



Research papers

Deep chlorophyll maximum and plankton community response to oceanic bottom intrusions on the continental shelf in the South Brazilian Bight



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ABSTRACT

The continental shelf of the South Brazilian Bight (Lat 23–28.5°S) is subject to bottom intrusions of the oceanic and nutrient-rich South Atlantic Central Waters (SACW) in summer, to compensate for the Ekman transport of surface waters offshore by northeasterly winds. In winter, shelf waters tend to overturn vertically due to tidal circulation and Ekman convergence of outer-shelf waters driven by southerly winds. From 9 November 2005 to 22 June 2006 the shelf off Santa Catarina State was surveyed to investigate hydrographic conditions and the seasonal dynamics of the plankton cross-shelf distribution and community structure. A strong wind-driven onshore bottom intrusion of the SACW with the formation of two independent deep chlorophyll maximum (DCM) layers on the shelf was clear. Chlorophyll concentrations ranged from 0.07 to 6.2 mg m⁻³ and phytoplankton carbon biomass from 0.2 to 511 µgC L⁻¹, mostly as large centric diatoms and in spite of the numerical dominance of small pennates. The mid-shelf DCM was 12 m thick between 38 and 50 m (1–5% of irradiance) with mean chlorophyll concentrations up to 1.8 mg m⁻³. The DCM on the outer shelf was formed between 60 and 70 m depth (1–0.01% surface light) by small pennate diatoms and small phytoflagellates, with chlorophyll concentrations of 0.5–0.7 mg m⁻³. Both DCMs were maintained independently from January to April 2006, and dispersed in June due to water column turnover during cold seasons. In the mid-shelf, the DCM was geographically extended towards the inner shelf and became thicker compared to pre- and post-intrusion periods. The freshwater species *Aulacoseira granulata* and large centric diatoms including the invasive *Coscinodiscus wailesii* were frequent along the shelf throughout the sampling period. *Oncaea waldemari*, *Ctenocalanus vanus* and *Oithona plumifera* usually dominated the zooplankton, which ranged from 23 to 7970 individuals m⁻³. Abundances were always higher on the inner shelf regardless of the season of the year. Abundance on the mid-shelf peaked following the onset of the intrusion of the nutrient-rich oceanic SACW in the lower euphotic zone and the enhancement of the DCM. A 6-step circulation model of diatoms coupled with shelf hydrodynamics is proposed as the main mechanism of retention of diatoms in the shelf system. The model suggests that diatoms resuspended in the nearshore are transported offshore by Ekman forces toward oligotrophic waters, where they sink faster due to poor nutrient conditions. Sinking cells find better nutrient conditions in the pycnocline/nutricline layers, become shade-adapted and increase their buoyancy, contributing to the formation of the DCM. Resting cells sinking out of the euphotic zone reach near-bottom layers or the sediments, from where they are carried back onshore by oceanic intrusions of the SACW. We suggest how this hydrodynamic circulation pattern of diatoms may take place in other subtropical shelf systems dominated by western boundary currents.

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1. Introduction

The continental shelf of the South Brazilian Bight (23–28.5°S) is a part of the westernmost transitional zone between the subtropical and temperate domains of the western boundary current system (Lohrenz and Castro, 2005; Longhurst, 2006). Different water

masses interact with hydrographic gradients, creating important ecotones of biological enhancement in the euphotic zone over the entire shelf (Castro et al., 2006). Away from continental runoff, phytoplankton production depends on inputs of nutrients to the euphotic zone by meso-scale physical processes, which are regulated by the seasonal pattern of the wind field and the dynamics of the Brazil Current flowing over the shelf break. In the summer, the northeast winds cause Ekman transport of surface waters offshore. This is balanced by onshore bottom intrusions of nutrient-rich South Atlantic Central Water (SACW), which may be enhanced by cyclonic eddies and meandering of the Brazil Current along the continental slope (Castro and Miranda, 1998; Campos et al., 2000). The nutricline over the outer shelf (> 100 m) is periodically displaced shoreward, spreading the subsurface chlorophyll-rich layer over the inner- and mid-shelf areas (Brandini, 1990; Brandini et al., 1989; Castro et al., 2006). Despite the numerical dominance of diatoms reported in earlier investigations (Brandini, 1988a; Brandini et al., 1989; Fernandes and Brandini, 1999, 2004), micro-flagellates concentrate at tidal fronts on the middle shelf, and picocized flagellates dominate the upper oligotrophic layers (Brandini et al., 1989). About 70% of the biomass of herbivorous mesozooplankton in the South Brazil Bight (SBB) is dominated by copepods (Lopes et al., 2006). Thus, a diatom-copepod dominated planktonic food web is enhanced in the shelf ecosystem of the SBB during summer periods from December to March where new production (*sensu* Dugdale and Goering, 1967) is concentrated at the deep chlorophyll maximum (DCM) along the nutricline. In winter periods (June–August), new production is limited by smaller contribution of nutrients (mostly phosphate and silicate) from the continental drainage of the La Plata plume (Braga et al., 2008) and benthic regeneration, compared to the higher nutrient inputs from the summer intrusions.

Despite the regularity with which the SACW intrusions enhance nutrient input to the euphotic layers over the mid-shelf during the summer seasons, its effects on the plankton community structure and dynamics over the continental shelf are still poorly understood. During the annual cycle, the hydrography along the cross-shelf off Santa Catarina State, as representative of the mid-portion of the SBB, was surveyed during five sampling cruises in order to follow the seasonal development of the DCM and its effect on the seasonal dynamics of the plankton assemblage. This study was carried out to address the following questions: (i) what is the spatial (horizontal and vertical) magnitude of the DCM in summer compared to periods when SACW intrusions are absent, (ii) which phytoplankton and zooplankton species dominate at the DCM layers during summer intrusions of the SACW, and (iii) how the abundance and cross-shelf distribution of plankton assemblages are regulated by the hydrographic regime over an annual cycle.

2. Material and methods

2.1. Field work

Five oceanographic cruises were conducted between November 2005 and June 2006 with the RV “Soloncy Moura” across the shelf off the Santa Catarina coast (26°45’S). On each cruise we sampled 15 stations from the isobaths of 20–140 m (Fig. 1). Vertical profiles of in situ photosynthetically available radiation (E_0) and natural fluorescence flux (F_f) were obtained with submarine PAR and natural fluorescence (PNF) sensors (Biospherical Instruments Profiling Natural Fluorometer model PNF-300). Chlorophyll concentrations (in mg m^{-3}) were calculated from the measurements of E_0 , F_f and two constants of the software for the PNF-300, following the equation:

$$\mu\text{g Chlor L}^{-1} = \frac{F_f}{^{\circ}a_c(\text{PAR}) \cdot \phi_f \cdot E_0}$$

where F_f =natural fluorescence data; E_0 =in situ photosynthetically available radiation; $^{\circ}a_c$ (PAR)=chlorophyll-specific absorption coefficient= $0.04 \text{ m}^2 \text{ mg}^{-1}$; ϕ_f =quantum yield of fluorescence= 0.045 .

Salinity and temperature data were obtained with an InterOcean CTD/S4. Factory laboratory calibration showed high precision of the measurements of pressure (± 0.1 decibar), temperature (± 0.02 °C) and salinity (± 0.02). Hydrographic properties (T , C and p) were converted to salinity (S) and sigma- t (σ_t) according to the Practical Salinity Scale (PSS-78) and the International Equation of State of Sea Water (IES-80). 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 (Fig. 1). These data were confirmed by modeling winds (model NCEP/NCAR) at a fixed position (26°30’S; 48°30’W) near the sampling transect. The depth of the upper mixed layer (Z_m , i.e., the physically homogeneous upper layer above the pycnocline) was calculated according to Montégut et al. (2004), and the chlorophyll heterogeneity index (CHI) was calculated according to Richardson (2005).

2.1.1. Phytoplankton

Net samples were collected at all stations, with vertical trawls of a conical plankton net with 20 μm mesh and diameter of 30 cm, from the bottom of the DCM to the surface. Samples were fixed with 0.4% formaldehyde in 200-ml polyethylene bottles. Using a Hydro-Bios water sampler of 1.2 L volume, water samples were

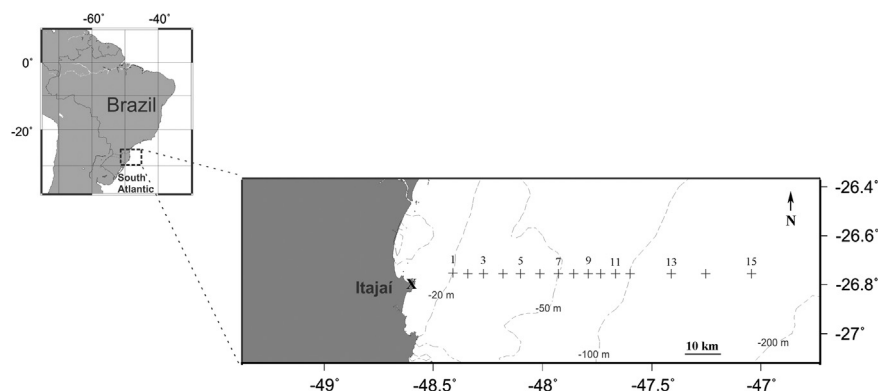


Fig. 1. Study transect off Santa Catarina, central South Brazilian Bight, with sampling stations (#1–15) visited between November 2005 and June 2006. The cross over Itajaí city indicates the position where wind data was obtained.

collected at 5 m as representative of the upper mixed layer (hereafter, UML) and at the peak concentration of the DCM according to the fluorescence profile previously determined, for study of the taxonomic composition and quantitative analysis of densities and biomass of the phytoplankton. Water aliquots were removed from the water-sampler, fixed with 0.8% acetic lugol (Edler, 1978) and stored in amber glass bottles for later laboratory analyses. In June, phytoplankton samples for Utermöhl analyses were collected only at 5 m in the upper mixed layer because a clear DCM was not present.

2.1.2. Zooplankton

Zooplankton was collected at three depth intervals, with vertical hauls of a WP-2 net (200 μm mesh) with closing mechanism: (i) through the upper mixed zone, (ii) through the DCM, and (iii) through the bottom layer below the thermocline. The filtered volume in each depth interval was obtained with a Hydro-Bios flowmeter. All organisms were transferred to 1000-ml polyethylene bottles and fixed with a 4% formaldehyde solution buffered with borax for later laboratory analyses.

