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**ECOSYSTEMS**

# Benthic macrofauna associated to the invasive bivalve *Mytilopsis leucophaeata* (Dreissenidae) in a coastal lagoon in Rio de Janeiro, Brazil

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**Abstract:** The invasion record for the estuarine bivalve *Mytilopsis leucophaeata* in Brazil is in Rio de Janeiro city, including the Rodrigo de Freitas Lagoon, where high densities of this invader were registered. This work aimed to (1) assess the composition and structure of the benthic macrofauna associated with this invader in Rodrigo de Freitas Lagoon, (2) analyze the spatiotemporal variation of richness, density and diversity of the associated benthic community, and (3) correlate changes on the density of the associated benthic species with some water quality variables and the density of *M. leucophaeata*. Clusters of *M. leucophaeata* were collected monthly (two years) in four sites. Nine taxa associated with *M. leucophaeata* were found; *Heleobia* sp. (Gastropoda) and *Melita mangrovi* (Amphipoda) showed the highest densities. The structure of the benthic macrofauna slightly differed among sampling sites, but not between dry and wet seasons. The water quality parameters, specific patterns of each taxon and high densities of *M. leucophaeata* contribute to variations in density of the associated species. Oscillations in the densities of *M. leucophaeata* and the native bivalve *Brachidontes darwinianus* suggest some agonistic relationship between them, such as a competition for space.

**Key words:** Biological invasion, engineer species, dark false mussel, estuary, Rodrigo de Freitas Lagoon.

## INTRODUCTION

Ecosystem engineers are species that may lead to considerable changes in the availability of resources for other species; such modifications may be biotic or abiotic, and the most common ones are related to the expansion or creation of new habitats (Jones et al. 1994, Sousa et al. 2009, Darrigran & Damborenea 2011). Some bivalves are regarded as engineer species owing to their typical gregarious behavior and high biomass production, affecting ecosystems and communities at various levels, i.e., increasing species richness and environment heterogeneity (Gutiérrez et al. 2003, Prado & Castilla 2006, Linares et al. 2017). Filter-feeding of massive populations of invasive bivalves may also interfere with local biodiversity, and adverse effects are recurrently recorded on the concentration of suspended particles and over the composition and structure of plankton communities (Karatayev et al. 2007, Sousa et al. 2013, Modesto et al. 2019).

The number of aquatic invasive species is escalating worldwide as a result of the increasingly exchange of goods and growing globalization process. The introduction of non-native bivalves is mainly related to inadequate management of ballast water or biofouling of ship hulls (Teixeira et al. 2010, Seebens et al. 2013, Teixeira & Creed 2020). Among the aquatic environments, estuarine systems are often the most affected for the introduction and spreading of non-native bivalves (Nehring 2006). Although detrimental impacts are frequent and commonly observed soon after the establishment of the invader (e.g., predation or competition effects over native species), some positive ones (e.g., predatory or competitive release; habitat improvement) might also occur (Rodriguez 2006, Boltovskoy et al. 2018).

The estuarine dark false mussel *Mytilopsis leucophaeata* (Conrad, 1831) is native from the Gulf of Mexico and Atlantic coast of North America, but has invaded several sites in Europe, Asia and America (Kennedy 2011, Forsström et al. 2016, Fernandes et al. 2018, Lodeiros et al. 2019). The few confirmed records for the established non-native populations of *M. leucophaeata* in Brazil are restricted for two coastal systems of the Rio de Janeiro city: Rodrigo de Freitas Lagoon (Rizzo et al. 2014, Fernandes et al. 2018) and Marapendi Lagoon (Fernandes et al. 2020). Contrasting with low densities usually found in its native range, dense clusters of *M. leucophaeata* are often registered within the invaded sites (Kennedy 2011, Van der Gaag et al. 2017). Several ecological and economic impacts are recorded for *Mytilopsis* species, such as competition with native species, changes on planktonic communities, financial losses in aquaculture, and biofouling in pipes of power-generating stations (Lin & Yang 2006, Aldridge et al. 2008, Florin et al. 2013, Cai et al. 2014, Freitas-Galeão & Souza 2015).

The benthic fauna associated to invasive populations of *M. leucophaeata* has been increasingly addressed, but most studies are restricted to identification of the taxa living over *M. leucophaeata* shells (Kelleher et al. 1999, Heiler et al. 2010) or to record the co-occurring bivalves with *M. leucophaeata* (Rajagopal et al. 2005, Brzana et al. 2017). Few recent studies have properly assessed the benthic fauna associated to clusters of *M. leucophaeata* (Richardson & Hammond 2016, Brzana et al. 2017), or to invasive populations of other *Mytilopsis* species (G.M.R. Freitas, unpublished data, Cai et al. 2014, Magni et al. 2019, Queiroz et al. 2020).

