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ECOSYSTEMS

Short-term variation of plankton spatial distribution at a subtropical mixed estuarine system

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Abstract: The horizontal distribution of plankton communities in a subtropical mixed estuarine system over one tidal cycle was investigated. Hydrological and planktonic samples were obtained twice on 17 July 2007 in a transect with ten stations in the Babitonga Bay estuary, south Brazil (~26°S). Hydrological variables did not vary spatially or tidally during samplings. However, in the cluster analyses both phyto and zooplankton were structured according to their estuarine position and in the inner stations also by the tidal condition. Phytoplankton abundances were higher during flood tide in the inner estuary (max. 122,583 ind.L^{-1}), where diatoms dominated, particularly *Diploneis bombus*. However, the density at ebb tide increased towards outer estuary (max. >100,000 ind.L^{-1}) and flagellates, mostly *Gymnodinium* spp., became abundant. Zooplankton abundances were higher at intermediate stations during both tides (max. 13,691 ind.m^{-3}). The innermost stations were dominated by the copepod *Acartia tonsa*, while in the outermost stations *Temora turbinata* and the polychaete larvae *Loimia* sp. dominated. The results demonstrate how variable the estuarine plankton horizontal structure can be over short time-scales even in mixed estuarine systems under relatively homogeneous conditions, highlighting the importance to consider such temporal scales for a more accurate understanding of the dynamics of these communities.

Key words: Babitonga Bay, mixed estuaries, phytoplankton, plankton dynamics, tidal variation, zooplankton.

INTRODUCTION

The time-scales for physical processes in estuaries are variable and driven primarily by the relative intensity of daily tidal fluctuations and seasonal changes in the freshwater flow (Boero 1994, Day et al. 2013). Tidal oscillation is especially important for plankton variability (Menéndez et al. 2012, 2015, Day et al. 2013), and rapid fluctuations in physical-chemical factors may be experienced by organisms through the tidal cycle in both horizontal and vertical axes (Laprise & Dodson 1993). Thus, biological responses to environmental variability in estuaries are difficult to predict because of the simultaneous and multifactorial relationships of environmental variables (Elliott & McLusky 2002). Besides this, interspecific differences mostly in salinity tolerance also account for shifts in the species dominance along the estuary and/or the tidal condition, emphasizing the role of this variable in the spatial and/or short-scale temporal structuring of these communities (Telesh 2004, Telesh & Khlebovich 2010, Menéndez et al. 2012, 2015, Day et al. 2013).

Numerous studies have focused on short-term plankton variability in estuaries (Dalal & Goswami 2001, Menéndez et al. 2012, Guenther et al. 2012, 2015, Sin & Jeong 2019). Most of such studies have sampled one fixed station many times all over the tidal cycle (Chandran 1985, Garcia-Soto et al. 1990, Bernát et al. 1994, Araujo et al. 2008, Marques et al. 2009, Guenther et al. 2012, Menéndez et al. 2012, 2015, Sin & Jeong 2019). This approach allows describing fine temporal changes in the assemblages, providing valuable information on the influence of tidal condition through time. However, it has limited spatial resolution, hampering a better understanding of how tidal cycle modifies the horizontal structure of plankton communities. Moreover, most of these studies have been conducted in estuaries with large physical-chemical gradients, and mixed estuaries with more homogeneous conditions have been considerably less studied. Thus, one question that remains open is how tide condition may affect the horizontal structure of the plankton assemblages in these estuaries.

The Babitonga Bay estuary (BBE) is a mixed subtropical estuary situated at a high priority area for conservation on the Brazilian coast (IBAMA 1998, MMA 2007). The region has a marked seasonality both in temperature and rainfall, with a rainy summer and a dry winter (Cremer et al. 2006, Alvares et al. 2013). Previous studies in the BBE have showed that the salinity gradient is one of the most important factors structuring the horizontal distribution of planktonic communities (Brandini et al. 2006, Costa & Souza Conceição 2009, Nogueira Júnior & Oliveira 2017). However, plankton distribution has been previously analyzed only considering seasonal time-scale, and nothing is locally known about short-term dynamics (Nogueira Júnior & Costa 2019). In the present study, we aim to test differences in the horizontal structure of the phyto and zooplankton assemblages during ebb and flood tide in this mixed estuary. We developed the present study in the winter and neap tide to be representative of a condition of reduced continental runoff and lower tidal range, respectively.

MATERIALS AND METHODS

Study area

The Babitonga Bay estuary (BBE; 26°13’44”S 48°40’40”W), southern Brazil, is a permanently open basin with 21 km in length, maximum width of 2 km in the central channel and area of 1567 km^2 (Supplementary Material - Figure S1) (IBAMA 1998). The depth in the central channel is 10 m, with the maximum of 28 m at the mouth. The innermost area of the estuary is shallower (<5 m), composed of extensive mangroves and tidal flats (Noernberg et al. 2020). Although the estuary receives water flows from many rivers, it is considered vertically homogeneous to weakly stratified estuary in its physical-chemical parameters (IBAMA 1998, Noernberg et al. 2020). The microtidal regime is mixed with semidiurnal dominance (with duration of nearly six hours between low and high tide). The mean tidal height is 0.84 m and the maximum is 1.9 m during spring tide, with tide amplification in the innermost portions (Truccolo & Schettini 1999, Knie 2002). The average annual rainfall is around 2265 mm, reaching higher values in spring-summer (October to March), average of 672 mm, and lower ones in autumn-winter (April to August), average of 190 mm (Cremer et al. 2006).

Sampling methods

The samplings occurred on 17 July 2007 in 10 stations ~2-4 km apart from each other, during the winter and neap tide, over one tidal cycle. Samplings were performed twice in shallow estuarine waters: i) during the day in the flood tide (~9:30-13:00) from the inner to the outer estuary in the transect (station 1 to 10; Figure S1);

ii) during the night in the ebb tide (~18:00-21:30) from outer to the inner estuary (station 10 to 1). The samples from station 10 during the ebb tide were lost and consequently were not included in the present study. During the samplings the wind blew mostly from SSE and the highest speed was 3.6 m/s at 18:00 and the lowest was 0.3 m/s at midnight. The tidal amplitude varied from 0.1 m at 9:24 to 1.6 m at 17:38. Wind and tidal data used in the present study is available at the National Meteorological Institute (INMET) and at the Brazilian Navy Hydrography Center, in the São Francisco do Sul Harbor station (26°14.7'S, 48°38.4'W), respectively.