2.2. Laboratory work

Net phytoplankton aliquots were oxidized and mounted on slides and coverslips following Hasle and Fryxell (1970). Taxonomic identifications followed Round et al. (2000), Landucci and Ludwig (2005), Sar et al. (2007), Tomas (1997) and Tenenbaum et al. (2004). Phytoplankton cells were counted in Utermöhl (1958) sedimentation chambers using a Zeiss model ED-03 inverted microscope with phase-contrast optics. Coastal samples were sedimented in 10-ml chambers for at least 12 h, and oceanic samples in 50-ml chambers for 24 h (Hasle, 1978). Nano-size cells (2–20 μm) were counted at 400 \times magnification over diameter transects until a minimum of 100 cells was reached. Micro-size cells (>20 μm) were counted at 160 \times magnification over the entire bottom area of the Utermöhl chamber or in half the chamber, depending on cell density, in order to reach a minimum count of 300 cells. Cell densities (except picoplankton of <2 μm) per liter were calculated according to Semina (1978). Mean linear dimensions of all taxa counted were obtained from 20 randomly selected cells with an ocular micrometer, based on the geometric shapes proposed by Hillebrand et al. (1999). From these shapes, cell volumes were calculated using the software ALGAMICA 4.0 (Gosselain et al., 2000). Cell volumes were converted into cell carbon according to Eppley (1972). Zooplankton samples were analyzed under a stereomicroscope; and crustaceans were identified and counted in 1/4 to 1/32 aliquots, until at least 300 individuals were counted. Taxonomic identification followed Björnberg (1981), Huys and Boxshall (1991), Bersano and Boxshall (1994) and Boltovskoy (1999). Densities of organisms were expressed as ind m^{-3} .

2.3. Statistical treatment

Using the software PRIMER v.6 (Clarke and Warwick, 2001), a similarity matrix based on Sørensen's presence/absence index was constructed from the diatom data for each of the five cruises. These matrices were used to generate non-metric multidimensional scaling (MDS) plots. The same matrices were also used to generate clusters, which were overlaid on the MDS.

In order to evaluate the interactions among the most abundant zooplankton species and environmental characteristics, a canonical correspondence analysis (CCA) was conducted. We included average temperature, salinity and water density in the sampled strata, distance from the coast, average chlorophyll (mg m^{-3}) in

the sampled strata, integrated chlorophyll in the euphotic zone (mg m^{-2}) as possible explanatory variables, as well the chlorophyll heterogeneity index (CHI) and the temperature stratification index ($\text{TSI} = \Delta T / \Delta h$ ($^{\circ}\text{C}/\text{m}$), where ΔT and Δh are difference of water temperature and water depth, respectively, between the upper and lower edges of the thermocline), which may be considered as indicators of the presence of DCM.

Before the analysis, explanatory variables were centered (mean=0) and standardized (SD=1) to put them on the same scale, and species data were square-root transformed. A Monte Carlo randomization procedure was used to test if each of the explanatory variables contributed a significant fraction of the variability ($P < 0.05$ after 999 runs). Only significant variables were included in the model. The CCA was run in the software CANOCO 4.5.

3. Results

3.1. Hydrography

Here, the 20 $^{\circ}\text{C}$ isotherm was used to define the upper limit of the thermocline below which the nutrient-rich SACW dominates the bottom layers over the shelf. Southerly winds predominated in November and December, changing to north-northeasterly winds in early January (Fig. 2), causing a strong onshore intrusion of the SACW (Fig. 3). The shoreward limit of the intrusion can be determined by the bottom insertion of the tidal-front, locally called the Deep Thermal Front (DTF, *sensu* Castro et al., 1987). In November, the DTF was positioned over the 80-m isobath and the thermocline was more defined seaward. Overall, the density field over the shelf (see Fig. 4, left-hand side) closely followed the spatial pattern of temperature which varied from <16 $^{\circ}\text{C}$ in bottom layers on the outer shelf dominated by the cold SACW to >26 $^{\circ}\text{C}$ in the upper mixed layer in January 2006. Higher temperatures were usually observed in the coastal mixed layers in the summer. Salinities ranged from 33 to 37, and were lowest near the coast when the halocline was well defined in the top 30 m from coast to mid-shelf areas, forming the Surface Haline Front (SHF, *sensu* Castro et al., 1987), separating coastal and shelf mixed waters from the outermost stratified Tropical Water of the Brazil Current. On the inner side of the DTF, tidal circulation maintains a mixed layer from surface to bottom whereas the side outward from the front is constantly stratified, with the upper mixed layer of different depths. Physical stratification (Fig. 4, left-hand side) was enhanced throughout the shelf in January by the bottom intrusion of the SACW, caused by the persistence of northeast upwelling-favorable winds from early January. Thermoclines were still conspicuous in late summer (March–April) over the mid- and outer shelf, but physical stratification decreased over the inner shelf due to tidal and wind mixing, with temperatures between 24 and 25 $^{\circ}\text{C}$. The DTF was gradually displaced seaward from the 50–60 m in March to the 70–80-m isobath in April. In June 2006, a large water body with salinities <34.5 extended from the coast to the mid-shelf due to advection of less saline waters from the La Plata River pushed northward by persistent southerly winds. The DTF was still over the 80-m isobath, but the SHF was displaced to almost 130 km offshore. Tropical waters were entrained toward the coast beneath this body of La Plata water and the SACW (Miranda, 1982; Castro and Miranda, 1998). As SACW intrusions were not observed, surface temperatures ranged between 21 and 22 $^{\circ}\text{C}$, and were lower on the coast due to winter cooling. The thermocline/pycnocline remained on the outer shelf above the SACW.

Based on the ratio of the depths of the euphotic and the upper mixing zone ($Z_{\text{eu}}/Z_{\text{m}}$), light was almost always available across the

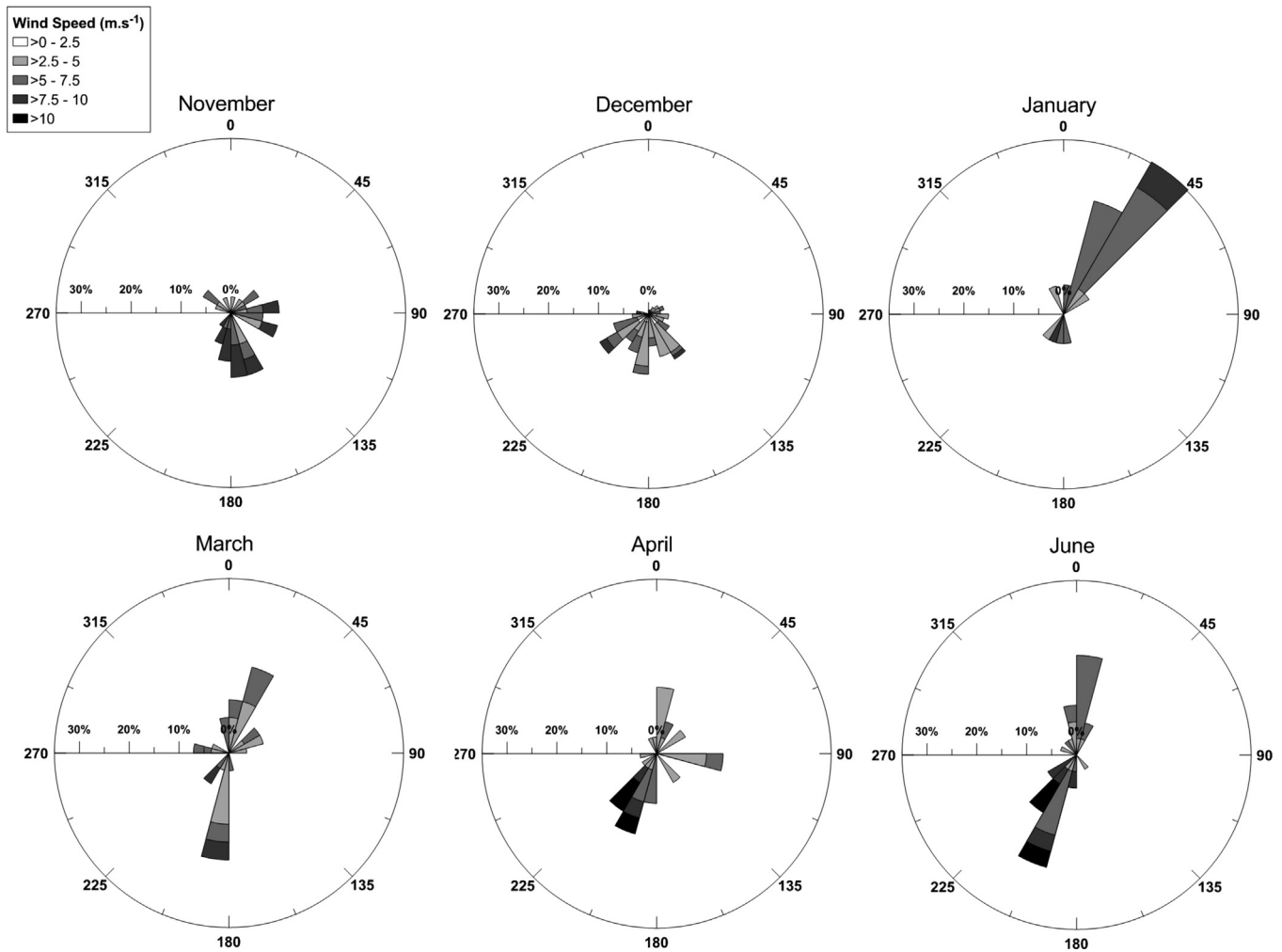


Fig. 2. Wind field off Santa Catarina, central South Brazilian Bight, between November 2005 and June 2006.

shelf. In most sampling cruises it penetrated deeper than the mixing zone ($Z_{eu}/Z_m > 1$, Fig. 4), particularly on the outer shelf where the ratios were usually highest. In November, the euphotic zone was well mixed on the inner shelf and part of the mid-shelf ($Z_{eu} = Z_m$), and subsequently the Z_{eu} was three times deeper than the mixing layer in a narrow band of the cross-shelf between 80 and 100 km offshore over the 80–90-m isobaths. Oceanward the Z_{eu} decreased again, becoming just slightly deeper than the Z_m . Light availability was greatest in January simultaneously to SACW summer intrusions, when the Z_{eu} was on average three times deeper than the mixing zone along the entire cross-shelf, up to a maximum of 7.8 over the 100 m isobath. The effect of the SACW intrusion was markedly greater on the inner- and mid-shelf up to 90 km offshore.

3.2. DCM magnitude and distribution across the shelf

In the nearshore area, the DCM was not well defined as in the mid- and outer-shelf regions, where they were always below 5% of surface light intensity and were sometimes sufficiently thick to reach depths below the euphotic zone, from 0.1% to 0.01% surface light (Fig. 5, right-hand side). In November 2005 a mean chlorophyll concentration of the DCM of 0.43 mg m^{-3} was detected that began 25 km offshore between 30 and 37 m depth and reached the mid-shelf slightly deeper, between 37 and 57 m (mean of 0.61 mg m^{-3}). Peak concentrations were up to 1 mg m^{-3}

at 54 m depth over the 60 m isobath at approximately 68 km offshore. A minor DCM was formed on the outer shelf between 50 and 62 m, with mean chlorophyll concentrations of 0.32 mg m^{-3} . The DCMs developed separately from two independent nuclei, one over the mid- and the other over the outer shelf. The mid-shelf nucleus was shallower, occupying a 12-m thick layer between 38 and 50 m, and was dominated by large centric diatoms in terms of carbon biomass, but numerically by small pennate cells with mean chlorophyll concentrations of 1.8 mg m^{-3} . The deeper nuclei on the outer shelf were formed between 60 and 70 m depth by small pennate diatoms and nano-sized phytoflagellates, with chlorophyll concentrations of $0.5\text{--}0.7 \text{ mg m}^{-3}$. These DCMs with different general phytoplankton compositions were maintained independently from January to April 2006, and dispersed in June when concentrations were $> 0.25 \text{ mg m}^{-3}$ between the 40-m isobath and the outer transect. The chlorophyll-rich layer during this period coincided with warmer residual tropical waters entrained between the upper, lighter La Plata water and the deeper SACW.

