most abundant species, except in March. Others including *Solmaris corona*, *Aglaura hemistoma*, *Corymorphia gracilis* and Rhopaloniematidae sp. 1 were also abundant in samples from at least one of the cruises (Table S1 in Supplementary material). Among siphonophores, *Diphyes bojani* and *Muggiae kochi* were the most abundant (37.3% and 34.7% respectively), alternating in dominance in the different cruises. In addition to them, *Bassia bassensis*, *Abylopsis tetragona*, *Abylopsis eschscholtzii* and *Enneagonon hyalinum* accounted for more than 5% of the number of individuals in at least one of the five cruises (Table S2 in Supplementary material).

Medusae species richness (up to 12 species per sample) and abundance (up to 2450 ind. 10 m^{-3}) were higher on the inner shelf up to the 60-m isobath in all cruises (Figs. 3 and 4). High values

were also found farther offshore in June, mainly following the predominance of the CW. Medusae were less diverse and abundant during intrusion periods (Figs. 3 and 4), and reached their highest values in November and June when the influence of the SACW was limited to more offshore waters. This general pattern reflects the distribution of the dominants *L. tetraphylla* (up to 2312 ind. 10 m^{-3}) and actinula larvae (up to 659 ind. 10 m^{-3}). The former was widespread, occurring over the entire shelf, but clearly associated with CW, while the latter was exclusive to the CW, almost disappearing when the SACW reached the inner shelf in January (Fig. 5). Other common medusae such as *Corymorphia gracilis* also predominated in November in coastal waters (up to 250 ind. 10 m^{-3}), and were less abundant over the middle shelf and rare over the outer shelf or under the influence of cold water (Fig. 6).

A few common medusae species had different distribution patterns; *S. corona* occurred in low abundances ($< 35\text{ ind. }10\text{ m}^{-3}$) of small individuals (1–5 mm in diameter) over the inner shelf during November and June; and low (January) to high (March) densities (up to 838 ind. 10 m^{-3}) of large medusae ($> 20\text{ mm}$ in diameter) were found offshore in association with the SACW (Fig. 5). *A. hemistoma* was less common in deeper layers under the SACW influence, otherwise it was spread over the entire shelf (up to 100 ind. 10 m^{-3}), except in January when it was almost restricted to offshore waters (Fig. 6). Rhopaloniematidae sp. 1 was found nearly exclusively during the June cruise, between the 35- and 120-m isobaths throughout the water column (up to 78 ind. 10 m^{-3} ; Fig. 6).

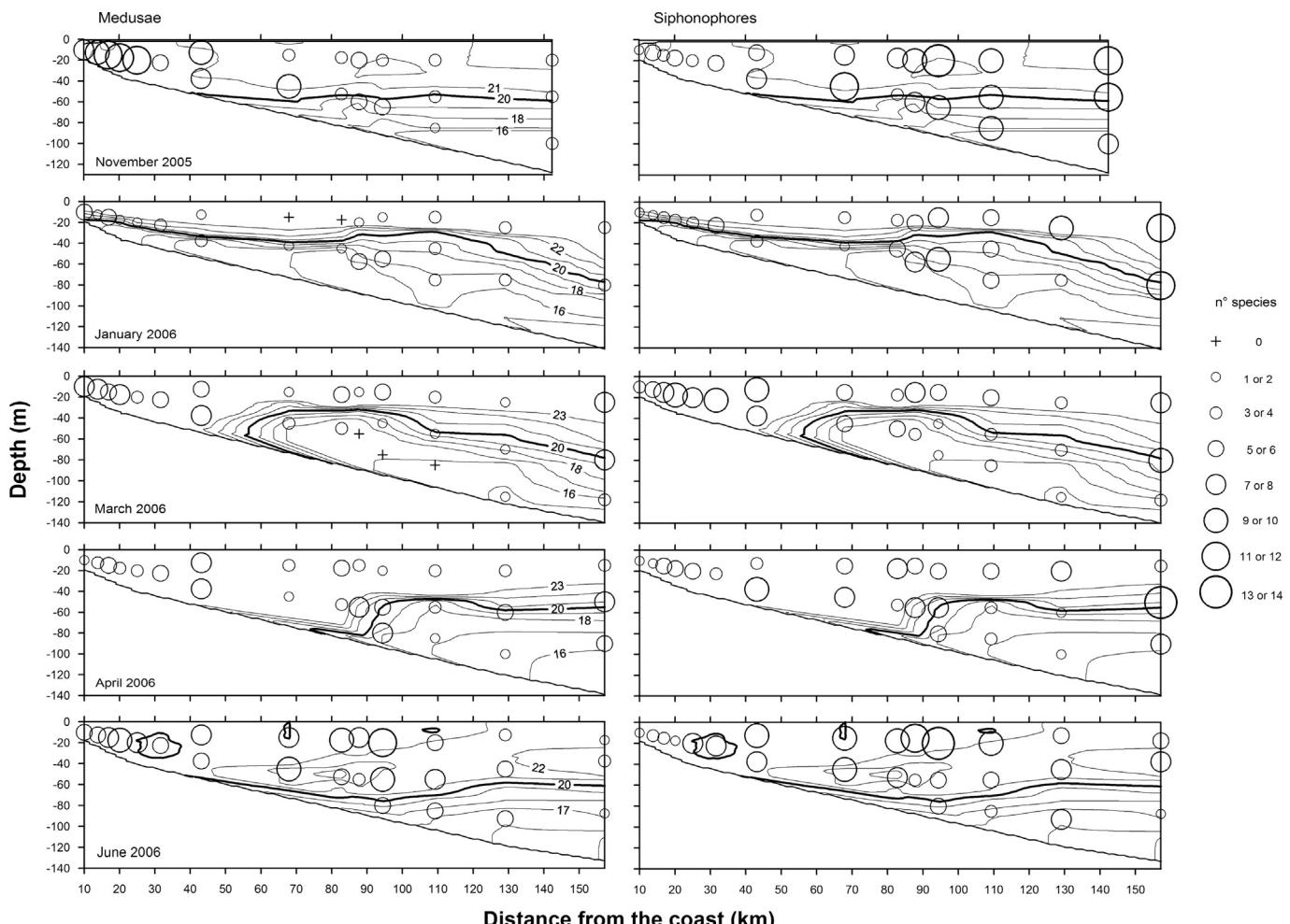


Fig. 3. Number of species of medusae and siphonophores off Santa Catarina, South Brazilian Bight, between November 2005 and June 2006, overlaid on the temperature ($^{\circ}\text{C}$) profile. The bold line indicates the $20\text{ }^{\circ}\text{C}$ isotherm which differentiates between colder South Atlantic Central Water and Tropical Water (Castro et al., 2006a, 2006b).