This work aims to assess the composition and structure of the benthic macrofauna associated to *M. leucophaeata* in Rodrigo de Freitas Lagoon, an urban, estuarine and multi-impacted coastal system located in Rio de Janeiro city to which high densities of this non-native bivalve were recorded (Rizzo et al. 2014). In addition to analyzing the spatiotemporal variation of richness, density and diversity of the associated benthic community, the relationship of the density of the associated benthic species with some water quality variables and the density of *M. leucophaeata* is also addressed. The potential impacts of the dark false mussel on the composition and structure of benthic macrofauna are also briefly discussed.

## MATERIALS AND METHODS

### Study site

The Rodrigo de Freitas Lagoon (22°57’02”–22°58’09”S, 43°11’09”–43°13’03”W) is a coastal and urban system situated in the Rio de Janeiro city, showing several recreational areas and high levels of human occupation on its margins (Enrich-Prast 2012). This estuarine system receives diffuse inputs of domestic sewage from vicinities or through inflowing of polluted rivers (Baptista-Neto et al. 2011, Braz et al. 2012, Soares et al. 2012). Most of the original perimeter of this lagoon was changed due to grounding (Enrich-Prast 2012).

The current area of Rodrigo de Freitas Lagoon is 2.2 km², with an estimated volume of 6,200,000 m³ and mean depth of 2.8 m (Domingos et al. 2012, RIOÁGUAS 2013). The single direct connection between the lagoon and sea is controlled by floodgates, leading to a low water renewal and high concentrations of organic matter and suspended particles (Soares et al. 2012, RIOÁGUAS 2013). Rodrigo de Freitas Lagoon is a mesohaline system and its brackish waters (6–25 ppt) are thermally stratified according to dry and wet seasons (Soares et al. 2012). During a brief period in the beginning of the XX century, the lagoon had very low salinity levels, typical of freshwater systems (Oliveira et al. 1957).

## Methodology

Field works were performed monthly between March 2016 and March 2018. During the 2016 Olympic Games conducted in Rio de Janeiro, the access to the Rodrigo de Freitas Lagoon was partly closed, hindering the samplings in July and August of this year; additional samplings were done in November 2016 and July 2017. Four sampling sites (P1 to P4) were distanced by 1.0 to 2.5 km along the margin (Fig. 1). The highest marine influence is expected to occur at P1 (the site closest to the connection with the sea), whereas P2 is situated near the discharge of a polluted river; P3 is a deck used to the practice of rowing, located near a dump of pluvial waters, and P4 is situated within a recreational area with paddle boats. Clusters of *M. leucophaeata* were collected after scraping the hard substrata, with the aid of a spatula and a quadrat of 0.04 $m^2$. Three replicates were collected in each site. Samplings were conducted in the morning (09:00 to 11:00 am), regardless of tide levels, as the water level is altered by the artificial system of floodgates in this lagoon. Clusters of the invasive bivalve were collected about 0.5 to 1.0 m below the water surface. Water temperature, conductivity, salinity, pH, chlorophyll *a* and dissolved oxygen were measured through a multi-parameter probe (YSI 6-6920-V2-4).

The sampled clusters of *M. leucophaeata* were kept in plastic bags and stored in a freezer (-20°C) for posterior sorting of the associated macrofauna. The taxonomic identification was based on available literature (e.g. Oliveira 1953, Loyola-e-Silva 2005, Rios 2009, Senna et al. 2012) and confirmed by taxonomists (see Acknowledgments). Photographs were made using a Zeiss AxioCam ICc5 camera coupled to a Zeiss Discovery V20 stereomicroscope. The specimens were counted, stored in 70% ethanol and catalogued in the collections of MNRJ (Museu Nacional do Rio de Janeiro) and UERJ (Universidade do Estado do Rio de Janeiro).

The mean densities of *M. leucophaeata* were obtained as in Maia-Neto et al. (2020), whereas mean densities of the associated fauna were calculated for each species through the averaged abundance of individuals per area of each replicate (N = 3). Dry season was set as between April to September whereas the wet season as between October and March, following a 10-year monitoring study on the water quality of the Rodrigo de Freitas Lagoon (Soares et al. 2012).

