UNIVERSIDADE DO SUL DE SANTA CATARINA
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS AMBIENTAIS

ANDRÉ SILVA FRANCISCO

El Niño Southern Oscillations and Pacific Decadal Oscillation as drivers of the decadal dynamics of benthic macrofauna in two subtropical estuaries (South Brazil)

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Orientador: Dr Sérgio A. Netto

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André Silva Francisco

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André S. Francisco

El Niño Southern Oscillations and Pacific Decadal Oscillation as Drivers of the Decadal Dynamics of Benthic Macrofauna in Two Subtropical Estuaries (Southern Brazil)

André Silva Francisco and Sérgio A. Netto*

Marine Science Laboratory, University of Southern Santa Catarina, UNISUL, Av Acácio Moreira 787, Dehon, Tubarão, Santa Catarina, 88704-900, Brazil

**Corresponding author; e-mail: sergio.netto@unisul.br*

Authors contributions ASF and SAN designed the study, performed research and analyzed data. ASF wrote the manuscript with substantial contributions from SAN. All authors edited the manuscript.

RESUMO

O El Niño- Oscilação Sul (ENSO) e a Oscilação Decadal do Pacífico (PDO) são oscilações climáticas em grande escala que afetam as teleconexões atmosféricas e oceânicas e desencadeiam eventos meteorológicos em diferentes escalas temporais e espaciais, tanto em áreas tropicais como extratropicais. Ao longo de 11 anos (2007 a 2017), a influência dos ENSO eventos (El Niño, La Niña e neutro) e diversidade (canônico e Modoki) e do PDO (fases positiva e negativa) sobre variáveis meteorológicas e invertebrados macrobênticos foi analisada em dois tipos de estuários subtropicais do sul do Brasil. Apesar de sua proximidade geográfica (85 km de distância), os estuários exibiram nítidas diferenças meteorológicas determinadas por processos orográficos, embora ambos tenham sido afetados pelo PDO e ENSO. A macrofauna bêntica dos estuários, um dominado por maré e outro dominado por rio, foi claramente distinta com maior riqueza de espécies no primeiro. A variabilidade de longo prazo da macrofauna bêntica em ambos os estuários foi fortemente influenciada pela oscilação decadal da temperatura da superfície do mar do Pacífico (PDO) e ENSO. Entretanto os sinais do PDO e ENSO diferiram entre os estuários estudados. O estuário dominado por maré foi primeiramente influenciado pelo PDO, e apenas secundariamente pelo ENSO. Já o estuário do dominado por rio exibiu comportamento oposto, com eventos ENSO como principal força moduladora da variabilidade decadal dos invertebrados macrobênticos. Os resultados também mostraram ainda que PDO e ENSO possuem efeitos combinados para ambos estuários, com maiores dissimilaridades da macrofauna durante períodos construtivos (PDO Positivo/EL Niño vs PDO Negativo /La Niña).

Palavras-chave: Variabilidade longo prazo, Comunidade estuarina, Variabilidade Climática, Biodiversidade bêntica, Ambiente costeiro.

ABSTRACT

The El Niño-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) are large-scale climatic phenomena affecting atmospheric and oceanic teleconnections, and thus triggering weather events at different temporal and spatial scales, both in tropical and extratropical areas. During 11 years (2007 to 2017), the influence of ENSO events (El Niño, La Niña and Neutral), ENSO diversity (canonical and Modoki) and PDO (positive and negative phases) on meteorological conditions and macrobenthic invertebrates were analyzed in two distinct (tide-dominated and river-dominated) subtropical estuaries of southern Brazil. Despite their geographical proximity (only 85 km apart), and although both were affected by the PDO and ENSO, the estuaries exhibited clear meteorological differences determined by orographic processes. The benthic estuarine macrofauna was clearly distinct and with higher species richness in the tide-dominated estuary. The long-term variability of benthic macrofauna in both estuaries was strongly influenced by the PDO and ENSO events. However, the signs of PDO and ENSO effects differed between the studied estuaries. The tide-dominated estuary was primarily influenced by the PDO, and only secondarily by the ENSO. On the other hand, the river-dominated estuary showed an opposite behavior, with ENSO events as the main modulating force of decadal variability of macrobenthic invertebrate community. Our results also showed that PDO and ENSO events have combined effects on both estuaries, with higher macrofauna dissimilarities during constructive periods (PDO Positive/EL Niño vs. PDO Negative/La Niña).

Key words: long-term variability; Estuarine communities; climate variability; benthic biodiversity; coastal environment.

INTRODUCTION

The El Niño-Southern Oscillation (ENSO) is the most important signal in the interannual variability of the global ocean-atmosphere system, fluctuating between anomalously warm (El Niño) and cold (La Niña) sea surface temperature (SST) conditions (Bjerknes 1969; Yeh and others 2018). Based on the location of the maximum SST anomaly cells on the Pacific, there are at least two ENSO types, canonical (or conventional) and Modoki (Ashok and others 2007; Ashok and others 2009; Yeh and others 2018). During a typical canonical ENSO, the warm (El Niño) or cold (La Niña) SST anomaly is primarily in the eastern tropical Pacific. In contrast, during El Niño Modoki events, cold SST anomalies prevail both in the eastern and western Pacific, whereas warm SST anomalies in the central Pacific. In La Niña Modoki events, the opposite phase of the El Niño Modoki, a colder central Pacific is flanked by warm anomalies on both eastern and western regions. The ENSO Modoki has been more frequent since the late 1990s and it has been relate to either natural (Yeh and others 2011) and anthropogenic forces (Yeh and others 2009; Kim and Yu 2012).

The evolution, development, and intensification of the canonical and Modoki events are dynamically and temporally different (Marathe and others 2015). As the intensity and location of their associated SST induced heating are distinct, the atmospheric teleconnections and impacts on tropical and midlatitude climate also differ. Nevertheless, both processes disrupt severely the global weather patterns and regional climate- e.g., influence on tropical cyclone genesis (Magee and others 2017), precipitation on South America (Tedeschi and others 2013), and Australia (Cai and Cowan 2009).

In addition to year-to-year variations associated to ENSO, SSTs in the tropical Pacific also fluctuate on large timescales due to the Pacific Decadal Oscillation (PDO, Mantua and Hare 2002). The strength and frequency of both ENSO types (i.e., canonical and Modoki) are strongly influenced by the PDO. For example, the positive (warm) phase of the PDO is associated with an enhanced frequency of El Niño events, while the negative (cool) phase is shown to be more favorable to the development of La Niña events (Verdon and Franks 2006). The PDO related SST and atmospheric circulation patterns in the tropical Pacific resemble those of the ENSO, but with a larger meridional extension on the eastern side of this ocean basin and a higher persistence (PDO measured in years/decades while ENSO in months; Mantua and Hare 2002). The PDO and the ENSO might have combined effects such as in the anomalous precipitation in South America (Kayano and others 2019), and act constructively (strong and well-defined anomalies) when they are in the same phase (warm or cold) and or destructively (weak and noisy anomalies) when they are in opposite phases (Kayano and others 2019; Lee and others 2019), affecting many coastal ecosystems worldwide.