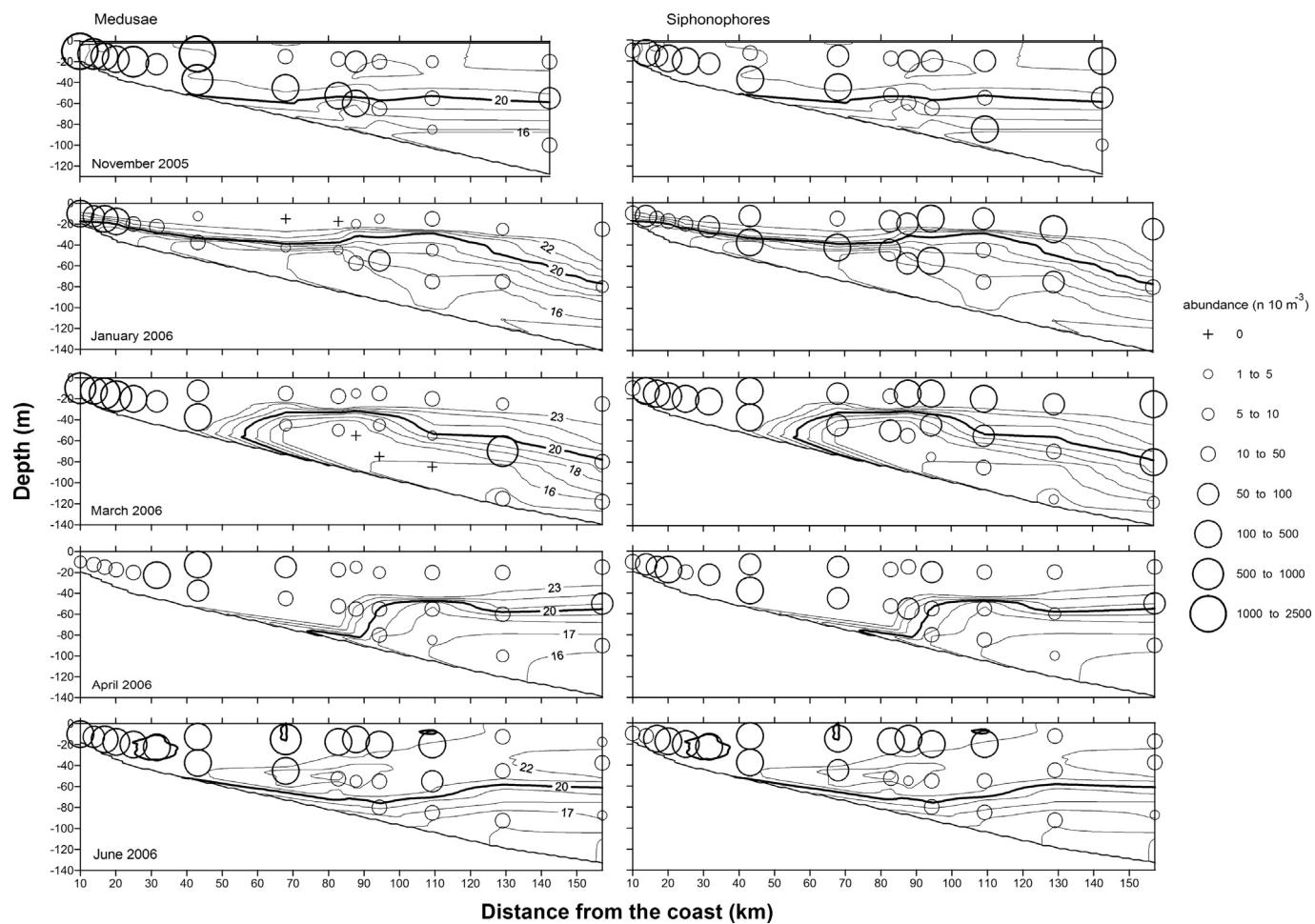


Fig. 4. Abundance ($n 10 m^{-3}$) of total medusae and siphonophore populations off Santa Catarina, South Brazilian Bight between November 2005 and June 2006, overlaid on the temperature ($^{\circ}C$) profile. The bold line indicates the $20^{\circ}C$ isotherm which differentiates between colder South Atlantic Central Water and Tropical Water (Castro et al., 2006a, 2006b).

Siphonophores were more diverse (up to 14 spp.) and abundant (up to $313 \text{ col. } 10 m^{-3}$) on the mid- to outer shelf. Typically few (< 5) species were found at the coastal stations, although high (up to $234 \text{ col. } 10 m^{-3}$), almost monospecific, densities could be found on the inner shelf (Figs. 3 and 4). The two most abundant species, *D. bojani* and *M. kochi*, were widespread over the shelf, but with different spatial and seasonal preferences. The former was more abundant (up to $243 \text{ col. } 10 m^{-3}$) when the influence of the SACW over the shelf increased, between January and April, mainly between 40 and 110 km offshore. *M. kochi* was less abundant with the SACW influence toward the coast, reaching its highest abundances (up to $234 \text{ col. } 10 m^{-3}$) in November and July in the most coastal stations up to 40 km offshore, and becoming scarce farther offshore (Fig. 7).

Most of the other siphonophore species were more typically found over the middle and outer shelf, associated with warm waters (Figs. 7 and 8). *B. bassensis* was widespread on all cruises, without pronounced seasonal variation, and was typically more abundant at the isobaths > 70 m (up to $40 \text{ col. } 10 m^{-3}$). *A. tetragona* and *E. hyalinum* were almost absent from the innermost stations, with high densities of the former (up to $92 \text{ col. } 10 m^{-3}$) in the lower layers under the influence of the cold SACW. *A. eschscholtzi* (up to $21 \text{ col. } 10 m^{-3}$) was less abundant in January, when it was found mainly offshore. In the other cruises it occurred all across the transect, but was less common in the lower layer under the SACW influence (Fig. 8).

The CCA showed significant ($p=0.001$) associations between environmental characteristics and the abundance of the 26 most

abundant planktonic cnidarians. According to the Monte Carlo routine, cnidarian distribution was unrelated ($p > 0.05$) to integrated chlorophyll, mollusks, polychaetes, decapods and ostracods. Therefore these variables were not included in the analysis. The variance explained by the selected variables was 38.7%, and 35.3% was explained by the first four axes (Table 1).

Species were distributed throughout the plane defined by axes 1 and 2 according to their affinities to the parameters included in the analysis. Therefore species located close to axis origins such as *A. hemistoma*, *Cordagalma ordinata*, *Nanomia bijuga*, *Rhopalone-matidae* sp. 1, and *Sphaeronectes köllikeri* showed a low or variable association with these parameters (Fig. 9). The first CCA axis explained 18.8% of the variation in species abundance, and was positively correlated with distance from the coast, TSI and CHI, and negatively with copepods and cladocerans. The second CCA axis explained 10.2% of the species variation, and correlated negatively with temperature and positively with chlorophyll (Table 1; Fig. 9). Thus, species such as *S. corona* and *A. tetragona* were associated with lower temperatures, and increasing distance from the coast and TSI; while others such as *Eudoxoides spiralis*, *A. eschscholtzi*, and *B. bassensis* were associated with higher temperatures and distance from the coast. *D. bojani*, *Proboscidactyla ornata* and *Chelophyes appendiculata* were mainly related to distance from the coast and CHI, while *L. tetraphylla*, *M. kochi*, *C. gracilis*, *Clytia* spp., *Obelia* spp. and actinula larvae were mainly negatively associated with distance from the coast, CHI and TSI, and positively with copepods and cladocerans (Fig. 9).

