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Effects of coastal upwelling on the structure of macrofaunal communities in SE Brazil

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ABSTRACT

The effects of coastal upwelling on the structure of macrofaunal communities were investigated in two shallow bays in SE Brazil. Water, sediment and fauna samples were collected at four time-points corresponding to austral summer, fall, winter and spring, respectively. Water column temperature and salinity profiles indicated that upwelling occurred in summer–spring (December and November), but not in fall–winter (April and August). The structure of macrofaunal communities differed consistently between these periods. The sediment content of labile organic matter did not vary as a function of upwelling and could not explain the changes in macrofaunal communities. Rather it appeared that macrofaunal community structure was determined by organic matter quality (i.e. phytoplankton composition), physical disturbance regimes and bottom-water temperature. Physical disturbance caused by S–SE winds, warm water temperatures (up to 26 °C) and resuspension-driven phytoplankton blooms during non-upwelling were associated to higher density (2511 ± 2525 ind m−2) and dominance of small opportunistic species such as spionid, paraonid and capitellid polychaetes. In contrast, stable hydrodynamic conditions, diatom blooms and lower water temperatures (down to 18 °C) during upwelling resulted in lower density of macrofauna (796–1387 ind m−2) and a shift in species composition to relatively large-sized magelonids and carnivorous polychaetes. Therefore, organic matter quality, physical disturbance regimes, and bottom-water temperature were the major factors regulating the life-cycles, composition and density of macrofaunal communities in these less productive subtropical upwelling systems.

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1. Introduction

Benthic macrofauna (i.e. animals retained by a 0.5 mm mesh) are important components of the food-webs in coastal marine ecosystems. They assimilate energy contained in organic detritus and thereby act as a second trophic level transferring energy from primary production to animals of higher trophic levels, such as commercially important benthic megafauna including prawns, crabs and demersal fishes (De Léo and Pires-Vanin, 2006; Rocha et al., 2003). In tropical and subtropical zones, marine ecosystems function under meso-oligotrophic conditions, and the limited input of organic detritus derived from phytoplankton greatly affects the structure of benthic macrofaunal communities. Under these conditions benthic macrofauna are typically characterized by high diversity, but low biomass of individuals (Alongi, 1989; Sanders, 1968). In meso-oligotrophic areas, primary productivity and the input of organic detritus to the seabed are strongly dependent on nutrients regenerated in the water and sediment, discharged by run-off from land or transported with oceanic water to the coast during upwelling events (Braga and Müller, 1998; Silveira et al., 2000).

The coastal areas of SE Brazil are strongly influenced by a seasonal upwelling of a deep, cold and nutrient-rich water mass; the South Atlantic Central Water (SACW) (Castro-Filho et al., 1987). During late spring to early summer in November–December, predominant winds from the E–NE quadrant induce the upwelling of SACW from the continental slope towards the coast by Ekman transport (Castro-Filho et al., 1987). SACW is therefore often registered up to 10 m depth along the coast below a strong thermocline in mid-water (Braga and Müller, 1998; Castro-Filho et al., 1987). SACW flows towards the coast in close contact with the sea bottom and becomes enriched with inorganic nutrients produced by organic matter mineralization in the water column and sediments. Thus, besides having a low temperature compared to surface water, SACW typically has low oxygen and high nitrate levels (Braga and Müller, 1998). When SACW with up to ~5 μM nitrate reaches the euphotic zone, it triggers phytoplankton blooms and the sediments may temporarily receive increased amounts of labile organic matter (Aidar et al., 1993; Sumida et al., 2005), providing a rich source of energy to the benthic fauna. Furthermore, upwelling conditions during spring–summer are characterized by more stable environmental conditions, i.e. calm winds and hydrodynamics, compared to non-upwelling
conditions in the rest of the year, when frequent passage of cold fronts causes stronger hydrodynamic forcing and sediment resuspension in the coastal zone (Gaeta et al., 1999; Mahiques et al., 1998).

SACW upwelling may influence benthic fauna communities along SE Brazilian coasts by changing the amount and quality of food delivered to the sediments. The phytoplankton biomass in spring–summer during coastal upwelling ranges from 3 to 12 mg chlorophyll m⁻³ in SE Brazil (Aidar et al., 1993; Gonzalez-Rodriguez et al., 1992). Other important coastal upwelling zones in the eastern boundary Pacific and Atlantic Oceans are extremely productive and phytoplankton biomass reaches levels up to 5-fold higher compared to those in SE Brazil (Chavez and Messié, 2009; Pennington et al., 2006). Much is known about how increased primary productivity affects benthic fauna in high-productive upwelling areas (Levin et al., 2009), but limited information is available on the ecological community structure of benthic macrofauna in less productive upwelling systems along SE Brazilian coasts (Quintana et al., 2010; Venturini et al., 2011).

This study investigates the effects of a seasonal upwelling on the availability of labile organic matter (i.e. microalgal-derived material) and associated impacts on the structure of macrofaunal communities along two shallow coastal bays in SE Brazil. We hypothesized that summer upwelling events increases labile organic matter content in the sediment resulting in higher density of organisms and shifts in dominance of macrofaunal species compared to non-upwelling seasons. To test this hypothesis, benthic macrofauna, sediment and water parameters were sampled four times during a year in two shallow-water bays (4–19 m depth), representing summer, fall, winter and spring. SACW upwelling was assessed by temperature and salinity profiles in the water column. Labile organic material was measured as chlorophyll-a concentrations in the sediment. Temporal changes in density and species distribution of macrofauna were detected by multivariate analysis and coupled to concurrent changes in environmental data.