Phytoplankton was sampled with vertical hauls using a conical plankton net with 20 µm mesh and mouth diameter of 30 cm, from near the bottom to the surface. Samples were fixed with 0.4% formaldehyde. Using a bottle sampler, water samples were taken from the subsurface for the 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. Subsurface water samples were taken and filtered with Whatman filters (25 mm diameter, GF/F) for latter chlorophyll-*a* measurements in the laboratory.

Zooplankton samples were taken by five-minute oblique hauls through most of the water column using a cylindrical-conical plankton net, with 60 cm mouth diameter, 200 µm mesh-size, and a calibrated Hydrobios mechanic flowmeter attached (the average volume filtered was ±SD 24±8.2 m^3 ranging between 10 and 38 m^3). The zooplankton collected was preserved in 4% buffered formaldehyde solution.

Vertical profiles of temperature, salinity, pH, dissolved oxygen and total dissolved solids were obtained at each station with a multiprobe YSI-556 MS.

Laboratory and data analyses

In the laboratory, net phytoplankton aliquots were oxidized and mounted on slides and coverslips (Hasle & Fryxell 1970). Taxonomic identifications followed mainly Tomas (1997), Round et al. (2000), Tenenbaum et al. (2004), Landucci & Ludwig (2005), and Sar et al. (2007). Phytoplankton cells were counted in Utermöhl (1958) 10 mL sedimentation chambers using a Zeiss model ED-03 inverted microscope with phase-contrast optics (Hasle 1978).

Nano-sized cells (2–20 µm) were counted at 400x magnification over diameter transects until a minimum of 100 cells was reached. Micro-size cells (>20 µm) were counted at 160x magnification over the entire bottom area of the Utermöhl chamber or in half the chamber, depending on cell density, to reach a minimum count of 300 cells. Cell densities per liter were calculated according to Semina (1978). Chlorophyll-*a* was read in the laboratory on a Turner Designs – Trilogy calibrated fluorometer (Parsons et al. 1984).

Zooplankton was identified and counted from 10 mL aliquots of each sample, counting 300 organisms at least. The specimens were identified to the lowest taxonomic level possible (following mainly Boltovskoy 1981, 1999). The density of zooplankton was standardized as individuals.m^{-3}, considering the filtered volume of water. Zooplankton wet weight was estimated from three 10 mL aliquots of each sample. Large macroscopic gelatinous zooplankton were manually removed and the aliquots were rinsed with distilled water in a 100 µm sieve, latter they were dried with blotted paper (Boltovskoy 1981, Omori & Ikeda 1994), and weighed using a digital analytical balance with precision of 0.1 mg.

Multivariate patterns of phytoplankton and zooplankton assemblages were determined and visualized using hierarchical agglomerative clustering techniques based on the Bray-Curtis similarity measures after square-root transformation. The similarity percentage analysis (SIMPER) was used to identify the species that mostly contributed to similarities within each identified group (Clarke & Gorley 2006). These analyses were performed using the PRIMER V.6 software. In order to test the influence of the explanatory variables on dominant phyto and zooplankton taxa, we used a constrained-ordination analysis (Lepš & Šmilauer 2003), using the software CANOCO ver. 4.5. The length of the gradient was short suggesting that most species would exhibit a linear response to the explanatory variables and thus we used the redundancy analysis (RDA; Jongman et al. 1995, ter Braak & Šmilauer 1998, Lepš & Šmilauer 2003). The RDA was performed for phytoplankton and zooplankton separately. The explanatory variables for phytoplankton included total abundance of zooplankton (ind.m^{-3}), temperature (°C), salinity, dissolved oxygen (mg L^{-1}), total dissolved solids (g L^{-1}), and pH. For zooplankton, the following explanatory variables were tested: total abundance of phytoplankton (cells L^{-1}), temperature, salinity, dissolved oxygen, total dissolved solids, and pH. Before the analyses, the explanatory variables were centered and standardized and the response variables were square root-transformed. The significance ($P<0.05$) of the canonical axes were tested using the Monte Carlo randomization procedure (999 runs) (Lepš & Šmilauer 2003).

RESULTS

Hydrological variables

The water column was vertically homogeneous during samplings, thus only average values

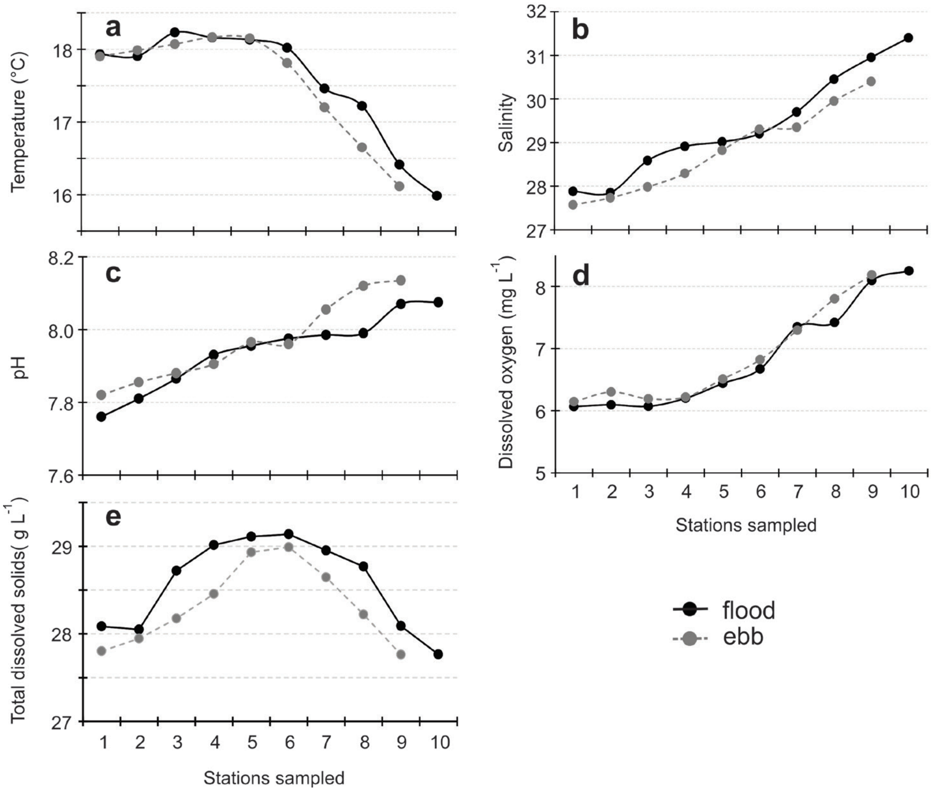

Figure 1. **Average (between subsurface and bottom) values of temperature (a), salinity (b), pH (c), dissolved oxygen (d), and total dissolved solids (e) at each sampling station and tide condition in the Babitonga Bay estuary.**