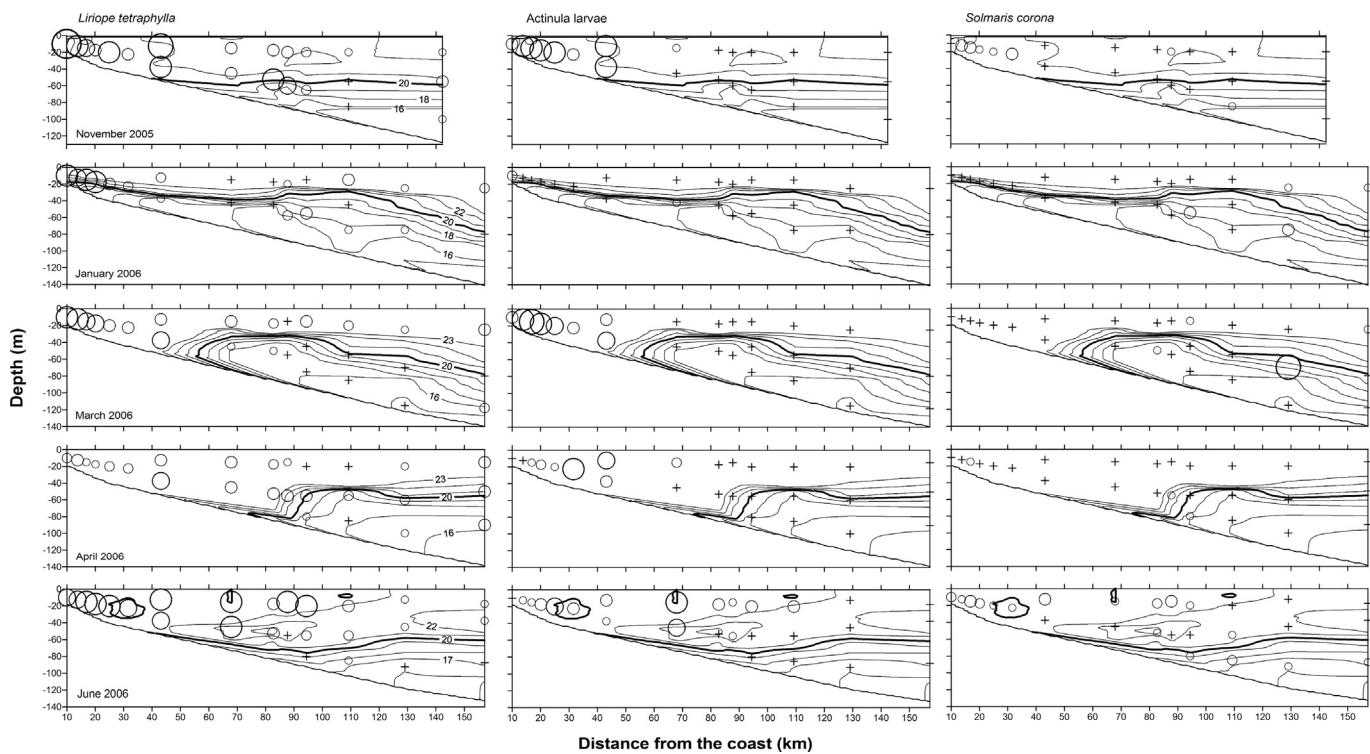


Fig. 5. Abundance ($n \text{ } 10 \text{ m}^{-3}$) of the hydromedusae *Liriope tetraphylla*, actinula larvae, and *Solmaris corona* off Santa Catarina, South Brazilian Bight, between November 2005 and June 2006, overlaid on the temperature ($^{\circ}\text{C}$) profile. The bold line indicates the 20°C isotherm which differentiates between colder South Atlantic Central Water and Tropical Water (Castro et al., 2006a, 2006b). Abundance classes as in Fig. 4.

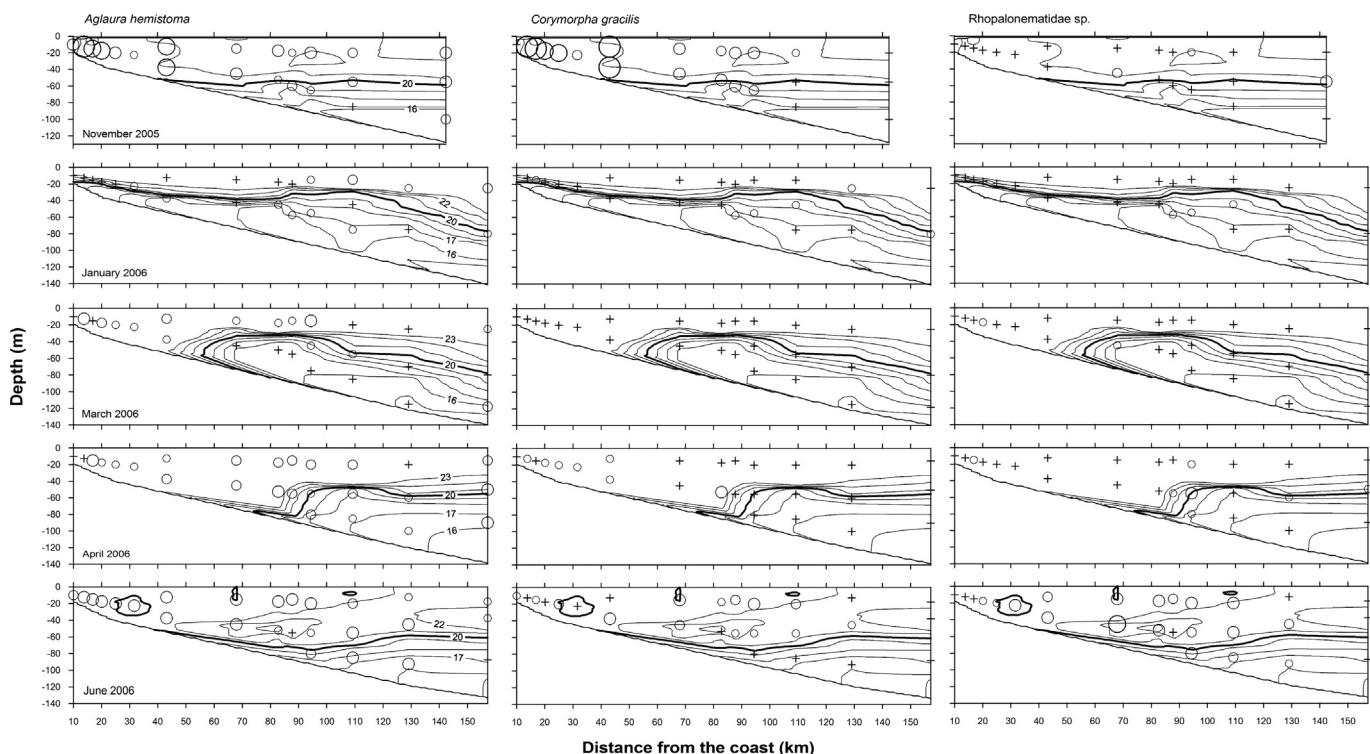


Fig. 6. Abundance ($n \text{ } 10 \text{ m}^{-3}$) of the hydromedusae *Aglaura hemistoma*, *Corymorphidae sp.*, and *Rhopalonematidae sp.* off Santa Catarina, South Brazilian Bight, between November 2005 and June 2006, overlaid on the temperature ($^{\circ}\text{C}$) profile. The bold line indicates the 20°C isotherm which differentiates between colder South Atlantic Central Water and Tropical Water (Castro et al., 2006a, 2006b). Abundance classes as in Fig. 4.