3.3. Integrated chlorophyll in the water column

Regardless of season, integrated chlorophyll concentrations over the euphotic zone (Z_{eu} , hereon defined as down to 1% surface light) varied from 3.4 to 42.6 mg m^{-2} ; below the euphotic zone, between 1% and 0.1% surface light, from 0.3 to 26.6 mg m^{-2} ; and farther downward between 0.1% and 0.01% surface light, from

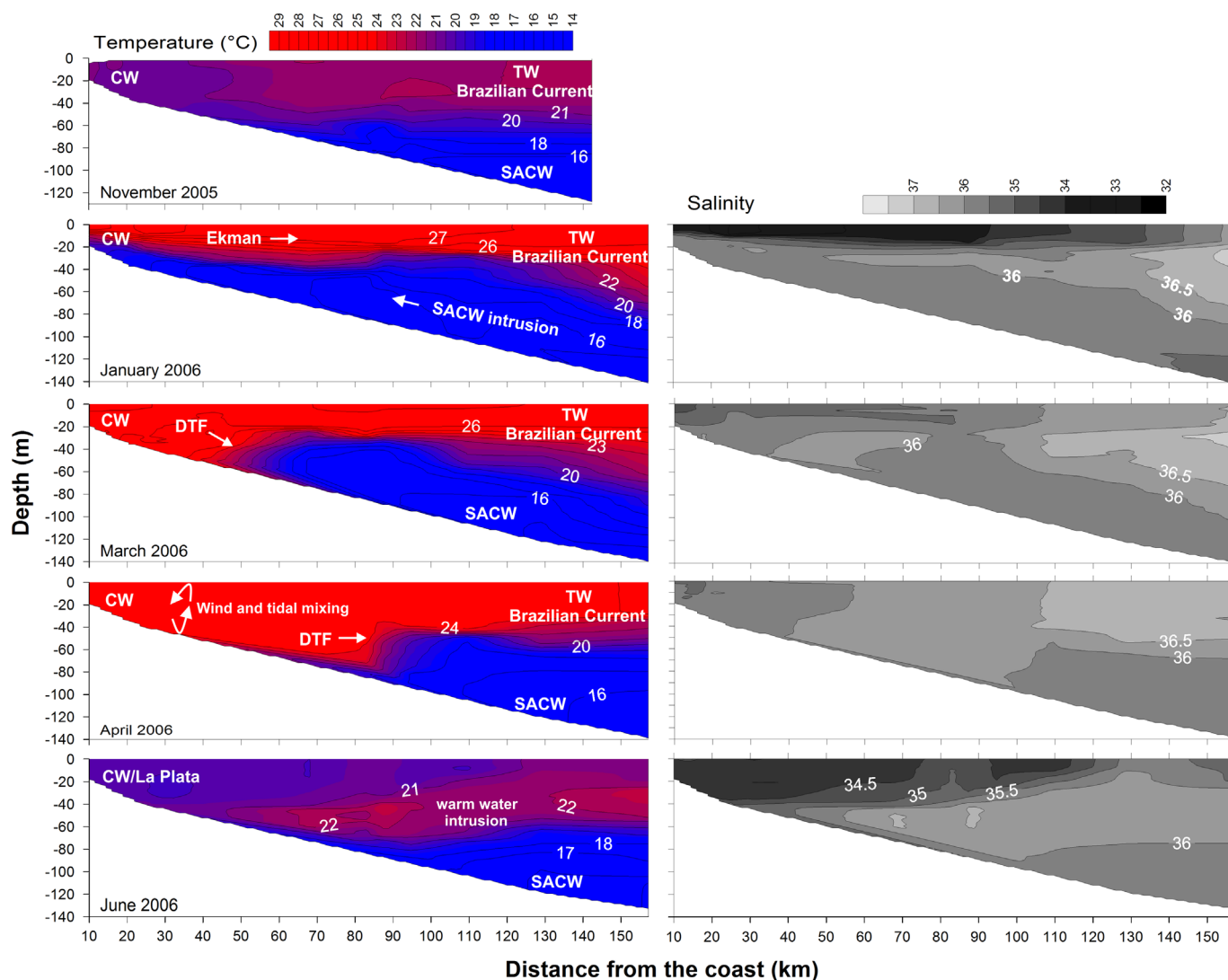


Fig. 3. Cross-shelf distribution of temperature and salinity off Santa Catarina, central South Brazilian Bight, between November 2005 and June 2006 (CW – coastal water; TW – Tropical Water; SACW – South Atlantic Central Water).

0.3 to 9.2 mg m^{-2} (Fig. 6). Farther from shore but still on the inner shelf, chlorophyll concentrated at the bottom, usually starting over the 30 m isobath (November, January) or farther offshore over the 50 m isobath (March, April). Following the cross-shelf distribution, the bottom DCM of the inner shelf spread oceanward, met the DTF, and began to climb up the thermocline/pycnocline seaward of the mid-shelf (see Figs. 3 and 4, left-hand side). There, concentrations in the euphotic zone ranged from 10 to 15 mg m^{-2} , except for the maximum of 20.4 mg m^{-2} observed over the 100 m isobath at 108 km offshore. The main difference between integrated chlorophyll concentrations on the mid-shelf, before and after the summer intrusion, was that chlorophyll became more concentrated below the Z_{eu} from 1% to 0.01% surface light. This was clear in January but especially in March, when chlorophyll concentration on the mid-shelf was markedly higher ($6\text{--}9 \text{ mg m}^{-2}$) from 0.1% to 0.01% surface light in comparison to January ($1.4\text{--}3.4 \text{ mg m}^{-2}$). In April the same trend continued on the mid- and outer shelf, except the maximum of 20.4 mg m^{-2} found in the Z_{eu} over the 100 m isobath (108 km offshore). Even so, integrated chlorophyll was still higher than in the same period along the transect, with $> 10 \text{ mg m}^{-2}$ at depths between 1% and 0.1% surface light over the 100–120 isobath and $> 5 \text{ mg m}^{-2}$ at depths between 0.1% and 0.01% surface light over the 90–100 m isobaths.

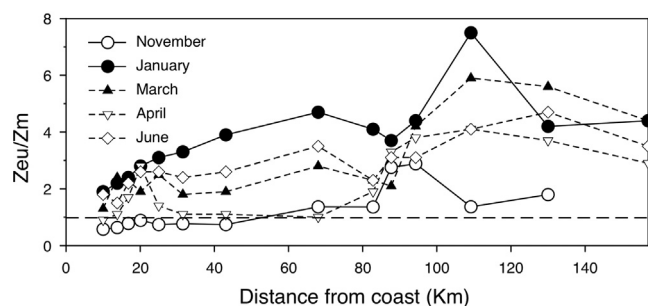


Fig. 4. Ratio of the depth of the euphotic zone over the upper mixing zone (Z_{eu}/Z_m) across the shelf off Santa Catarina, central South Brazilian Bight, between November 2005 and June 2006.

3.4. Phytoplankton abundance and biomass

Diatoms and flagellates (nano-phytoflagellates and dinoflagellates) contributed differently to total phytoplankton density along the transect (Fig. 7, left-hand side). In November, prior to the intrusion, centric cells dominated the UML near the coast but pennates numerically dominated along the mid-shelf at the UML and DCM, with densities up to $5 \times 10^5 \text{ cells L}^{-1}$. The only exception was over the 40 and 120 m isobaths, where flagellates dominated

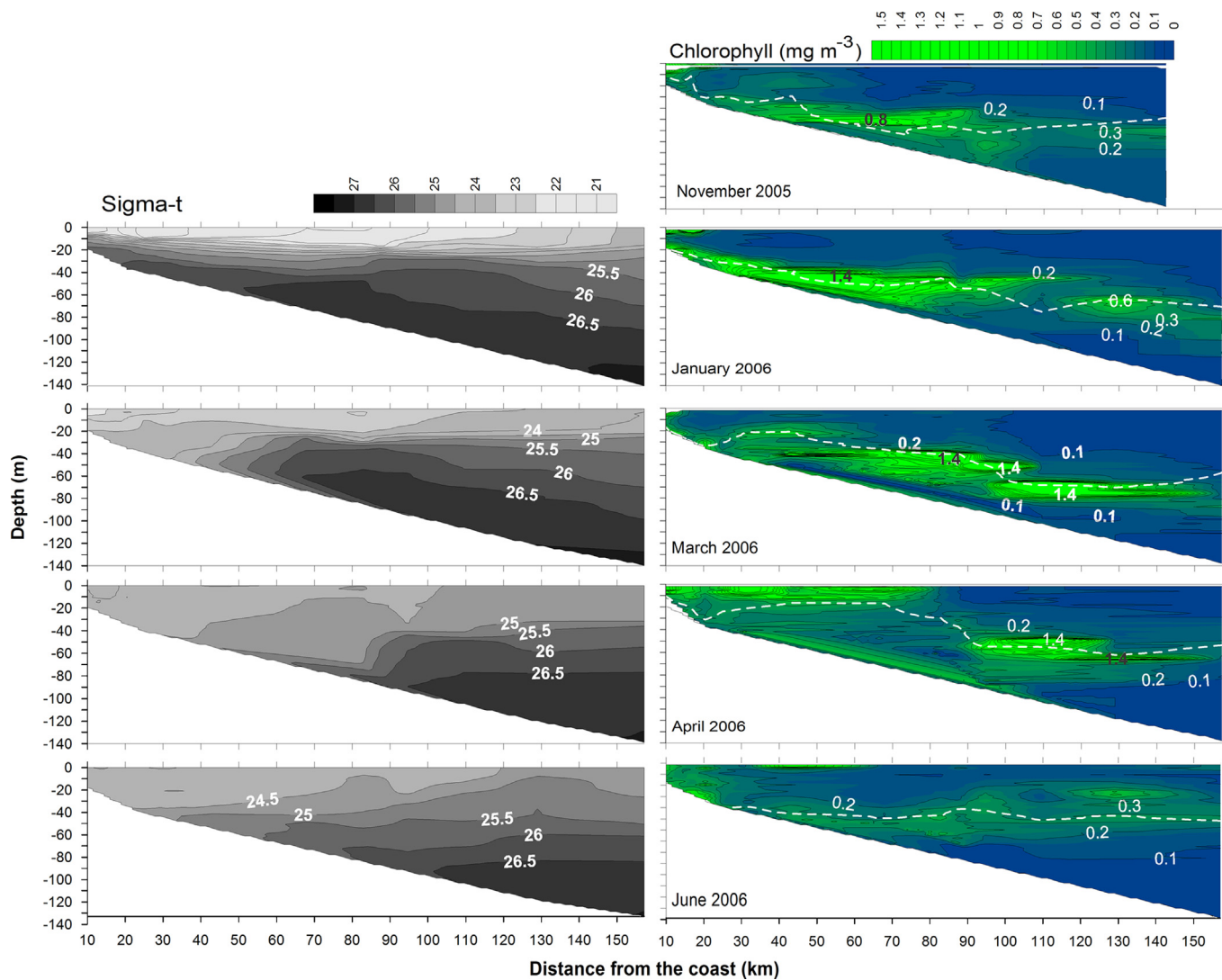


Fig. 5. Cross-shelf distribution of density (Sigma-t) and chlorophyll (mg m^{-3}) off Santa Catarina, central South Brazilian Bight, between November 2005 and June 2006. The tracked white line represents the 1% surface light along the transect.