of hydrological variables are presented. The hydrological variables were also mostly horizontally homogeneous and similar in both tide conditions (Figure 1). Mean temperature was slightly higher towards the inner estuary, with a maximum of 18.3°C at station 3, about 2°C warmer than the outermost station (Figure 1a). As expected, salinity, dissolved oxygen, and pH were lower in the inner estuary, increasing in the outer estuary. Salinity varied from the mean of 27.5 to 31.4 (Figure 1b), dissolved oxygen from 6 to 8.4 mg L^{-1} (Figure 1c) and pH from 7.8 to 8.1 (Figure 1d). Total dissolved solids was higher in the intermediate stations reaching values around 29 g L^{-1} (Figure 1e).

Phytoplankton

Maximum chlorophyll-*a* values were recorded at station 2 during flood and ebb tide (Figure 2a, b; 2.3 and 2.2 mg m^{-3}, respectively) and minimum at station 9 and 10 (0.7 and 0.9 mg m^{-3}, respectively). During flood tide, phytoplankton total abundances tended to increase in the inner estuary, reaching highest values between 110-123,000 cells L^{-1} in the stations 1-3, nearly three times higher than in the ebb tide in the same stations (Figure 2c, d). However, relatively high abundance (80,711 cells L^{-1}) was also recorded at station 9. During ebb, phytoplankton abundances tended to increase towards the estuarine mouth, reaching the maximum of 85,000 ind.L^{-1} at station

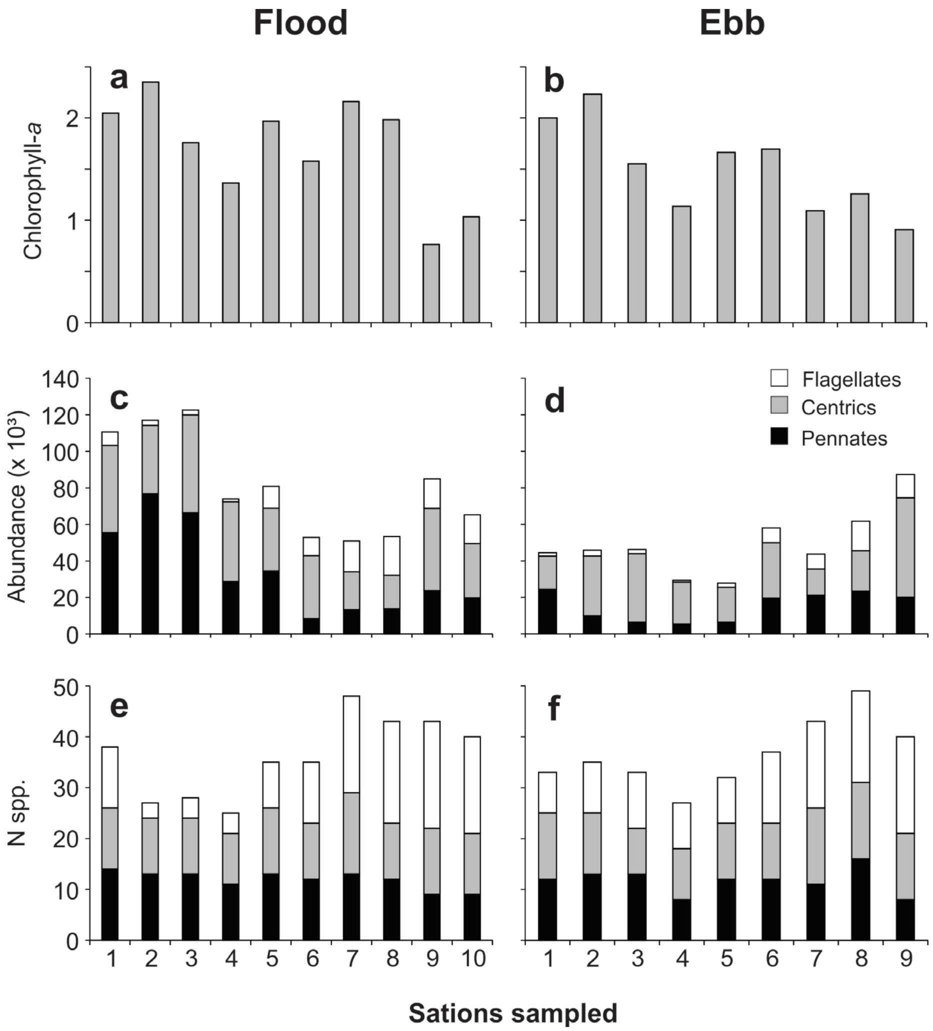

Figure 2. Chlorophyll-*a* concentration (a, b; mg m^{-3}), total phytoplankton abundance (10^3 cells L^{-1}; c, d) and number of species (e, f) at each sampling station and tide condition (flood and ebb tide) in the Babitonga Bay estuary.

9. Abundance was dominated by diatoms in all stations and tidal condition, with centrics and pennates as the most representative groups. Flagellate abundance was usually comparatively lower, tending to increase in the outer estuary in both tide conditions (Figure 2c, d).

A total of 91 species of phytoplankton were found (Table SI). Maximum number of species was 48 and 49 at station 7 and 8, and minimum of 25 and 27 species at station 4, during flood and ebb tide respectively (Figure 2e, f). In general, the total number of centric and pennate species did not vary between samplings stations, oscillating between 10-16 for centric and between 9-15 species for pennates. Flagellates occurred mostly in the outer estuary, increasing the number of phytoplankton species at these stations (Figure 2e, f).

The cluster analysis identified four distinct assemblage groups for phytoplankton (Figure 3a). The groups reflected the spatial distribution of the outer stations (group 4 – stations 9-10; group 3 stations 7-8) and the tide condition for the intermediate and innermost stations (group 2 stations 1-6 during the ebb tide; group 1 stations 1-6 during the flood). Within groups 1 and 2 occurred a tendency to a further subdivision at the ~50% similarity level, in both cases separating the stations 1-4 from the 5-6. According to the SIMPER routine the diatoms *Diploneis bombus* and *Paralia sulcata*, were the most important species for the formation of the groups 1 and 2 (Figure 3a). *Diploneis bombus* was also the most important species for group 3, along with the dinoflagellate *Gymnodinium* spp. and the diatom *Fallacia* spp. For group 4, *Thalassionema nitzschoides* and *Gymnodinium* spp. were the most representative species.