Estuaries are transitional ecosystems that mediate transfers of energy and materials between the terrestrial environment and the adjacent ocean. This interaction shapes an ecosystem with complex physicochemical characteristics, high productivity and values of natural goods and services among the highest of natural ecosystems (Day and others 2013). Estuaries support an abundant and diverse fauna, including benthic macroinvertebrates, which play key roles in the flow of energy, nutrients cycling, and in benthic-pelagic coupling (Day and others 2013). In addition to local natural and man-made processes that modulate the estuarine benthic communities, large-scale meteorological processes, such as the ENSO, may also directly influence the dynamics of these ecosystems (Pollack and others 2011; Netto and others 2018). This is because ENSO events may interfere in the freshwater inflow, change wind intensity and direction favoring water flow into or off the estuary and thus impacting hydrodynamics, primary production (Odebrecht and others 2017), and sediment load (Ha and others 2018).

Studies evaluating the impacts of ENSO events on estuarine benthic communities are limited. These studies have adopted different approaches: 1- to contrast the effects of specific and usually extreme events on the fauna (Colling and others 2007; Pinotti and others 2011); 2- to relate long-term benthic variability to changes in some processes or environment parameters caused by ENSO events (Currie and Small 2005; Pollack and others 2011). Under both scenarios, only the canonical ENSO was considered, but all studies showed negative impacts of ENSO on estuarine macrofauna abundance and diversity. An unexploited subject, however, is how ENSO variation (i.e., canonical or Modoki) and the frequency/recurrence of these events (PDO) may interact and affect estuarine assemblages. Moreover, the studies relating ENSO and estuarine macrofauna have focused in a single estuary. Although estuaries share many common features, they can also differ widely, and we can hypothesize that different estuaries are not equally susceptible to the effects of the same ENSO event, as the effects may largely depend on intrinsic factors, such as the inlet and drainage basin sizes, orographic precipitation, and length:width ratio.

In this study, we investigated whether the ENSO events (El Niño, La Niña, and neutral), ENSO diversity (canonical and Modoki), and PDO (cold and warm phases) influence the temporal (decadal) variability of macrobenthic invertebrates in two geomorphologically distinct but geographically close estuaries in Southern Brazil. Decadal variability of PDO and ENSO events from 2007 to 2017 are described and the long-term dynamics of the benthic macrofauna between the estuaries area compared and related to these large-scale processes.

METHODS

Study Site

Our model systems were two subtropical and microtidal estuaries, Itajaí-Açu estuary and the Babitonga Bay, that are located 85 km away from each other in Santa Catarina State, South Brazil. These estuaries are markedly different in the size of their watersheds and their hydrodynamic drivers (Figure 1). The Itajaí-Açu estuarine river (26°54.7'S 48°38.1'W) is meandering, narrow (about 250 m) and drains an area of 15,500 km². This estuary is highly stratified and the river discharge is the main hydrodynamic driver, with minor tidal mixing (Schettini 2002). During periods of low river discharge, the estuary has a high sediment trapping efficiency and the salinity intrusion can extend up to 30 km from the river mouth (Schettini and Toldo 2006). On the other hand, during episodic river floods, marine waters are flushed off the estuary basin and river-borne materials are directly transported to the inner shelf (Schettini 2002). Sediments in the lower reaches of the Itajaí-Açu estuarine river consists mainly of silt and clay material (> 70 %) and total organic content is around 10%. However, sedimentary facies change significantly depending on the river discharge, with increase of fine sands during periods of low discharge, and riverine muddy and sand during high discharge (Schettini and Toldo 2006). Values of salinity in the lower estuary, range from 0 to 36; mean air temperature oscillates between 24°C in the summer and 16°C in the winter; total annual mean precipitation is 1600 mm (Schettini 2008). Most of the marginal areas of the Itajaí-Açu estuarine river are urbanized, and maintenance dredging of the channel for the Itajaí harbor is relatively common.

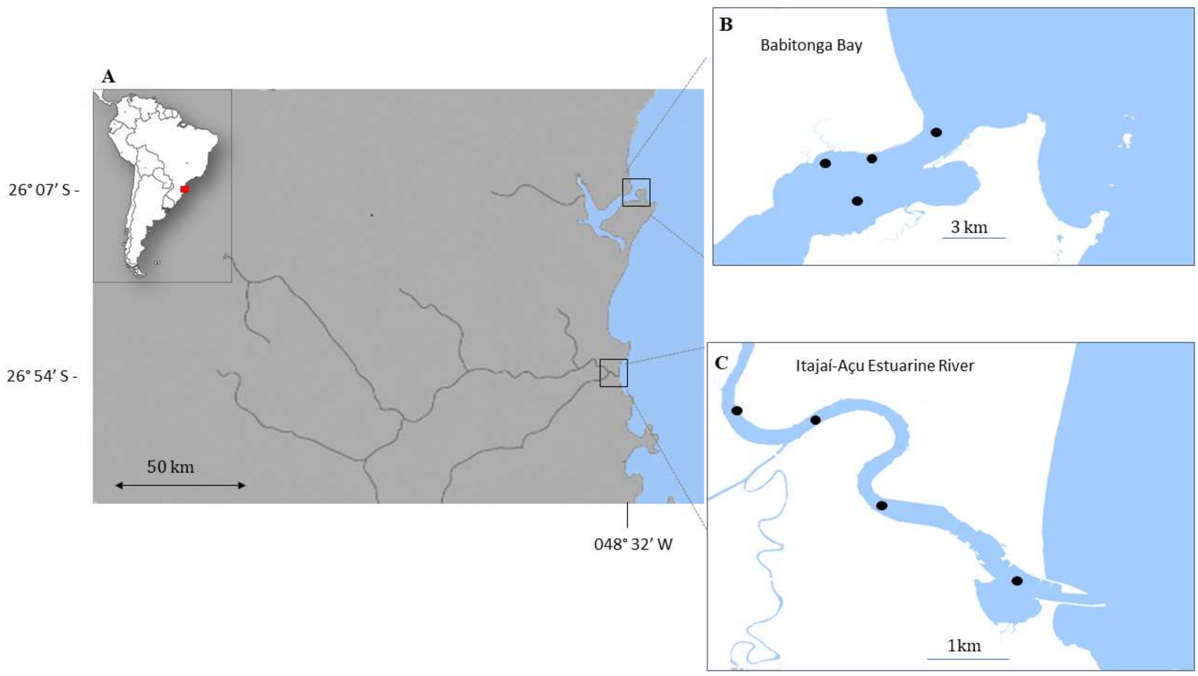


Figure 1. Map showing (a) the two studied estuaries in the Santa Catarina State, their watershed, and location of sampling sites for (b) the Babitonga bay and (c) the Itajaí-Açu estuarine river, Southern Brazil.

