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Mesozooplankton distribution, especially copepods, according to water masses dynamics in the upper layer of the Southwestern Atlantic shelf (26°S to 29°S)

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ABSTRACT

Zooplankton in shelf waters is dominated by a highly diverse assemblage of copepods, followed by a variety of organisms sorted according to the environmental conditions. Epipelagic copepod, chaetognath and cladoceran species assemblages in the upper 100 m layer, together with mesozooplankton major groups were characterized in relation to dynamics of the water masses in the subtropical domain of the Brazilian shelf. Water samples for nutrients and chlorophyll, measurements of temperature, salinity and fluorescence (Rosette/CTD) and zooplankton samples were collected in four transects (26°S to 29°S), ~ 250 km long, across the shelf, during early summer. Intrusions of the cold South Atlantic Central Water (~ 15 m) was evidenced by the large abundance (> 3000 ind.m^{-3}) of the small copepod *Oncaea venusta*, highlighting the role of small omnivorous copepods in the coastal upwelling at ~ 26°S. Low-salinity waters (< 34.5) were observed up to 120 km off the bay area at ~ 29°S, together with a high abundance of *Temora turbinata*. At the slope, the dominance of the Tropical Water increased the prevalence of *Clausocalanus furcatus*. The chaetognath *Flaccisagitta enflata* and the cladoceran *Penilia avirostris* in the inner shelf and the cladoceran *Evadne spinifera* in the outer shelf were also dominant species in the area. Zooplankton assemblages were related to different oceanographic scenarios, associated with coastal upwelling, coastal and estuarine plumes, shelf and slope areas. These assemblages were mainly comprised of epipelagic and tropical species; however, the recurrent presence of copepod, cladoceran and chaetognath cold-water species reinforced the transitional character of the area. In addition, there was a clear cross-shelf gradient, with an increasing contribution of large copepods, siphonophores, salps and euphausiids toward the ocean. The characteristic tropical species assemblages emphasise the dominant role of small metazoans in the pelagic food webs driven by the dynamics of the water masses. The species assemblages also established the species distribution baseline in the subtropical Brazilian shelf.

1. Introduction

Coastal environments and water mass interactions may create important subregions of intense biological responses at several trophic levels, from plankton to nekton (Schettini et al., 1998; Acha et al., 2004). The properties of water masses are widely used around the world to evaluate ecological processes that control primary and secondary production and define distinct zones of the epipelagic ecosystem (Boltovskoy, 1999; Longhurst, 2007; Acha et al., 2015). For instance, zooplankton species richness increased according to water mass interactions in the Mediterranean Sea (Brugnano et al., 2010), the intensity of El Niño effects was defined by different water mass indicator species (Cruz et al., 2011) and water masses structured biogeographic patterns of zooplankton communities and copepod biodiversity in the China Sea (Chen and Liu, 2015).

At the extreme south of the Brazilian 8000 km long shelf, different water masses coexist in the water column associated with different oceanographic processes that act on plankton communities, such as the proximity of Subtropical Convergence, the brackish water outflow of the La Plata River and Patos Lagoon, cyclonic eddies and the meandering of the Brazil Current (Gaeta and Brandini, 2006; Möller et al., 2008; Muelbert et al., 2008; Piola et al., 2008). The Santa Catarina shelf (26°S to 296°S) outlines the boundary between two large areas with different oceanographic features: the Southern Subtropical Shelf (SSS),

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characterized by the Plata Plume Water (PPW), and the South Brazilian Bight (SBB), distinguished by the shelf break and coastal upwelling of the South Atlantic Central Water (SACW) (Acha et al., 2004). Upwelling zones in the SBB extending from Cape Frio (23°S) to Cape Santa Marta Grande (29°S) are marked by salty and nutrient-rich SACW intrusions, especially in summer (Matsuura, 1986; Campos et al., 2013). This drives the subsurface chlorophyll maxima, zooplankton biomass and the diatom-copepod dominance (Odebrecht and Djurfeldt, 1996; Resgalla et al., 2001; Brandini et al., 2014), and sustains the spawning of the Brazilian sardine *Sardinella brasiliensis* (Kurtz and Matsuura, 2001). Strong horizontal and vertical density gradients resulting from the expansion of the PPW enlarges the habitat of *Engraulis anchoita* larvae (Macedo-Soares et al., 2014) further north than Cape Santa Marta Grande. On the other hand, due to the freshwater decrease, copepods and ichthyoplankton (Muelbert et al., 2008), crab and shrimp larvae (Brandão et al., 2015) aggregate in the Subtropical Shelf Front of the SSS. These studies suggested that the water mass dramatically influences the trophic dynamics by improving the development of distinct plankton assemblages and larval transport and survival.

The copepods are one of the keystone trophic links in marine ecosystems generating about 70%, and up to 97%, of the herbivorous pelagic biomass in the SBB (Lopes et al., 2006) and in the southwestern Atlantic Ocean (Boltovskoy, 1999), respectively. This large secondary production may reach top predators, generating up to 30% of the total chaetognath biomass (Liang and Vega-Pérez, 2002). Small copepod species (< 1 mm) are the most abundant metazoans on Earth (Turner, 2004), and are linked to the potential size of fisheries (Bradford-Grieve et al., 1999), as the Brazilian sardine larvae prey on small species and copepodites (Kurtz and Matsuura, 2001). Although the copepod role in zooplankton communities has been studied worldwide (Thor et al., 2005; Miyashita et al., 2009; Fernández de Puelles et al., 2014; Oliveira-Santos et al., 2016) and several studies on zooplankton distributions were conducted in the SBB and in the Cape Frio upwelling (reviewed in Lopes et al., 2006), there is limited knowledge on the role of the Cape Santa Marta Grande upwelling on the coastal ecosystem nearby (Campos et al., 2013).

The spatial distribution of ichthyoplankton (Macedo-Soares et al., 2014), decapod larvae (Brandão et al., 2015) and the sea–air CO_2 flux dynamics (Ito et al., 2016) progressively added evidence about the drivers of the planktonic communities in the southwestern subtropical Atlantic shelf. These recent studies showed that water mass dynamics determined ichthyoplankton and meroplankton assemblages and the sources/sinks of CO_2 release to the atmosphere. In this context, we investigated the mesozooplankton association with water mass dynamics off the Santa Catarina shelf, as a surrogate of the transitional area between two major oceanographic regimes. We aimed to address: (i) the major water masses and oceanographic features during summer; (ii) how the mesozooplankton is regulated by the oceanographic structure; and (iii) which copepod species and zooplankton taxa characterize the coastal processes and the shelf ecosystem.

2. Material and methods

2.1. Study area

The Santa Catarina shelf and slope (Fig. 1B) is at the northern limit of the Southern Brazilian Shelf and is considered a transitional environment between tropical and subtropical conditions. The Cape Santa Marta Grande represents the border of the SBB (23°S to 28°40'S) and the SSS (28–35°S) (Fig. 1A). The CSM has a relatively steep and narrow continental shelf under the influence of the Brazil Current. Intense northeast winds in summer affect the water mass structure resulting in upwelling episodes in its south (Matsuura, 1986; Campos et al., 2013). The PPW and the Sub-Antarctic waters (Subtropical Shelf Front) reach the southern Santa Catarina shelf in winter and promote the major seasonal dynamics during an annual cycle (Möller et al., 2008; Piola et al., 2008). The northern shelf is strongly influenced by continental inputs from the Babitonga Bay estuary surrounded by extensive mangroves and the Itapocu, Itajaí and Tijucas rivers (Carvalho et al., 1998; Schettini et al., 2005).

The longstanding water masses occurring on the continental shelf are the warm Tropical Water (TW = T ≥ 18.5 °C, S ≥ 36), which flows southward in the upper portion of the Brazil Current, near the shelf break with high-temperature, high-salinity, low-nutrient concentration and high-oxygen concentrations. The cool SACW (T ≤ 18.5 °C, S ≥ 35.3), which also flows southward into the lower portion of the Brazil Current (200–500 m), has low-temperature, high-salinity and high-nutrient concentrations, especially nitrate. The Subtropical Shelf Water (STSW = T > 18.5 °C, 35.3 < S < 36) results from mixing of the continental and oceanic waters (TW) and spreads throughout the neritic region (Hille et al., 2008; Möller et al., 2008; Piola et al., 2008).