the UML samples. In January, pennate diatoms maintained their numerical dominance on the inner- and mid-shelf, but centrics became as important as pennates in the UML along the inner shelf and also at the DCM over the 70 m isobath (72 km offshore). On the outer shelf, flagellates dominated both in the UML and at the DCM. Late in the summer (March–April), the numerical dominance of diatoms decreased and flagellates occupied the mid-shelf UML in March except over the 80 m isobath (87 km offshore), and both the mid-shelf UML and DCM in April. In June, phytoplankton analyses were carried out only for the UML, which were numerically dominated by flagellates, with small diatoms (mostly pennates) contributing $< 1 \times 10^5$ cells L^{-1} .

Phytoplankton carbon (except picoplankton) ranged from < 2 to $164 \mu\text{gC L}^{-1}$ with a maximum in the inner- and mid-shelf regions, decreasing on the outer shelf (Fig. 7, right-hand side). Phytoplankton carbon was mostly concentrated in diatoms (31–90% C), with flagellates usually contributing $< 10\%$ of total phytoplankton C except in June when they contributed up to 70% of total phytoplankton C. Though numerically less important, centric diatoms contributed more than pennates to the C biomass of total phytoplankton except at the DCM over the 60 m isobath (68 km offshore). In January and March, pennates also contributed substantially to the phytoplankton biomass at the UML over the 45 m isobath (32 km offshore) and at the DCM on the near coast

over the 30-m isobath. However, centric diatoms were still the dominant group in these locations. In November prior to the intrusion, biomass varied between 10 and $80 \mu\text{gC L}^{-1}$ with the DCM between 20 and 70 km offshore. Following the intrusion in January, diatoms accumulated twice as much C in the mid-shelf area, both at the DCM and in the UML, with the maximum reaching $170 \mu\text{gC L}^{-1}$ over the 45 m isobath (32 km offshore). In March, biomass decreased to half the levels observed in January and was mostly concentrated at the DCM. In April, the diatom C stock decreased even more throughout the transect except at a few mid-shelf stations over the 50–80 m isobath (43–90 km offshore), but much below the ranges observed in January and March. In June, the diatom biomass was very low and the contribution of pennates increased along the entire shelf, even at the outermost stations 109 km offshore, probably in response to the advection of La Plata waters.

3.5. Diatom community structure

A total of 105 species of diatoms, 26 species of dinoflagellates, filamentous *Trichodesmium* sp., and a few silicoflagellates of the genus *Dyctiocha* were found (Table S1, Supplementary material). Unfortunately, the fixation of Utermöhl samples with acetic lugol did not preserve coccolithophorids. Therefore, these were not

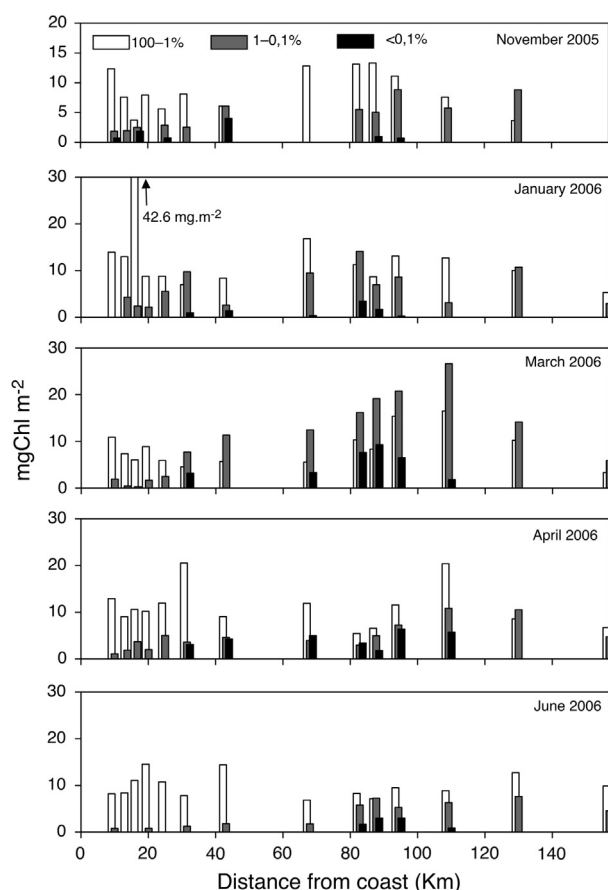


Fig. 6. Integrated chlorophyll concentrations over different light layers across the shelf off Santa Catarina, central South Brazilian Bight, between November 2005 and June 2006. White, gray and black bars indicate integrated chlorophyll over 100–1, 1–0.1 and < 0.1% of surface irradiance, respectively. The number besides the white bar in January 2006 shows the highest integrated chlorophyll concentrations for that particular station and light layer. Note the different scales on the y-axes.

included in the analyses of phytoplankton distribution. Although commonly identified in shelf samples of the SBB the coccolithophorids have been shown to represent a minor component of the phytoplankton in previous studies (Brandini, 1988b; Brandini et al., 1989).

Diatoms contributed 29–90% and 31–90% of phytoplankton density and carbon biomass, respectively. They were dominated by a mix of coastal-estuarine centrals (*Thalassionema nitzschioides*, *Thalassiosira nanolineata*, *Thalassiosira* spp., *Chaetoceros didymus*, *Chaetoceros decipiens*, *Chaetoceros* spp., *Cylindrotheca closterium*, *Guinardia striata*, *Paralia sulcata*, *Hemiaulus indicus*, *Asterionella glacialis*, *Aulacoseira granulata*, *Leptocylindrus danicus* and *Coscinodiscus* spp.) and pennates (*Diploneis* sp., *Nitzschia* spp. including the *Pseudonitzschia* group, *Bacillaria paxillifera*, *Pleurosigma* sp., *Fragilariopsis doliolum* and unidentified small pennates). *Skeletonema costatum* was identified only at near-coastal stations. Shelf species of the genus *Hemiaulus* (*Hemiaulus hauckii*, *Hemiaulus membranaceus* and *H. indicus*) were always present in the inner-shelf assemblages.

Diatoms were not only dominant in abundance and biomass, but were also a very diverse group with the highest species richness in the nearshore waters, decreasing offshore (Fig. 8). Diatoms species richness was also comparatively high in mid-shelf stations during the summer intrusion in comparison to other sampling periods. In the same period, it was almost twice as high in the UML as at the DCM. The Shannon diversity index (H') ranged

from < 0.5 to 3.08, with different patterns of cross-shelf distribution according to season. In November, prior to the intrusion, the highest H' values were observed on the inner shelf, decreasing seaward. During the January intrusion, H' values remained high even away from the coast, reaching maxima > 2.0 in both the UML and DCM over the 60 m isobath. Typical coastal/estuarine species contributed most to both UML and DCM phytoplankton assemblages on the mid-shelf, and H' was very similar in both layers.

The typical freshwater genus *Aulacoseira* was frequent and sometimes dominant. This diatom was frequently identified at inner- and mid-shelf stations, in both the UML and the DCM. This was more evident during the January summer intrusion, when it was found from nearshore to the outer shelf, as indicated in the bottom plot of Fig. 8. Its contribution for the diatom assemblage decreased from March onward. The invasive *Coscinodiscus wailesii* was frequent, although in low numbers. This species was earlier identified in November at the DCM over the 100 m isobath (108 km offshore). Although in low densities (up to 120 cells L^{-1}), they were frequently found in both the UML and DCM following the January intrusion, until late summer (March–April). Large centric diatoms such as *Coscinodiscus* spp. and *H. indicus*, although not abundant numerically, contributed substantially to total phytoplankton C biomass.

In late summer, diversity was reduced in both the UML and DCM over the mid-shelf, similar to the lower indexes usually observed in the UML and the DCM on the outer shelf, where flagellates tend to dominate the phytoplankton. In March and April, maximum diversity was restricted to the inner-shelf area. In June, the advection of La Plata water strongly affected the diversity of diatom, which decreased overall along the cross-shelf and, as stated above, pennate diatoms and nano-flagellates numerically dominated the phytoplankton assemblage. In November, prior to the SACW intrusion, the stations were separated into at least three groups sharing 40% of diatom community similarity, based on Sørensen's presence/absence index (Fig. 9). During SACW intrusion in January, however, all stations shared at least 40% in the similarity of diatoms species composition, suggesting the assemblage was more mixed in this period along the cross-shelf.

3.6. Zooplankton composition and cross-shelf dynamics

A total of 73 crustacean taxa, including 59 copepod taxa, were identified along the transect during the entire study period (Table S2, Supplementary material). Copepods represented at least 80% of the overall zooplankton abundance. The most abundant taxon was the copepod *Oncaea waldemari*, which represented between 24.6% and 41.3% respectively in March and January; followed by *Ctenocalanus vanus*, between 9.2% and 22.1% in January and June; and *Oithona plumifera*, between 3.4% and 12.7% in November and January. Other taxa with > 5% relative abundance in at least one cruise were the cladoceran *Penilia avirostris* and the copepods *Clausocalanus furcatus*, *Temora stylifera*, and *P-calanus* (copepodites of *Paracalanus*, *Ctenocalanus*, and *Clausocalanus*).