The Babitonga bay (26º7'S/ 48°32'W) is an estuarine complex with a single and relatively large inlet (about 2 km) and draining an area of 1,198 km^2 (Figure. 1b). Stratification and mixing processes inside the Babitonga bay are primarily regulated by tidal currents, although freshwater discharge during heavy rainy periods might also change stratification patterns (Lana and others 2018). Well-defined gradients of salinity and sediments extends from the inlet, euhaline with sandy bottoms (> 90%) with low total organic content (around 2%), to the oligohaline inner bay with muddy-sand bottoms and higher (around 5%) total organic content (Vieira and others 2008). The orographic effect due to close proximity of the Serra do Mar mountain range to the Babitonga bay increases precipitation (1400–5300 mm/year of rainfall annual) and humidity (over 85%) in the region; mean air temperature varies between 26°C in the summer and 18°C in the winter (Vieira and others 2008).

Benthic Fauna Sampling and Samples Processing

Sampling was carried out in 4 sites in the outer Itajaí-Açu estuarine river (Estuarine river) and Babitonga bay (Bay) from 2007 to 2017 (Figure 1b, c). Most of the sampling was, but some missing periods (Estuarine river: 2007 twice, and 2009, 2010, and 2015 – three times; Bay: 2009 – 3 three times, and 2017 twice). Macrofauna samples (3 replicates in each site) were taken with a 0.022 m^2 van Veen grab at depths ranging between 8 and 12 m. In total we collected 443 samples in the Estuarine river and 492 in the Bay (total of 935 samples). After collection, samples were fixed in 10% formalin for at least 48 h, sieved on a 0.5-mm mesh net, preserved in 70% ethanol, and sorted using a dissecting microscope. All invertebrates were identified to the lowest possible taxonomical level and counted.

Environmental Data

Average monthly data of air temperature, precipitation, pressure, surface runoff and eastward wind velocity trends for each estuary were obtained from the Giovanni online data system, developed by the NASA Goddard Earth Sciences Data and Information Services Center (NASA GES DISC, https://giovanni.gsfc.nasa.gov/giovanni/). Data of air temperature, precipitation, pressure, and eastward were obtained from satellite and estimated using MERRA-2 Model M2TMNXFLX v5.12.4 (Molod and others 2015), while surface runoff from the Noah 3.6.1 model in the Famine Early Warning Systems Network (FEWS NET) Land Data Assimilation System (FLDAS, McNally 2018). The data collection from Estuarine river were limited by the coordinates of the Data Bounding Box 50.25W, -27.15S, -48.65W, -26.85S, while the data from Bay were from 48.75W, -26.05S, -48.43W, -26.08S. For both areas data was obtained from January 2007 to December 2017.

ENSO events were analyzed using the Oceanic Niño Index (ONI) and ENSO Modoki data (El Niño Modoki Index, EMI). The ONI, provided by the National Oceanic and Atmospheric Administration (NOAA), is a 3-month running mean anomalies of SST data (Huang and others 2017) in the Niño 3.4 region (5ºN-5ºS, 120º-170ºW). Monthly data on the EMI, provided by the Japan Agency for Marine-Earth Science and Technology (JAMSTEC), are based in a tripolar variation in the SST (we also calculated a 3-month running mean anomalies) of the regions: A- 165°E–140°W, 10°S–10°N; B- 110°W–70°W, 15°S–5°N; C- 125°E–145°E, 10°S–20°N (Ashok and others 2007). As an indicator of ENSO events frequency over the studied period we use PDO index, which in positive phase is associated with an enhanced frequency of El Niño events, and in negative phase is favorable for the development of La Niña events (Lin and others 2018). Monthly PDO data obtained from NOAA are based on the reconstruction of SST and the PDO index also available at the NOAA website (https://www.ncdc.noaa.gov/teleconnections/pdo).

Data Analysis

The characterization of El Niño, La Niña and neutral, if canonical or Modoki, conditions were determined according to values of the SST anomalies and their arrangement in the regions A, B, C and Niño 3.4. The monthly averaged values between ONI and EMI (ONI/EMI) were used as proxy of variability for ENSO events during the studied period, as the ONI/EMI was significantly correlated with the ONI (r^2=0.97) and EMI (r^2=0.85). The threshold of ±0.5ºC defined periods of El Niño (higher than 0.5ºC), La Niña (lower than -0.5ºC) and Neutral (between 0.5ºC and -0.5ºC). If warmer (or cold) SST anomalies in the central equatorial Pacific were flanked by colder (or warmer) than in the western and eastern tropical Pacific the event was classified as El Niño (La Niña) Modoki, otherwise as canonical. Based on this procedure, we ended up with 5 different ENSO events: Neutral (N), El Niño canonical (ENC), El Niño Modoki (ENM), La Niña canonical (LNC) and La Niña Modoki (LNM).

Initially differences in macrofaunal assemblages and environmental variables between the two estuaries were examined. To visualize the similarities of the macrobenthic invertebrates between Estuarine river and Bay, similarity matrices from the abundance data were constructed based on the Bray-Curtis similarity measure. Ordination was done by nMDS, and the significance of differences in macrofauna assemblages, number of taxa, diversity, and density between estuaries performed by a one-way permutational analysis of variance (PERMANOVA, Anderson and others 2008). The similarity percentages routine SIMPER, (Clarke and Gorley 2006) was then applied to define those species that contributed most to the observed dissimilarities between estuaries. For the univariate measures, PERMANOVAs were run on Euclidean distance matrices and for the macrofaunal assemblages on Bray-Curtis similarity measure matrix, both with 9999 permutations, and the residuals permuted under a reduced model (Anderson and others 2008).

In order to visualize differences and relationships of the environmental variables (air temperature, precipitation, surface runoff, pressure, and eastward wind velocity) between the Estuarine river and Bay, a Principal Coordinate Analysis (PCO, Gower 1966) was applied to a Euclidian distance matrix. The significance of the differences in the environmental variables between estuaries was tested with PERMANOVA run on Euclidean distance matrices with 9999 permutations (Anderson and others 2008).

For each estuary, the effects of ENSO events and PDO on the macrofaunal and environmental variables were then investigated. Differences in number of taxa, diversity (H′), density, and macrofaunal assemblages, and in environmental data between ENSO types (N, ENC, ENM, LNC and LNM) and PDO phases (positive and negative) were tested with a one-way PERMANOVA using the same procedure as described above. In order to visualize macrofaunal patterns in response to different ENSO events in warm and cold phases of the PDO for each estuary, we performed a PCO on the Bray-Curtis similarities among centroids in a two-dimensional space (Anderson and others 2008). Similarly, variation of the environmental data in different ENSO events during PDO phases were also analyzed by PCO, but instead on Euclidean distance matrices among centroids in a two-dimensional space (Anderson and others 2008).

In order to identify the contribution of predictor variables to the temporal variability of macrofauna in each estuary a distance-based linear model routine (DistLM, Legendre and Anderson 1999) was applied. The DistLM was based on similarity matrices of macrofauna abundance data and the predictors include PDO, ENSO, air temperature, precipitation, surface runoff, pressure, and eastward wind tendency. Initially we used forward selection, an adjusted R^2 criterion and 9999 permutations. Based on these results, a new model routine with forward regression as selection procedure, and Akaike Information Criterion (AIC) as the selection criterion, was used to determine the most parsimonious models predicting macroinvertebrate communities, and to the distance-based redundancy analysis (dbRDA) models (McArdle and Anderson 2001; Anderson and others 2008).