2. Material and methods

2.1. Study area

The study area is located in Ubatuba at the Tropical/Subtropical boundary in SE Brazil (Fig. 1). Ubatuba is composed of several small enclosed bays and is surrounded by the Serra do Mar mountain chain, which extends to the shore throughout most of the region and limits the extension of intertidal flats and drainage systems (Mahiques et al., 1998). The coastal water (CW) in Ubatuba has a salinity of 32–36 and temperatures of ≥ 25 °C (Castro and Miranda, 1998). Since there are only few, small-sized rivers present in the coastal bays, the freshwater and nutrient run-off is minimal, resulting in meso-oligotrophic characteristics of the CW (Castro and Miranda, 1998; Gaeta et al., 1999). Nutrient concentrations (e.g. nitrate, ammonium, phosphate) are low during most of the year and the phytoplankton is dominated by nanoflagellates (Aidar et al., 1993; Gaeta et al., 1999). In spring–summer, however, the upwelling of the cold and nutrient-rich SACW (salinity ≤ 36.4 and temperatures ≤ 20 °C) to the euphotic zone and higher rainfall can drive sporadic blooms of opportunistic diatoms (Aidar et al., 1993; Castro-Filho et al., 1987; Gaeta et al., 1999). Sporadic nutrient enrichment of the water column may also occur during short-term sediment resuspension events, which are frequent during passage of cold fronts (i.e. strong S–SE waves, 4–6 times per month) in the period without SACW upwelling. These resuspension events can also increase water column nutrient levels, stimulate primary productivity and influence the depth distribution of organic matter into the sediments (Aidar et al., 1993; Gaeta et al., 1999; Quintana et al., 2010; Gallucci and Netto, 2004). The physical disturbance level and potential for sediment resuspension in Ubatuba bays are determined by the shape of the shoreline and the orientation to the open sea (Bureone et al., 2003; Mahiques et al., 1998). Bays oriented in S–SE direction are more exposed to...
physical disturbances generated by the S–SE waves than bays oriented in E–NE.

In this study, two shallow water bays, Fortaleza and Ubatuba bays, located near Ubatuba City, Brazil, were investigated (Fig. 1). Fortaleza Bay is located in a non-urbanized area and is influenced by freshwater input from one river. The bay opening is oriented S–SE and thus the hydrodynamics is partly controlled by swells (S–SE waves) during the passage of cold fronts. Ubatuba Bay is located in a more urbanized area and is influenced by four small rivers and the bay opening is oriented in E–NE direction. This bay has a constriction in the shoreline dividing it into two parts (Fig. 1), the inner part, which is sheltered from storms and S–SE waves and the outer part, which is exposed to S–SE waves.

2.2. Water and sediment sampling

Water and sediment samples were collected from a research vessel (R/V Veliger II) in December 2004, and April, August, and November 2005 (corresponding to early summer, fall, winter and spring, respectively). Four stations in each bay were positioned in a shore-to-ocean transection within bays (Fig. 1). Stations F1, F2, F3 and F4 were located in Fortaleza, and stations U5, U6, U7 and U8 in Ubatuba (Fig. 1).

On each sampling occasion water temperature and salinity profiles were measured by a CTD (Conductivity, Temperature and Density, Falmouth®). The profiles were used to identify the presence of specific water masses pre-defined according to temperature and salinity characteristics (Castro-Filho et al., 1987). Besides the temperature and salinity, dissolved oxygen (DO) and nitrate concentrations were used as additional indicators to detect SACW. Typically, SACW has high nitrate concentrations (4–12 μM and low DO (<200 μM) compared to other water masses (Aidar et al., 1993; Braga and Müller, 1998). DO and nitrate were measured on water samples taken 1 m above the bottom, using van Dorn bottles. Immediately after retrieval, 100 mL were transferred to Winkler bottles and fixed with Winkler reagents. Afterwards, 1–2 L of water were filtered through a GF/F filter. Nitrate samples were taken from the filtrate and stored at −20 °C. Wind velocity and direction were obtained from Caraguatatuba, the closest city to Ubatuba (ca. 25 km), every 6 h during the sampling days (available at http://sinda.crn2.inpe.br/PCD, Brazilian National Space Research Institute – INPE).

Sediments were sampled with a multicorer that provided three acrylic core liners (9.6 cm inner diameter, 60 cm long) every time it was retrieved. Sediment cores collected from one drop of the multicorer were always used for different purposes to avoid pseudo-replication. A total of 9 cores were retrieved from each station during every sampling: one for grain size; three for chlorophyll-a (Chl-a) and total organic matter (TOM); five for macrofauna. The cores were sliced at 0–2, 2–5 and 5–10 cm intervals and sediment was collected for analysis of grain size, TOM, Chl-a and macrofauna. The vertical resolution applied in this study did not reveal any clear pattern in all measured variables, probably due to the effects of sediment resuspension on most of the stations. Therefore, for comparative purposes, all results were depth integrated to 10 cm. Sediment samples for grain size, TOM and Chl-a were stored at −20 °C. Macrofauna samples were sieved on board using a 0.5 mm mesh. The material retained on the mesh was transferred to plastic jars and preserved with 70% ethanol.