In general, zooplankton densities were always higher over the inner shelf (Fig. 10), independently of seasons, with the highest levels in January (2500–7970 ind m^{-3}) and lowest in April (< 2000 ind m^{-3}). Mid-shelf zooplankton abundances had maxima between 1529 ind m^{-3} in June and 6730 ind m^{-3} in January, when zooplankton concentrate in the DCM. Outside the 100 m isobath, maximum zooplankton densities ranged between 1072 ind m^{-3} in November and 2192 ind m^{-3} on the UML in April. Cold water from the bottom layer with high influence of the SACW usually contained lower zooplankton densities, represented mainly by *C. vanus* and *O. plumifera* (not shown). The abundance of the copepods drove that of the total zooplankton. The most abundant species overall, *O. waldemari*, was widespread,

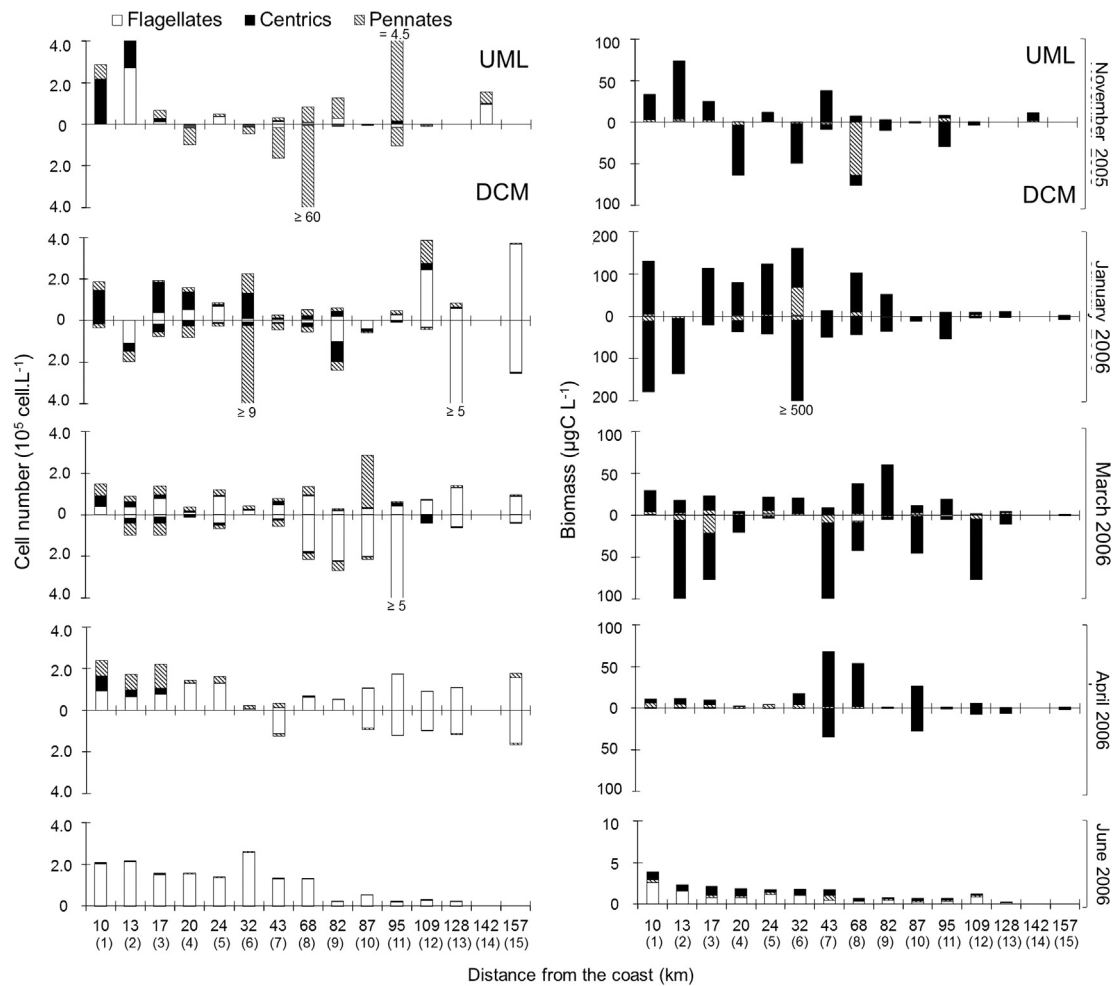


Fig. 7. Cross-shelf distribution of diatoms (centric and pennate) and total flagellate densities (left-hand side) and biomass (right-hand side) off Santa Catarina, central South Brazilian Bight, between November 2005 and June 2006. DCM, Deep Chlorophyll Maximum; UML, Upper Mixed Layer. Station numbers are indicated in brackets on the x-axes. Note the different scales on the y-axes.

occurring in all but two samples; it was concentrated mainly on the inner shelf, where maximum densities ranged between 588 ind m^{-3} in March and 3848 ind m^{-3} in January (Fig. 10). Away from the inner shelf, the abundance of *O. waldemari* was typically lower, increasing in January between the 50 and 80 m isobaths (between 258 and 2558 ind m^{-3}) peaking in the DCM. Medium to high densities (up to 835 ind m^{-3}) between the 50 and 120 m isobaths were also observed in the UML in June. The second most abundant species, *C. vanus*, reached relatively high densities during November on the inner (between 29 and 871 ind m^{-3}) and mid-shelf (between 137 and 1108 ind m^{-3}) mainly at the DCM. During January *C. vanus* was abundant in the inner shelf up to the 50 m isobaths where it peaked at the DCM (1306 ind m^{-3}). During the other cruises *C. vanus* was concentrated between 50 and 90 m isobaths, mainly in the DCM, except by the June peak of 919 ind m^{-3} in the 20 m isobath. Outside the 100 m isobath, *C. vanus* was not abundant, with densities typically lower than 50 ind m^{-3} , except by the peak of 627 ind m^{-3} during January on the 140 m isobath DCM (Fig. 9). *O. plumifera* was abundant only during January at coastal stations (up to 882 ind m^{-3}) and between the 50 and 70 m isobaths in the DCM (between 578 and 1088 ind m^{-3}). *P. avirostris* had a typical coastal distribution, occurring almost exclusively on the inner shelf and reaching its highest densities during November (up to 1071 ind m^{-3}) and January (up to 1078 ind m^{-3}).

After the Monte Carlo test, the Canonical Correspondence Analysis showed significant associations between environmental characteristics and the abundance of the 50 most abundant zooplankton taxa ($P=0.001$). Species distributions were only weakly related to salinity and water density. Therefore we excluded these variables from the analysis, in order to incorporate the samples from the first cruise, when salinity data were not available. Analyses of four tested CCA ordination axes shown in Table S3 (Supplementary material) explained 23.2% of variance in species abundance.

The first ordination axis correlated mainly with the distance from the coast and to a lesser extent with the TSI and CHI, and negatively with chlorophyll. The second axis was positively correlated with the TSI and temperature (Table S3; Fig. 11). The copepods *Paracalanus* spp., *O. waldemari*, *Calocalanus pavo*, *Calanoides carinatus*, *T. stylifera*, *Cl. furcatus*, *P. calanus*, *Paracalanus* spp., and *O. plumifera* were located close to the axes origin, indicating a low or variable association with the environmental parameters. Species such as the copepods *Lubbockia squillimana*, *Haloetilus* spp., *Aetideus giesbrechti*, *Acrocalanus longicornis*, *Rhincalanus nasutus*, and *Mecynocera clausi* were highly associated with increasing distance from the coast (Fig. 11). Those on the left side of the plot were species with more coastal affinities such as the copepods *Centropages furcatus*, *Corycaeus giesbrechti*, *Euterpina acutifrons*, *Oithona nana*, *Calanopia americana*, *Temora turbinata*,

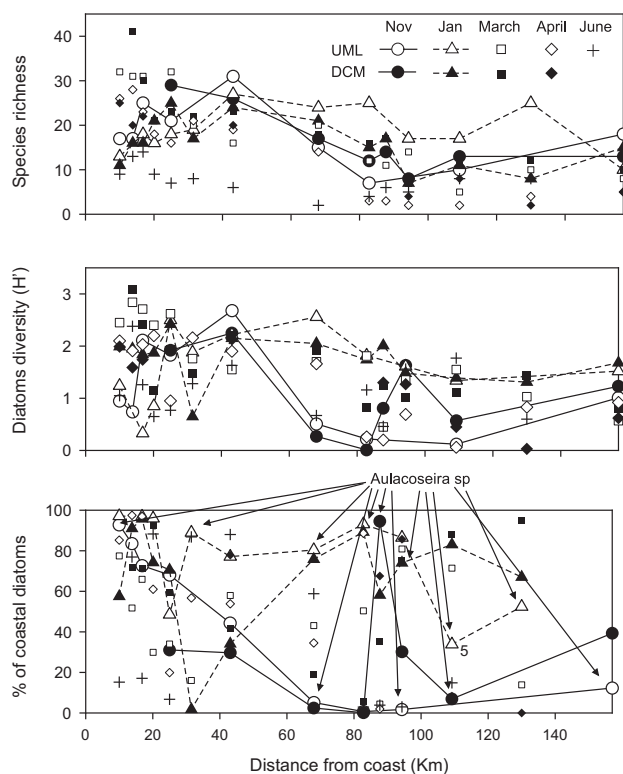


Fig. 8. Cross-shelf distribution of diatom species richness, diatoms diversity H' and % of coastal species of diatom off Santa Catarina, central South Brazilian Bight, between November 2005 and June 2006. UML, Upper Mixed Layer; DCM, Deep Chlorophyll Maximum. Setae on the bottom plot indicate higher frequency of *Aulacoseira granulata* in January 2006.

the cladoceran *P. avirostris*, and the decapod *Lucifer* spp. The vertical axis was mainly defined by the temperature and TSI positively and integrated chlorophyll negatively. Species such as the copepods *Sapphirina nigromaculata*, *Scolecithrix danae*, *Lucicutia flavicornis*, and *Corycaeus lautus* and the cladoceran *Evadne spinifera* were positively related to TSI; and others such as *Centropages brachiatus*, and *E. acutifrons* were negatively associated with TSI. Gammarids, ostracods, and the copepod *Labidocera fluviatilis* were associated with high temperatures, while Euphausiacea and the copepods *C. vanus*, *Microsetella rosea*, and *M. norvegica* were associated with lower temperatures and higher integrated chlorophyll values.

4. Discussion

The South Brazilian Bight is a typical western boundary shelf where the hydrography and plankton cross-shelf distribution closely resemble those found in the South Atlantic Bight off the southeastern USA. Hence, we consider it the most appropriate to compare with our results (see review by Lohrenz and Castro, 2005). The meandering of the Brazil Current and its associated eddy-induced shelf-break upwelling more or less mirror the role that the Gulf Stream (GS) plays in the hydrodynamics off the southeastern USA, except that the Brazilian shelf is broader (up to 200 km) and the shelf break is deeper (ca 200 m) (Castro and Miranda, 1998). Yet, analogous to the hydrographic features observed here, surface salinity fronts and seasonal intrusions of oceanic and nutrient-rich GS waters control the cross-shelf dynamics of plankton production and composition (Atkinson, 1977; Atkinson et al., 1984; Yoder et al., 1983, 1985; Yoder, 1985; Paffenhöfer, 1985).

Assuming the SACW to be a source of nutrients (Castro et al., 2006), a deeper Z_{eu} on the inner and mid-shelf might have been enriched by the oceanic intrusion in comparison to November. The gradual decrease of the mean Z_{eu}/Z_m ratio in the cross-shelf section between the 40- and 90-m isobaths from November to April, was due to vertical mixing and erosion of the pycnocline by tidal and wind stirring. From there toward the outer shelf, residual tidal circulation and wind mixing is not strong enough to disrupt the thermocline and the clear waters allow light to penetrate deeper into the water column in relation to the upper mixed layer. Therefore, it is clear that the intrusions of SACW improve light conditions for phytoplankton growth, mostly in the inner- and mid-shelf regions, between 40 and 90 km.