The Monte Carlo test indicated significant relationships between the canonical axes of the RDA and the environmental variables (P<0.001). The first four canonical axes explained 61.5% of the total variance of the phytoplankton assemblage. The first axis explained 37.8% and was mostly negatively related to temperature and total dissolved solids (Table SII, Figure 4a). The second axis explained a further 12.1% of the data variance and was mostly negatively related to zooplankton abundance and total dissolved solids. The third and fourth axes were mostly positively related to pH and dissolved oxygen and negatively to temperature, and together explained a further 11.6% of the assemblage variance (Table SII). Temperature was positively related mostly to *Skeletonema costatum* and *Dynophysis acuminata*, and also to *Eucampia zodiacus*, *Thalassiothrix* sp., and *Pleurosigma angulatum* in a lesser extent. Temperature was negatively associated with *Gymnodinium* spp., *Fallacia* spp. and *Prorocentrum* spp. Higher values of total dissolved solids were mainly associated with *Diploneis bombus*, *Thalassiosira mala* and *Actinoptychus senarius*, while lower values were related to *Actinocyclus normanii* and *Thalassionema nitzschoides*. *Pleurosigma angulatum*, unidentified pennate, *Eucampia zodiacus* and *Thalassiothrix* spp. were negatively associated with salinity, dissolved oxygen and pH (Figure 4a).

Zooplankton

Higher zooplankton biomass (>80 mg m^{-3}) was observed at intermediate stations (5, 6 and 7) in both tides, especially during ebb when reached the highest value of 164 mg m^{-3} at station 6 (Figure 5a, b). Minimum values were registered at station 9 during flood tide (5.4 mg m^{-3}) and 1 during ebb (3 mg m^{-3}). In general, zooplankton was more numerous in the intermediate-outer stations during both tide conditions, with highest values at stations 5, 6, and 8 (max. of 13,691 ind.m^{-3} during ebb tide at station 6; Figure 5c-f). During the flood tide, maximum abundance was recorded at station 5 (7870

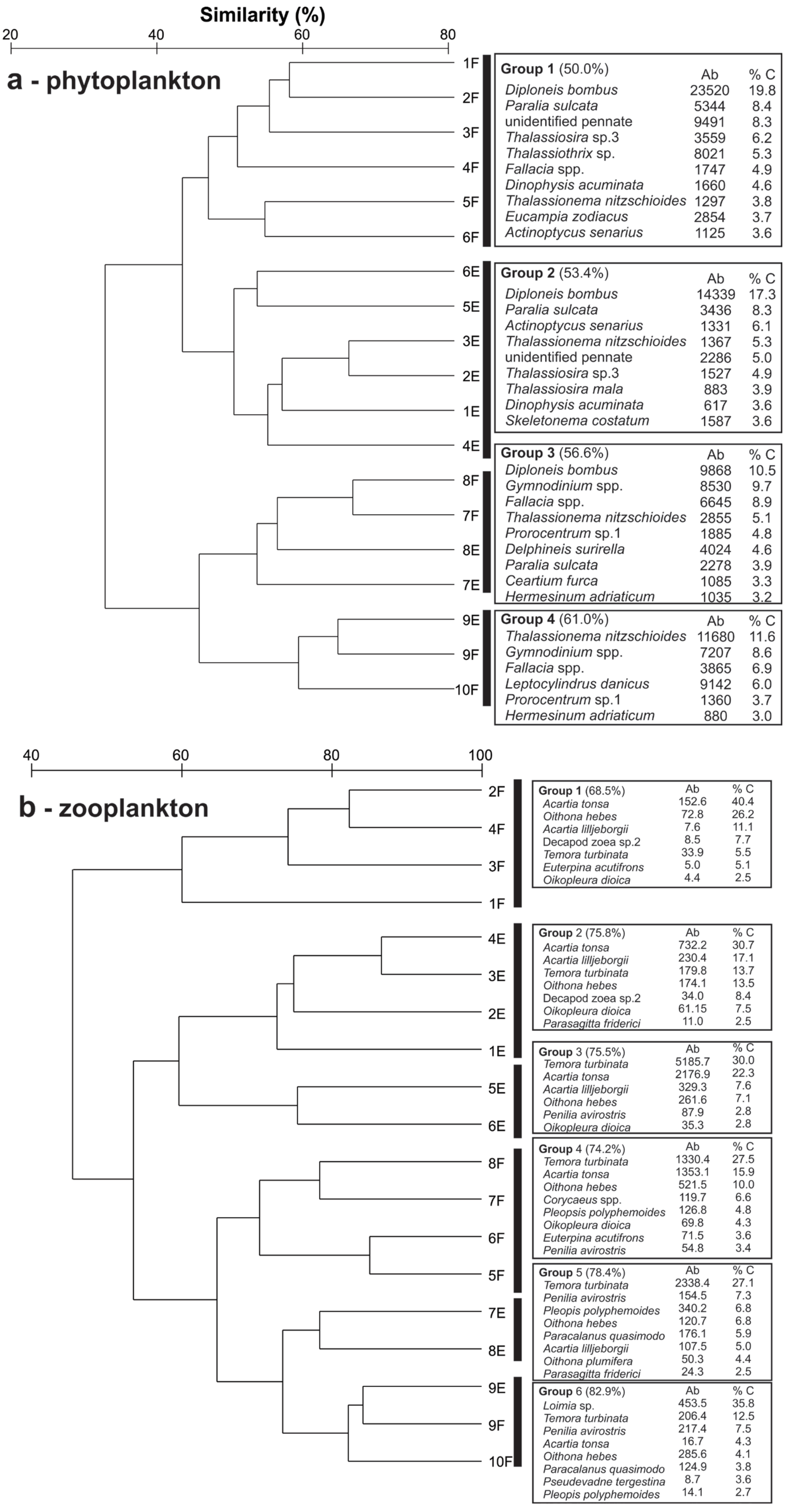

Figure 3. Hierarchical clustering between samples based on Bray-Curtis similarity (%) of phytoplankton (a) and zooplankton (b) assemblages from the Babitonga Bay estuary showing the formed groups and the results of the SIMPER analysis (boxes). Between parentheses is shown the average similarity within each group and the mean abundance (Ab) and percentage of contribution (% C) of each species to the formation of the groups; f - flood tide, e - ebb tide.