2.2. Field and laboratory work

Sampling was conducted during early austral summer from December 12th to 20th 2010 at 25 oceanographic stations distributed in four cross-shelf transects over the Santa Catarina continental shelf aboard the Brazilian R. V. *Cruzeiro do Sul* (Fig. 1). Vertical profiles of salinity, temperature, oxygen and fluorescence were registered with a conductivity-temperature-depth (CTD) profiler Sea Bird Electronics Model 911 Plus with auxiliary sensors. Water samples were collected in 5-L Niskin bottles of the rosette system to determine the concentration of chlorophyll and inorganic nutrients (ammonium, nitrite, nitrate, phosphate, silicate) at selected depths (3 m or 5 m, at the chlorophyll maximum depth and at the base of the mixed layer). Nutrients were estimated by colorimetric analysis following the methods of Aminot and Chaussepied (1983) and chlorophyll-a concentration by spectrophotometry according to Welschmeyer (1994).

Zooplankton samples were collected through vertical hauls from the maximum fluorescence depth up to the surface at locations where the oceanic bottom was deeper than 20 m, from 10 m above the sea floor when the water column was homogenous and from about 10 m depth at shallow stations (up to 20 m). A conical-cylindrical plankton net was used with a 0.5 m diameter mouth and 200 µm mesh size, equipped with a General Oceanics® flowmeter. The samples were immediately fixed in 4% buffered seawater-formaldehyde solution. The maximum fluorescence depth varied from 10 to 95 m and the plankton sampling depth ranged from 14 to 107 m, considered as upper layer. The distance from the coast varied from 11 to 280 km. The mean volume of water filtered by the net was 31.1 ± 14.1 m^3.

Zooplankton was quantified through wet biomass and displacement biovolume (Boltovskoy, 1981). Samples were subsampled with a Folsom splitter (McEwan et al., 1954) in fractions of ½ or ¼, before counting. Aliquots of 10 mL were taken from a known volume of the fractions (500–800 mL) to sort copepods, and sometimes chaetognaths and cladocerans (Frontier, 1981). The other taxa were counted in the whole fraction. For all the zooplankton taxa, including copepods, at least 100 individuals in each sample were counted or sorted for further identification. Zooplankton samples were identified and quantified under a stereomicroscope and microscope (10× and 40× magnification). The identification criteria employed were Onbé (1999) for Cladocera; Björnberg (1981), Bradford-Grieve et al. (1999), Campos-Hernández and Suárez (1999) and Dias, Araujo (2006) for Copepoda; Alvariño (1967), and Casanova (1999) for Chaetognatha; and Boltovsky (1981, 1999) for general zooplankton.

2.3. Data analyses

Major zooplankton taxa and species abundance were standardized to the number of individuals per m^3. The copepod taxa were selected according to the frequency of occurrence (FO > 60%), relative abundance (RA > 1%) or absolute abundance (AA > 300 ind.m^{-3}) for

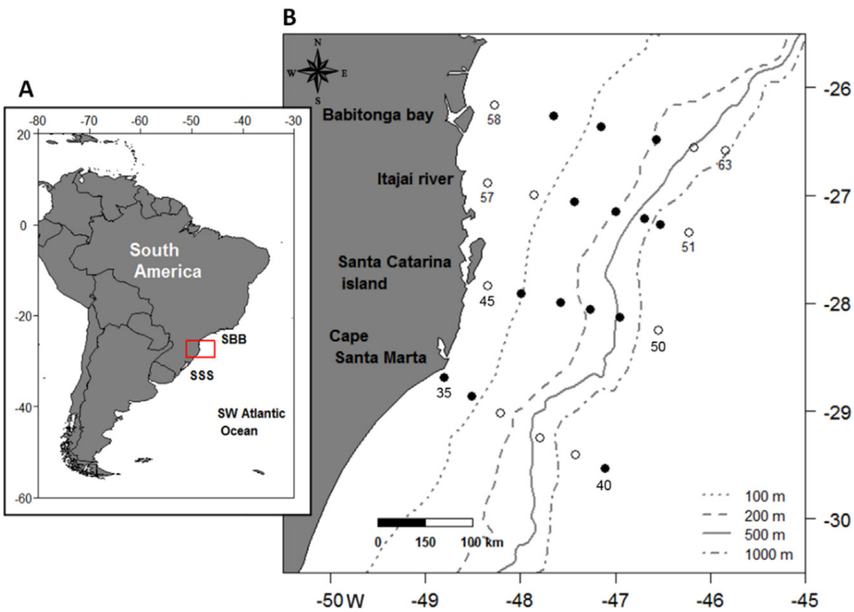

Fig. 1. (A) Location of the study area in the Southwest Atlantic Ocean and between the South Brazilian Bight (SBB) and the Southern Subtropical Shelf (SSS). (B) Position of the 25 oceanographic stations of Santa Catarina shelf from Babitonga Bay (26°S) to Cape Santa Marta Grande (29°S). Black bullet points are night samples and the white ones are day samples.

further statistical analyses. The cross-shelf stations were categorized according to the isobaths: inner shelf to 100 m, outer shelf between 100 and 500 m and slope deeper than 500 m. The inner shelf may also be referred as a "coastal station". The water masses were characterized according to the thermohaline index following Piola et al. (2008) and Möller et al. (2008). The mixing triangle method for calculating the percentage of water masses (Mamayev, 1975) was used for TW, SACW and PPW (see Möller et al., 2008). The indices of TS for each water mass were PPW (17 °C, 24), SACW (5.6 °C, 33.9) and TW (26.8 °C, 37.8). A 3-day mean (December 10, 18 and 19, 2010) composition image of sea surface chlorophyll-a concentration (SSC) was provided by sensor MODIS and was used to delineate spatial gradients in log-transformed chlorophyll values by applying an edge detection filter to the mean image. Total zooplankton abundance was plotted on the SSC image to verify the association between surface log-transformed chlorophyll (and gradients) with zooplankton spatial variability. A correlation matrix was calculated using the following variables: total zooplankton, copepod abundance, and surface values of chlorophyll, temperature, salinity and percentage of water mass. Only correlation values statistically significant at 95% confidence level were considered for discussion. All computations were made for n = 25.

Cluster analysis was used to define faunistic areas (groups of stations) plotted spatially in our sampling area, and included Copepoda, Cladocera and Chaetognatha species and the major mesozooplankton groups (Oikopleuridae and Fritillaridae, invertebrate larvae, Siphonophorae, nauplii, Euphausiacea and Thaliacea). Cluster analysis was based on the Bray-Curtis similarity and UPGMA linkage classification (Field et al., 1982). Prior to the analysis, abundance data were transformed by applying a square-root function. The Similarity Profile Routine (SIMPROF) was used to test for the presence of sample groups (or more continuous sample patterns) in *a priori* unstructured sets of samples (Clarke et al., 2008). Groups of samples are separated (at $p < 0.05$) by a permutation procedure with a frequency of 999 permutations.

In order to further examine the associations among the dominant zooplankton taxa and the environmental variables, a canonical correspondence analysis (CCA) was applied (Legendre and Gallagher, 2001). This analysis focused mainly on the environmental affinities of the assemblages formed in the cluster groups. Temperature, salinity, chlorophyll, distance from the coast, nutrients (ammonium, nitrate, nitrite, phosphate, and silicate) and the oxygen stratification index were included as explanatory variables. Chlorophyll and nutrients used in the analyses were integrated, whereas temperature and salinity were expressed as the mean value in the water column, from the depth of chlorophyll maxima to the surface (10 m depth). The oxygen stratification was calculated using the surface oxygen value and the value for the bottom of the oxycline, and respective depths. The statistical significance of the analysis was tested using the Monte Carlo permutation procedure, performing 999 permutations. The colinearity between the explanatory variables was verified through the variance inflation factor (VIF), where the variables with a VIF value > 20 were considered strongly co-linear and consequently removed from the analysis. All multivariate analyses were performed in the R program using the *Vegan* and *HH* packages (Oksanen et al., 2013; Heiberger, 2013; R Development Core Team, 2011).