Although nutrients were not measured in this investigation, the seasonal differences in their magnitude are well reported (Brandini, 1988a, 1990; Gaeta and Brandini, 2006; Castro et al., 2006; Braga et al., 2008). In summer, the continental input of nutrients to the inner shelf (< 50 m depth) is higher following the rainy periods, although restricted to the near coast; whereas the oceanic inputs from the SACW fuel the new production at the base of the euphotic layers in the offshore areas. In winter, massive sources of nutrients, mostly phosphate and silicate, also arrive laterally from the La Plata River outflow, which is reinforced by southwesterly winds (Brandini, 1990; Ciotti et al., 1995; Brandini et al., 2007; Braga et al., 2008; Möller et al., 2008). Braga et al. (2008) reported summer mean concentrations of nitrate, phosphate and silicate in the upper euphotic zone (0–50 m depth) ranging, respectively, from 0.6 to 4.2, 0.3 to 0.4 and 3.7 to 4.5 μM . In winter, the mean concentrations of nitrate were similar to that in summer (from 2.9 to 3.6 μM), but phosphate and silicate were higher, ranging from 0.6 to 0.7 and 5.3 to 9.2 μM , respectively, due to the influence of the La Plata outflow. Higher mean concentrations of phosphate and silicate in these upper layers were associated with local and remote continental drainage. Below 50 m concentrations of nitrate, phosphate and silicate were > 9.1, 0.8 and 5.0 μM due to the presence of the SACW. Their ranges are in accordance with earlier data obtained by Brandini (1990) at the same latitudes as the SBB.

As observed earlier by Brandini (1990) and recently by Braga et al. (2008), the La Plata water reaches the SBB with very low nitrate concentrations, due to rapid absorption by phytoplankton along the Uruguayan and the southernmost Brazilian coast (34–30 °S) where surface chlorophyll concentrations are much higher, usually > 5 mg m^{-3} (Ciotti et al., 1995; Piola et al., 2008a; Garcia and Garcia, 2008) than at the surface of the SBB. The main nutrient contribution of the La Plata plume to the upper Z_{eu} of the SBB is residues of phosphate and silicate, unused due to the nitrate limitation in surface waters. Therefore, anomalous higher surface nitrate concentrations in mid- or outer shelf areas are mostly due to the effect of upward movements of the SACW into the lower euphotic layer caused by cyclonic eddies, shelf break upwelling and onshore bottom intrusions (reviewed by Castro et al., 2006). The regression of nutrient concentrations against temperature below the 20 °C isotherm (i.e., the SACW) conformed to linear relationship, with nitrate and phosphate having $r^2 > 0.9$ and silicate $r^2 > 0.75$ (Gonçalves and Brandini, unpublished). The mean ratio of N:P in the SACW has been estimated as 13.6 (Castro et al., 2006) which is slightly below the Redfield ratio of 16. Therefore, intrusions of the SACW into the SBB not only improve light conditions, but also the nutrient status of the lower euphotic layers where DCMs are formed.

The summer intrusion did not affect the inner-shelf integrated chlorophyll concentrations, as on the mid-shelf. Higher mean integrated chlorophyll concentrations in the water column of the nearshore stations, including the exceptional peak of 42.6 mg m^{-2} observed over the 30 m isobath (17 km offshore) in January, were

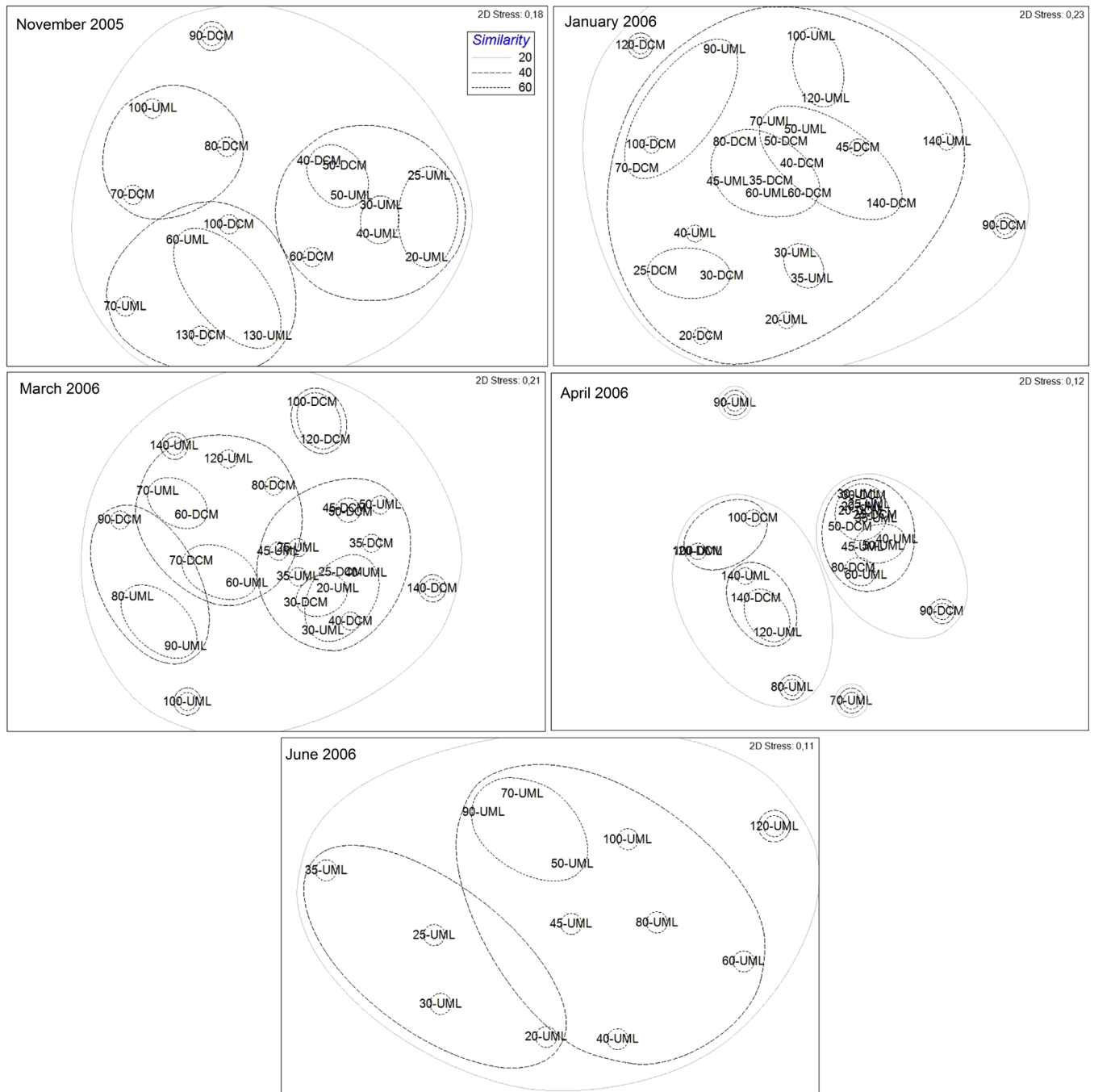


Fig. 9. Sørensen similarity analyses of diatom assemblage across the shelf off Santa Catarina, central South Brazilian Bight, between November 2005 and June 2006. UML, Upper Mixed Layer. DCM, Deep Chlorophyll Maximum.

probably more associated with the higher continental runoff in summer rainy seasons than with nitrate-depleted intrusions arriving on the inner shelf (Brandini et al., 2007).

4.1. Phytoplankton cross-shelf dynamics

Odebrecht and Djurfeldt (1996) reported the dominance of large centric diatoms (e.g., *Coscinodiscus* and *Thalassiosira*) in the DCM at inner- and mid-shelf stations of the southern Brazilian shelf, particularly off Santa Catarina, some distance south of our sampling transect. Many species of these genera formed the bulk of the large centric diatom assemblage in the mid-shelf DCM, sometimes contributing to the greater phytoplankton biomass although numerically less important. One of them was *C. wailesii*,

an invasive species from the tropical Pacific, which has been spread worldwide by ballast water (Nehring, 1998) and became established in estuarine lagoons of southeastern Brazil in the late 1980s (Fernandes et al., 2001). It was remarkable to find *C. wailesii* at the DCM far from the coast over the 100 m isobath in November 2006, and spread over the entire mid-shelf, although in low numbers (20–170 cells L^{-1}), following the summer intrusion. The possible impact of this large invasive centric diatom on the plankton tropho-dynamics and export rate of production to the benthic system (Smetacek, 1985) is a matter of concern and deserves further investigation.

It is also remarkable that *A. granulata*, a typical freshwater and estuarine species, which dominates the phytoplankton of lakes, rivers, and estuaries worldwide (Hoetzel and Croome, 1996; Perez

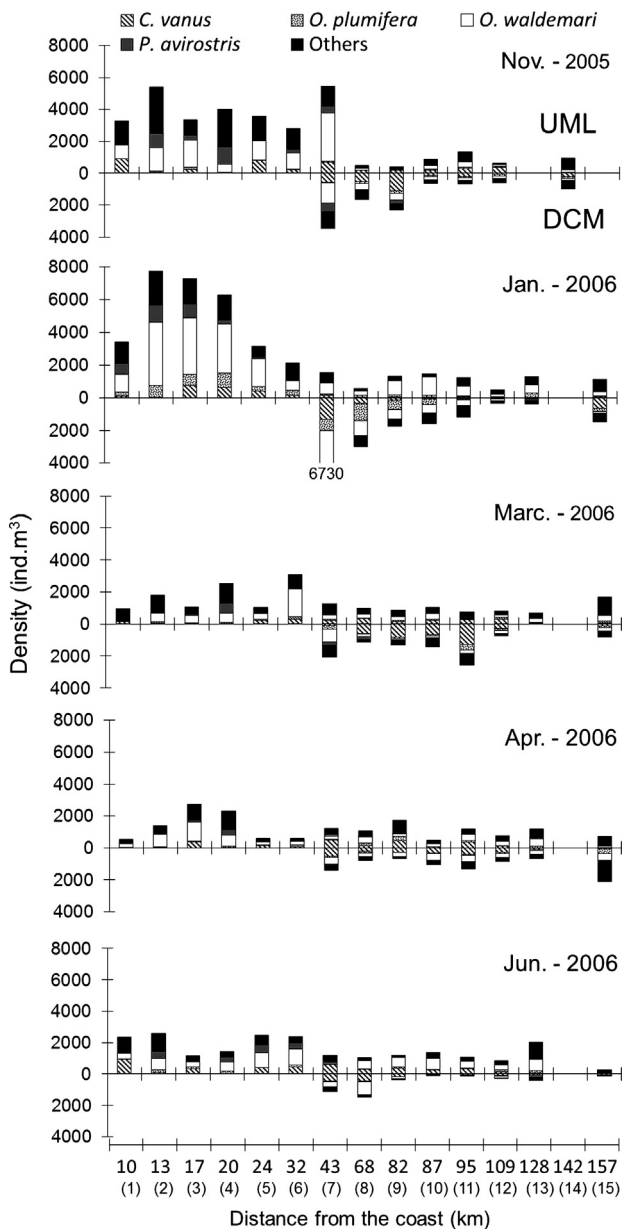


Fig. 10. Cross-shelf distribution of planktonic crustacean off Santa Catarina, central South Brazilian Bight, between November 2005 and June 2006. UML, Upper Mixed Layer. DCM, Deep Chlorophyll Maximum. Station numbers are indicated in brackets on the x-axis. Note the different scales on the y-axes.