RESULTS

PDO and ENSO Events

Between January 2007 and end-2013, the PDO index was mostly negative, with La Niña (14 months of LNC and 20 LNM) representing 40% of the events (Fig. 2). Increasing PDO values from mid-2009 through mid–2010 corresponded with El Niño condition (1 month of ENC and 6 of ENM) (8.3% of the events from 2007 to 2014). Neutral conditions characterized 51% of the months of the entire period, particularly from late-2012 through end-2014. The PDO switched to a positive phase from early-2014 through mid-2016, when observed positive SSTAs were up to 1.95°C. This switch was associated to a strong El Niño condition (15 ENC and 2 ENM) from late-2014 through early-2016. A new and short LNM event (4 months) followed the decrease of the PDO. During mid-2016 and 2017, SSTAs fluctuated from moderately negative to moderately positive, signaling neutral ocean condition.

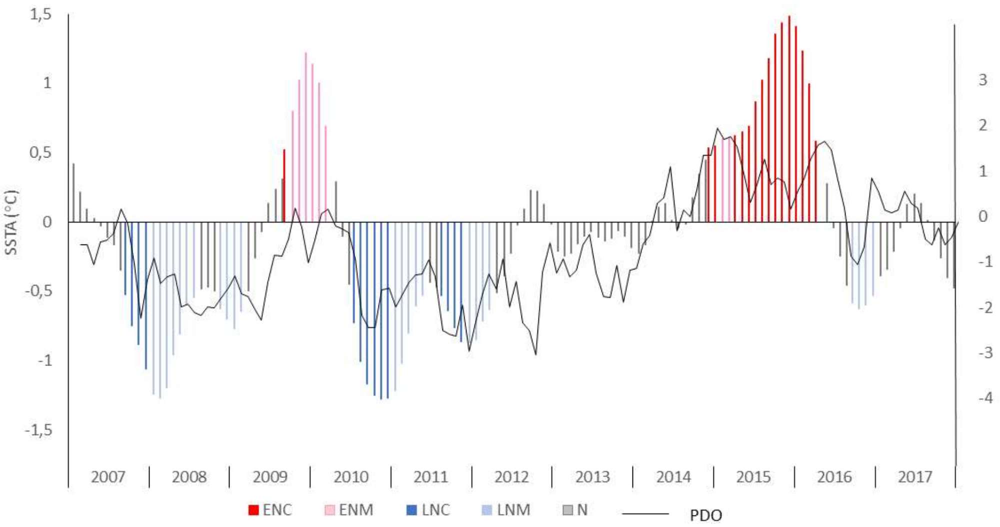


Figure 2. Monthly average of sea surface temperature anomalies (SSTA) indicating the ENSO events El Niño canonical (ENC), El Niño Modoki (ENM), La Niña canonical (LNC), La Niña Modoki (LNM) and neutral (N) conditions, and the Pacific Decadal Oscillations (PDO) from January 2007 to December 2017.

Environmental Variables

The principal coordinate analysis of the environmental variables (precipitation, temperature, pressure, runoff, and eastward winds tendency) showed a clear distinction between the Estuarine river and Bay (Fig. 3). Data variability over the entire study period (i.e., 11 years) was higher in the Bay. Moreover, all environmental variables differed significantly between estuaries, except for eastward winds (Table 1). Average monthly precipitation, temperature, pressure and runoff were higher in the Bay than in the Estuarine river.

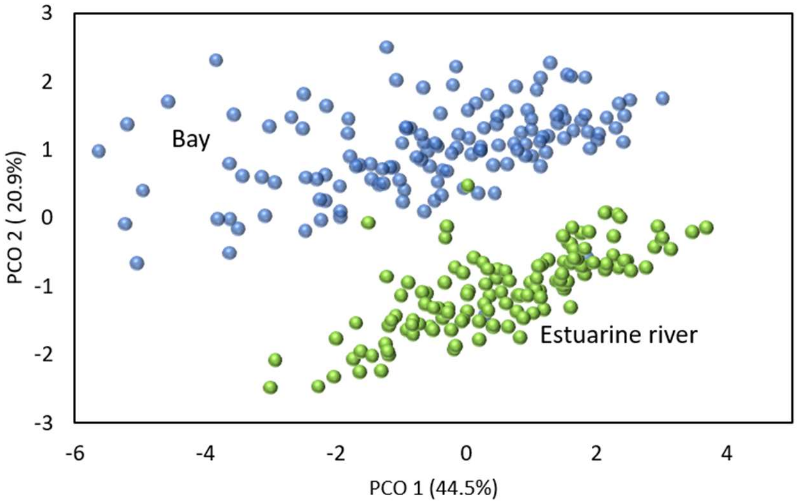


Figure3. Principal coordinates analysis (PCO) of the environmental data from Babitonga bay and Itajaí-Açu estuarine river from 2007 to 2017.

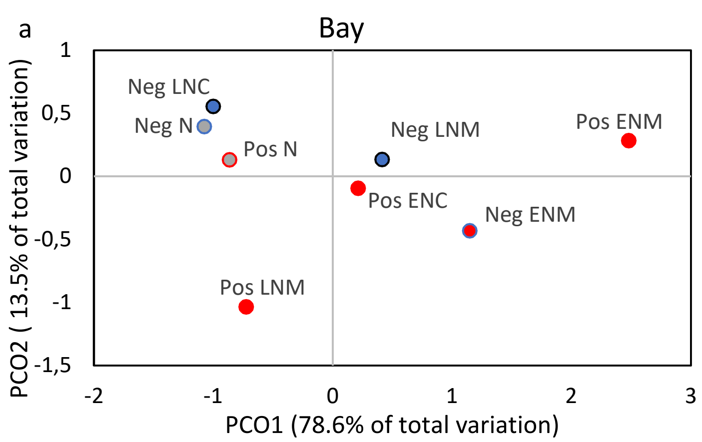
Table 1. Mean values (± SD) of the environmental variables, and summary results of the PERMANOVA tests for differences between the Babitonga bay (B) and Itajaí-Açu estuarine river (Er). Bold values -significant differences at p<0.05

Variables	Bay	Estuarine river	Pseudo-F	P(MC)
Precipitation (mm)	253 (±123)	221 (±95)	5.56	**0.028** (B>Er)
Temperature (ºC)	20 (±2.8)	18 (±3.1)	9.19	**0.004** (B>Er)
Pressure (hPa)	990 (±2.9)	970 (±2.7)	3206	**0.001** (B>Er)
Runoff (Kg $m^{-2}.s^{-1}$)	$1.9x10^{-5}$(±1.9 $x10^{-5}$)	$9.7x10^{-6}$(±8.3 $x10^{-6}$)	32.06	**0.001** (B>Er)
Eastward Wind ($m.s^{-2}$)	9.6 $x10^{-6}$ (±8.5 $x10^{-6}$)	$1.1x10^{-5}$ (±8.9 $x10^{-6}$)	2.46	0.113