3. Results

3.1. Oceanographic features and water masses

Detailed descriptions of the physical oceanography during the cruise can be found in Macedo-Soares et al. (2014), Brandão et al. (2015) and Ito et al. (2016). Here, we summarize the mesoscale oceanographic features of the Santa Catarina continental shelf.

The water-mass structure in the 25 occupied stations is shown in the T-S diagram (Fig. 2). In the larger-scale sampling program from 21° to 33°S, the following water masses were found: Plata Plume Water (PPW), Subtropical Shelf Water (STSW), Tropical Water (TW) and South Atlantic Central Water (SACW). See Macedo-Soares et al. (2014), Brandão et al. (2015) and Ito et al. (2016) for details. However, this study covers a geographic area where STSW, TW and SACW dominated since PPW is encountered south of the study area in summer.

A strong vertical stratification was observed in the water column during summer (Fig. 3). The warm and low-salinity STSW was confined to the inner and outer shelf surface waters. Beyond the outer shelf to the slope, salty and warm TW occupied the surface layer, being replaced by SACW around 80 m and deeper than 150 m in the Santa Catarina Island (SCI; 28°S) transect, thus forming a sharp thermocline separating both the warm STSW and TW from the cool SACW in the intermediate layers.

Features such as thermal fronts, upwelling and estuarine plumes were detected in the coastal zone (Fig. 3). The thermal front between STSW and SACW was identified by the 18 °C isotherm (Kurtz and Matsuura, 2001). The thermal front ran along the shelf at around 50–75 m depth, being sharper in both Itajaí (IR) and Babitonga Bay (BB)

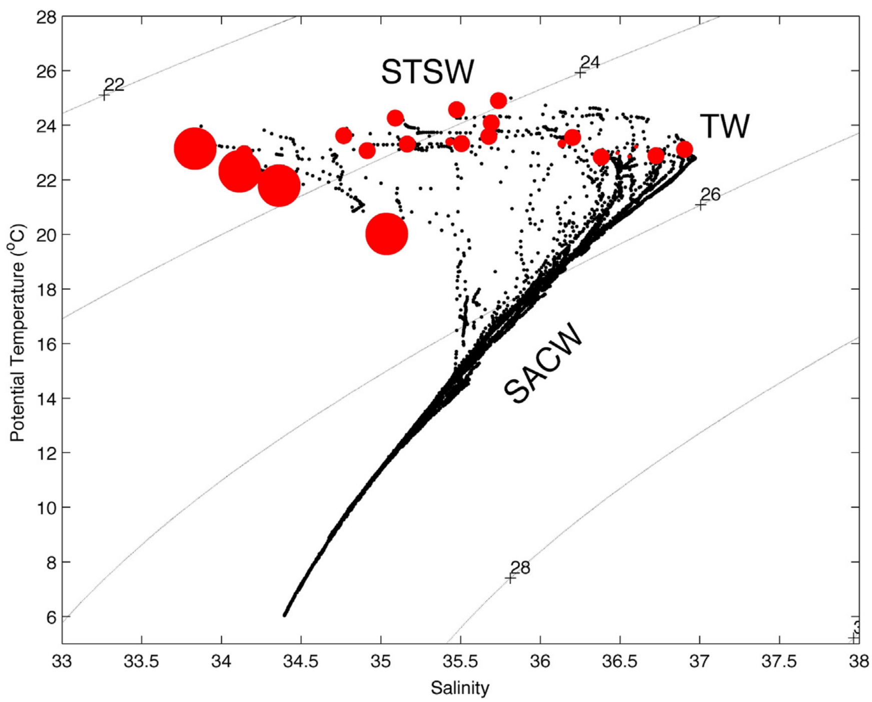

Fig. 2. Temperature-salinity (0–500 m) diagram from stations 35–63 (black). The TS diagram also shows the abundance of total zooplankton (red bullets), with values placed on surface TS values of each station. The diameter used for the red bullets is linearly dependent on measured abundance. TW, STSW and SACW stand for Tropical Waters, Subtropical Shelf Waters, and South Atlantic Central Waters, respectively. The PPW appeared further south of the study area and therefore is not shown in the figure. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article)

transects. The vertical temperature profile showed the intrusion of SACW in the shelf, due to the coastal upwelling near Cape Santa Marta (CSM; 29°S) where SACW is found in the 15 m depth. Low-salinity waters (34) off BB (26°S) extended up to 90 km toward the inner shelf in the upper 25 m depth (Fig. 3).

3.2. Association of zooplankton abundance and the water masses

Zooplankton abundance ranged from 193 to 7437 ind.m^{-3} (mean 1333 ind.m^{-3} ± 1398 ind.m^{-3}). In general, abundance was highest at all coastal stations over the inner shelf (Fig. 4). Over the outer shelf, zooplankton abundances were equally high in all transects, except in IR at Station 55 and CSM at Station 38. Over the slope, the abundance decreased abruptly, especially in SCI, where TW was deeper (Fig. 3), and in IR, where the lowest abundances were recorded. Abundance was highly correlated with chlorophyll concentration (Table 1), and values were higher in vicinities of chlorophyll frontal zones (black lines; Fig. 4) especially in the upwelling zone, at Station 35, which strongly contributed to the high correlation coefficient ($r = 0.93$, $p < 0.05$, $N = 25$).

Zooplankton and copepod abundance distributions were very similar, except at an outer BB station (St. 62), a shelf station (St. 37) in CSM, and the coastal station (St. 45) of SCI (Fig. 4a), where copepod values decreased relative to zooplankton. Copepods had the highest abundance (up to 6417 ind.m^{-3}) in the upwelling at CSM (St. 35) and lower values on the slope toward the northern area (Fig. 4b). Cladocerans and chaetognaths mostly concentrated over the inner shelf, showing a strong coast–ocean gradient (Fig. 4c, d).

The association of zooplankton abundance and the water masses showed that the highest abundance was observed in the coastal station influenced by the cold water due to an upwelling event close to CSM (Fig. 2). The significant negative correlations between zooplankton and both temperature ($r = -0.66$, $p < 0.05$, $N = 25$) and TW ($r = -0.64$, $p < 0.05$, $N = 25$) reinforced this observation (Table 1). The higher the temperature the lower was the zooplankton abundance. Intermediate abundances were found in the presence of STSW, which dominated most of upper water column over the inner shelf. In general, the abundance pattern followed the water mass distribution toward the ocean and thus was higher at the inner shelf stations and lower at the slope stations.

Copepod abundance followed the zooplankton abundance patterns (Fig. 4), which is reflected by the similar correlation results. There was no correlation between zooplankton and STSW, since this water mass resulted from a mixture between PPW (not shown in Fig. 2) and TW in the triangle of mixture of water masses. Nevertheless, STSW is presented over the inner shelf. The well-known summer prevailing winds (not shown here) over the SSS lead to a southward retreat of PPW, allowing TW, STSW and SACW to dominate over the inner shelf, and the later upwells in the CSM vicinities during strong northeasterly wind events.

3.3. Mesozooplankton community structure

Eleven zooplankton taxa were identified as main groups: Chaetognatha, Cladocera, Copepoda, Euphausiacea, invertebrate larvae, nauplii, Siphonophorae, Thaliacea, and Larvacea (divided into Oikopleuridae and Fritillaridae). Among these, the dominant groups were Copepoda (90%), Cladocera (2%) and Chaetognatha (2%). The others represented only 6% of the total (Table S1, Supplementary material). Excluding the copepod contribution, invertebrate larvae were important in the innershelf on all four transects, reaching maxima of 57% in IR and 41% in CSM, followed by crustacean nauplii (~ 10% in BB and CSM). Larvaceans, siphonophores, thaliaceans and euphausiids were especially abundant in the outer shelf toward the slope (Fig. 5).