Group 1 (50.0%)	Ab	% C
Diploneis bombus	23520	19.8
Paralia sulcata	5344	8.4
unidentified pennate	9491	8.3
Thalassiosira sp.3	3559	6.2
Thalassiothrix sp.	8021	5.3
Fallacia spp.	1747	4.9
Dinophysis acuminata	1660	4.6
Thalassionema nitzschioides	1297	3.8
Eucampia zodiacus	2854	3.7
Actinoptycus senarius	1125	3.6

Group 2 (53.4%)	Ab	% C
Diploneis bombus	14339	17.3
Paralia sulcata	3436	8.3
Actinoptycus senarius	1331	6.1
Thalassionema nitzschioides	1367	5.3
unidentified pennate	2286	5.0
Thalassiosira sp.3	1527	4.9
Thalassiosira mala	883	3.9
Dinophysis acuminata	617	3.6
Skeletonema costatum	1587	3.6

Group 3 (56.6%)	Ab	% C
Diploneis bombus	9868	10.5
Gymnodinium spp.	8530	9.7
Fallacia spp.	6645	8.9
Thalassionema nitzschioides	2855	5.1
Prorocentrum sp.1	1885	4.8
Delphineis surirella	4024	4.6
Paralia sulcata	2278	3.9
Ceartium furca	1085	3.3
Hermesinum adriaticum	1035	3.2

Group 4 (61.0%)	Ab	% C
Thalassionema nitzschioides	11680	11.6
Gymnodinium spp.	7207	8.6
Fallacia spp.	3865	6.9
Leptocylindrus danicus	9142	6.0
Prorocentrum sp.1	1360	3.7
Hermesinum adriaticum	880	3.0

Group 1 (68.5%)	Ab	% C
Acartia tonsa	152.6	40.4
Oithona hebes	72.8	26.2
Acartia lilljeborgii	7.6	11.1
Decapod zoea sp.2	8.5	7.7
Temora turbinata	33.9	5.5
Euterpina acutifrons	5.0	5.1
Oikopleura dioica	4.4	2.5

Group 2 (75.8%)	Ab	% C
Acartia tonsa	732.2	30.7
Acartia lilljeborgii	230.4	17.1
Temora turbinata	179.8	13.7
Oithona hebes	174.1	13.5
Decapod zoea sp.2	34.0	8.4
Oikopleura dioica	61.15	7.5
Parasagitta friderici	11.0	2.5

Group 3 (75.5%)	Ab	% C
Temora turbinata	5185.7	30.0
Acartia tonsa	2176.9	22.3
Acartia lilljeborgii	329.3	7.6
Oithona hebes	261.6	7.1
Penilia avirostris	87.9	2.8
Oikopleura dioica	35.3	2.8

Group 4 (74.2%)	Ab	% C
Temora turbinata	1330.4	27.5
Acartia tonsa	1353.1	15.9
Oithona hebes	521.5	10.0
Corycaeus spp.	119.7	6.6
Pleopsis polyphemoides	126.8	4.8
Oikopleura dioica	69.8	4.3
Euterpina acutifrons	71.5	3.6
Penilia avirostris	54.8	3.4

Group 5 (78.4%)	Ab	% C
Temora turbinata	2338.4	27.1
Penilia avirostris	154.5	7.3
Pleopis polyphemoides	340.2	6.8
Oithona hebes	120.7	6.8
Paracalanus quasimodo	176.1	5.9
Acartia lilljeborgii	107.5	5.0
Oithona plumifera	50.3	4.4
Parasagitta friderici	24.3	2.5

Group 6 (82.9%)	Ab	% C
Loimia sp.	453.5	35.8
Temora turbinata	206.4	12.5
Penilia avirostris	217.4	7.5
Acartia tonsa	16.7	4.3
Oithona hebes	285.6	4.1
Paracalanus quasimodo	124.9	3.8
Pseudevadne tergestina	8.7	3.6
Pleopis polyphemoides	14.1	2.7

ind.m^{-3}). The lowest densities were recorded in the innermost station (station 1) for both tides, with minimum of 23 and 279 ind.m^{-3} respectively during flood and ebb tide. Copepods dominated the zooplankton, with maximum of 7684 ind.m^{-3} at station 5 and 12,700 ind.m^{-3} at station 6, during flood and ebb tide respectively (Figure 5c, d). In general, copepods represented 87.5% of the total zooplankton except for station 9 during the flood tide, when they were only 14% and polychaetes 83%. Polychaetes occurred abundantly from the intermediate stations towards the estuarine mouth, reaching densities >400 ind.m^{-3} at the stations 8-10 during the flood tide and at station 9 during ebb (Figure 5e, f). Cladocerans also were more abundant in the outer estuary, reaching up to 600 ind.m^{-3} during ebb tide at station 8 and 350 ind.m^{-3} during flood tide at station 7. Decapod larvae were more abundant at the intermediate estuary, especially during ebb tide, reaching 462 ind.m^{-3} at station 6.

A total of 64 species of zooplankton were sampled (Table SIII). As well as for phytoplankton, higher zooplankton diversity was registered in the outer estuary, with a maximum of 30 and 33 species at station 9 in both tide conditions and minimum of 8 in the flood tide (station 1) and 14 in the ebb (station 2) (Figure 5g, h). Copepods (maximum of 12 spp.), polychaetes (max. 5 spp.) and other taxa were more diverse in the outermost stations. Decapods were more representative in the intermediate-outer estuary, reaching a total of 10 spp. at station 5 during ebb tide and 5 spp. at station 7 during both tides (Figure 5g, h).

As for phytoplankton, the cluster analysis identified distinct zooplankton assemblages structured according to the horizontal distribution and/or tide condition of the samples (Figure 3b). Six groups were formed at 55% similarity level. Two groups were formed by inner stations (1-4) according to the tide condition (group 1 - flood; group 2 - ebb). Group 3 was formed by the stations 5 and 6 during ebb; group 4 by the stations 5-8 during flood tide; group 5 by the stations 7 and 8 during ebb tide, and group 6 included the outermost stations (9 and 10) during both tides conditions. *Acartia tonsa* was the main species contributing to the similarity in group 1 and 2. *Oithona hebes* was also important for group 1, and *Acartia lilljeborgi* for group 2. Group 3 was mainly composed by *Temora turbinata* and *Acartia tonsa*. The copepods *Temora turbinata, Acartia tonsa*, and *Oithona hebes* were also the most representative species from group 4. For group 5 *Temora turbinata* was also the most representative species. Group 6 was mainly formed by the polychaete *Loimia* sp. and the copepod *Temora turbinata*, along with the cladoceran *Penilia avirostris* (Figure 3b).