## Statistical analyses

Species richness, Shannon-Weaver´s diversity (H’) and uniformity (J’) were calculated to be used as ecological descriptors of associated benthic community (Moreno 2001). Excel 2016 graphics were built to show the spatiotemporal variation of these three ecological descriptors, mean density of the associated species, and the six water quality variables. Simple linear regressions were performed between mean density values of *M. leucophaeata* (independent variable) with mean density of the total benthic macrofauna and with mean densities of each associated species (dependent variables). A correlation test was made to verify a possible competition between *M. leucophaeata* and the native bivalve *Brachidontes darwinianus* (d’Orbigny, 1842),

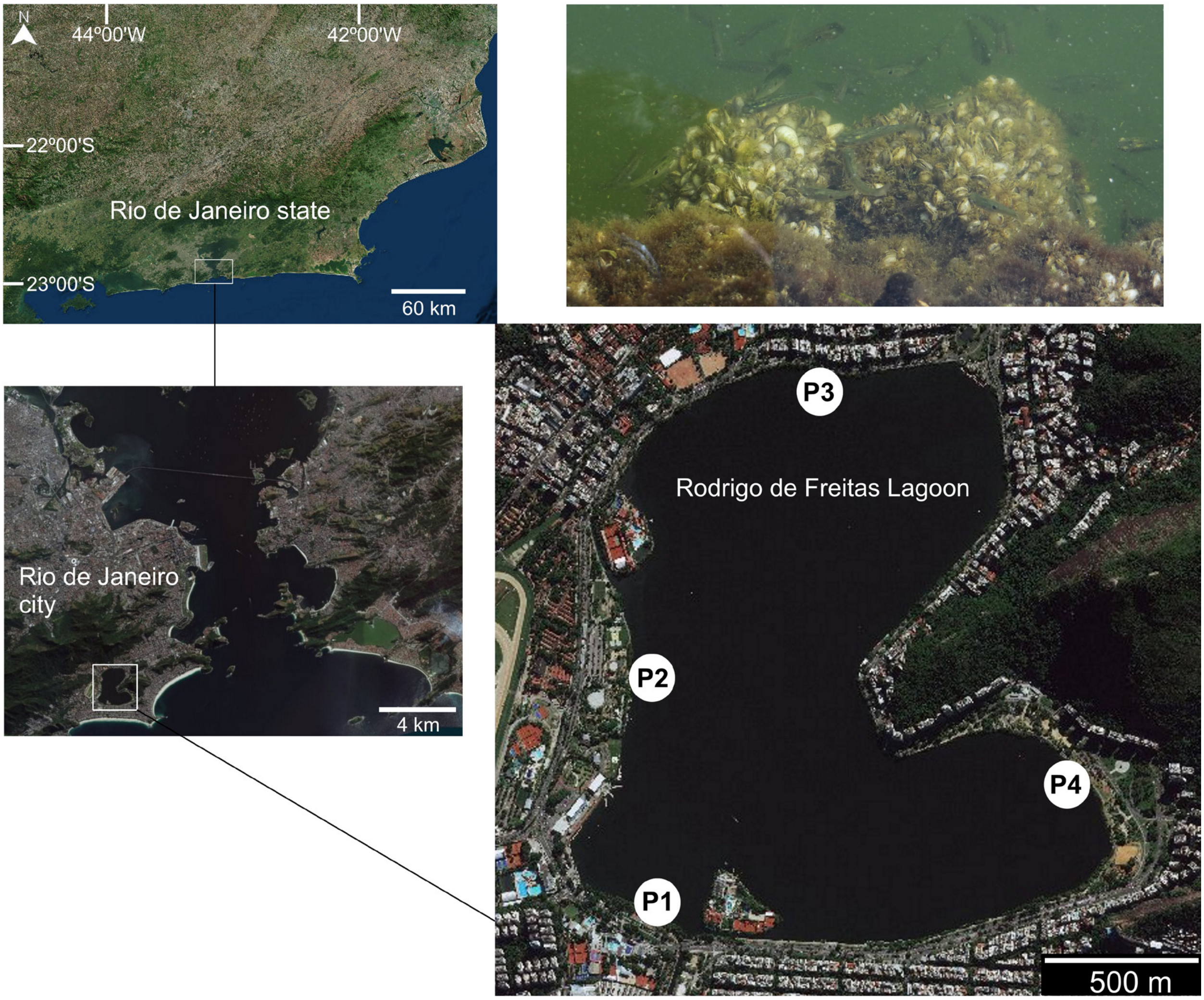

**Figure 1. Satellite images of the Rodrigo de Freitas Lagoon (modified from ArcGIS Online), showing the four sampling sites (P1 to P4). Top right: clusters of *M. leucophaeata* in Rodrigo de Freitas Lagoon.**

regarding separately the density of the first samplings (March 2016–April 2017) and the latter ones (May 2017–March 2018) of each sampling site. Other linear regressions were conducted to explore possible relationships within the associated species. All univariate analyses were performed in the software PAST 3.26