A total of four cladoceran species (Table S2) and eight chaetognath species (Table S3) were identified in the samples. Among the cladocerans, higher abundances of *Penilia avirostris* occurred at the coastal stations (St. 36, 45 and 58), while higher abundances of *Evadne spinifera* were found in the outer region (St. 39; Fig. 6). The chaetognath species *Flaccisagitta enflata* and *Ferosagitta hispida* were spread over the whole area, but the dominant *F. enflata* peaked mostly in the inner shelf, whereas high values of *F. hispida* were found along the SCI and IR transects. The species *Mesosagitta minima* and *Serratosagitta serratodentata* were abundant in the outer shelf and slope stations (Fig. 6). The zooplankton coastal–ocean gradient in CSM was unique. Invertebrate larvae (40%, of which 28% were brachyuran zoea), crustacean nauplii (10%) and chaetognaths (*F. enflata* = 13%) were associated with the coastal upwelling (St. 35), and *E. spinifera* (St. 39, 58%), larvaceans (St.

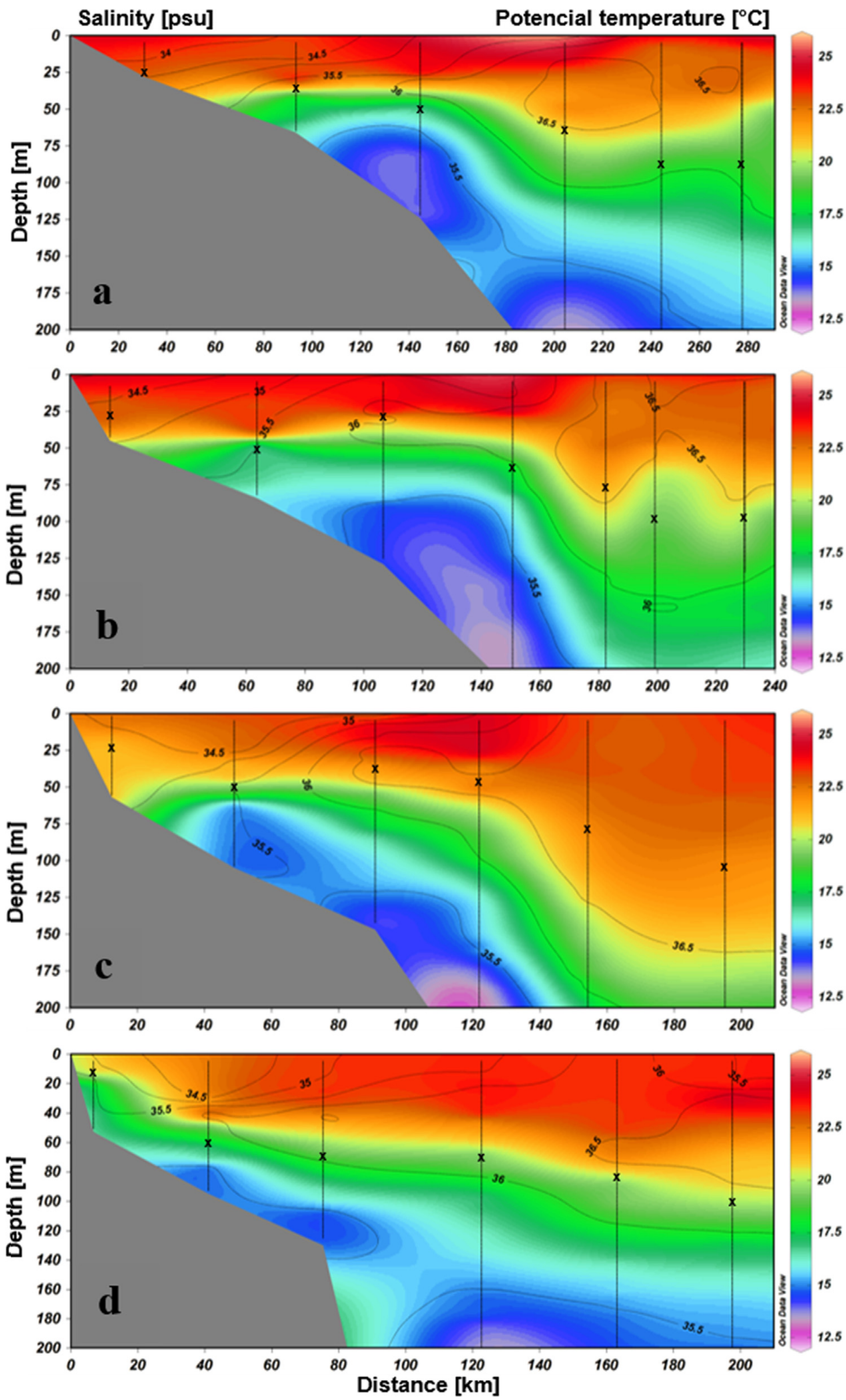

Fig. 3. Cross-shelf vertical distributions of temperature and salinity at the Santa Catarina shelf. (a) Babitonga Bay, (b) Itajaí River, (c) Santa Catarina Island and (d) Cape Santa Marta. The "x" indicates starting depth of the vertical hauls for plankton sampling.

40, 30%) and siphonophores (St. 37, 17%) were found over the outer shelf and slope (Figs. 5 and 6). Furthermore, this transect had the lowest proportion of *F. enflata* in the inner shelf and the highest in the outermost station (St. 40, 16%) compared to the other transects. The coastal station of IR was also particularly different, as invertebrate larvae comprised about 60% and *F. enflata* 20% of the total abundance.