The Monte Carlo test indicated significant relationships between the canonical axes of the RDA and the environmental variables ($P<0.001$). The first four canonical axes explained 84.0% of the total variance of the zooplankton assemblage (Table SIV). The first axis explained 52.9% and was mostly positively related to dissolved oxygen, salinity, pH and negatively to temperature. The second axis explained 20.3% of the data variance and was mostly positively related to phytoplankton abundance and negatively to total dissolved solids (Table SIV; Figure 4b). *Loimia* sp., *Penilia avirostris*, *Paracalanus quasimodo*, *Corycaeus* spp. and bivalvians were negatively related to temperature and positively mostly to salinity and dissolved oxygen. Differently, species such as *Oithona hebes*, *Acartia tonsa*, *Acartia lilljeborgi* and *Oikopleura dioica* had the opposite distribution, positive with temperature and negative with salinity, dissolved oxygen and pH (Figure 4b). Phytoplankton abundance was mostly negatively associated with *Temora turbinata*, but also to *Paracalanus crassirostris* and *Pleopis* polyphemoides. in a lesser extent.

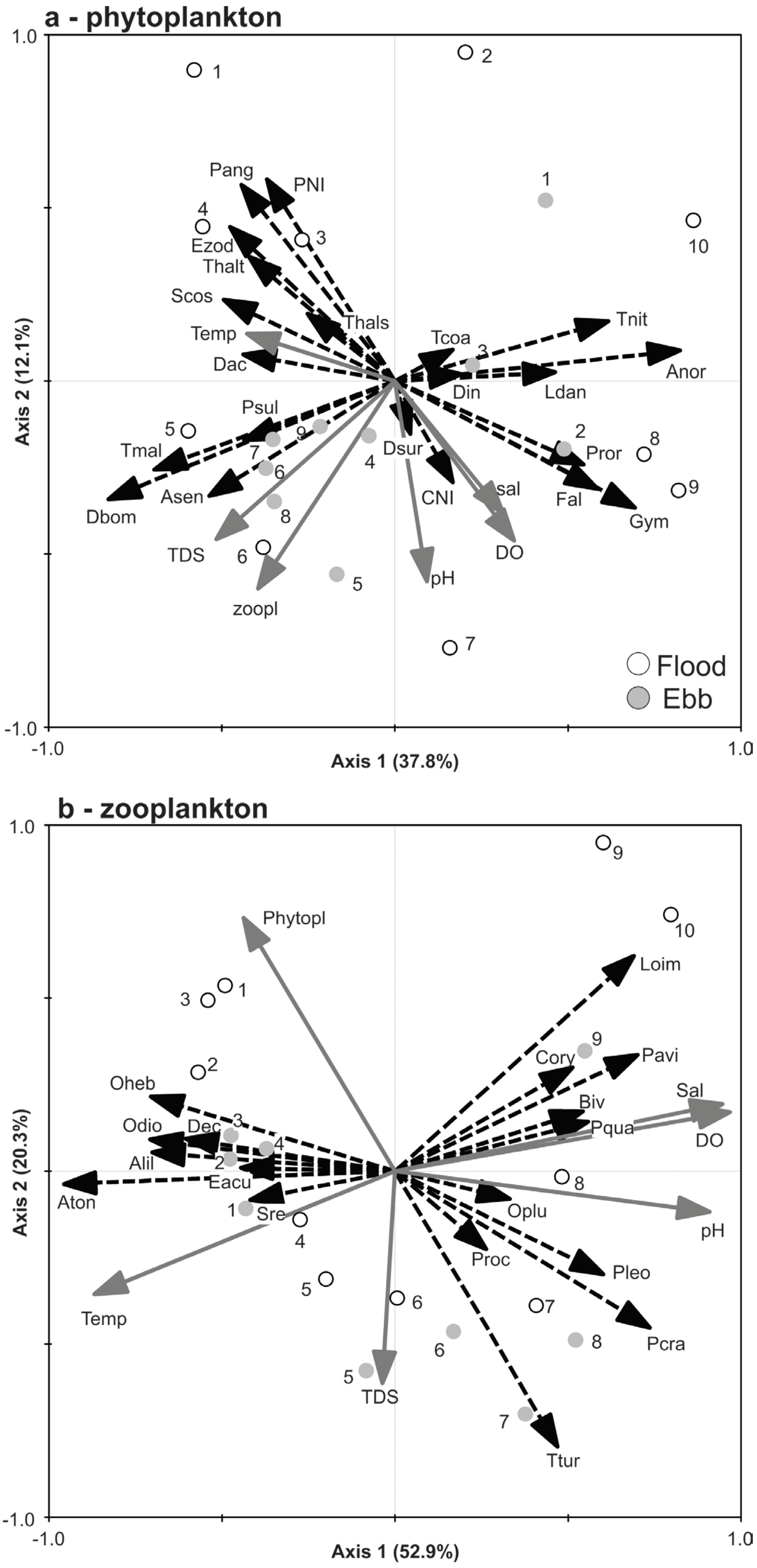

Figure 4. Ordination diagrams of the Redundancy Analysis of the phyto (a) and zooplankton (b) assemblages from Babitonga Bay estuary showing the first and second canonical axes. Dotted black vectors are the explanatory variables and grey vectors are the dependent variables. Circles represent the distribution of the stations during flood (open circles) and ebb (gray circles) tide. The percentage of the species data variation explained by each axis is shown in parentheses. **Explanatory variables codes:** sal = salinity; DO = dissolved oxygen; zoopl = total zooplankton abundance; TDS = total dissolved solids; temp = temperature; phytopl = total phytoplankton abundance. **Phytoplankton taxa codes:** Anor = *Actinocyclus normanii*; Asen = *Actinoptychus senarius;* CNI = centric diatom not identified; Dac = *Dinophysis acuminata*; Dbom = *Diploneis bombus;* Din = dinoflagette not identified; Dsur = *Delphineis surirella;* Ezod = *Eucampia zodiacus;* Fal = *Fallacia* spp.; Gym = *Gymnodinium* spp.; Ldan = *Leptocylindrus danicus;* Pang = *Pleurosigma angulatum;* PNI = Pennate not identified; Pror = *Prorocentrum* spp.; Psul = *Paralia sulcata;* Scos = *Skeletonema costatum;* Tcoa = *Tryblionella coarctata;* Thals = *Thalassiosira* spp.; Thalt = *Thalassiothrix* sp.; Tmal = *Thalassiosira mala*; Tnit = *Thalassionema nitzschioides.