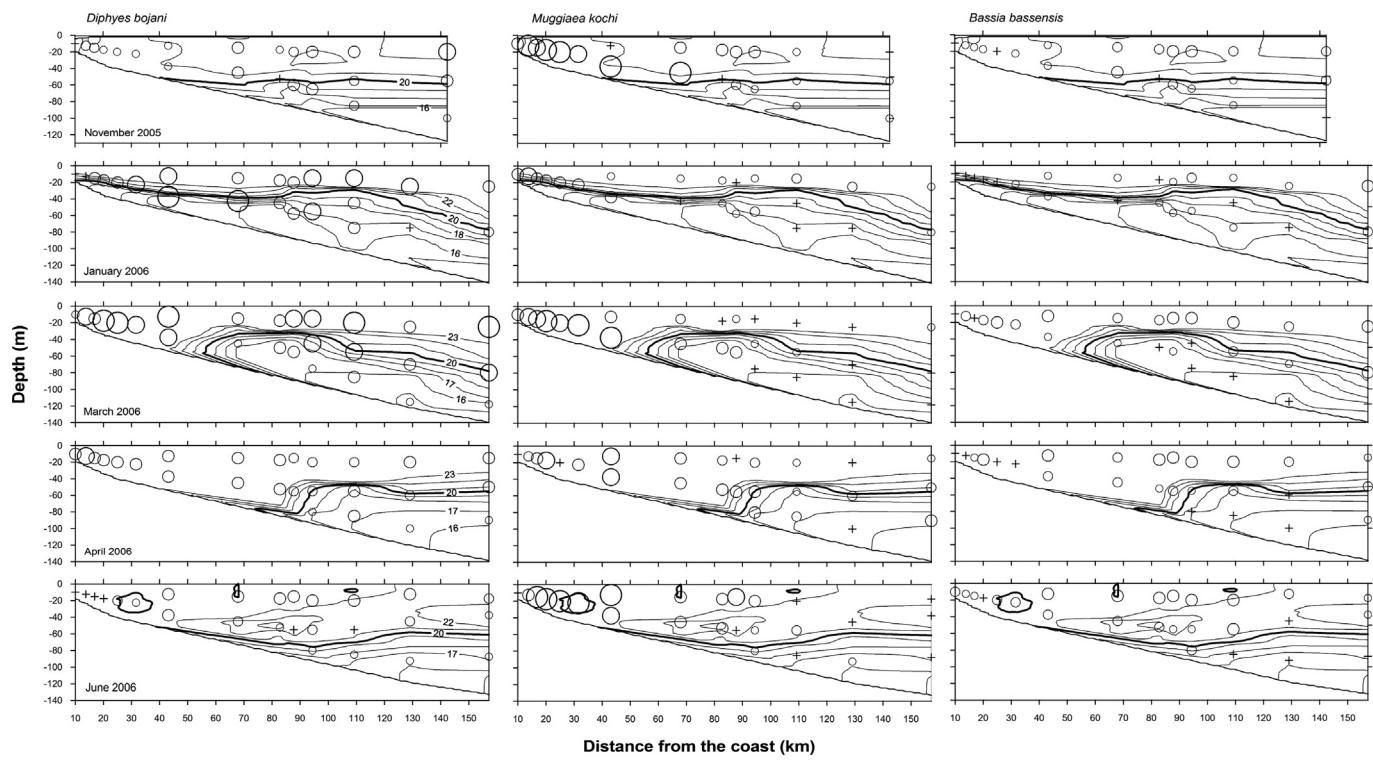


Fig. 7. Abundance ($\text{col. } 10 \text{ m}^{-3}$) of the siphonophores *Diphyes bojani*, *Muggiaeae kochi*, and *Bassia bassensis* off Santa Catarina, South Brazilian Bight, between November 2005 and June 2006, overlaid on the temperature ($^{\circ}\text{C}$) profile. The bold line indicates the 20°C isotherm which differentiates between colder South Atlantic Central Water and Tropical Water (Castro et al., 2006a, 2006b). Abundance classes as in Fig. 4.