3.4. Copepod composition and distribution

A total of 78 taxa and 69 species were identified in the samples

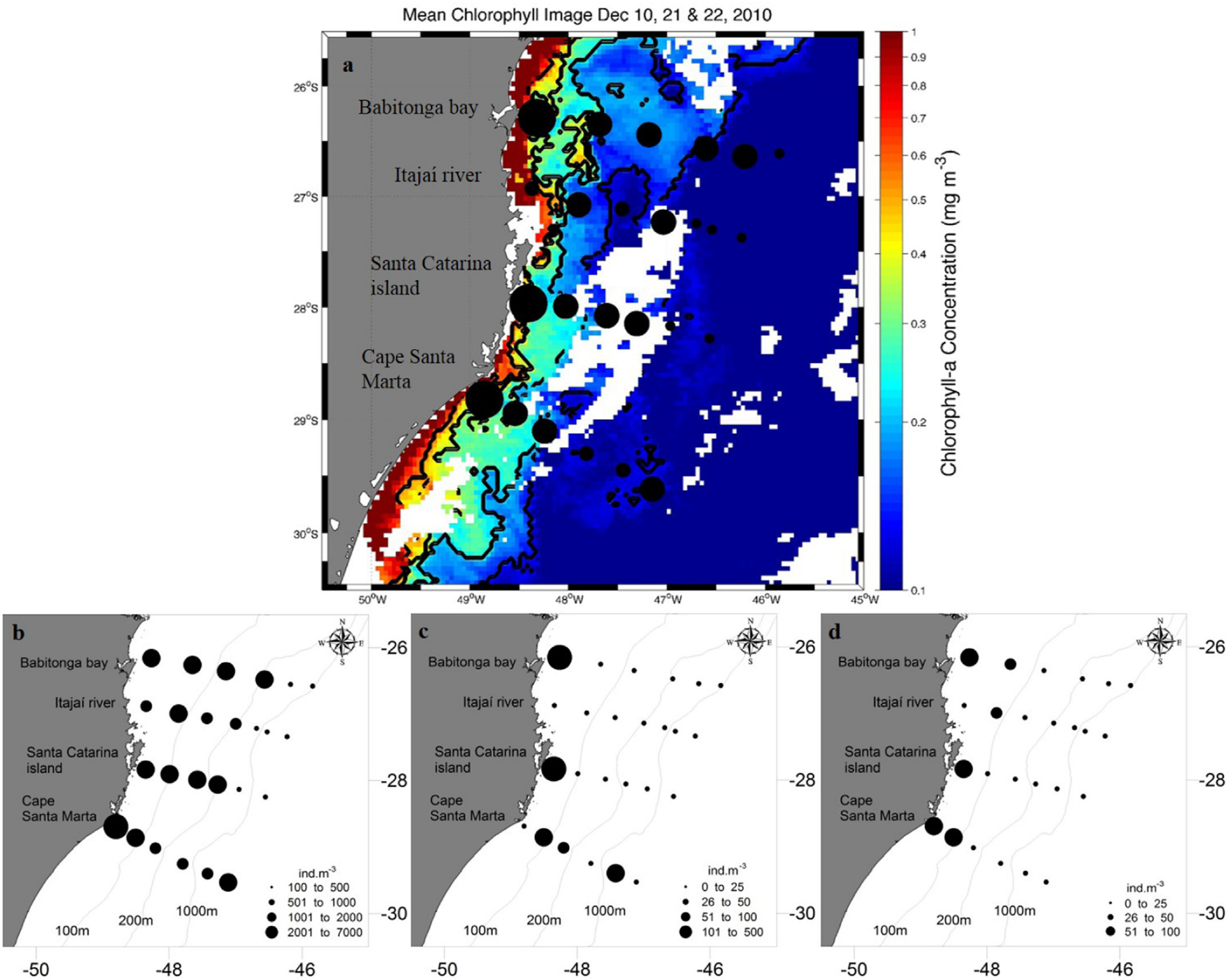

Fig. 4. Total zooplankton (a), Copepoda (b), Cladocera (c) and Chaetognatha (d) abundance distribution off the Santa Catarina shelf. Total zooplankton abundance plotted on satellite mean MODIS image of SSC derived from 3 distinct days in December 2010. The image also shows the lines (black) of strong gradients of log-transformed chlorophyll values.

(Table S4). Among the copepod species, 17 taxa were selected by their high abundance and frequency of occurrence (FO), accounting for almost 90% of the total abundance. These species are listed according to their relative abundance (RA) as: *Oncaea venusta* (21%), *Clausocalanus furcatus* (19%), *Temora turbinata* (8%), *Temora stylifera* (7%), Clausocalanidae copepodites (7%), *Oithona plumifera* (6%), *Calocalanus pavoninus* (6%), *Farranula gracilis* (4%), *Ctenocalanus vanus* (2%), *Corycaeus giesbrechti* (2%), *Subeucalanus pileatus* (1%), *Oncaea media* (1%), *Paracalanus aculeatus* (1%), *Clytmnestra scutellata* (1%), *Corycaeus* copepodites (1%), *Corycaeus speciosus* (0.6%), and *Mecynocera clausi* (0.5%). The last two were selected as they had an FO higher than 60%.

The copepods *Oncaea venusta* and *Clausocalanus furcatus* were widespread distributed. *O. venusta* occurred from the inner to the outer shelf, but was dominant in the inner shelf, and displayed high abundance at the CSM coastal station (3020 ind.m^{-3}). *C. furcatus* was often very abundant between the inner and outer shelf (mean abundance 203 ind.m^{-3}), but was less abundant over the inner shelf of SCI, where *P. avirostris* was dominant (St. 45 and 46, Fig. 6). *C. pavoninus* was present at most locations, although abundance decreased toward the slope and almost disappeared in the CSM. *T. turbinata* and *T. stylifera* were mainly dominant over the inner shelf of BB and SCI, where a similar zooplankton composition had already been described (Figs. 5 and 6), although *T. turbinata* reached the highest abundance at the CSM coastal station. *O. plumifera* occurred all over the shelf, while Clausocalanidae

Table 1
Matrix of Correlation Coefficients. Statistically significant values at 95% confidence level are marked in bold (n = 25). TW, PPW, and SACW stand for Tropical Waters, Plata Plume Waters, and South Atlantic Central Waters, respectively.

	Zooplankton abundance (ind.m^{-3})	Copepods (ind.m^{-3})	Surface Temperature (°C)	Surface Salinity	Surface Chlorophyll (mg.m^{-3})	PPW (%)	TW (%)	SACW (%)
Zooplankton abundance (ind.m^{-3})	1	**0.99**	**− 0.66**	− 0.3	**0.93**	0.27	**− 0.64**	0.28
Copepods (ind.m^{-3})	**0.99**	1	**− 0.62**	− 0.27	**0.92**	0.25	**− 0.6**	0.27

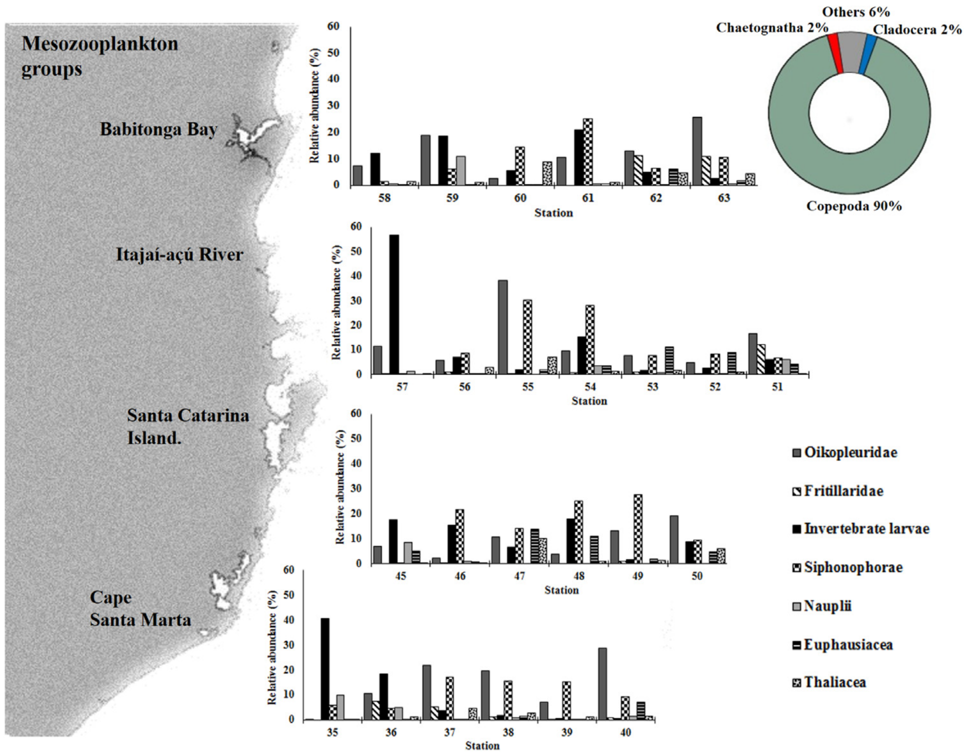

Fig. 5. Mesozooplankton composition based on relative abundance of the main groups off the Santa Catarina shelf, excluding the copepod contribution. Dominant zooplankton taxa are highlighted in the upper right.

(most copepodites of *Clausocalanus* spp.) occurred from the outer shelf to the slope only at BB and IR.