2.3. Laboratory analysis

DO was determined by Winkler titration and nitrate was analyzed spectrophotometrically (Grasshoff, 1999; Strickland and Parsons, 1972). Grain size was analyzed by sieving and pipetting techniques (Suguio, 1973). The statistical parameters of the grain types were obtained following Folk and Ward (1957) and classified using the triangular diagram of Shepard (1954). Sediment subsamples were analyzed for TOM and chlorophyll-a (Chl-a). TOM content was quantified gravimetrically as the weight loss after combustion (500 °C for 3 h). Chl-a in sediment was extracted from wet subsamples (1–2 g) with 90% acetone (24 h in the dark at 4 °C). The absorbance of Chl-a extracts was measured on a spectrophotometer (665 and 750 nm) before and after acidification (10% HCl), and final Chl-a concentration was calculated according to Lorenzen (1967). Preserved macrofaunal samples were sorted under a dissection microscope, and fauna was quantified and identified to the lowest possible taxonomic level. Polychaetes, the most abundant group of macrofauna, were classified into trophic feeding groups, i.e. surface deposit feeders, sub-surface deposit feeders, carnivores and omnivores according to Fauchald and Jumars (1979) and Muniz and Pires (1999). Ash-free biomass of polychaetes was determined by difference in dry weight before and after combustion at 500 °C for ca. 3 h.

2.4. Statistical analysis

To identify significant differences between bays and sampling dates, two-way ANOVA tests were performed on water (i.e. bottom temperature, salinity, DO and nitrate) and sediment data (i.e. median grain size, TOM, Chl-a, total macrofaunal density and feeding groups density). Four stations were analyzed to cover spatial differences within each bay and to detect potential effects of upwelling in the two bays through time. Therefore, water and sediment data obtained from the stations of each bay were tested together in the two-way ANOVA. When necessary the data were square root (x) or log (x + 1) transformed to meet the assumption of normality. All tests were performed with a significance level α = 0.05 using SigmaPlot 11.0.

Multivariate analyses were applied to environmental and fauna data. General patterns of SACW influence in the systems were tested by principal component analysis (PCA) applied to environmental data (indicators of SACW: temperature, salinity, DO and nitrate in the bottom water, wind direction — in degrees, chlorophyll-a in sediments) and total density of macrofauna. One-way analysis of similarity (ANOSIM) was performed (Clarke, 1993) to verify differences in species density between the groups observed in the PCA. Similarity percentage analysis (SIMPER) was used to identify the species that contributed most to the difference among groups observed in the PCA (Clarke, 1993). In addition, a biotic-environmental matching (Bio-Env) analysis was performed to identify the environmental variable or group of variables that best explained the variation of macrofaunal species (Clarke, 1993). The significance of correlation coefficients (ρw) obtained by Bio-Env were verified by the permutation analysis RELATE. All multivariate macrofaunal community analysis, i.e. PCA, ANOSIM, BIO-ENV and RELATE were performed using Primer 6.0 & Permanova + (Clarke and Warwick, 2001).

3. Results

3.1. Winds and water column

Average wind speed was similar throughout the year (4–5 m s⁻¹), while wind direction changed consistently among sampling dates. In December and November winds were predominantly from E. In April, the dominating wind direction changed to SE and in August winds were mainly from S–SE.

Temperature and salinity profiles in the water column showed upwelling of SACW occurred in summer and spring (December and November). SACW was detected at all sites except the shallowest stations (F1 and U5 at 4–5 m water depth, Table 1). In contrast, Coastal Water (CW) was detected on all stations in April and August. Bottom-water temperature was similar between bays, but varied from 18 to 24 °C in upwelling and from 22 to 26 °C in non-upwelling periods (Table 1), with lows and highs recorded in December (16.6–18.5 °C) and April (21.4–28 °C), respectively (p < 0.001). Salinity did not vary
significantly between bays (Table 1), but was lower in November (32–34) compared to the other months (34–35) (p < 0.001).

Lower DO and higher nitrate were also used to trace the presence of SACW at the study sites over time. In both bays, nitrate was consistently higher in December and November (ranging 0.2–5.8 μM), indicating the presence of SACW, than in April and August (0.2 to 1.4 μM, p < 0.05, Table 1). Accordingly, DO was consistently lower in Ubatuba Bay than Fortaleza Bay (later on referred as Ubatuba and Fortaleza, respectively) in December (139 to 237 μM) and also in August (62 to 112 μM) (p < 0.05).

3.2. Sediment characteristics

The percentage of sand and silt + clay in the sediment did not vary temporally on individual stations, but varied spatially within bays (Table 2). In Fortaleza, the shallower stations had sandy sediment (median grain size of 31–67 μm) whereas muddy sediment (median grain size of 26–29 μm) was typical at the deeper stations F3 and F4. An opposite pattern was observed in Ubatuba, where sandy sediments predominated at the deeper stations and muddy sediments at the shallower stations (Table 2). In both bays, the sandy stations (F3, F4, U7 and U8) were mainly composed by fine and very fine sand, since 35–100% of total sediment was composed of particles with 62–177 μm (Folk and Ward, 1957). At muddy stations (F1, F2, U5 and U6) 68–96% of total sediment consisted of silt-clay particles <62 μm (Folk and Ward, 1957).