* **Zooplankton taxa codes:** Alil = *Acartia lilljerborgi*; Aton = *Acartia tonsa*; Biv = Bivalve; Cory = *Corycaeus* spp.; Eacu = *Euterpina acutifrons*; Dec = Decapoda sp.2; Loim = *Loimia* sp.; Odio = *Oikopluera dioica*; Oheb = *Oithona hebes*; Oplu = *Oithona plumifera*; Pavi = *Penilia avirostris*; Pcra = *Paracalanus crassirostris*; Pleo = *Pleopis polyphemoides*; Pqua = *Paracalanus quasimodo*; Proc = *Procerastea* spp.; Sre = *Stauridiosarsia reesi*; Ttur = *Temora turbinata.*

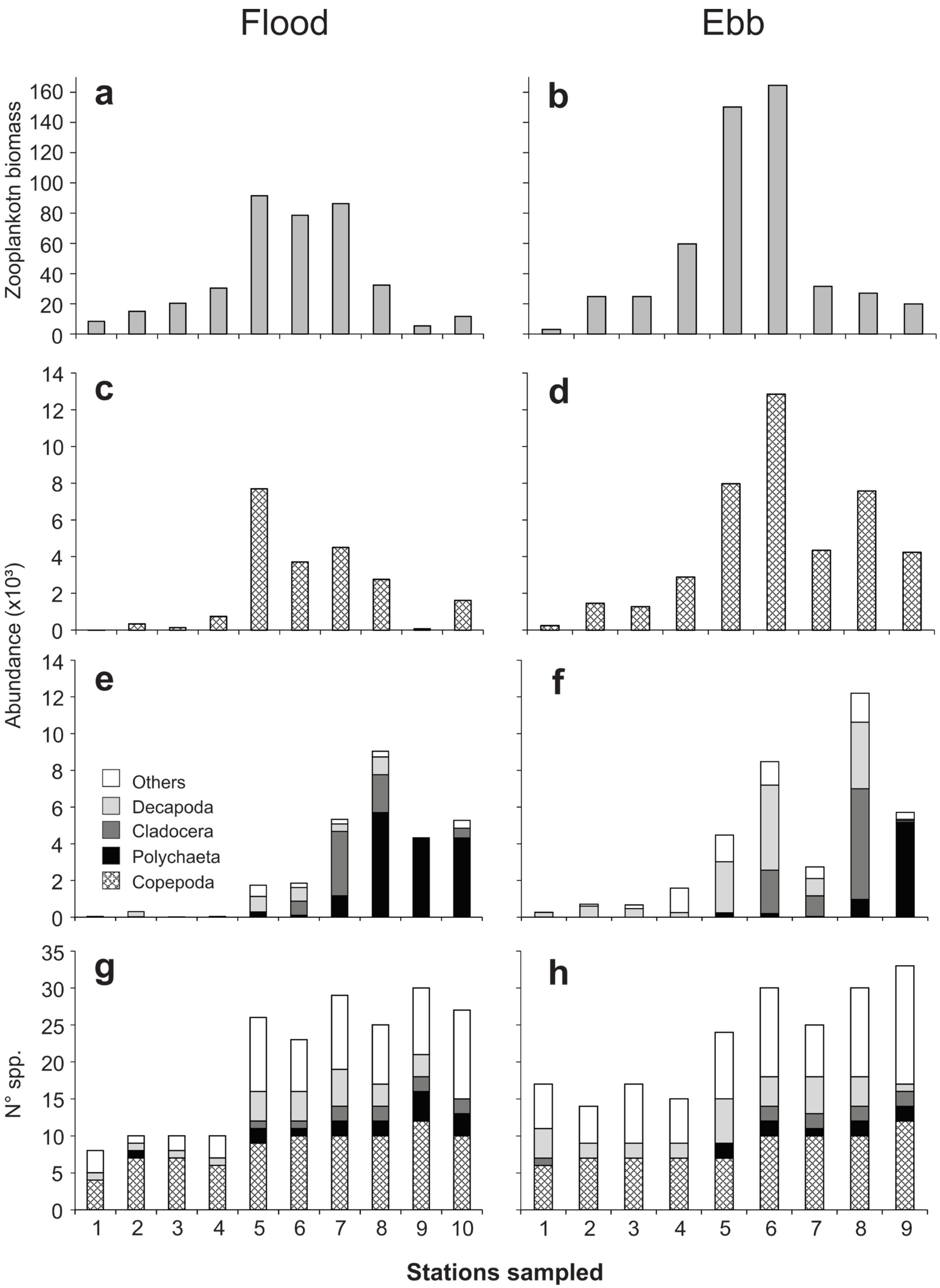

Figure 5. Zooplankton biomass (mg m^{-3}; a, b), copepods abundance (10³ ind. m^{-3}; c, d), zooplankton abundance without copepods (10³ ind. m^{-3}; e, f), and number of species of main higher taxa (g, h) at each sampling station and tide condition in the Babitonga Bay estuary.

DISCUSSION

In the present study, both spatial gradients and tidal oscillations were important to structure the plankton assemblages at a short-term perspective, in spite of the relatively small environmental variability during our samplings. Phyto and zooplankton formed relatively similar patterns following the estuarine horizontal gradients and/or tide condition (Figure 3a, b). From cluster results, we observed that the tidal variation influenced the planktonic community structure in the inner sites and such influence was less noticeable near the estuarine mouth. In general, the innermost stations (1-5) were split according to the tidal condition while in the other stations the pattern of clustering followed mostly the transect stations.

The analysis of plankton distribution at a short-term perspective is complex and highly influenced by local advection and turbulent mixing processes (Garcia-Soto et al. 1990, Dalal & Goswami 2001, Menendez et al. 2012). Diel and/or tidal zooplankton vertical migration also may include further complexities to our data (Anger et al. 1994, Meester & Vyverman 1997, Mecalco-Hernández et al. 2018). However, our samplings integrated the whole water column diminishing the bias these migrations may cause, and thus the observed patterns are unlikely to have been strongly influenced by them.