The other species had low abundances and restricted distributions in the inner and outer shelf or slope. *C. giesbrechti*, *P. aculeatus*, *C. scutellata* and *S. pileatus* occurred mainly over the inner shelf, while *O. media*, *C. speciosus* and *M. clausi* occurred exclusively over the outer shelf and slope. *C. vanus* was recurrent over the outer shelf in all transects, particularly in the southern region. Additionally, 16 large copepod species

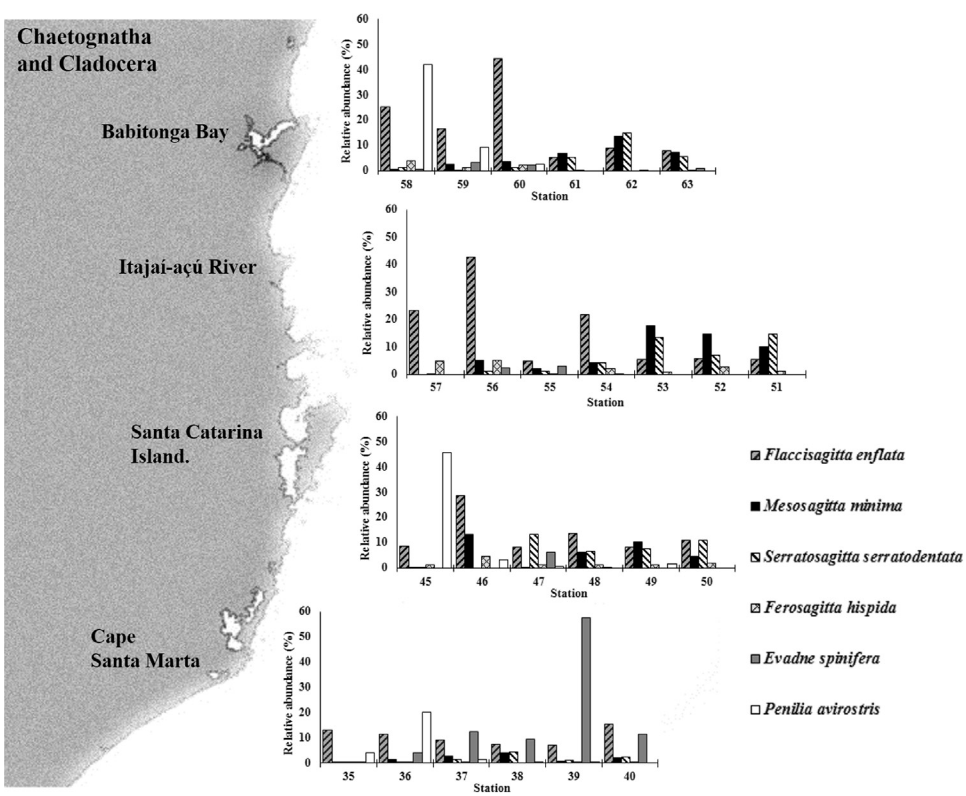

Fig. 6. Cross-shelf relative abundance (%) of chaetognath and cladoceran species off Santa Catarina shelf, excluding the copepod contribution.

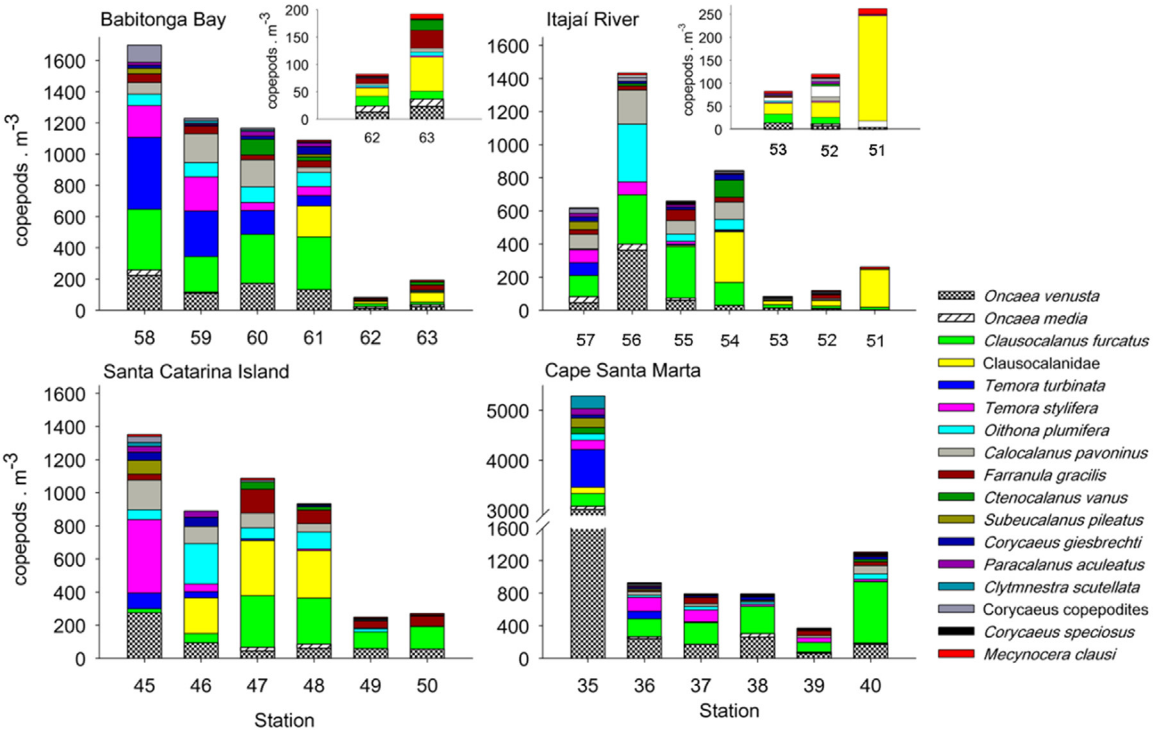

Fig. 7. Cross-shelf distribution of the dominant copepod species off the Santa Catarina shelf. Babitonga Bay and Itajaí River slope stations are highlighted in the upper right. Note the difference in the abundance scales for each graph.

(> 1.5 mm) were found preferentially over the outer shelf (e.g., *Nannocalanus minor* and *Neocalanus gracilis*) (Table S2). However, they were not considered in the following multivariate analysis due to their low abundance.

3.5. Zooplankton community and environmental conditions

The spatial distribution of different zooplankton taxa, especially the copepods, cladocerans, and chaetognaths, showed strong inshore–offshore and north–south patterns that were statistically consistent with the results from the SIMPROF test. The cluster plot showed a cross-shelf division highlighted by five groups (Fig. 8).

The shallow station in CSM (St. 35) under the influence of the SACW intrusion was solely in Group 1. On the inner shelf, Group 2 included zooplankton under the influence of coastal conditions. The outer shelf and CSM slope stations under the influence of STSW were clustered in Group 3. Slope Groups 4 and 5 were formed by oceanic warm-water species under the influence of TW toward the south or north (Fig. 8).

In the CCA (Fig. 9), the distance from the coast mainly created the first ordination axis (39%), thus representing the cross-shelf gradient.

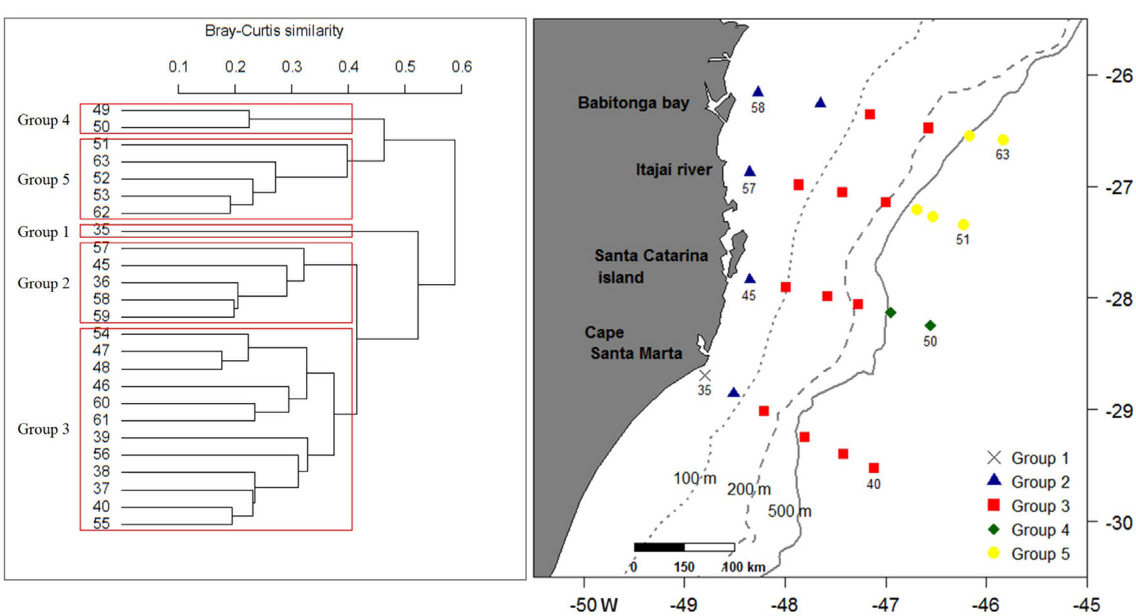

Fig. 8. Cluster analysis and geographical location of the dominant Copepoda, Cladocera, Chaetognatha species and the major mesozooplankton groups off the Santa Catarina shelf.