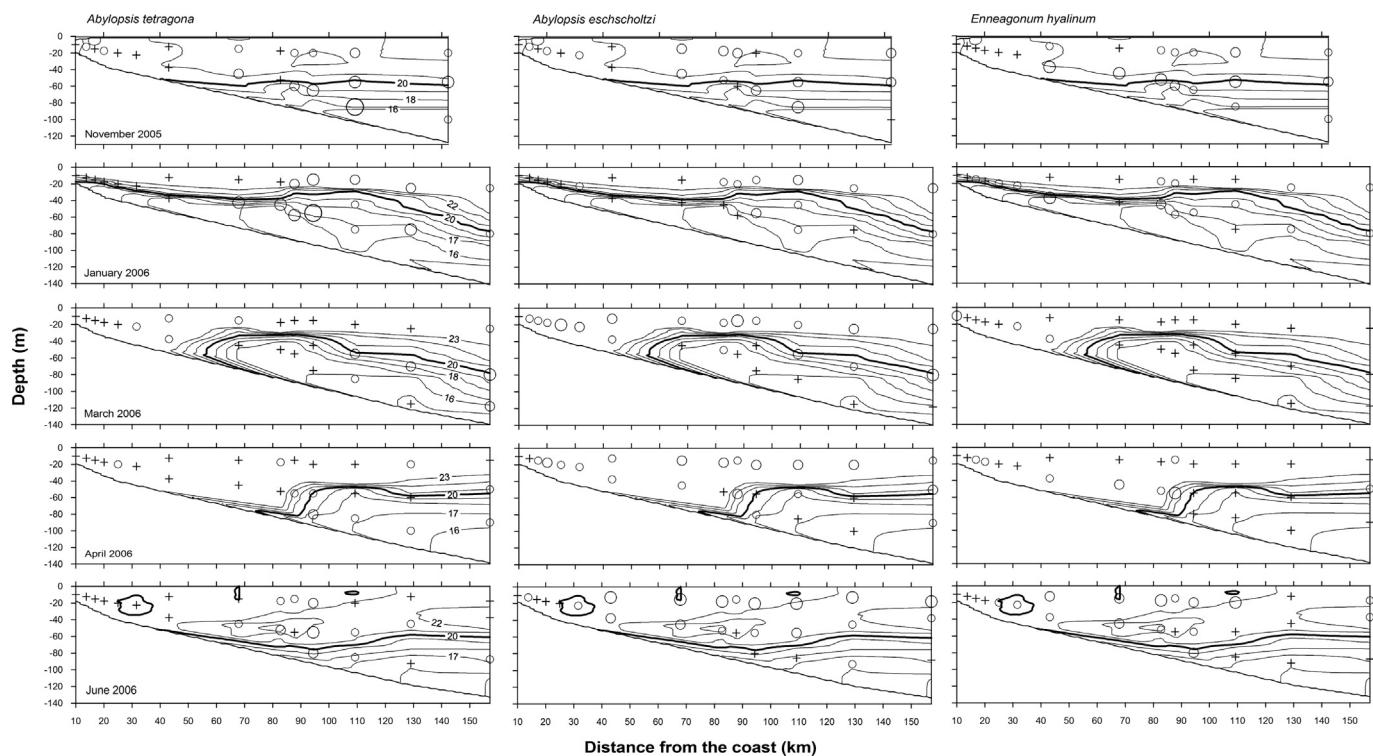


Fig. 8. Abundance ($\text{col. } 10 \text{ m}^{-3}$) of the siphonophores *Abylopsis tetragona*, *A. eschscholtzi*, and *Enneagonum hyalinum* off Santa Catarina, South Brazilian Bight, between November 2005 and June 2006, overlaid on the temperature ($^{\circ}\text{C}$) profile. The bold line indicates the 20°C isotherm which differentiates between colder South Atlantic Central Water and Tropical Water (Castro et al., 2006a, 2006b). Abundance classes as in Fig. 4.

Table 1

Results of the Canonical Correspondence Analysis performed between environmental variables and the 26 most abundant planktonic cnidarian taxa.

CCA summary	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.258	0.106	0.053	0.033
Species-environmental correlations	0.901	0.826	0.628	0.512
% Of variance explained (species data)	18.8	10.2	4.3	2.0
Accumulated variance (%)				
Of species data	18.8	29.0	33.3	35.3
Of species-environmental variables	50.7	72.3	83.1	89.8
Correlations of environmental variables				
Distance from the coast	0.891	-0.105	-0.388	-0.074
Temperature stratification index	0.845	0.298	0.273	-0.254
Temperature	-0.160	-0.730	0.604	-0.170
Cladocerans	-0.588	0.121	0.038	-0.064
Copepods	-0.577	0.292	0.216	-0.398
Chlorophyll stratification index	0.539	-0.102	0.332	0.549
Chlorophyll	-0.250	0.416	0.553	0.306

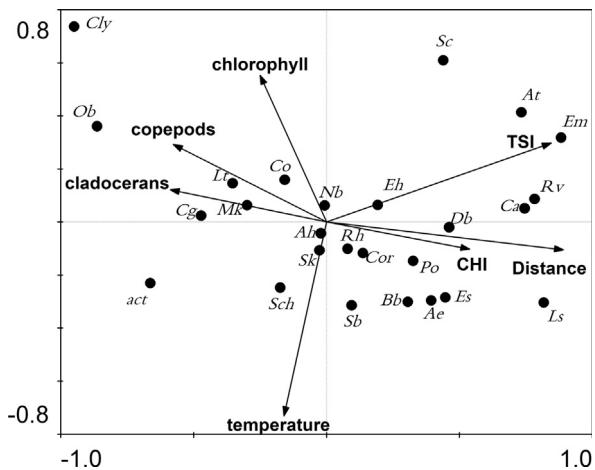


Fig. 9. Ordination plot of the first and second axes of the Canonical Correspondence Analysis between the 26 most abundant planktonic cnidarian species (circles) and the selected explanatory variables (vectors). Species codes: act=actinula larvae; Ae=Abylopsis eschscholtzii; Ah=Aglaura hemistoma; At=Abylopsis tetragona; Bb=Bassia bassensis; Ca=Chelophyses appendiculata; Cg=Corymorphia gracilis; Cly=Clytia spp.; Co=Cunina octonaria; Cor=Cordagalma ordinata; Db=Diphyes bojani; Em=Eudoxoides mitra; Eh=Enneagonum hyalinum; Es=Eudoxoides spiralis; Ls=Lensis subtilis; Lt=Liriope tetraphylla; Mk=Muggiaea kochii; Nb=Nanomia bijuga; Ob=Obelia spp.; Po=Proboscidactyla ornata; Rh=Rhopalonematidae sp. 1; Rv=Rhopalonema velatum; Sb=Solmundella bitentaculata; Sc=Solmaris corona; Sch=Sulculeolaria chuni; and Sk=Sphaeronectes köllikeri. Codes for environmental variables: CHI=chlorophyll heterogeneity index; TSI=temperature stratification index; and distance=distance from the coast.

4. Discussion

Our study showed that the coast–ocean gradient of environmental factors is clearly perceptible and is an important driver of planktonic cnidarians, as observed elsewhere for other assemblages (Gili et al., 1988; Pagès and Gili, 1991, 1992; Pagès et al., 2001). As suggested by our data, this gradient can be particularly important on a wide shelf such as the SBB (up to ~200 km). As shown by the CCA, the factors that most influenced the cnidarian distribution, abundance, and species composition across the shelf were TSI, CHI, temperature, and prey availability (Fig. 9). These first two indices are indicative of the presence of a three-layered system: an upper mixing layer, an intermediate thermocline with a deep chlorophyll maximum, and a cold bottom layer, indicative of the SACW presence.

The cnidarian assemblage studied here is typical of the SBB, mostly dominated by coastal species from tropical and subtropical waters (Vannucci, 1957, 1963; Bouillon et al., 2004), which closely

overlap the distribution of copepods and cladocerans, their potential prey. The high biomass of zooplankton on the inner shelf year-round (Lopes et al., 2006; Miyashita et al., 2009) possibly contributes to the development of dense cnidarian populations in the nearshore stations. The salinities <35 at the inner-shelf stations may restrict most siphonophore species, which are typically oceanic and sensitive to diluted waters (Mackie et al., 1987); *M. kochii* and *N. bijuga* are one of the few common and abundant siphonophores in nearshore environments, and they may even be found inside estuaries in salinities down to nearly 20 (Nogueira Júnior, 2012). Other aspects also differ sharply between the nearshore and offshore pelagic environments, including a typically stratified three-layered ecosystem in offshore areas versus a vertically mixed water column inshore, and a diatom-based food chain inshore versus phytoplankton offshore (Castro et al., 2006a; Gaeta and Brandini, 2006).