et al., 1999; Marshall, 2009; Wang et al., 2009), including the southbound La Plata River plume (Gomez et al., 2004), occurred off the coast in high numbers and in good physiological conditions based on microscopic observations. In November > 8000 cells L^{-1} were counted in the DCM over the mid-shelf (80 m isobath), and following the summer intrusion in January, its abundance increased along the entire cross-shelf DCM, reaching up to 14,000 cells L^{-1} over the 45 m isobath (21 km offshore) and 6000 cells L^{-1} at the DCM over the 90 m isobath (84 km offshore). The advection of the La Plata plume during winter seasons along the southernmost part of the SBB (Castro et al., 2006; Piola et al., 2008b) has a marked effect on the shelf phytoplankton abundance and composition (Brandini, 1988a; Ciotti et al., 1995). The surface La Plata plume was clearly identified during the June cruise (see Fig. 3), as occurs almost every winter (June–August). Seeding of

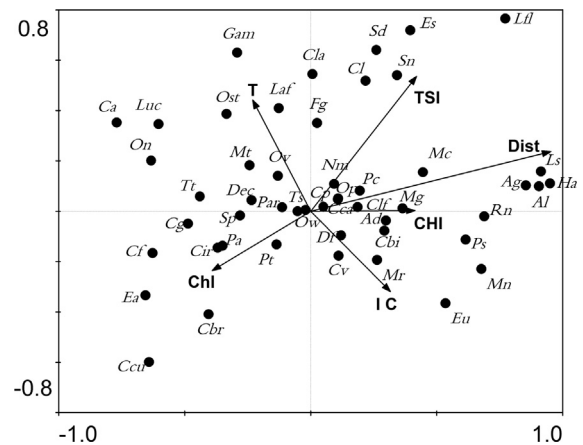


Fig. 11. Ordination diagram for the canonical correspondence analysis axes 1 and 2, showing the association of the 50 most abundant crustacean zooplankton species (circles) with environmental variables (represented by vectors). Species codes: Es=*Evadne spinifera*, Pa=*Penilia avirostris*, Pt=*Pseudoevadne tergestina*, Ad=*Acartia danae*, Al=*Acalanulus longicornis*, Ag=*Aetides giesbrechti*, Cbr=*Centropages brachiatus*, Cca=*Calanoides carinatus*, Ca=*Calanopia americana*, Cp=*Calocalanus pavo*, Cbi=*Candacia bippinata*, Ccu=*Candacia curta*, Cf=*Centropages furcatus*, Clf=*Clausocalanus furcatus*, Cg=*Corycaeus giesbrechti*, Cla=*Corycaeus latus*, Cl=*Corycaeus lautus*, Cv=*Ctenocalanus vanus*, Df=*Drepanopus forcipatus*, Ea=*Euterpina acutifrons*, Fg=*Farranula gracilis*, Ha=*Haloptilus* spp., Laf=*Labidocera fluviatilis*, Ls=*Libinia squillimana*, Lfl=*Lucicutia flavicornis*, Mn=*Microsetella norvegica*, Mg=*Macrosetella gracilis*, Mc=*Mecynocera clausi*, Mt=*Mesocalanus tenuis*, Mr=*Microsetella rosea*, Nm=*Nannocalanus minor*, On=*Oithona nana*, Op=*Oithona plumifera*, Ow=*Oncaea waldemari*, Ov=*Oncaea venusta*, Par=*Paracalanus* spp., Ps=*Paraeucalanus sewelli*, Pc=*P. calanus*, Rn=*Rhincalanus nasutus*, Sn=*Sapphirina nigromaculata*, Sd=*Scolecithrix danae*, Sp=*Subeucalanus pileatus*, Ts=*Temora stylifera*, Tt=*Temora turbinata*, Cir=Cirripedia, Dec=Decapoda, Eu=Euphausiacea, Gam=Gammaridae, Luc=*Lucifer* spp., Ost=Ostracod. Environmental variables codes: Chl=chlorophyll; T=temperature; Dist=distance from the coast; CHI=Chlorophyll heterogeneity index; TSI=temperature stratification index; IC=integrated chlorophyll.

diatoms from the La Plata plume, where diatoms represent up to 87.6% of the phytoplankton shelf assemblage (Carreto et al., 2008), must be a common process of mixing typical tropical with temperate phytoplankton assemblages (Brandini, 1988b; Fernandes and Brandini, 2004) and increasing diatom diversity. We did not observe *Aulacoseira* cells in our June transect, and we cannot explain how these cells arrived on our sampling transect. Yet it is remarkable that they survived, even in small numbers, under the much higher salinity conditions of the shelf. There are no other reports about the occurrence of this freshwater genus so far from a coast, except in South African waters (Eileen Campbell, personal communication).

Flagellates made only a minor contribution to shelf biomass. Dinoflagellates, coccolithophorids, and nano-flagellates ($< 20 \mu\text{m}$) usually form the bulk of the flagellate community in shelf systems, where they may be more abundant in more stable and nutrient-rich shelf fronts (Pingree et al., 1968). This has also been reported previously in the SBB, where a mixed population of dinoflagellates, coccolithophorids, and large diatoms tends to accumulate in the upper mixed layers of the surface salinity front (Brandini et al., 1989). In our investigation we were unable to show this, due to insufficient sampling resolution. Although they always dominate numerically at the surface and at the DCM on the outer shelf, flagellates are less important in terms of biomass during the summer stratification condition, when diatoms accumulate at the DCM, driven by the mid-shelf intrusion. When the DCM and the bulk of the diatoms collapse on the mid-shelf in late summer and early autumn due to zooplankton grazing, sinking of nutrient-depleted cells or physical dispersion by tidal and wind induced water turnover, flagellates tend to occupy the void left by diatoms.

4.2. Zooplankton cross-shelf dynamics

A mixture of coastal and oceanic epipelagic crustaceans, mostly copepods, was identified in this investigation, which is typical of southwest Atlantic shelf. As discussed above, the diverse physical processes in the SBB promote year-round fertilization of the euphotic zone with new nutrients, either local or from remote land runoff in winter (e.g., the La Plata plume) or oceanic sources during the summer stratified seasons. Therefore, we expect food not to be limiting for small herbivorous copepods to maintain their reproduction throughout the year. Pioneer populations or resting stages are always ready to respond rapidly to a more intense enrichment such as summer intrusions, as reported by Paffenhöfer (1983) for the southeastern USA shelf and by Miyashita et al. (2009) for the SBB. The most abundant species, are reported as abundant in many regions of the SBB (Valentin, 1984, 1989; Lopes et al., 1999, 2006; Ávila et al., 2009; Miyashita et al., 2009), with *O. waldemari*, *P. avirostris*, and *T. stilyfera* predominating in coastal waters, *C. vanus* and *O. plumifera* mainly on mid-shelf in the DCM and *Cl. furcatus* offshore. A pattern of cross-shelf distribution of planktonic crustacean assemblages was clear, as indicated by the distance from the coast being the most explicative variable in the CCA analysis. Such coast-ocean gradient also has high influence on planktonic cnidarians (Nogueira et al., 2014) and is expected given the large shelf (180 km) off Santa Catarina. The decreasing in abundance and increasing in diversity towards the ocean, as observed here, are common patterns on zooplankton both in the SBB (Lopes et al., 1999) and elsewhere (Li et al., 2012 and references therein).

To the north of our study transect, an early attempt to describe the cross-shelf distribution of zooplankton clearly distinguished neritic from oceanic zooplankton assemblages in response to contrasting hydrographic regimes across the shelf (Valentin, 1984). The herbivores *C. carinatus* and *C. vanus*, two common species in African upwelling zones (Gibbons and Hutchings 1996), dominate neritic assemblages during upwelling episodes, together with omnivorous copepods and cladocerans (e.g., *Corycaeus amazonicus*, *Eucalanus pileatus*, *Clausocalanus acuticornis* and *P. avirostris*). Simultaneously in the adjacent offshore domain, out of the upwelling influence, zooplankton are less abundant but highly diversified and dominated by warm-water species such as *Cl. furcatus*, *C. pavo* and *M. clausii*. In the wider and shallow shelf system of the central SBB, represented by our study transect, coastal salinity fronts due to long residence of the continental drainage and the bottom intrusions maintain strong vertical stratifications in physical and biotic gradients as the major driving forces of vertical zooplankton distribution. Yet, features described in Cabo Frio region were similar to those observed here (Valentin, 1984, 1989): (i) *Cl. furcatus* was indeed more abundant on the outer end of the shelf dominated by warm oligotrophic waters. Mazzochi and Paffenhöfer (1998) demonstrated experimentally how this small calanoid is adapted to low phytoplankton concentrations and therefore may dominate the copepod population in oligotrophic waters; (ii) *C. vanus* dominated the mid-shelf chlorophyll-rich intrusion usually accumulating on the DCM, although inner-shelf populations also persisted throughout the seasons, as reported by Valentin (1989); and (iii) the cladoceran *P. avirostris* was also representative of the neritic assemblage, being always abundant on the inner shelf. It was remarkably frequent although not abundant in the DCM layers of the mid- and outer shelf.

Using empirical models of copepod production and biomass, Miyashita et al. (2009) reported the indirect growth of the copepod population in response to oceanic intrusions of the SACW on the shelf off Santos, where the hydrographic regime is similar to our study transect. Although Miyashita and co-workers did not directly associate copepod production with food availability at the

DCM, they reported twice as much copepod abundance and biomass in the summer-stratified period as in the previous autumn, non-intrusion period. They concluded that the major effect of bottom SACW intrusions is to enhance food for the dominant *O. plumifera* and *O. waldemari* and the calanoids *C. vanus* and *Cl. furcatus*; although, as stated above, this last copepod does not require particularly rich phytoplankton conditions to reproduce successfully Mazzochi and Paffenhöfer (1998). These species dominated our sampling transect, some of them clearly more concentrated at the DCM (e.g., *O. plumifera* and *C. vanus*). Mazzochi and Paffenhöfer (1998) also reported that *Cl. furcatus* was more associated with warm surface waters, as we did here. These findings are in agreement with the earlier studies of Valentin (1984) and Lopes et al. (1999), which also indicated that these species are common and abundant in coastal and mid-shelf regions, affected by oceanic intrusions of the SACW. Off the southeast coast of the USA, bottom intrusions also support dense concentrations of small copepods (Paffenhöfer, 1983, 1985). In our investigation, small cyclopoid copepods and copepodites were always abundant across the shelf during all sampling cruises, with no apparent relationship to the chlorophyll-rich summer intrusion. However, copepodite abundance must have been greatly underestimated because the mesh size of our net was too large to sample efficiently small copepods and larval stages (Miyashita et al. 2009).