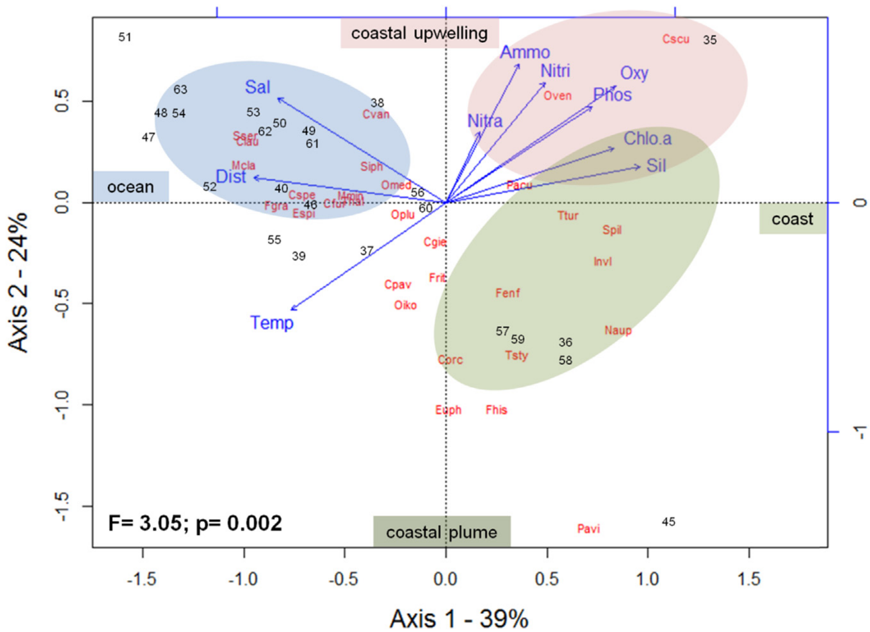

Fig. 9. Canonical Correspondence Analysis ordination of the dominant mesozooplankton taxonomic groups and species Invertebrate larvae (Invl), Oikopleuridae (Oiko), Fritillaridae (Frit), Siphonophorae (Siph), Nauplii (Naup), Euphauseacea (Euph), Thaliacea (Thal), *Subeucalanus pileatus* (Spil), *Calocalanus pavoninus* (Cpav), *Paracalanus aculeatus* (Pacu), *Clausocalanus furcatus* (Cfur), *Ctenocalanus vanus* (Cvan), Clausocalanidae (Clau), Temora stylifera (Tsty), *Temora turbinata* (Ttur), *Oithona plumifera* (Oplu), *Oncaea media* (Omed), *Oncaea venusta* (Oven), *Corycaeus giesbrechtii* (Cgie), *Corycaeus* sp. copepodites (Corc), *Farranula gracilis* (Fgra), *Penilia avirostris* (Pavi), *Evadne spinifera* (Espi), *Ferosagitta hispida* (Fhis), *Flaccisagitta enflata* (Fenf), *Mesosagitta minima* (Mmin), *Serratosagitta serratodentata* (Sser) in relation to environmental variables salinity (sal), distance from shore (Dist), temperature (Tem), ammonium (Ammo), nitrite (Nitri), nitrate (Nitra), oxygen (Oxy), phosphate (Phos), chlorophyll a (Chlo a), silicate (Sili).

This pattern was in contrast to those for silicate and chlorophyll. The second axis (24%) represented the nutrient-rich waters of the cold coastal upwelling, in contrast to the low salinity and high temperature waters of the coastal plume.

The species with oceanic affinities, such as the copepods *C. furcatus*, *C. vanus*, *F. gracilis*, *C. speciosus*, Clausocalanidae and *M. clausi*, the chaetognaths *M. minima* and *S. serratodentata*, the cladoceran *E. spinifera*, and the Thaliacea and Siphonophorae were positively correlated with distance and salinity in Axis 1, as most in the outer shelf and slope clustered in Groups 4 and 5 (Fig. 8).

In Axis 1, the coastal Station 45 was positively correlated with nutrients and the highest abundance of cladoceran *P. avirostris* (Fig. 6). In Axis 2, the copepods *O. venusta* and *C. scutellata* were associated with upwelling environmental features at Station 35 (group 1), such as higher phosphate, oxygen, nitrate, nitrite and ammonium. *C. scutellata* reached the highest abundance (Fig. 7) and was strongly related to higher oxygen stratification and phosphate.

The negative part of Axis 2 was related to the coastal stations also defined by Group 2.

The cladoceran *P. avirostris,* the chaetognaths *F. enflata* and *F. hispida,* the copepods *T. stylifera* and *Corycaeus* copepodites were negatively correlated with salinity and distance to the coast. In addition, coastal associations were also related positively to silicate and chlorophyll, invertebrate larvae and the copepods *S. pileatus* and *T. turbinata*. The latter species were abundant and mainly alternated their dominance between the coastal stations (Fig. 7).

The CCA analysis describes the coupling of the cross-shelf gradient properties with the zooplankton assemblages, which flourished in productive waters with continental input in contrast to assemblages established under high salinity and temperature conditions far from the coast. Moreover, we found dominant species in the cold, salty and nutrient-rich waters of the CSM coastal upwelling and special zooplankton assemblages in the warm, less saline and intermediate nutrient waters under the influence of Babitonga Bay and Itajai River waters.

4. Discussion

The association of the mesozooplankton with the dynamics of the water masses during summer was assessed in the transitional subtropical area of the South Brazil Shelf. The zooplankton community in the upper layers showed a typical coast–ocean gradient, where the abundance and the species turnover followed the patterns of the mesotrophic coastal (chlorophyll frontal zones) to the oligotrophic waters of the Brazil Current. The zooplankton assemblages in the upper layers has an important role in the pelagic realm. Copepod peak abundance in different subtropical and tropical oceans was closely related to chlorophyll maximum, mainly around 30 −100 m (Paffenhöfer and Mazzocchi, 2003). Besides, the highest richness of zooplankton off Brazilian coast was also observed in the first 250 m, decreasing down to 2300 m depth (Bonecker et al., 2014). Copepoda, Cladocera and Chaetognatha were the top three epiplankton (94%) and were closely related to unique coastal processes, thus consolidating their role in the shelf ecosystem.

The shelf near Cape Santa Marta presents strong seasonal variability under the influence of upwelling events. This physical process occur in pulses associated with changes in the wind field and interspersed with the presence of STSW during austral summer (Campos et al., 2013). In addition, *Haloptilus longicornis*, *Lucicutia gaussae* and *Ctenocalanus vanus* often appear on the shelf during upwelling events (Lopes et al., 2006) and are common species in the Cape Frio (Valentin, 1984, Guenther et al., 2008), in the Benguela upwelling (Gibbons and Hutchings, 1996; Peterson, 1998) and also in the CSM upwelling and the inner shelf. The herbivorous copepod *Paracalanus quasimodo* increases its dominance with the bloom of diatoms at Cape Frio (23°S) (Rosa et al., 2016), while the detritivore *Oncaea venusta* was dominant in the CSM. Our results showed that the magnitude of copepod abundance is similar in both upwelling systems, although there is a shift of the dominant species. Species shift can occur due to environmental decadal changes, upwelling cycle and species interactions. *Oncaea* and *Corycaeus* species are usually carnivores (Turner, 2004) and control the dominance of *P. quasimodo* both during upwelling and downwelling in Cape Frio (Rosa et al., 2016).