The clearly contrasting general distribution patterns of medusa and siphonophore abundance and species richness (Figs. 3 and 4) may be related to their life cycles. While most medusae are meroplanktonic with a typical benthic polypoid stage (the Hydroidolina), siphonophores and Trachyline medusae are holoplanktonic (Bouillon et al., 2006). Holoplanktonic species numerically dominated in both coastal (e.g., *L. tetraphylla* and *M. kochii*) and offshore (e.g., *D. bojani*, *A. tetragona*, *S. corona*) areas, with higher diversity offshore. In contrast, meroplanktonic species such as *Corymorphia forbesi*, *Obelia* spp., *Clytia* spp., *Cirrhovenia tetraneura*, *Stauridiosarsia reesi*, *Eucheilota* spp., and *Aglauropsis kawari* were mainly restricted to the inner-shelf stations, where suitable substrate for the polyps is probably easier to find, greatly increasing the diversity of planktonic cnidarians in shallow waters.

The dominant species in the present study, the hydromedusa *L. tetraphylla* and the siphonophores *D. bojani* and *M. kochii*, are typically reported as the most abundant medusae and siphonophore species in the SBB ecosystem in other studies. Other abundant species such as *A. hemistoma*, *Abylopsis* spp., *C. gracilis*, *B. bassensis* and *S. corona* are also common and sometimes abundant in Brazilian waters, and may dominate the planktonic cnidarian community depending on the latitude, distance from the coast, and the local oceanographic structure (Vannucci, 1957, 1963; Moreira, 1973; Navas-Pereira, 1981; Abreu and Nogueira, 1989; Cordeiro and Montú, 1991).

The presence of actinula larvae in the plankton has not been previously reported in SBB or in the southwestern Atlantic, except for a few individuals in an estuary (Nogueira Júnior, 2012). The general absence of previous records of this organism is noteworthy, since it has a coastal distribution and reached high densities, up to 659 ind. 10 m^{-3} , among the most numerous cnidarians in this study. The correct identity of these larvae is not possible to determine without molecular studies or raising them to the next stage (whether a polyp or a medusa; see Bouillon et al., 2004, 2006). However, the seed population is certainly coastal, and their general morphology is quite similar to that described for some species of *Ectopleura* (e.g., Schuchert, 2010). The hydroid fauna of the SBB shallow areas is relatively well known (Migotto et al., 2002; Haddad and Marques, 2009), and *Acharadria crocea* (= *Ectopleura crocea*) is the only actinula-producing-hydroid abundant in the region, and therefore the most probable identity of these larvae. This hydroid concentrates in dense populations along the shoreline and produces large quantities of actinulae during winter and spring (Bornancin, 2011), which is in accordance with the seasonal pattern observed here.

With the exception of a few species such as *S. corona* (see below) and *A. tetragona*, low abundance and species richness characterized the waters below the thermocline, under SACW influence. This is a common distributional feature of planktonic

cnidarians over stratified shelf ecosystems (Pagès and Gili, 1991, 1992; Palma and Apablaza, 2004). Similarly, reductions in the number of planktonic cnidarian species and abundance have been reported during upwelling or stratified situations elsewhere (Gili et al., 1987; Gasca and Suárez, 1991; Pagès and Gili, 1992). However, Miglietta et al. (2008) found higher densities of medusae in upwelling than in non-upwelling periods off Panama Bay.

The SACW intrusion particularly affected the distribution and abundance of coastal species; for instance, *L. tetraphylla*, actinula larvae, *M. kochi*, *C. gracilis*, and Rhopalonematidae sp. 1, *Clytia* spp. and *Obelia* spp. were restricted to the nearshore and were less abundant during the intrusion. Indeed, the CCA analysis indicated that these species in general were associated with low levels of TSI and CHI, usually observed in the nearshore stations, and therefore negatively associated with the presence of SACW. Similarly to the cnidarian species, other coastal taxa such as the cladocerans and doliolids tended to reduce their abundance and be limited to the near-coast (Nogueira Júnior, 2011; Brandini et al., 2014). The reduction in their abundance on the inner shelf during the SACW intrusion may be associated with two main factors: (i) the intrusion reduced the extent of their optimal niche (CW) over the shelf, and most of their population may be more restricted to very shallow areas where CW still predominates; (ii) the surface Ekman transport of CW (Castro et al., 2006b) carries its associated planktonic biota offshore, which may dilute the density of the coastal species over an extensive area. In coastal upwelling off Chile, large fractions of zooplankton populations may be transported offshore due to wind-driven advection (Escribano and Hidalgo, 2000). In January the SHF (*sensu* Castro et al., 1987) was located more than 100 km distant from the coast, and coastal diatoms dominated offshore waters in the same period (Brandini et al., 2014). Although we do not have enough data to prove mechanisms of transport across the shelf, wind-driven movements of water masses are widespread during summer in SBB and the main responsible to the SACW onshore intrusion (Matsuura, 1986; Castro et al., 1987, 2006a, 2006b).

In contrast to the coastal assemblages, the species with more-offshore affinities (those lying on the right side of Fig. 9) tended to be favored by the SACW intrusion, increasing their abundance and distribution over the shelf due to the increase in food availability on the mid- and outer shelf following the enhancement of the deep chlorophyll maximum layer (Brandini et al., 2014). These species were dominated by siphonophores, which may reproduce asexually when food is abundant (Mackie et al., 1987; Carré and Carré, 1991), rapidly taking advantage of the increase in food availability. In fact, these siphonophores populations such as *D. bojani*, *A. tetragona*, *A. eschscholtzi*, *Eudoxoides mitra*, *E. spiralis*, *C. appendiculata* were dominated by the asexually produced eudoxoids during the intrusion periods. Moreover, the environmental changes caused on the shelf by the SACW intrusion simulate in nearshore areas the stratified conditions that are typical of offshore waters, favoring the development of typical offshore species in more-coastal waters.

Temperature seems to affect the vertical occupation of oceanic species. *E. spiralis*, *B. bassensis*, *A. eschscholtzi*, *Sulcoleolaria chuni* and *Solmundella bitentaculata*, were mostly sampled in the upper layer, associated with high temperatures as shown by the CCA analysis (Fig. 9). In contrast, *D. bojani*, *P. ornata*, *C. appendiculata*, *E. mitra*, and *R. velatum* were evenly distributed throughout the water column regardless of temperature. *S. corona* and *A. tetragona* were associated with lower temperatures, and are typical of the cold bottom layer. This is the first report about vertical distribution of planktonic cnidarians on Brazilian offshore waters and is in general agreement with reports of their vertical occupation and preferred hydrographic conditions observed elsewhere (Gili et al., 1987, 1988; Pagès and Gili, 1991, 1992; Pagès, 1992; Palma and Apablaza, 2004).

High abundances of large *S. corona* were found exclusively in areas under the influence of the SACW, suggesting that this medusa can be considered an indicator of the SACW. The distribution of this species was particularly interesting, with low concentrations of small medusae (< 10 mm in diameter) on the inner shelf, and high concentrations of large (mainly 20–40 mm) medusae offshore under the influence of the cold SACW. Such a contrasting distribution between small and large medusae is hard to explain, and perhaps they actually correspond to different, closely related species. The general morphology of the inner-shelf population is very similar to that of the offshore one, except for the smaller number of tentacles. Because the number of tentacles increases with the size of the medusa (Russell, 1953), these small juveniles were identified together with the larger ones as *S. corona*. However, at least three species have been recorded in SBB, and the taxonomy of the local members of the genus is unresolved (Vannucci, 1957, 1963). Detailed morphological and molecular studies comparing these two populations are needed to determine whether they belong or not to the same species.