TOM was higher in sediments from Ubatuba (1 to 12%) than Fortaleza (1 to 7%) and was lowest in November in both bays (p < 0.05) (Table 2). Chl-a was 77% higher in Ubatuba (14.5 ± 13.2 μg g⁻¹) than in Fortaleza (3.3 ± 2.0 μg g⁻¹) (p < 0.05), with no significant temporal change (Table 2). Accordingly, no major enhancement of chl-a was observed between upwelling and non-upwelling periods in any bay (Table 2).

3.3. Benthic macrofaunal communities

The temporal patterns of total macrofaunal density and species composition were similar in the two bays. Total density varied significantly 2–3 times over the year (p < 0.05). The highest density occurred during non-upwelling conditions in April (2525 ± 1029 ind m⁻²) and August (2511 ± 680 ind m⁻²), and the lowest during upwelling in December (1387 ± 540 ind m⁻²) and November (796 ± 386 ind m⁻²) (Fig. 2). The macrofaunal community was composed by a total of 153 species, including 89% rare (frequency of occurrence <10%) and 11% common species (10–50% frequency of occurrence) (Guille, 1970). Polychaetes were the most abundant group (60–90%), followed by mollusks (10–20%), crustaceans (8–15%), echinoderms (1–3%) and others (sipunculids, hemichordates and nemerteans 2–4%). In December, the macrofauna in both bays was mainly composed by magelonid polychaetes (Magelona posteroelongata, Magelona papillicornis and Magelona variolnellata), lumbrinerids (Ninoe brasiliensis), goniadids (Goniada sp.), small crustaceans (amphipods and tanaidaceans) and bivalves (Nucula semiorbata). In April, the community was composed of tellinid bivalves (Tellina versicolor), brittle stars (Amphipoda australis), amphipods (Amphelus capensis) and various polychaetes including opportunistic species (among others Fauveliopsis sp., M. papillicornis, Mediomastus capensis, Porcelliothis australis, Acanthosoma simplex, Sphiophanes missionis). In August, macrofauna was fully dominated by opportunistic polychaetes such as A. simplex, M. capensis and S. missionis. In November, the community shifted back to a composition of magelonids, lumbrinerids, goniadids, small crustaceans and bivalves as observed in December, but densities were lower.

Shifts in dominance between trophic groups of polychaetes were evident between upwelling and non-upwelling conditions (Table 3). Surface deposit feeders were significantly more abundant in April (1127 ± 755 ind m⁻²) and August (1189 ± 504 ind m⁻²) compared to December (378 ± 369 ind m⁻²) and November (274 ± 187 ind m⁻²) (p < 0.05) and were mostly represented by the species A. simplex and S. missionis (Fig. 2, Table 3). Surface deposit feeders followed the same trend with significantly higher densities in April (303 ± 110 ind m⁻²) and August (331 ± 214 ind m⁻²) compared to December (79 ± 59 ind m⁻²) and November (79 ± 70 ind m⁻²) and were mostly composed by the capitellid polychaete M. capensis (Table 3). Total carnivores including small pilargid species Sigarama grubii, and Synelmis sp. were less abundant in November (29 to 288 ind m⁻², p < 0.05) (Fig. 2), whereas larger carnivores such as the lumbrinerid N. brasiliensis and gonidiid Goniada sp. were mostly 2–4 times more

<table>
<thead>
<tr>
<th>Station</th>
<th>Water depth (m)</th>
<th>Upwelling – December + November</th>
<th>Non-upwelling – April + August</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>T (°C)</td>
<td>S</td>
<td>DO (μM)</td>
</tr>
<tr>
<td>F1</td>
<td>4</td>
<td>34.4</td>
<td>33.2</td>
</tr>
<tr>
<td>F2</td>
<td>9</td>
<td>20.7</td>
<td>34.0</td>
</tr>
<tr>
<td>F3</td>
<td>11</td>
<td>19.6</td>
<td>34.6</td>
</tr>
<tr>
<td>F4</td>
<td>18</td>
<td>18.3</td>
<td>35.4</td>
</tr>
<tr>
<td>U5</td>
<td>5</td>
<td>23.7</td>
<td>34.2</td>
</tr>
<tr>
<td>U6</td>
<td>9</td>
<td>19.7</td>
<td>34.9</td>
</tr>
<tr>
<td>U7</td>
<td>13</td>
<td>18.7</td>
<td>35.1</td>
</tr>
<tr>
<td>U8</td>
<td>19</td>
<td>18.3</td>
<td>35.3</td>
</tr>
</tbody>
</table>

Table 1
Summary of environmental conditions in the bottom-water registered during upwelling in summer-spring (December 2004 and November 2005) and non-upwelling in fall-winter (April and August 2005). Values represent average of temperature (T), salinity (S), dissolved oxygen (DO) and nitrate in the bottom water (n = 2).