Our results also suggest that seeding populations of *O. waldemari* are more concentrated in the nearshore in early summer, extending their niche toward the mid-shelf along the colder bottom layers in response to oceanic intrusions, while *C. vanus* concentrate always along DCM following the intrusion. After the intrusion event when phytoplankton abundance and biomass have markedly decreased, probably due to sinking and grazing pressure by dominant copepods, in March and April, *O. waldemari* abundance reduces while relatively high densities of *C. vanus* persist along the mid-shelf DCM. *O. plumifera* is also one of the most common copepods and apparently it also responds rapidly, extending its niche along the chlorophyll-rich intrusion.

Growth and accumulation of plankton organisms do not necessarily coincide along cross-shelf gradients. On the regional scale, diatoms (followed by herbivorous copepods) seem to profit from the hydrodynamic scenario described here for the SBB in the summer 2005–2006, but they accumulated only in specific niches. In the tidally mixed nearshore and at the DCM, light conditions and nutrient availability combine to favor the growth of diatoms. However, accumulation also depends on factors other than growth, such as decreasing sinking rates and low grazing pressure by copepods, which were not measured in this investigation. Therefore, we can only speculate on how these physical and biological driving forces combine to form the diatom-rich DCM in the mid- and outer-shelf regions.

The cross-shelf dynamics of phytoplankton composition and abundance observed here suggest the following 6-step model (Fig. 12) to explain not only the formation of a diatom-rich DCM but also the cycling of diatom populations between the inner- and mid-shelf sections of the SBB: (1) In early summer, cells in the near-shore area are constantly resuspended by tidal and wave mixing; (2) While in suspension, their horizontal distribution may be extended away from coast along with the SHF by Ekman transport driven by northeast winds (Castro et al., 1987, 2006); (3) As they move oceanward they find nutrient-depleted waters in the upper mixed layer and, losing buoyancy due to poor nutritional conditions, they start to sink downward. Increasing sinking rates by nutrient-depleted diatoms and vice-versa are well known in historical investigations (Steele and Yentsch, 1960; Smayda, 1970; Bienfang et al., 1982; Smetacek, 1985); (4) In contrast, sinking rates decrease at the top of the pycnocline, where nutrient

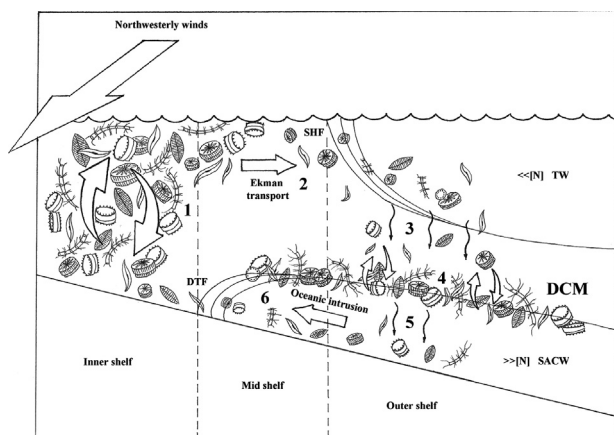


Fig. 12. Schematic representation of the shelf hydrodynamic loop model based on the diatom distribution and community structure along the cross-shelf off Santa Catarina, central South Brazilian Bight, between November 2005 and June 2006. SHF, Surface Haline Front; TW, Tropical Water; DCM, Deep Chlorophyll Maximum; SACW, South Atlantic Central Water; DTF, deep thermal front; [N], nutrient concentration; Numbers indicate the following steps around the loop: (1) diatom resuspension in the nearshore waters by tidal and wave mixing; (2) offshore Ekman transport of diatom cells during summer northeasterly winds; (3) nutrient-depleted diatoms lose buoyancy and sink; (4) cell sinking rates decrease at the top of the pycnocline/nutricline and accumulate at the DCM; (5) below the DCM, cells become light-limited and sink downward to bottom layers; and (6) diatom resting stages are carried back to nearshore waters by the oceanic intrusion of the SACW.

concentrations are higher and light conditions are still satisfactory to maintain growth, forming the DCM. [Bienfang et al. \(1983\)](#) have reported the increase of buoyancy of shade-adapted diatoms growing under low light intensities and how this contributes to formation of DCM. [Brandini et al. \(1989\)](#) reported maximum dissolved oxygen concentrations just above the DCM in the same region, suggesting that growth rather than the sinking rate is responsible for the formation of the DCM on the shelf of the SBB; (5) Turbulence in the UML decreases gradually downward ([Mann and Lazier, 2006](#)) and cells of the DCM below $< 1\%$ surface light become light-limited, and hence sinking rates increase toward the bottom layers; (6) Sinking cells (and resting stages) still in suspension may be carried by the oceanic intrusion of SACW, finding their way back to nearshore where light again becomes available due to vertical mixing, closing the loop.

The following evidence supports this “shelf hydrodynamic loop” of diatoms in the SBB: (i) summer northeasterly winds are the major force moving surface waters along with tidally resuspended diatoms offshore, by Ekman transport. This “seeding step” of estuarine phytoplankton to the open shelf was suggested long ago for the shelf off the eastern USA ([Marshall, 1982, 1984](#); [Malone et al., 1983](#)), and offshore wind driven advection was also detected for some coastal zooplankton in the SBB during this study ([Nogueira et al., 2014](#)); (ii) typical coastal/estuarine species, usually abundant in the nearshore and coastal lagoons ([Fernandes and Brandini, 2004](#); [Procopiak et al., 2006](#)) were common at the surface and at the DCM of mid-shelf regions, contributing between 50% and 90% of the diatom community. This was confirmed by the high degree of mixing of the diatom assemblage in January (at both the UML and the DCM), sharing at least 40% in the species composition along the entire transect (see [Fig. 8](#)). In addition, a surface low-salinity layer was clearly detected along the transect in January (see [Fig. 3](#)) when the 36.5 isohaline representing the SHF (*sensu* [Castro et al., 1987](#)) was located far (ca 130 km) offshore; (iii) Low-Light High-Nutrient conditions along the DCM resemble nearshore benthic habitats dominated by shade-adapted pennate diatoms ([Queiroz et al., 2004](#)). Although shade-adapted pennate diatoms do not contribute as much as centric species to

phytoplankton biomass, they grow faster at the DCM and increase their chlorophyll/cell content; (iv) Unfortunately, no data from sediment-trap experiments on the Brazilian shelf are available, that might support the argument of mass sedimentation of diatom cells following the oceanic intrusions. Yet we can suggest evidence for phytoplankton sinking based on the partitioning of the integrated water-column chlorophyll data depicted in [Fig. 6](#). In late-summer periods, substantial amounts of chlorophyll are concentrated below the Z_{eu} in the mid-shelf region, indicating that sinking of phytoplankton cells proceeds continuously after the intrusion enrichment; (v) The onshore summer intrusions is the hydrodynamic mechanisms that diatoms and (perhaps) their resting stages can be transported back to the nearshore. Our results lack simultaneous hydrodynamic data, and we can only rely on the physical oceanographic studies that have been done in the SBB in recent decades. Nevertheless, the DTF shown in [Fig. 3](#) between the bottom insertion of the 19 and 20 °C isotherms, was sited at 80 km offshore over the 70-m isobath in November, prior to the intrusion. In January it had moved to 20 km offshore over the 35-m isobath, i.e., moving 60 km shoreward in approximately 72 days (the time interval between the November 6 and January 17 cruises). To match this distance with the time interval, the mean intrusion cross-shelf velocity must be ca 1 cm s^{-1} . This is a very low current speed, yet is sufficient to generate the laminar flow necessary to transport diatoms and their resting stages in suspension in the SACW back to shore. It is within the range of 0.2–2.0 cm s^{-1} used in erosion experiments by [Ziervogel and Foster \(2006\)](#) to confirm the lateral transport of benthic diatoms from shallower to deeper areas of the Mecklenburg Bight in the Baltic Sea.

5. Conclusions

Particle dynamics, wind-driven Ekman transport offshore, and bottom intrusions of oceanic waters are common processes in shelf systems worldwide ([Lohrenz and Castro, 2005](#); [Longhurst, 2006](#); [Mann and Lazier, 2006](#)). These processes are important for the circulation of phytoplankton in upwelling systems of eastern boundary shelves, particularly the diatoms, which are the most important primary producers in these ecosystems. Upon stress due to temporary nutrients or light limitation, diatom blooms produce fast sinking resting spores to avoid being washed away from the upwelling system by offshore wind-driven surface waters ([Villac and Kaczmarek, 2011](#)). We propose a similar mechanism in western boundary systems where such a “hydrodynamic loop of diatoms”, here observed in the SBB may also take place. It seems that diatom life cycles have evolved following such a loop, to avoid massive losses of neritic diatom cells from the shelf waters, and simultaneously maintaining themselves near their primary resources (e.g., light and nutrients) as they do in major upwelling systems ([Garrison, 1981](#); [Pitcher, 1990](#)). Diatoms are able to survive in dark shelf sediments for many years ([Smetacek, 1985](#); [Lewis et al., 1999](#)), which easily matches the temporal scale of the hydrodynamic loop proposed here. Each summer intrusion may contribute a little to a multi-year scale transport mechanism of diatoms and their resting stages back to the coast, where they find their way into estuaries and coastal lagoons by tidal currents. Obtaining further current data will be crucial to confirm this hydrodynamic-loop scenario and its efficiency for diatom retention along the shelf system as a whole, from the innermost shallow areas down to the outermost and deepest shelf waters. In addition to maintaining the constant seeding of diatoms along the cross-shelf, it prevents loss of cells from the shelf, as has been documented in the western North Atlantic ([Falkowski et al., 1994](#); [Sarmiento and Gruber, 2006](#) and references therein).

It remains to be confirmed whether herbivorous copepods and the shelf zooplankton assemblages in general may also rely on similar processes to follow their food sources. It has been widely reported how the retention of copepods and their resting stages in estuarine habitats is driven by vertical migrations coupled with tidal circulation as a mechanism to avoid dispersion to the outer shelf, where food is less abundant than inside the estuaries (Wooldridge and Erasmus, 1980; Hough and Naylor, 1991; Kimmerer et al., 1998; Plourde et al., 2002). However, our evidence of an extension of the cross-shelf distribution niche of dominant copepods in the SBB related to the chlorophyll-rich intrusions, may not indicate a similar hydrodynamic loop of copepods and their resting eggs. Further studies are need to determine whether an analogous hydrodynamic loop exists by which copepods, similarly to diatoms, may repopulate shelf plankton assemblages in western boundary shelf systems.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.csr.2013.08.002>.

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