PDO and ENSO Influence on the Environmental Variables

The eastward wind velocity trends were significantly higher during the warm phases of the PDO in both estuaries (Table S1). The other environmental variables did not vary significantly between the PDO phases. On both estuaries, the mean air temperature was significantly higher during the El Niño events (canonical and Modoki) and lower during LNC (mean differences between LNC and ENM/ENC were around of 3ºC; Tables S2, S3 and S4). The precipitation was also significantly higher during El Niño events. However, on the Bay, the periods of LNM were as rainy as in El Niño conditions. Lower precipitation values were detected during LNC and N periods on both estuaries. Variations on the surface runoff generally followed the precipitation, significantly higher during ENM and LNM on the Bay, and during ENC on the Estuarine river, and lower during LNC and N conditions. Mean air pressure was higher during periods of ENSO Modoki events, particularly ENM, decreasing during the other events in both estuaries. Significantly lower eastward wind velocity trends were detected during LNC, and higher during El Niños and, on the Bay, also during LNM (Tables S2, S3 and S4).

Differences in the environmental data between ENSO events within PDO phases were evident in the distribution across the first two axes of the PCOs for the Bay and Estuarine river (Fig. 4). For the Estuarine river, the first PCO axes explained most of the variation (more than 70%) and were strongly associated with the ENSO events, with LNC and neutral condition on the negative portion of the PCO 1, and El Niño events with the positive values. However, on the Bay, the rainy LNM on the negative phase of the PDO showed higher similarities with the El Niño events, in contrast to the LNM during the warm phase of the PDO. Moreover, for both estuaries, the PCO also showed high similarity between the LNC in the negative phase of the PDO with neutral conditions (Fig. 4).



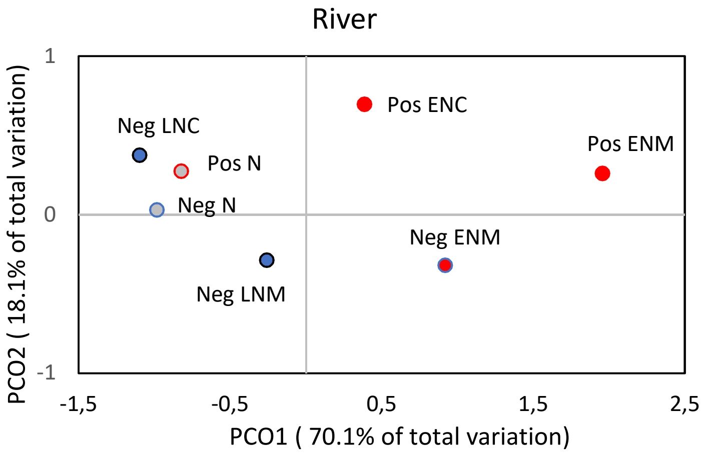


Figure 4. Principal coordinates analysis (PCO) of distances among centroids indicating the similarities of the environmental variables for the (a) Babitonga bay and (b) Itajai-Açu estuarine river. Pos- positive phase of PDO; Neg- negative phase of PDO; N- Neutral conditions; ENC- El Niño canonical; ENM- El Niño Modoki; LNC- La Niña canonical. Red dots- El Niños; Blue dots- La Niñas; Gray dots- neutral conditions. Red line around dots- positive PDO; Blue line around dots- negative PDO.

Benthic Macrofauna

The macrobenthic communities of the Babitonga bay and Itajaí-Açu estuarine river clearly differed (Fig. 5) and the PERMANOVA tests (for both composition and abundance) confirmed it (P(MC) < 0.0001). From a total of 146 taxa recorded in the estuaries, 142 were registered in the Bay and 44 in the Estuarine river; 28% of the taxa (42) occurred in both estuaries, 62% (102 taxa) were registered exclusively in the Bay and 1.3% (2 taxa) were registered only in the Estuarine river. The most abundant taxa in the Bay, polychaetes of the family Syllidae (22.5% of the macrofauna) and Cirratulidae (8,6%), and the lancet *Branchiostoma* sp. (6.4%), accounted for 37.5% of the total macrofauna. In the Estuarine river, the gastropod *Heleobia australis* (72% of the macrofauna), the tanaidean *Monokalliapseudes schubarti* (8.8%) and the Capitellidae polychaete *Heteromastus similis* (4.9%) accounted for 85.75% of the total macrofauna. The number of taxa and diversity were significantly higher in the Bay than in the Estuarine river, while density values did not differ.

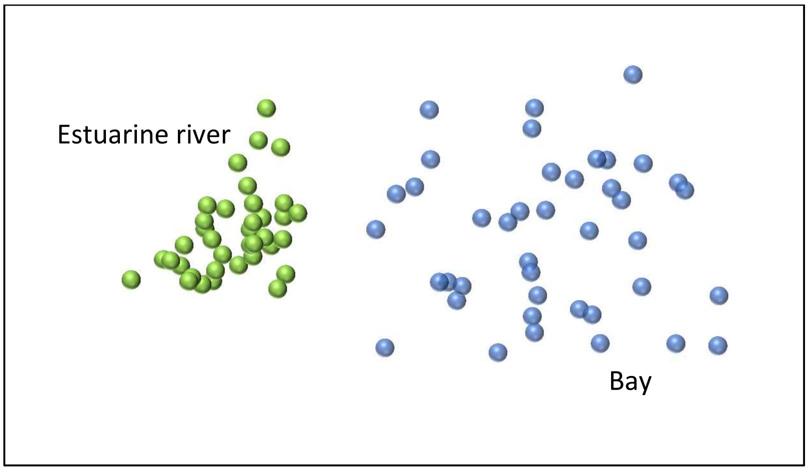


Figure 5. MDS ordination (stress 0.15) of log-transformed macrobenthic data from the Babitonga bay and Itajaí-Açu estuarine river.

PDO and ENSO Influence on Benthic Fauna

Significant differences for the macrofauna between PDO phases were detected for both estuaries. In the Bay, cold phases were characterized by higher the densities of Spionidae and Magelonidae (*Magelona* sp.) polychaetes (SIMPER analysis, data not shown), and significantly higher number of taxa and diversity (Table 2). On the other hand, warm phases in the Bay were differentiated by higher densities of Syllidae polychaetes and ophiuroids. In the Estuarine river, cold phases were characterized by the *H. similis* and *H. australis*, while warm phases were characterized by *M. schubarti*. Macrofaunal densities were higher during warm phases of the PDO in the Estuarine river (Table 2).