<table>
<thead>
<tr>
<th>Station</th>
<th>Sand (%)</th>
<th>Silt + Clay (%)</th>
<th>TOM (%)</th>
<th>Chl-a (μg g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>F1</td>
<td>82 ± 1</td>
<td>18 ± 1</td>
<td>1.3 ± 0.1</td>
<td>2.7 ± 0.5</td>
</tr>
<tr>
<td>F2</td>
<td>38 ± 14</td>
<td>62 ± 14</td>
<td>5.3 ± 0.9</td>
<td>3.6 ± 1.1</td>
</tr>
<tr>
<td>F3</td>
<td>38 ± 12</td>
<td>62 ± 12</td>
<td>6.9 ± 1.6</td>
<td>3.2 ± 0.8</td>
</tr>
<tr>
<td>F4</td>
<td>17 ± 2</td>
<td>83 ± 2</td>
<td>4.1 ± 0.3</td>
<td>2.6 ± 0.5</td>
</tr>
<tr>
<td>U5</td>
<td>21 ± 7</td>
<td>75 ± 10</td>
<td>6.0 ± 1.0</td>
<td>15.9 ± 3.1</td>
</tr>
<tr>
<td>U6</td>
<td>45 ± 54</td>
<td>55 ± 54</td>
<td>7.9 ± 1.9</td>
<td>21.2 ± 1.0</td>
</tr>
<tr>
<td>U7</td>
<td>73 ± 0</td>
<td>27 ± 1</td>
<td>4.4 ± 0.5</td>
<td>5.9 ± 1.2</td>
</tr>
<tr>
<td>U8</td>
<td>100 ± 0</td>
<td>0</td>
<td>1.7 ± 0.4</td>
<td>0.8 ± 0.1</td>
</tr>
</tbody>
</table>

Table 2
Summary of environmental conditions in the sediment during upwelling in summer and spring (December 2004 and November 2005) and non-upwelling in fall and winter (April and August 2005). Values represent average of % sand, % silt + clay, total organic matter (TOM) and chlorophyll-a (Chl-a) in the sediment (n = 6) ± standard error.
abundant in December and November than in April and August (Table 3). Omnivores were present in low densities with an average of 61 ind m$^{-2}$ in both bays and on all sampling dates and were mostly represented by nereidid species such as Neanthes bruaca (data not shown).

The ash-free biomass of total polychaetes was in both bays higher in April and August (208 to 489 mg m$^{-2}$) than in December and November (170 to 327 mg m$^{-2}$) (Table 4). However, the mass per individual was lower in April and August (0.07 to 0.21 mg ind$^{-1}$ m$^{-2}$) than in December and November (0.24 to 0.33 mg ind$^{-1}$ m$^{-2}$) (Table 4).

### 3.4. General environmental and community patterns

When all relevant environmental data from water column (bottom temperature, salinity and DO–SACW indicators) and sediment (depth-integrated chl-a and total macrofaunal density — response to SACW upwelling) were analyzed together in the PCA, two groups of data were identified (Fig. 3). The first group, Group I, included Fortaleza and Ubatuba stations sampled during April and August (Fig. 3). The second group, Group II, included stations sampled during December and

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**Fig. 2.** Density of total macrofauna, surface deposit-feeders, subsurface deposit-feeders and carnivores in Fortaleza and Ubatuba bays throughout the sampling dates. Values represent average ± standard error ($n = 5$).
November (Fig. 3). The first (PC1) and second principal components (PC2) explained 37 and 28%, respectively of total data variability, and indicated marked environmental differences between upwelling (Group II) and non-upwelling (Group I) conditions (Fig. 3). In PC1, wind direction, temperature, and sediment chl-a had the most negative loadings and co-varied with total macrofaunal density, while nitrate had the most positive loadings (Fig. 4). In PC2, DO and temperature had the most positive loadings, while nitrate and salinity had the most negative loadings and co-varied with total macrofauna (Fig. 4).

ANOSIM results (Global R = 0.21, p = 0.02), performed with the two group of stations formed in the PCA, showed that density and composition of macrofauna were significantly different. SIMPER analysis revealed that Group I (April and August) and Group II (December and November) had a total dissimilarity of 88% (Table 5). The species that

Fig. 3. PCA plots of the first two axes of stations in Fortaleza and Ubatuba bays throughout the sampling dates (D: December, A: April, Au: August and N: November). Ellipses separate group I, represented by stations of Fortaleza and Ubatuba during April and August (Non-up.: non-upwelling); and group II (Up.: upwelling), represented by stations of both bays in December and November. Size-corresponded bubble plots of wind direction (°), temperature (°C), concentration of nitrate (μM), dissolved oxygen (μM), and chlorophyll-a in sediments (μg g⁻¹) show their variations in Fortaleza and Ubatuba bays throughout the sampling dates.
mostly contributed to the dissimilarity (total – 50% cumulative contribution) were the polychaetes *A. simplex*, *M. capensis*, *M. papillicornis*, *S. missionensis*, *Cirratulidae* sp., the amphipod *Scoloplos* sp., the amphipod *Amphelisca paria* and the bivalves *Nucula semiornata* and *Tellina* sp. (Table 5). The average similarity between species within groups was 23% for Group I and 9% for Group II. Group I was dominated by the opportunistic polychaetes *M. posterolongata, A. simplex* and *S. missionensis*, which contributed with up to 49% of the cumulative similarity (Table 6). Group II was represented by the polychaetes *A. simplex, N. brasiliensis, M. posterolongata* and *M. papillicornis*, which accounted for ~48% of cumulative similarity (Table 6).