A Non-metric Multidimensional Scaling (nMDS) analysis was performed, through PAST 3.26, on the data matrix of benthic species (mean density; square-root transformed) to appraise possible changes of the associated community among sampling sites and seasons. Bray-Curtis dissimilarity index was used as distance measure of the nMDS (999 permutations). Analysis of Similarities (ANOSIM) were applied to test for the significance of the spatial and temporal pattern shown by nMDS.

Partial Redundancy Analysis (RDA) was applied on the matrix of benthic community density to address the relationship between the density of macrofauna benthic species and water quality variables. Time as used as covariable (i.e. measured as days after the first sampling date) to deal with possible effects of temporal autocorrelation on species density and environmental variables. Conductivity was removed from the analysis since it was highly correlated with salinity (Pearson's` r = 0.99). Species data were $\log_{10}$ x + 1 transformed whilst environmental data were normalized (i.e. centered and reduced by standard deviation). The stepwise forward selection criterion was used priorly (Monte Carlo`s test; 999 permutations) to detect which environmental variables have significant contributions ($p < 0.05$) to the model, and the significance of RDA axis was tested through Monte Carlo's test (999 permutations).

Generalized linear models (GLMs) were used to assess the relationship of the density ($\log_{10}$ x + 1 transformed data) of each benthic species with the suite of environmental variables simultaneously. Thus, the unconstrained scores (i.e. full variation of the water quality variables) of the first two environmental axes of the RDA were retrieved (i.e. controlled thus for potential temporal autocorrelation) and used as independent variables, while the density of benthic species was used as dependent variables in all GLM analyses. Gaussian distribution was performed and a 95% confidence interval ($p \leq 0.05$) was assumed. GLMs were chosen using the stepwise selection procedure, through the Akaike information criterion (AIC). RDAs and GLMs were performed with CANOCO 4.5 (Lepš & Šmilauer 2003).

### Genetic confirmation

An unidentified crab species was found associated to clusters of *M. leucophaeata*. Three individuals of this crab were thus DNA-sequenced for the cytochrome c oxidase subunit I (COI), following general procedures described in Fernandes et al. (2018), to confirm its taxonomic identity. DNA was extracted by a salting-out technique and purified with a Macherey-Nagel commercial kit. DNA amplification was achieved with primers HCO2198 and LCO1490 (Folmer et al. 1994) and sequenced by Macrogen Inc. (Seoul, South Korea) for both directions. A BLAST search was conducted in NCBI website, matching, at 99.8%–100% of accuracy, the identity with a sequence of a panopeid crab (reference number: KF682792). All three generated sequences are available in GenBank (reference numbers: MN498019–MN498021).

## RESULTS

The benthic macrofauna samples associated to the invasive bivalve *M. leucophaeata* were composed of 95,396 individuals belonging to nine taxa: *Cassidinidea fluminensis* (Mañe-Garzón, 1944) (Isopoda), *Melita mangrovi* Oliveira, 1953 (Amphipoda), *Sinelobus stanfordi* (Richardson, 1901) (Tanaidacea), *Eurypanopeus dissimilis* (Benedict & Rathbun, 1891) (Decapoda), *Amphibalanus* spp. (Cirripedia), *Heleobia* sp. (Gastropoda), *Brachidontes darwinianus* (Bivalvia), *Alitta succinea* (Leuckart, 1847) (Polychaeta) and Chironomidae larvae (Diptera) (Fig. 2). The gastropod *Heleobia* sp., with 3,017 (± 1,922 S.D.) individuals/m$^2$, and the amphipod *M. mangrovi*, with 1,734 (± 689 S.D.) individuals/m$^2$ were the species with the highest mean density.