Table 2. Permutational analysis of variance (PERMANOVA) testing the effects of the PDO on the macrofauna associations and univariate descriptors. S – number of taxa; H´- diversity; N – density. Bold values -significant differences at p<0.05. W- warm PDO phase; C- cold PDO phase

	Bay					River				
	df	SS	MS	Pseudo-F	P(MC)	df	SS	MS	Pseudo-F	P(MC)

Macrofauna	1	30456	30456	11.5	**0.0002**	1	6736.3	6736.3	4.81	**0.001**
Res	490	1.20E6	2632.2			441	6.10E5	1399.4		
S	1	61.029	61.029	4.51	**0.035**	1	1.115	1.11	0.56	0.45
Res	490	6616.2	13.502		(W<C)	441	1.60E9	3.70E6		
H´	1	2.575	25.375	5.27	**0.023**	1	3.00E6	3.00E6	0.81	0.38
Res	490	235.6	0.4809		(W<C)	441	1.60E9	3.70E6		
N	1	1.40E6	1.40E6	1.27	0.271	1	3.00E6	3.00E6	0.81	0.38
Res	490	5.30E8	1.10E6			441	1.60E9	3.70E6		

The macrobenthic communities also differed significantly among ENSO events in the Bay and Estuarine river (Table 3 and Table S5). In the Bay, while the Syllidae and Cirratuidae polychaetes were the taxa that contributed most for the similarities between El Niño events (Modoki and canonical), *Magelona* sp., Spionidae polychaetes and *Branchiostoma* sp. distinguished the La Niña conditions (SIMPER analysis, data not shown). The number of taxa and diversity of the macrofauna in the Bay were significantly higher during ENM, LNM and LNC, and lower during ENC. In the Estuarine river, differences among ENSO events were mainly evident during the ENM, when macrobenthic communities showed significantly lower number of taxa and densities. Moreover, while *M. schubarti* contributed most for the similarities between the ENC in the Estuarine river, the cold events (LNM and LNC) were distinguished by capitellid polychaetes and the gastropod *H. australis*.

Table 3. Permutational analysis of variance (PERMANOVA) testing the effects of the ENSO events on the macrofauna associations and univariate descriptors. S – number of taxa; H´- diversity; N – density. Bold values -significant differences at p<0.05

	Bay					River				
	df	SS	MS	Pseudo-F	P(MC)	df	SS	MS	Pseudo-F	P(MC)
Macrofauna	4	45852	11463	4.38	**0.0002**	4	27113	6778.3	4.97	**0.0002**
Res	487	1.2E6	2616.8			438	5.9E5	1362.5		
S	4	199.2	49.816	3.74	**0.005**	4	6.5349	1.63	5.18	**0.0008**
Res	487	6478	13.302			438	138.1	0.31		
H´	4	10.7	2.698	5.77	**0.0004**	4	1.03	0.25	1.66	0.159

Res	487	227.4	0.46			438	68.2	0.15		
N	4	5.6E6	1.40E6	1.28	0.254	4	146.5	36.6	5.62	**0.001**
Res	487	5.3E8	1.09E6			438	2854.9	6.518		

The interaction of ENSO events with PDO phases influenced the macrobenthic communities in different ways between estuaries (Fig. 6). For the Bay, the first PCO axis explained 48% of the data variation and it was mainly associated with the variability between the cold and warm phases of the PDO. It can also be noted a high similarity of the fauna during the PDO cold phases, characterized by a fauna with greater diversity in LNC, LNM, and neutral. Conversely, the PDO warm phases showed a higher faunal variability which was distinguished by the low number of taxa, especially during LNM (Fig. 6a). The axis 2 explained 24.7% of the variation and was associated with the El Niño events and positive neutral conditions (positive axis), and La Niñas and negative neutrality (negative axis). For the Estuarine river, the PCO 1 explained 74.8% of the macrofauna variation and was mainly related to the ENSO events, with high dissimilarity of ENM in the warm phase of the PDO, also characterized by low density and diversity. In the PCO 2 (16% of the macrofauna variation), the positive values of the axis were associated to the positive phase of the PDO whereas the negative values with the cold phase (Fig. 6b).

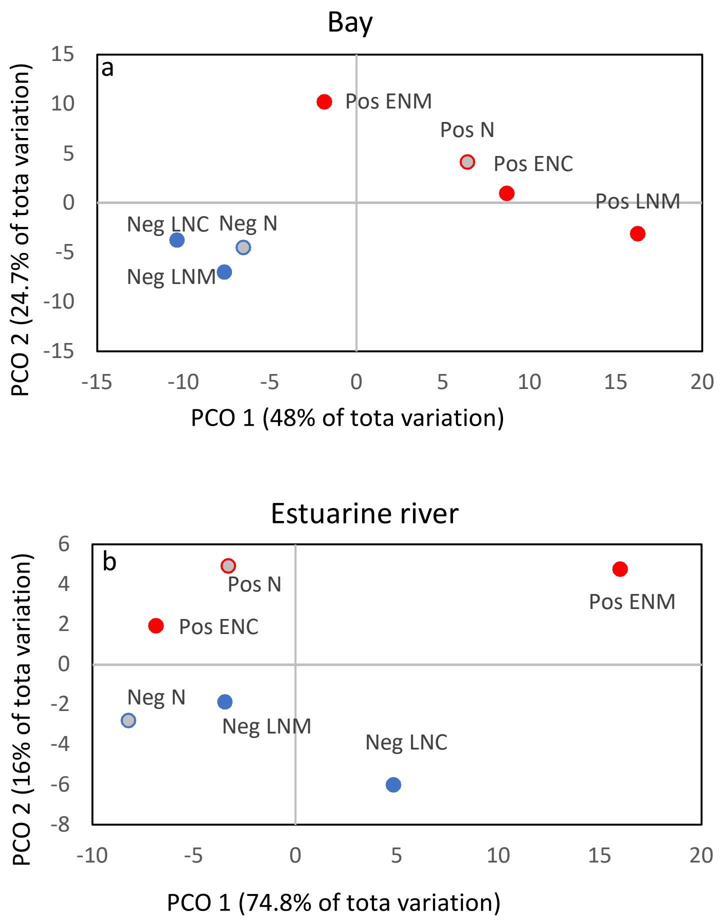


Figure 6. Principal coordinates analysis (PCO) of distances among centroids indicating the similarities of the macrofauna for (a) Babitonga Bay and (b) Itajaí-Açu estuarine river. Pos- positive phase of PDO; Neg- negative phase of PDO; N- Neutral conditions; ENC- El Niño canonical; ENM- El Niño Modoki; LNC- La Niña canonical. Red dot- El Niños; Blue dots- La Niñas; Gray dots- neutral conditions. Red line around dots- positive PDO; Blue line around dots- negative PDO.

Interrelationships among PDO, ENSO, Environmental Variables, and Macrofauna

The DistLM analysis detected significant correlations between macrofaunal structure and some predictor variables for the Bay and Estuarine river (Table 4). For the Bay, marginal tests evaluating the contribution of individual variables to macrofaunal assemblages revealed significant contribution of the PDO (14%) and ENSO (9.6%). However, the sequential test and the Best procedure evaluating the effects of all predictors combined, showed that the PDO was responsible for explaining significantly the variation in the invertebrate community composition (14.14%). For the Estuarine river, the DistLM analysis showed in the marginal testes that ENSO (3.34%) and PDO (3.05%) had a significant relationship with the variability in the macrofaunal community. Both sequential and Best procedure, however, showed that only ENSO significantly explained the fauna variability (3.34%) when all predictors were combined.