5. Concluding remarks

Our study is the first attempt to couple hydrographic patterns to cnidarian species in the SBB, with a comprehensive spatial (including vertical) and temporal coverage relevant to the scale of the seasonal SACW onshore intrusion. In conclusion, our data showed that the abundance, distribution, and general taxonomic composition of both medusae and siphonophores were strongly influenced by onshore intrusions of this oceanic water mass. The intrusion favored the development of both warm and cold water cnidarian species with offshore affinities over the shelf, and simultaneously reduced the abundance and geographic extent of coastal species. This may be due to (i) the increase in the productivity and food availability along the deep chlorophyll maximum, which is fueled by the intrusion (see Brandini et al., 2014), and (ii) the coast-ward extension of the stratified conditions typical of the outermost offshore areas. Further understanding of cnidarian population dynamics is necessary to construct a more accurate trophic model for the pelagic ecosystem off the SBB. Some insights are presented herein, but data on production and consumption rates must be obtained in order to reach a correct assessment of the role of these delicate organisms in the energy flow of SBB shelf ecosystems and analogous western current boundary systems.

Acknowledgments

We thank the crew of the R.V. "Soloncy Moura" and the students of the plankton laboratory (CEM-UFPR, MPL) for their invaluable help during the cruises. MNJr was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Grant no. 140945/2007-5), and by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, Grant no. 2011/09880-8). JCUC was supported by Grant number CRN 2076 from the Inter-American Institute of Global Change Research, which is supported by the USA National Science Foundation (Grant GEO-0452325). This investigation received funds from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq Project 474165/2004-3). Janet Reid revised the English text.

Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.csr.2014.02.022>.