Most of the species captured in the present study are euryhaline and typically found in warm brackish-water ecosystems worldwide (Devassy & Goes 1988, Sassi 1991, Huang et al. 2004, Li et al. 2006, Madhu et al. 2007, Araujo et al. 2008, Dias et al. 2018). The abundance and diversity levels, as well as species composition and assemblage structure of both zoo and phytoplankton found here can be considered as typical of winter conditions from BBE and other nearby Southwestern Atlantic subtropical estuaries (Montú & Cordeiro 1988, Brandini et al. 2006, Miyashita et al. 2012, Salvador & Bersano 2017, Nogueira Júnior & Costa 2019).

The abundant centric diatoms *Diploneis bombus* and *Paralia sulcata* were the most important phytoplankton species for the formation of the inner groups in both flood and ebb tide (groups 1 and 2). These species are commonly found at tidal flats and salt marshes (McQuoida & Nordberg 2003), including tropical and subtropical estuaries from southwestern Atlantic (Procopiak et al. 2006, Haraguchi et al. 2015, Gonçalves-Araujo et al. 2018). Tidal flats and salt marshes are mainly found in the inner – and shallower – regions of the BBE (Vieira & Horn Filho 2017), which may have contributed to an increase in their abundance at this portion in the present study. Among the mechanisms responsible for suspending benthic microalgae on the water column, waves generated by winds (Holland et al. 1974) and tidal currents (Shaffer & Sullivan 1988) are common. Previous studies already discussed that the turbulence may favor microalgae suspension and its entrainment into the water column, especially during flood tide when currents are stronger in the BBE (Truccolo & Schettini 1999), and during winter also with stronger winds (Brandini et al. 2006). Indeed, the positive relation of both *D. bombus* and *P. sulcata* to total dissolved solids in the water column in the present study (Figure 4a) also support this view and suggest an association with resuspension processes.

The copepods *Acartia tonsa* and *Oithona hebes* dominated zooplankton communities in the inner stations in both tide conditions, while *Temora turbinata* was more important in the outer estuary. The cyclopoid *O. hebes* is commonly found in mangrove habitats (Rocha 1986), while the calanoids *A. tonsa* and *T. turbinata* preferentially colonize areas of the inner and outer estuary, respectively (Lopes et al. 1998, David et al. 2005, Brandini et al. 2006, Miyashita et al. 2012). Indeed, *A. tonsa* and *O. hebes* were related to lower values of salinity, dissolved oxygen and pH (Figure 4b) registered in the innermost stations in the estuary.

In the outer and deeper estuary, the pennate diatom *Thalassionema nitzschioides* and the dinoflagellate *Gymnodinium* spp. were the most important phytoplankton species. They are indeed commonly associated with intermediate and higher salinities and are mainly found in the outer estuarine portions (Mani & Khrishnamurty 1989) and shelf waters (Gonçalves-Araujo et al. 2018). For zooplankton, the high densities of the copepod *Temora turbinata* and the cladoceran *Penilia avirostris* in the outer portions also evidences the mixing of neritic coastal waters within the estuary (Li et al. 2006). Both species are very frequent and abundant at the adjacent shallow shelf (Brandini et al. 2014, Domingos-Nunes & Resgalla Jr 2017, Becker et al. 2018), being also commonly captured in the outer estuary (Brandini et al. 2006, Teixeira-Amaral et al. 2017, this study). The sites near the estuarine mouth (stations. 9-10; group 6) were largely defined by the polychaeta larvae *Loimia* sp., what is in accordance to previous observations in the BBE that associated this taxon with higher salinities in the outer BBE (Nogueira Júnior & Oliveira 2017).

Although the methodology applied here is adequate to assess the horizontal distribution of zooplankton, it is important to note that there are limitations. Due to the small boat used and distances between sampling stations (2-4 km), we spent about 3.5 hours at each transect and we could not observe finer spatiotemporal changes in the plankton assemblages. Besides this, only one day was investigated and more days of sampling in different environmental conditions are necessary. In any case, considering that the knowledge of the variability of the estuarine plankton composition and abundance at different temporal and spatial scales is a prerequisite for understanding the coastal dynamics, the present study is relevant because is a pioneering attempt to depict the horizontal pattern of plankton along a tidal scale in a subtropical, mixed estuary. Particularly considering that most of the previous studies analyzed large environmental gradients and short-temporal changes over a single or few stations (Chandran 1985, Guenther et al. 2015, Wan Maznah et al. 2016), hampering the understanding of tidal variations in the horizontal structuring of these communities.

In conclusion, our results suggest that the environmental gradients and tidal oscillation do structure the spatial patterns on plankton communities even in mixed estuaries under small gradients and relatively homogeneous conditions. We observed communities tending to group according to the horizontal estuarine gradients and tidal cycle, with higher differentiation between ebb and flood tide in the inner parts of the BBE for both phyto and zooplankton compartments. This may suggest influence of tidal oscillation on community structure was higher in the inner estuarine areas, what should be further tested. In mixed systems, the short-term plankton distribution seems to be species-dependent and further studies on biotic and abiotic regulations must be considered, like light and tidal currents influences, beyond their own ability to swim to migrate.

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SUPPLEMENTARY MATERIAL

Figure S1. Study area and sampling stations in the Babitonga Bay estuary.

Table SI. Phytoplankton taxa found in the Babitonga Bay estuary. RA: relative abundance. FO: frequency of occurrence. Species list according to the most abundant groups.

Table SII. Summary of the Redundancy Analysis (RDA) performed between the 21 most abundant phytoplankton taxa and six environmental explanatory variables from Babitonga Bay, Brazil.

Table SIII. Zooplankton taxa found in Babitonga Bay estuary. RA: relative abundance. FO: frequency of occurrence.

Table SIV. Summary of the Redundancy Analysis (RDA) performed between the 17 most abundant zooplankton taxa and six environmental explanatory variables from Babitonga Bay, Brazil.

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LSN analyzed and interpreted the data and wrote the manuscript; FB designed the study and helped in the data interpretation; MSS designed the study, performed the samplings, identified and quantified the phytoplankton; MNJ designed the study, performed the samplings, identified and quantified the zooplankton, analyzed and interpreted the data and wrote the manuscript.