Table 4. Results of the marginal test and sequential tests performed by DISTLM-forward analysis. The percentage of variance in faunal data explained by the variable is abbreviated as "% var." Values in boldface indicate significant correlation ($P < 0.05$)

Bay Marginal tests				Estuarine River Marginal tests			
Variable	Pseudo-F	P	% var	Variable	Pseudo-F	P	% var
Temperature	0.937	0.494	4.09	Temperature	13.366	0.22	1.5
Pressure	1	0.431	4.3	Pressure	1.88	0.09	2.14
Precipitation	0.728	0.766	3.2	Precipitation	1.7	0.11	1.9
Runoff	0.928	0.532	4.05	Runoff	0.75	0.58	0.8
Eastward wind	1	0.106	6.34	Eastward wind	1.3	0.22	1.4
ENSO	2	**0.0078**	9.62	ENSO	2.97	0.01	3.34
PDO	4	**0.0003**	14.14	PDO	2.7	0.02	3.05
Sequential tests				Sequential tests			
PDO	3.62	**0.0003**	14.14	ENSO	2.97	**0.015**	3.34
Pressure	1.19	0.25	4.6	Precipitation	3.51	**0.005**	3.8
Runoff	1.31	0.16	5.02	Temperature	1.26	0.25	1.38
Eastward wind	1.86	0.02	6.7	Eastward wind	2.47	**0.03**	2.26
Temperature	1.13	0.3	4.1	Pressure	1.12	0.32	1.2
Precipitation	1.14	0.29	4.13	PDO	1.14	0.31	1.22
ENSO	0.91	0.57	3.3	Runoff	0.77	0.57	0.8

The distance-based RDA ordination for the Bay (Fig. 7a) showed that the first two axes explained 13.3% of the total variability in the macrofauna community and 65.2% of the relationship between the macrofauna environmental variables (Fig. 7a). The first axis (responsible for 53% of the fitted model relating the macrofauna-environmental variables) strongly related to the PDO and represented the macrofauna variability during periods of cold phases (2007 to 2013, in the negative portion of the axis) and the warm and neutral phases from (2014 to 2017 in the positive portion of the axis). The second axis, responsible for 12.2%, represented the variability within the ENSO events, with the positively portion of the axis related to the runoff and pressure, and negative to air temperature (Fig 7a).

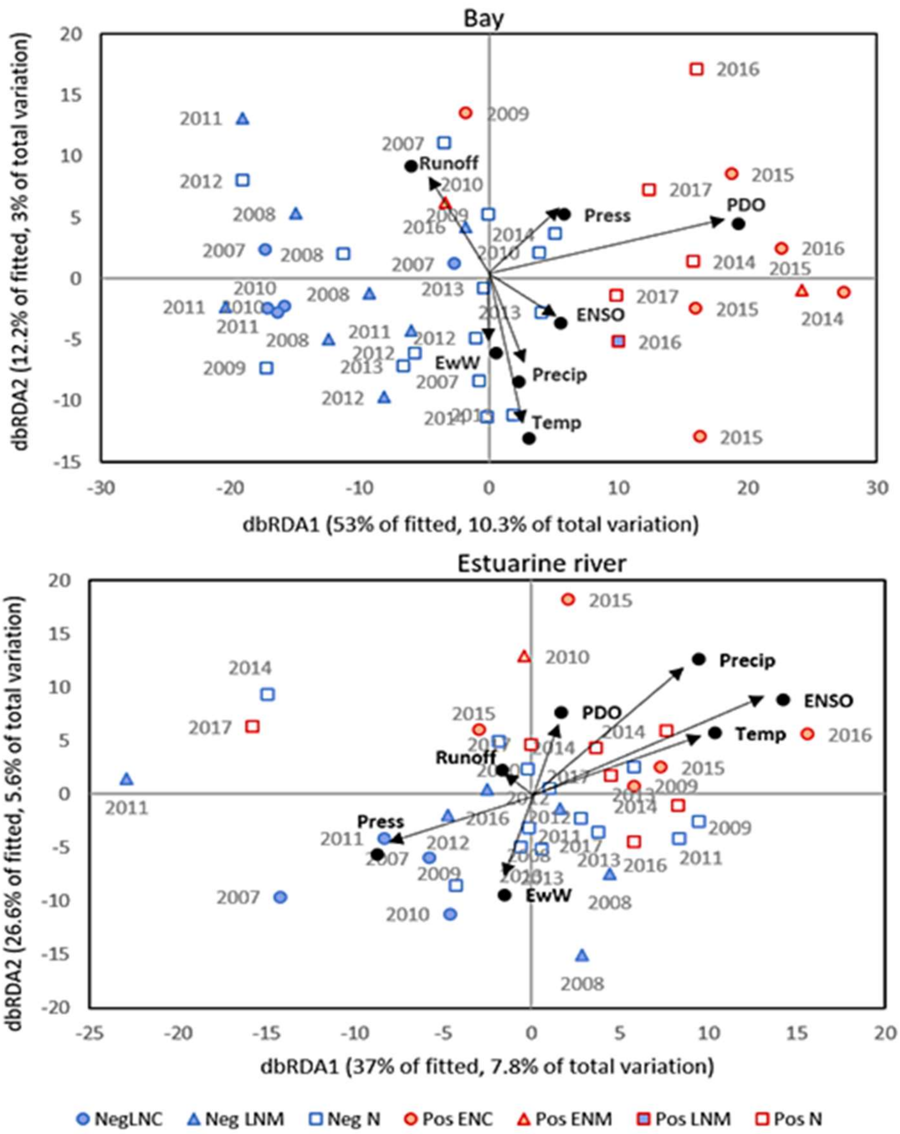


Figure 7. Distance-based redundancy analyses relating PDO, ENSO, environmental variables and macrofauna for the (a) Babitonga bay and (b) Itajaí-Açu estuarine river from 2007 to 2017. Pos- positive PDO; Neg- negative PDO; N- Neutral conditions; ENC- El Niño canonical; ENM- El Niño Modoki; LNC- La Niña canonical; LNM -La Niña Modoki.

For the Estuarine river, the first two axes of the dbRDA explained 13.4% of the total variability in the faunal data and 63.6% of the relationship between the macrofauna environmental variables (Fig 7b). The first axis (responsible for 37% of the fitted model) was strongly associated to the ENSO events and precipitation. The negative portion of the axis 1 showed that the macrofauna associated with events of higher values of pressure and eastward wind (LNC and LNM). On the dbRDA axis 2, responsible for 26.6%, represented the PDO phases where the variation of macrofaunal community was mainly related to precipitation.