References

- Abreu, P.C., Nogueira, C.R., 1989. Spatial distribution of Siphonophora species at Rio de Janeiro Coast, Brazil. Ciênc. Cult. 41 (9), 897–902.
- Bornancin, E., 2011. *Acharadria crocea* (Cnidaria: Hydrozoa): Integrative Study of Larval Settlement Ecophysiology and Ecological Niche Modeling (Master's thesis). University of São Paulo, São Paulo.
- Bouillon, J., 1999. Hydromedusae. In: Boltovskoy, D. (Ed.), South Atlantic Zooplankton. Backhuys Publishers, Leiden, pp. 424–512.
- Bouillon, J., Gravili, C., Pagès, F., Gili, J.-M., Boero, F., 2006. An introduction to Hydrozoa. Mémoires du Muséum national d'Histoire naturelle, Backhuys Publishers.
- Bouillon, J., Medel, M.D., Pagès, F., Gili, J.M., Boero, F., Gravili, C., 2004. Fauna of the Mediterranean Hydrozoa. Sci. Mar. 68 (2), 1–449.
- Brandini, F.P., 1990. Hydrography and characteristics of the phytoplankton in shelf and oceanic waters off southeastern Brazil during winter (July/August 1982) and summer (February/March 1984). Hydrobiologia 196, 111–148.
- Brandini, F.P., Lopes, R.M., Gutseit, K.S., Spach, H.L., Sassi, R., 1997. Planctonologia na plataforma continental do Brasil. Diagnose e revisão bibliográfica. Ministério do Meio Ambiente e da Amazônia Legal – IBAMA, Brasília.
- Brandini, F.P., Nogueira Jr, M., Simião, M., Codina, J.C.U., Noernberg, M.A., 2014. Deep chlorophyll maximum and plankton community response to oceanic bottom intrusions on the continental shelf in the South Brazilian Bight. Cont. Shelf Res. 89, 61–75.
- Carré, C., Carré, D., 1991. A complete life cycle of the Calyptoporid Siphonophore *Muggiae kochi* (Will) in the laboratory, under different temperature conditions: ecological implications. Philos. Trans. R. Soc. B 334 (1269), 27–32.
- Castro, B.M., Brandini, F.P., Pires-Vanin, A.M., Miranda, L.B., 2006b. Multidisciplinary oceanographic processes on the Western Atlantic continental shelf between 4°N and 34°S (4, W). In: Robinson, R., Brink, K.H. (Eds.), The Sea, vol. 14. The Global Coastal Ocean: Interdisciplinary Regional Studies and Syntheses. Harvard University Press, pp. 259–293.
- Castro, B.M., Lorenzetti, J.A., Silveira, I.C.A., Miranda, L.B., 2006a. Estrutura termohalina e circulação na região entre o Cabo de São Tomé (RJ) e o Chuí (RS). In: Rossi-Wongtschowski, C.L.B., Madureira, L.S.-P. (Eds.), O Ambiente Oceanográfico da Plataforma Continental e do Talude na Região Sudeste-Sul do Brasil. Editora da Universidade de São Paulo, São Paulo, pp. 11–120.
- Castro, B.M., Miranda, L.B., 1998. Physical Oceanography of the western atlantic continental shelf located between 4°N and 34°S – coastal segment (4,W). In: Robinson, A., Brink, K. (Eds.), The Sea, vol. 11. The Global Coastal Ocean: Regional Studies and Syntheses. Harvard University Press, pp. 209–251.
- Castro, B.M., Miranda, L.B., Miyao, Y., 1987. Condições hidrográficas na plataforma continental ao largo de Ubatuba: variações sazonais e em média escala. Bol. Inst. Oceanogr. 35 (2), 135–151.
- Cordeiro, T.A., Montú, M.A., 1991. Distribuição dos Siphonophorae: Calyphorphae (Cnidaria) em relação às massas de água ao largo dos estados do Paraná e Santa Catarina, Brasil (28°S–31°S). Nerítica 6 (1–2), 107–126.
- Escribano, R., Hidalgo, P., 2000. Spatial distribution of copepods in the north of the Humboldt Current region off Chile during coastal upwelling. J. Mar. Biol. Assoc. U.K. 80, 283–290.
- Gaeta, S.A., Brandini, F.P., 2006. Produção primária do fitoplâncton na região entre o Cabo de São Tomé (RJ) e o Chuí (RS). In: Rossi-Wongtschowski, C.L.B., Madureira, L.S. (Eds.), O Ambiente oceanográfico da Plataforma Continental e do Talude na Região Sudeste-Sul do Brasil. Editora da Universidade de São Paulo, São Paulo, pp. 219–264.
- Gasca, R., Suárez, E., 1991. Siphonophores of upwelling areas of the Campeche Bank and the Mexican Caribbean Sea. Hydrobiologia 216/217, 497–502.
- Gili, J.M., Pagès, F., Fusté, X., 1991. Mesoscale coupling between spatial distribution of planktonic cnidarians and hydrographic features along the Galician Coast (Northwestern Iberian Peninsula). Sci. Mar. 55, 419–426.
- Gili, J.M., Pagès, F., Riera, T., 1987. Distribución de las especies más frecuentes de sifonóforos calcíforos en la zona norte del Mediterráneo occidental. Invest. Pesq. 51 (3), 323–338.
- Gili, J.M., Pagès, F., Sabates, A., Ros, J.D., 1988. Small-scale distribution of a cnidarian population in the western Mediterranean. J. Plankton Res. 10 (3), 385–401.
- Haddad, M.A., Marques, A.C., 2009. Cnidaria. In: Rocha, R.M., Boeger, W.A. (Eds.), Zoologia. Estado da Arte e Perspectivas. Editora da UFPR, Curitiba, pp. 29–48.
- Hosia, A., Bamstedt, U., 2007. Seasonal changes in the gelatinous zooplankton community and hydromedusa abundances in Korsfjord and Fanafjord, western Norway. Mar. Ecol. Prog. Ser. 351, 113–127.
- Hosia, A., Stemmann, L., Youngbluth, M., 2008. Distribution of net-collected planktonic cnidarians along the northern Mid-Atlantic Ridge and their associations with the main water masses. Deep-Sea Res. II 55, 106–118.
- Lohrenz, S.E., Castro, B.M., 2006. Eastern ocean boundaries pan – regional overview. In: Robinson, A.R., Brink, H. (Eds.), The Sea, vol. 14. Harvard College, pp. 3–20.
- Longhurst, A.R., 2006. Ecological Geography of the Sea. Academic Press, San Diego.
- Lopes, R.M., Montú, M.A., Gorri, C., Muxagata, E., Miyashita, L., Oliveira, L.P., 2006. O zooplâncton marinho da região entre o Cabo de São Tomé (RJ) e o Chuí (RS). In: Rossi-Wongtschowski, C.L.B., Madureira, L.S.-P. (Eds.), O Ambiente Oceanográfico da Plataforma Continental e do Talude na Região Sudeste-Sul do Brasil. Editora da Universidade de São Paulo, São Paulo, pp. 265–358.
- Mackie, G.O., Pugh, P.R., Purcell, J.E., 1987. Siphonophore biology. Adv. Mar. Biol. 24, 97–262.
- Matsuura, Y., 1986. Contribuição ao estudo da estrutura oceanográfica da região sudeste entre Cabo Frio (RJ) e Cabo de Santa Marta Grande (SC). Ciênc. Cult. 38 (8), 1439–1450.
- McCune, B., 1997. Influence of noisy environmental data on canonical correspondence analysis. Ecology 78 (8), 2617–2623.
- Mianzan, H.W., Guerrero, R.A., 2000. Environmental patterns and biomass distribution of gelatinous macrozooplankton. Three study cases in the South-western Atlantic Ocean. Sci. Mar. 64 (1), 215–224.
- Miglietta, M.P., Rossi, M., Collin, R., 2008. Hydromedusa blooms and upwelling events in the Bay of Panama, Tropical East Pacific. J. Plankton Res. 30 (7), 783–793.
- Migotto, A.E., Marques, A.C., Morandini, A.C., da Silveira, F.L., 2002. Checklist of the Cnidaria Medusozoa of Brazil. Biota Neotrop. 2 (1), 1–30.
- Mills, C.E., 1995. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. ICES J. Mar. Sci. 52, 575–581.
- Miyashita, L.K., Melo Júnior, M., Lopes, R.M., 2009. Estuarine and oceanic influences on copepod abundance and production of a subtropical coastal area. J. Plankton Res. 31 (8), 815–826.
- Möller, 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. Cont. Shelf Res. 13 (30), 1607–1624.
- Moreira, G.S., 1973. On the diurnal vertical migration of Hydromedusae off Santos, Brazil. Publ. Seto Mar. Biol. Lab. 20, 537–566.
- Navas-Pereira, D., 1981. Distribuição das hidromedusas (Cnidaria, Hydrozoa) na região da plataforma continental do Rio Grande do Sul. In: Lunetta, J.E. (Ed.), Seminários de Biologia Marinha. Anais da Academia Brasileira de Ciências, São Paulo, pp. 221–276.
- Nogueira, C.R., Oliveira Jr, S.R., 1991. Siphonophora from the coast of Brazil (17°S to 24°S). Bol. Inst. Oceanogr. 39 (1), 6–69.
- Nogueira Júnior, M., 2011. Composição, migração vertical e distribuição espacotemporal do zooplâncton gelatinoso (Cnidaria, Ctenophora e Thaliacea) da plataforma Sudeste do Brasil. Tese de Doutorado, Universidade Federal do Paraná, Pontal do Paraná.
- Nogueira Júnior, M., 2012. Gelatinous zooplankton fauna (Cnidaria, Ctenophora and Thaliacea) from Baía da Babitonga (southern Brazil). Zootaxa 3398, 1–21.
- Pagès, F., 1992. Mesoscale coupling between planktonic cnidarian distribution and water masses during a temporal transition between active upwelling and abatement in the northern Benguela system. S. Afr. J. Mar. Sci. 12, 41–52.
- Pagès, F., Gili, J.M., 1991. Vertical distribution of epipelagic siphonophores at the confluence between Benguela waters and the Angola Current over 48 h. Hydrobiologia 216/217, 355–362.
- Pagès, F., Gili, J.M., 1992. Influence of Agulhas waters on the population structure of planktonic cnidarians in the southern Benguela region. Sci. Mar. 56 (2), 109–123.
- Pagès, F., González, H.E., Ramón, M., Sobral, M., Gili, J.M., 2001. Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by Bassia bassensis (Siphonophora: Calyphorphae). Mar. Ecol. Prog. Ser. 210, 13–24.
- Palma, S., Apablaza, P., 2004. Abundancia y distribución vertical del zooplankton gelatinoso carnívoro en una área de surgencia en el norte del Sistema de la Corriente de Humboldt. Invest. Mar. 32 (1), 47–70.
- Palmer, M.W., 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74 (8), 2215–2230.
- Pugh, P.R., 1984. The diel migrations and distribution within a mesopelagic community in the North East Atlantic. 7. Siphonophores. Prog. Oceanogr. 13, 461–489.
- Richardson, K., 2005. Seasonal distribution of primary production, phytoplankton biomass and size distribution in the Greenland Sea. Deep-Sea Res. I 52, 979–999.
- Russell, F.S., 1953. The Medusa of the British Isles. Anthomedusae, Leptomedusae, Limnomedusae, Trachymedusae and Narcomedusae, vol. I. Cambridge University Press, London.
- Schuchert, P., 2010. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 2. Rev. Suisse Zool. 117 (3), 337–555.
- Ter Braack, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67 (5), 1167–1179.
- Vannucci, M., 1957. On Brazilian hydromedusae and their distribution in relation to different water masses. Bol. Inst. Oceanogr. 8 (1–2), 23–109.
- Vannucci, M., 1963. On the ecology of Brazilian medusae at 25°lat S. Bol. Inst. Oceanogr. 13 (1), 143–184.