Small epipelagic copepod species dominated the overall zooplankton community. The widespread species, concentrated mainly on the inner and mid shelves (Groups 2 and 3), *Oncaea venusta*, *Temora turbinata*, *Temora stylifera*, *Oithona plumifera, Corycaeus giesbrechti, Calocalanus pavoninus* and *Ctenocalanus vanus* are typical in mixtures of coastal waters and TW (Lopes et al., 2006); and *Clausocalanus furcatus*, *Farranula gracilis* and *Corycaeus speciosus* are characteristic where the TW predominates (groups 4 and 5) (Dias et al., 2010). Among other holoplankton, the replacement of *P. avirostris*, *F. enflata* and *F. hispida*, which are abundant in warm coastal waters, by *E. spinifera* and *S. serrodentata* in shelf waters had been previously reported (Resgalla, 2008; Domingos-Nunes, Resgalla, 2012). However, *Fritillaria pelucida* and hydromedusae, typical of the Cape Frio coastal upwelling (Lopes et al., 2006) were not reported. In general, with the exception of the Cape Santa Marta upwelling, the species assemblies were similar to the structure of coastal and oceanic waters at the SBB off Rio de Janeiro (22°S) (Lopes et al., 1999; Dias et al., 2010) and São Paulo (24°S) (Eskinazi-Sant'Anna and Björnberg, 2006; Miyashita et al., 2009), and typical of the tropical/subtropical Southwest Atlantic Ocean (Björnberg, 1963, 1981; Bradford-Grieve et al., 1999). Furthermore, the species richness (69 species; 78 taxa) was higher than that reported in coastal and inner shelf studies in the SBB, which registered 44 species in the inner shelf and 58 taxa in the coastal waters to the north (Sartori and Lopes, 2000; Miyashita et al., 2009). In contrast, our results were similar to those of the deep ocean off the Campos Basin (22°S) of a highly diversified (89 taxa; 70 species) copepod assemblage also dominated by *C. furcatus*, *F. gracilis* and *O. venusta* (Dias et al., 2010). The most-abundant *Oncaea venusta* and *Clausocalanus furcatus* are ubiquitous species in the Brazil Current. They are widespread in the shelf domain over a huge latitudinal gradient from the northeastern (3°S to 7°S; Cavalcanti, Larrabázal, 2004) to the southeastern shelves (20.5°S to 24°S; Bonecker et al., 2014) as well as from the south Brazilian shelf (26°S to 29°S; our study area).

The transitional nature of the area was disclosed by the co-ocurrence at the shelf waters of dominant tropical species and few subtropical ones. Besides the dominance of numerous small copepod species, the warm-water copepods *Undinula vulgaris* and *Euchaeta marina* also shared the outer shelf and slope with other large cold-water species as *Aetideus giesbrechti*, *Paraeuchaeta scotti*, *Haloptilus longicornis*, *Heterorhabdus papilliger*, *Lubbockia squillimana*, *Neocalanus gracilis*, *Pleuromamma gracilis* (Table S2) that are common in water masses between 100 and 200 m of the Southwest Atlantic (Björnberg, 1981). The latter copepod species and the cold-water chaetognath *Serratosagitta serratodentata*, an indicator species of subtropical waters (Crelier and Daponte, 2004) and the oceanic cladoceran *Evadne spinifera* (Resgalla, 2008) were also typical species in the Brazil-Malvinas Confluence where tropical and cold-water faunas converge (Berasategui et al., 2005). The species assemblage found reflect the presence of the Brazil Current, the Atlantic upwelling zone and the proximity of the Subtropical Shelf Front (Acha et al., 2004). In fact, the distribution of tropical marine organisms in this region reach their southern limit of distribution in the Southwestern Atlantic, with the Santa Catarina shelf known as the southernmost limit of the tropical reef fish (Floeter et al., 2008; Anderson et al., 2015), crustaceans (Teschima et al., 2012; Giraldes and Freire, 2015), corallith (Capel et al., 2012) and rhodolith beds (Pascelli et al., 2013), showing the importance of this environment to biodiversity and conservation.

Copepod abundance (mean 1212 ind.m^{-3}) was much higher than previously observed in the area (153 ind.m^{-3}) (Domingos-Nunes, Resgalla, 2012). The abundance of copepodites and small species must have been underestimated due the large mesh size (300 μm) used by the latter authors. This is a usual problem for copepod ecology studies (Campaner, 1985; Miyashita et al., 2009; Dias et al., 2010). Failure to adequately account for small copepods may have serious implications for estimates of grazing impact on phytoplankton and microzooplankton, and for estimation of zooplankton fluxes and trophic interactions (Gallienne, Robins, 2001; Turner, 2004). Zooplankton communities were also dominated by small-size copepods in the western boundary current system in the subtropical North Pacific during winter, and there was a cross-shelf gradient strongly related to the highest mean temperature (Dai et al., 2016). As in our results, these authors showed the importance of small-size copepods in systems with low productivity and high energy transfer efficiency.

Neritic zones may contain embedded frontal interfaces caused by continental runoff, and embody mechanisms by which the physical energy of the ocean system can be converted to trophic energy to support biological processes (Acha et al., 2015). Zooplankton abundance was strongly correlated with chlorophyll concentrations on the inner shelf (Table 1), indicating that low-salinity plumes and seasonal intrusions of oceanic nutrient-rich SACW waters enrich chlorophyll frontal zones (Fig. 4). SACW intrusions carry onshore resting phytoplankton cells that had previously sank from the euphotic zone sustaining heterotrophic production in summer (Brandini et al., 2014). Maximum abundances of the small detritivore *Oncaea venusta* (3020 ind.m^{-3}) co-occurred with high concentration of engrauliid eggs, probably *E.anchoita* (Macedo-Soares et al., 2014) in the CSM upwelling. Further south small copepods were linked to eggs and larvae of *E. anchoita* (Marrari et al., 2004). *Oncaea* is also the main prey of the Brazilian sardine *Sardinella brasiliensis* (Kurtz and Matsuura, 2001). The enrichment of SACW intrusion leading to the chlorophyll peak and *Oncaea* patches may provide abundant prey for fish larvae.

During summer, a shallow thermocline occurs and the oligotrophic tropical water (Matsuura, 1986; Lopes et al., 2006) sustains the dominance of the warm-tolerant species (group 3; Fig. 9). High temperature and salinity induce the prevalence of the small *Clausocalanus furcatus*, known as a TW indicator species (Lopes et al., 2006), on the outer shelf and slope. In the 10-year-time-series research conducted at the northern Spain upwelling, the genus *Clausocalanus*, and the recent arrival of *Temora stylifera*, have served as baseline for monitoring water warming and stratification (Beaugrand et al., 2002; Bode et al., 2012). Warm-water copepod assemblages showed a northward displacement of more than 10° latitude in 40 years (Beaugrand et al., 2002), and the coastal upwelling and stratification disturbance drove the biomass and abundance of the main species (Bode et al., 2012). In fact, there are already projected changes of the Brazilian Current that may have important implications in the distribution of marine species (Pontes et al., 2016). Our data depicted the zooplankton distribution baseline for the transitional waters between the SBB and SSS, providing valuable insights for monitoring the vulnerable shelf ecosystems.

5. Conclusions

A mixture of coastal and oceanic epipelagic species, typical of neritic areas of the tropical and subtropical Southwest Atlantic improved the zooplankton diversity and abundance in the upper layers. The coexistence of numerous warm and cold-water species was related to the presence of the Atlantic upwelling zone, the Brazil Current and the proximity of the Subtropical Shelf Front characterizing the transitional nature of the area. Intrusions of the nutrient-rich South Atlantic Central Water were by far the most important processes controlling zooplankton community on shelf in summer. The highest abundances were due to small copepods such as copepodites and adults of the genera *Oncaea*, *Clausocalanus*, *Paracalanus* and *Temora*. Our findings indicated the importance of the small-size organisms in the subtropical zooplankton communities, leading towards an understading of the functioning of the epipelagial community. They work as a link from the microzooplankton to the larger zooplankton, and fish larvae. The small copepods probably occupy a higher trophic level in the oligotrophic oceans than in more eutrophic conditions. Since the area is the largest Brazilian fishing ground, the coupling of small copepods and fish larvae must be addressed properly. Further studies should address the role of feeding behaviour, temperature preference and also trophic interactions to determine the range of vertical distributions.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.csr.2018.06.011.

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