The nine taxa were found in all sampling sites (Table I). The highest mean density of individuals/m$^2$ (± S.D.) was recorded in P2 (1,427 ± 1,776), contrasting to the lowest one found in P4 (472 ± 537) (Table I). Species richness per month was always higher than four in any sampling site (Fig. 3a). Species density varied with sites and seasons, and peaks were observed in September 2016 for P2, June 2016 for P3, and a gradual increase for P3 that peaked in November 2017 (Fig. 3b). The mean value of the Shannon-Weaver (H') index was highest in P4 (H' = 1.33 ± 0.28 S.D.), whereas the lowest value appeared in P1 (H' = 1.07 ± 0.27 S.D.) (Fig. 3c). The same pattern was observed for the uniformity index (J') (Table I).

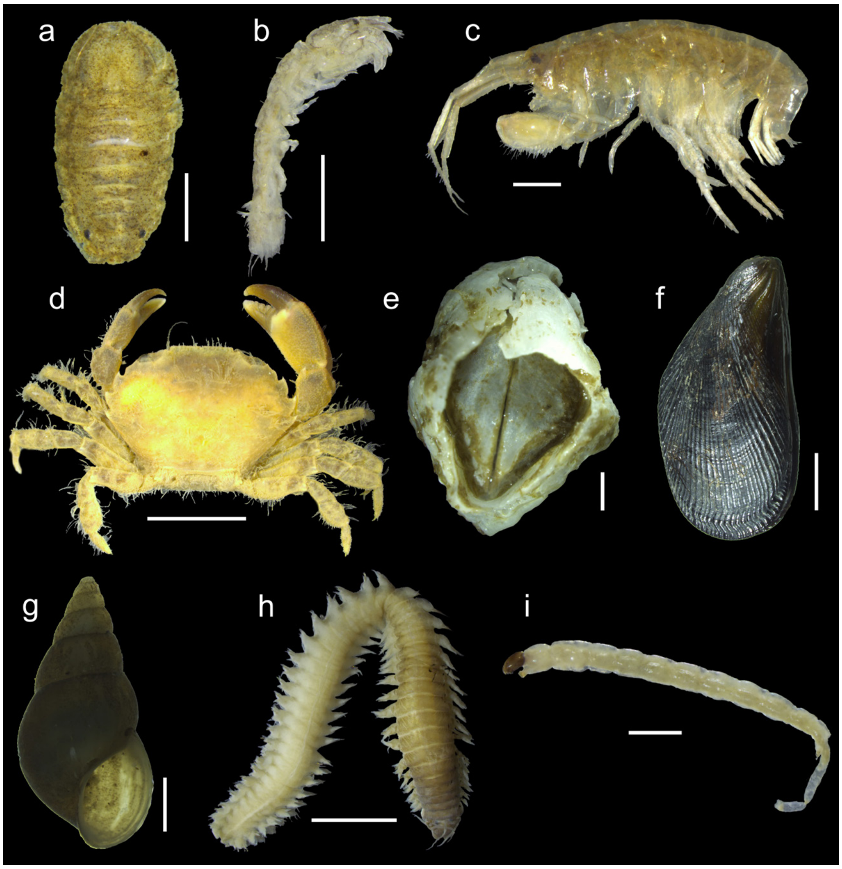

**Figure 2. Macrofauna benthic species associated to *Mytilopsis leucophaeata* in the Rodrigo de Freitas Lagoon. a. *Cassidinidea fluminensis* (Mañe-Garzón, 1944). b. *Sinelobus stanfordi* (Richardson, 1901). c. *Melita mangrovi* Oliveira, 1953. d. *Eurypanopeus dissimilis* (Benedict & Rathbun, 1891). e. *Amphibalanus* sp. f. *Brachidontes darwinianus* (d'Orbigny, 1842). g. *Heleobia* sp. H. *Alitta succinea* (Leuckart, 1847). i. Chironomidae larvae. Scale bars: a-c, g, i, 1 mm; d, f, h, 5 mm; e, 2 mm.**

*Amphibalanus* spp. and *S. stanfordi* showed high population oscillations (Fig. 4). High densities of *C. fluminensis* were found in the first sampling year, whereas high densities of *M. mangrovi*, *E. dissimilis*, *B. darwinianus* and *A. succinea* were recorded in the second year. *Heleobia* sp. showed high densities during all sampling periods. Low densities of Chironomidae larvae were found between January–October 2017 (Fig. 4).