The temporal changes in density and composition of macrofaunal species were mostly affected by the combination of sediment chl-a, temperature, salinity, nitrate and winds (Bio-Env analysis, $p_{\text{W}} = 0.360$) (Table 7). Temperature, salinity and nitrate are considered good indicators of the presence or absence of SACW in the system. The Weighted Spearman coefficients ($p_{\text{W}}$) were significant according to RELATE permutation analysis (Global $\rho = 0.371$, $p = 0.01$) (Clarke and Warwick, 2001) indicating significant correlations between macrofaunal species and the combination of variables tested in the Bio-Env analysis (Table 7).

### 4. Discussion

#### 4.1. Temporal dynamics of SACW

The seasonal upwelling of SACW in the study area is known to occur from November to March in the coastal and inner shelf areas of the Ubatuba region (Aidar et al., 1993; Braga and Müller, 1998; Gaeta et al., 1999). In this study, the presence of SACW was registered at depths below 10 m in December and November, associated with predominant winds from the E–NE quadrant. In April and August, wind direction shifted to SE, and as a consequence, SACW upwelling ceased and was replaced by CW. Fortaleza and Ubatuba bays were therefore influenced by two periods with different oceanographic conditions. These conditions were clearly visualized in the PCA analysis, which separated stations in December + November (Group I) from April + August (Group II) (Fig. 2). The first period was typical of spring–summer upwelling events (i.e. water temperatures < 20 °C, and high nitrate concentrations of ca. 1–6 μM) (Aidar et al., 1993; Braga and Müller, 1998). The second period was characteristic of fall–winter conditions with the predominance of CW, water temperatures >20 °C and low nitrate concentrations (0–1 μM) (Aidar et al., 1993; Braga and Müller, 1998). Upwelling of SACW was also observed from relatively low dissolved oxygen (DO) levels in December (158 to 216 μM). However, the lowest DO levels registered during August in Ubatuba were probably associated to high accumulation of organic matter and chl-a in the sediment compared to the other months (see next section).

#### 4.2. Sediment characteristics and organic matter content

The sediment characteristics in Fortaleza and Ubatuba bays reflected the influence of coastal hydrodynamic regime and physical energy level, which are coupled to the passage of cold fronts and associated S–SE waves (Gallucci and Netto, 2004; Mahiques et al., 1998). Since Fortaleza is geographically oriented S–SE, it is more impacted by S–SE waves than Ubatuba. The latter bay is affected differently by S–SE waves due to its E–NE orientated inner part and the S–SE exposed outer part (Fig. 1). This explains the distinct spatial distribution of sediments in the bays with sandy sediments in Fortaleza and outer part of Ubatuba (i.e. high content of very fine sand), and muddy sediments (i.e. high content of silt and clay), in the innermost part of
Ubata (Table 2). Organic (TOM) and chl-a content followed the distribution of fine sediment grains and also accumulated in the inner part of Ubata.

In contrast to our hypothesis, chl-a concentration in the sediment (i.e. content of labile organic matter) did not increase in response to SACW upwelling. This is similar to previous studies in nearby coastal areas showing that sediment chl-a concentration does not vary significantly over time (Muniz et al., 2013; Venturini et al., 2011). Regular blooms of phytoplankton, either supported by coastal upwelling in summer or by nutrient regeneration during the passage of cold fronts in fall and winter may provide a constant supply of fresh algal biomass to the sediments in the bays throughout the year (Quintana et al., 2014; Yoshinaga et al., 2008). Conversely, other typical coastal upwelling areas, e.g. Chilean coast, are marked by a strong seasonal change in primary production, where elevated amounts of phytoplankton biomass are transported to the sediments in summer during upwelling. Sediment Chl-a in Chilean upwelling areas, e.g. Chilean coast, are marked by a strong seasonal change in primary production, where elevated amounts of phytoplankton biomass are transported to the sediments in summer during upwelling. Sediment Chl-a in Chilean upwelling areas, therefore, reach levels up to one order of magnitude higher (i.e. 400 μg g⁻¹, Gutiérrez et al., 2000) than reported in this study (1 to 21 μg g⁻¹).

4.3. SACW upwelling effects on the structure of benthic macrofauna

Our hypothesis that upwelling of SACW increases availability of labile organic matter in the sediment resulting in increased density and shifts in dominance of macrofaunal species was not confirmed. The density of macrofauna was, in fact, lowest during SACW upwelling (average 800–1390 ind m⁻², December and November) and highest when upwelling was absent (average 2510–2525 ind m⁻², April and August). This pattern differs consistently from highly productive upwelling systems, where extremely high densities (74,000 ind m⁻²) of several species are recorded in response to massive loading of organic matter (Sellanes et al., 2007). The differing patterns of macrofaunal community structure between upwelling and non-upwelling conditions in this study may not, therefore, be directly linked to the amount of labile organic matter, but more related to organic matter quality (Venturini et al., 2011), physical disturbance regimes governed by winds and bottom-water temperature. These factors were also pointed out to explain most of the variability of macrofauna in PCA and Bio-Env analyses. There was a single occasion when DO levels were low in August (62–119 μM, stations US and U6), but macrofauna was apparently not adversely affected by this, since density was high and species composition in these stations was similar to the stations with high DO concentrations (Fig. 2, Table 1).