DISCUSSION

The results of this study showed clear differences in the macrobenthic associations between two geomorphologically different but geographically close estuaries in Southern Brazil, the euhaline sector of Babitonga bay, a tide-dominated estuary, and the low Itajaí-Açu estuarine river, a river-dominated estuary. Additionally, our results showed that, in the long-term, macrofauna variability at Babitonga bay and Itajaí-Açu estuarine river were strongly influenced by both PDO phases and ENSO types. However, the signals of the PDO and ENSO differed between the estuaries. While in the Babitonga bay the temporal variability of macrofaunal communities was primary linked with PDO phases, and only secondarily with ENSO events, in the Estuarine river they exhibited the opposite behavior, with ENSO events as the main driver of the decadal macrofauna variability. Moreover, and as already pointed out in previous climatic studies of ENSO-related teleconnections (Kayano and others 2018; Lee and others

2019), our results showed that, for both estuaries, PDO and the ENSO have combined effects, and that the higher macrofauna dissimilarities occurred during constructive periods (i.e., Positive PDO/El Niño vs. Negative PDO/La Niña).

Along the 11-year period (2007 to 2017) covered by this study, the PDO was clearly divided into a cold (2007 to 2013) and warm and more variable (2014 to 2017) phases. From all environmental variables analyzed, only the eastward wind tendency showed a significant difference between the PDO phases. The increase or decrease of the local easterly winds between phases is related to the oscillations of the anticyclone system on the Southern Atlantic between latitudes 30°S and 45°S (Grimm and Ambrizzi 2009; Reboita and others 2019). The local easterly winds, significantly higher during warm phases of the PDO, are also known to favor the increase of precipitation over the southern region of Brazil (Grimm and others 1998; Fernandes and Rodrigues 2018). In addition, the eastward wind tendency was the only environmental variable that did not vary between estuaries, suggesting that this large-scale atmospheric process can similarly affect both estuaries.

Most of the interannual climatic variability of Southern Brazil comes from ENSO-related teleconnections (e.g., Grimm and others 2000; Grimm 2019). Furthermore, local influences may play a significant role, as observed for the studied estuaries. The Babitonga bay region, about 85 km northward from the Itajaí-Açu estuarine river, is more rainy and warmer, with a clear orographic effect as a result of its proximity to the Serra do Mar mountain range. Still, in both estuaries all environmental variables varied significantly between different types of ENSO events, with higher values mainly recorded during EL Niño events, especially during ENSO Modoki, and lower values during LNC. Interestingly, on the Bay, periods of LNM also showed significantly higher values of precipitation, runoff and eastward winds. Although the intensification of meteorological processes (e.g., positive precipitation anomaly) during El Niño is usually related to ENC in Southern Brazil (e.g. Grimm and others 1998; Penalba and

Rivera 2016), some studies have also shown that other ENSO events including ENM and LNC with strong positive anomalies may be evident (e.g., Tedeschi and others 2013; Viegas and others 2019). As the location of the ENSOs associated SST-induced heating are distinct, the atmospheric teleconnections also differ (Tedeschi and others 2013). These temporal and spatially different convective processes interfere in the Walker and Hadley circulations, and Rossby wave activities, inducing anomalous circulations on the atmosphere, and resulting in changes in precipitation, pressure and temperature (Grimm and others 2019). Besides, changes in the large-scale systems (cyclones/anticyclones) during periods of ENM may also disrupt the climate in southern Brazil (Taschetto and others 2011; Reboita and others 2019).

The composition of the macrofauna associations, the number of taxa, and diversity of the Babitonga bay and Itajaí-Açu estuarine river were significantly distinct. The sampling program in our study focused in the euhaline sector of the Bay and in the outer Estuarine river. Differences in the composition of benthic fauna between estuaries may vary along their horizontal gradients, with higher similarities in inner portions and higher dissimilarities in the outer portion (Netto and Fonseca 2017; Beard and others 2019). In this study, differences in the species composition resulted from the larger inlet size (8 fold) and lower drainage basin (14 fold) that increase the marine influence and contribute to the stability of the estuarine gradient in the outer Bay.

One of the most important results of this study was the significant correlation between the decadal variability of the macrofauna and the long-term fluctuation of SST in the Pacific Ocean. For the Bay, the PDO was responsible for explaining 14% of the total variability of the macrofauna. This result is similar to those reported for corals (Rodriguez-Ramirez and others 2014), ichthyoplankton assemblages (Marshall and others 2019), and fish production (Mantua 2009) in some marine areas in the Pacific.

The benthic macrofauna of the Babitonga bay was significantly more diverse during the cold PDO. Moreover, during the PDO cold phase, and particularly during LNC events, the macrobenthic invertebrates showed lower variability in their structure than in warmer phase, probably reflecting the observed increase in the relative stability of the environment and decrease precipitation and runoff. Lower richness and diversity of the macrofaunal community during the warm PDO, especially in ENC events, were paralleled with an increase of Syllidae polychaetes abundances. The syllids constitute one of the most diverse polychaetes families and shifts of distribution and species composition have been associated to increase in temperatures (Bianchi 2007; Del-Pilar-Ruso and San Martín 2012; Pezy and others 2017). It is interesting to note that the variability of the macrofauna in LNM and LNC during cold PDO phases were clearly distinct (as showed by the dbRDA). During events of LNM, the macrofauna variability increased in a similar fashion of that observed during El Nino events in warm PDO. Although this increase in macrofauna variability during constructive periods of ENSO/PDO should be further investigated, it is likely that heavy rainfall periods on the Bay during LNM in cold PDO and El Niño in warm PDO be responsible for such variability.

The macrobenthic associations of the Itajaí-Açu estuarine river are numerically dominated (more than 80%) by *H. australis* and *M. schubarti*, all of them with opportunistic behavior (Bemvenuti and others 2005; Freitas-Júnior and others 2013). Different from the Bay, most of the decadal variability in the macrobenthic invertebrates of the Estuarine river was mainly associated with ENSO events and precipitation, as the river discharge is the main local hydrodynamic driver. The low estuary has been historically subjected to severe flooding during El Niño events (Ignacio and Toldo Junior 2013). In fact, during this study the macrofauna community collapsed after flooding and flood-induced scouring in ENM and ENC events. Although El Niño rainy events were the main factors responsible for the macrofauna variability, we also detected significantly differences between PDO phases. These differences were due to an increase of the densities of *M. schubarti* during warm PDO. *Monokalliapseudes schubartii*, an endemic estuarine tanaidean from South America (Drumm and Heard 2011) is already known to be affected by meteorological events, with intense recruitment during warm periods (Colling and others 2007; Freitas-Júnior and others 2013).

Long-term studies are critical for providing key insights into environmental processes, natural resource management, biodiversity conservation, and ultimately for predicting ecosystem responses. Most of subtropical coastal areas are deprived of such data, though global warming is already altering estuarine ecosystems at a regional scale (e.g., Brazil, Bernardino and others 2015). The interactions between global warming and the quasi-periodic PDO and ENSO oscillations, which range in mean temperature was around 3ºC in this study, are most likely to have a major effect on natural systems. The changes in the composition and diversity of macrofaunal invertebrates observed during the extremes El Niño, that is, warm PDO/La Niña during cold PDO phases resembles those observed by Kröncke and others (2019) in response to climate variability and ocean warming in the northern hemisphere.

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