The shift in macrofaunal trophic structure from low density surface deposit feeders and carnivores in December and November to high density and dominance of surface and subsurface deposit feeders in April and August (Fig. 2), suggests seasonal variability in organic matter quality and stimulation of macrofauna (Dauwe et al., 1998). Based on sediment content and composition of lipid biomarkers in the same two bays, it appears that frequent sediment resuspension in April and August sporadically enriches the sediment with organic matter derived from phytoflagellate blooms, whereas upwelling in December and November enriches the sediment with organic matter derived from diatoms (Quintana et al., 2014). Hence, the peak densities of the surface and subsurface deposit feeders (A. simplex, S. missionensis, M. capensis) were associated with the phytoflagellate blooms in April and August. A. simplex, S. missionensis and M. capensis are opportunistic and able to adapt reproductive features to rapidly exploit increased loading of fresh organic matter (Blair et al., 1996; Salen-Picard et al., 2002). In December and November, on the other hand, the low density of fauna and dominance of magelonids and the carnivore N. brasiliensis, which have a broad diet varying from detritus and diatoms to small crustaceans and bivalves (Fauchald and Jumars, 1979), was probably a response to the lower input of phytoflagellates and the presence of more diatoms in the sediment (Quintana et al., 2014). Our findings were also consistent with a system budget of energy flow in the area (Rocha et al., 2003), which shows that winter consumption of organic matter by deposit-feeding polychaetes is almost twice as high (41%) as during summer (23%).

The instability of the sediment during fall-winter months due to the passage of cold-fronts associated to S-SE winds could explain the increased dominance of small-sized opportunistic species such as paraonid, spionid and capitellid polychaetes (i.e. A. simplex, S. missionensis and M. capensis, respectively) observed in our study. The presence in high abundances and of small-sized fauna with short-life cycles is characteristic of environments affected by physical disturbances such as dredging (Hiddink et al., 2006; Kaiser et al., 2000). Accordingly, the average individual biomass of polychaetes during non-upwelling (fall-winter) decreased, indicating fast recruitment of smaller sized organisms compared to the spring-summer upwelling period (Table 4). During SACW upwelling in December and November,

### Table 4

<table>
<thead>
<tr>
<th>Ash-free biomass</th>
<th>Upwelling (December + November)</th>
<th>Non-upwelling (April + August)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fortaleza</td>
<td>Ubatuba</td>
</tr>
<tr>
<td>Total polychaetes (mg m⁻²)</td>
<td>327.4 ± 126.3</td>
<td>170.4 ± 44.0</td>
</tr>
<tr>
<td>Mass per individual (mg ind⁻¹ m⁻²)</td>
<td>0.33 ± 0.10</td>
<td>0.24 ± 0.08</td>
</tr>
</tbody>
</table>

### Table 5

Species that accounted for most of the differences between Groups I and II based on similarity analysis (SIMPER) of fourth-root transformed density data. The best discriminating species, i.e. with high average dissimilarity/standard deviation (Diss./SD = 0.80) are shown in bold text. Group I/Group II indicates whether densities are higher in Group I or II.

<table>
<thead>
<tr>
<th>Species</th>
<th>Diss./SD</th>
<th>%</th>
<th>Cumulative %</th>
<th>Group I/Group II</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aricidae simplex</td>
<td>0.90</td>
<td>5.94</td>
<td>5.94</td>
<td>Group I</td>
</tr>
<tr>
<td>Spiothanes missionensis</td>
<td>0.99</td>
<td>5.89</td>
<td>11.82</td>
<td>Group I</td>
</tr>
<tr>
<td>Mediomastus capensis</td>
<td>1.02</td>
<td>5.73</td>
<td>17.55</td>
<td>Group I</td>
</tr>
<tr>
<td>Ampelisca paria</td>
<td>0.88</td>
<td>4.42</td>
<td>21.98</td>
<td>Group I</td>
</tr>
<tr>
<td>Magelona posterolongata</td>
<td>0.78</td>
<td>3.98</td>
<td>25.96</td>
<td>Group I</td>
</tr>
<tr>
<td>Synelmis sp.</td>
<td>0.77</td>
<td>3.56</td>
<td>29.52</td>
<td>Group I</td>
</tr>
<tr>
<td>Magelona papilicornis</td>
<td>0.73</td>
<td>3.51</td>
<td>33.03</td>
<td>Group I</td>
</tr>
<tr>
<td>Sigambra grubii</td>
<td>0.76</td>
<td>3.46</td>
<td>36.51</td>
<td>Group I</td>
</tr>
<tr>
<td>Ninoe brasiliensis</td>
<td>0.71</td>
<td>3.27</td>
<td>39.77</td>
<td>Group I, II</td>
</tr>
<tr>
<td>Magelona papillicornis</td>
<td>0.79</td>
<td>3.43</td>
<td>38.84</td>
<td>Group I</td>
</tr>
<tr>
<td>Cirratulidae sp.1</td>
<td>0.70</td>
<td>3.11</td>
<td>42.88</td>
<td>Group I</td>
</tr>
<tr>
<td>Scoloplos sp.</td>
<td>0.07</td>
<td>3.10</td>
<td>45.99</td>
<td>Group I</td>
</tr>
<tr>
<td>Nucula seminata</td>
<td>0.56</td>
<td>2.61</td>
<td>48.60</td>
<td>Group I</td>
</tr>
<tr>
<td>Tellina sp.</td>
<td>0.51</td>
<td>2.10</td>
<td>50.70</td>
<td>Group I</td>
</tr>
</tbody>
</table>

### Table 6

Contribution of dominant species to the similarity within Group I (April + August) and II (December + November). Group I and II had average similarities of 27% and 10%, respectively.

<table>
<thead>
<tr>
<th>Species</th>
<th>Group I – April + August</th>
<th>Group II – December + November</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mediomastus capensis</td>
<td>18.2</td>
<td>Aricidae simplex</td>
</tr>
<tr>
<td>Aricidae simplex</td>
<td>15.6</td>
<td>Ninoe brasiliensis</td>
</tr>
<tr>
<td>Spiothanes missionensis</td>
<td>15.0</td>
<td>Magelona posterolongata</td>
</tr>
<tr>
<td>Magelona papilicornis</td>
<td>8.5</td>
<td>Magelona capensis</td>
</tr>
<tr>
<td>Total cumulative %</td>
<td>48.8</td>
<td>Total cumulative %</td>
</tr>
</tbody>
</table>

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the frequency of cold fronts is lower and therefore conditions calmer and sediment resuspension events rare. Conditions are thus favorable for recruitment of less abundant larger-sized and slower-growing macrofaunal species, such as magelonids and carnivorous polychaetes (e.g. *N. brasiliensis* and *Goniada sp.*).

This study also suggests that SACW upwelling plays a different role for a tropical shallow-water macrofaunal communities than providing fresh food derived from phytoplankton blooms. The lower bottom-water temperature during upwelling seems to have an important function for structuring macrofaunal communities. The – 10 °C drop in bottom-water temperature registered during SACW upwelling can be critical for the metabolism of marine invertebrates (Gillooly et al., 2001; Kristensen, 1983). Low temperatures are associated with high densities of relatively large top-carnivores of megafauna and may also prevent the occurrence of stenothermic macrofaunal species in the SE Brazilian inner shelf (De Léo and Pires-Vanin, 2006; Pires, 1992; Pires-Vanin, 1993). The temperature variation in Ubatuba region may therefore explain some of the changes in benthic macrofaunal composition. Magelonid polychaetes that were more abundant in December and November when the water temperature was colder are probably more resistant to temperature changes (i.e. eurythermic species) than, for example, the polychaete *M. capensis* that dominated in the warmer April and August. This pattern was also clearly visualized in the two groups of PCA and SIMPER analysis, where magelonid species were represented in group II (December + November) and *M. capensis* were represented in group I (April + August) (Table 6). For the polychaete *A. simplex*, the warmer temperature may have acted as a trigger for reproduction, since it was well represented in both groups I and II. To our knowledge, no information is available on the effects of temperature on these species or if this pattern is repeated in an inter-annual scale. Thus, care should be taken when comparing these results with macrofaunal communities from other coastal upwelling marine ecosystems.

### 5. Conclusion

The structure of benthic macrofaunal communities in the investigated shallow coastal systems was clearly influenced by two marked periods of distinct environmental conditions: (1) December + November during SACW-upwelling (summer and spring) and (2) April + August (fall and winter) when SACW-upwelling was absent. However, our hypothesis that SACW upwelling would result in higher availability of labile organic matter and high density of macrofauna was not confirmed, since sediment content of chi-a did not change through time. The differing patterns of macrofaunal community structure between upwelling and non-upwelling conditions, therefore, were not directly linked to the amount of labile organic matter, but more related to organic matter quality, physical disturbance regimes and bottom-water temperature. Physical disturbances, warmer temperatures and resuspension-driven phytoflagellate blooms during non-upwelling periods were associated with peak densities of total macrofauna and dominance of small-sized opportunistic species such as sponion, paraooid and capitellid polychaetes. On the other hand, more stable physical conditions and low temperature during upwelling led to low density of larger-sized magelonid and carnivore species. Therefore, organic matter quality, physical disturbance regimes and temperature were key factors for regulating the life-cycles, and hence the composition and density of macrofaunal communities, in these less productive coastal upwelling systems.

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### References


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**Table 7**

Summary of BEST analysis showing the combination of variables that best explains the density and species composition of macrofauna in both bays and their Weighted Spearman coefficients (ρw).

<table>
<thead>
<tr>
<th>No. of variables</th>
<th>ρw</th>
<th>Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>0.360</td>
<td>Chlorophyll-a, temperature, salinity, nitrate, winds</td>
</tr>
<tr>
<td>4</td>
<td>0.353</td>
<td>Chlorophyll-a, temperature, salinity</td>
</tr>
<tr>
<td>2</td>
<td>0.351</td>
<td>Salinity, nitrate</td>
</tr>
<tr>
<td>4</td>
<td>0.342</td>
<td>Chlorophyll-a, salinity, nitrate, winds</td>
</tr>
<tr>
<td>3</td>
<td>0.341</td>
<td>Temperature, salinity, nitrate</td>
</tr>
</tbody>
</table>