Most simple linear regressions of the mean density of *M. leucophaeata* with mean densities of the associated benthic macrofauna were not significant ($p > 0.05$). Linear regressions of the mean density of *M. leucophaeata* were significant for mean density of the total macrofauna ($r = -0.29$, $r^2 = 0.08$, $p = 0.002$), *A. succinea* ($r = - 0.20$, $r^2 = 0.04$, $p = 0.04$) and *M. mangrovi* ($r = -0.28$, $r^2 = 0.07$, $p = 0.004$), however with low $r^2$ values. Mean densities of *M. leucophaeata* and *B. darwinianus* were significantly correlated for the site P3. Density of *M. leucophaeata* was higher and directly associated with increased densities of *B. darwinianus* ($r = 0.61$, $p = 0.02$) in the first samplings, whereas densities of both species were inversely related in the latter samplings ($r = -0.58$, $p = 0.04$).

The spatiotemporal variation of the six water parameters is shown (Fig. 5). The ANOSIM test revealed that the structure of the benthic macrofauna slightly differed between sampling sites (Global $R = 0.24$, $p = 0.0001$), despite a considerable overlap of the groups showed in the nMDS (Fig. 6a). Most ANOSIM paired tests revealed significant differences among sampling sites, except between site P2 and P3 (Global $R = 0.02$, $p = 0.17$). No seasonal difference was observed for the composition and structure of

**Table I.** **Mean values of density of species and density of total macrofauna per sampling site, diversity (H'), uniformity (J') and values of richness. Numbers inside parentheses indicate standard deviations (± S.D.).**

| | **P1** | **P2** | **P3** | **P4** | **Mean density** |
|---|---|---|---|---|---|
| **CRUSTACEA** | | | | | |
| Isopoda | | | | | |
| *Cassidinidea fluminensis* | 42 (59) | 27 (39) | 5 (7) | 5 (9) | 19 (18) |
| Tanaidacea | | | | | |
| *Sinelobus stanfordi* | 91 (151) | 1,077 (927) | 552 (619) | 229 (265) | 487 (438) |
| Amphipoda | | | | | |
| *Melita mangrovi* | 819 (1,116) | 2,160 (2,498) | 2,358 (2,987) | 1,602 (1,486) | 1,734 (689) |
| Decapoda | | | | | |
| *Eurypanopeus dissimilis* | 9 (13) | 26 (46) | 58 (114) | 149 (153) | 60 (62) |
| Cirripedia | | | | | |
| *Amphibalanus* spp. | 1,631 (1,540) | 1,944 (1,738) | 1,566 (1,258) | 633 (491) | 1,443 (564) |
| **BIVALVIA** | | | | | |
| *Brachidontes darwinianus* | 144 (135) | 1,690 (2,135) | 1,619 (2,092) | 299 (311) | 938 (830) |
| **GASTROPODA** | | | | | |
| *Heleobia* sp. | 2,198 (1,970) | 5,572 (8,040) | 3,241 (4,360) | 1,059 (1,493) | 3,017 (1,922) |
| **POLYCHAETA** | | | | | |
| *Alitta succinea* | 119 (91) | 249 (274) | 209 (222) | 261 (155) | 209 (64) |
| **DIPTERA** | | | | | |
| Chironomidae larvae | 33 (71) | 100 (127) | 8 (13) | 13 (22) | 38 (42) |
| Mean density of macrofauna | 565 (816) | 1,427 (1,776) | 1,068 (1,184) | 472 (537) | 883 (447) |
| Diversity (H') | 1.07 (0.27) | 1.25 (0.34) | 1.15 (0.32) | 1.33 (0.28) | – |
| Uniformity (J') | 0.55 (0.16) | 0.61 (0.16) | 0.58 (0.15) | 0.67 (0.13) | – |
| Richness | 9 | 9 | 9 | 9 | – |

the associated benthic macrofauna (Global R = 0.02, p = 0.10; Fig. 6b).

Partial RDA was significant (F = 3.34; Monte Carlo test: p = 0.001 for all axes) revealing that, after the influence of temporal autocorrelation was taking into account, axis 1 and 2 accounted respectively for 47.3% and 33.5% of data variance on the composition and structure of the associated benthic macrofauna (Fig. 7). Chlorophyll *a* was not included in the model, since this variable did not contribute significantly to explaining the distribution of the associated macrofauna (Monte Carlo test: p = 0.39). Only the mean densities of *A. succinea* and *E. dissimilis* were positively and weakly correlated to RDA axis 1, and thus with increased values of salinity and oxygen, contrasting to the densities of Chironomidae larvae, which were negatively correlated to RDA axis 1, and thus with decreased values of salinity and oxygen. The other species were also negatively associated with RDA axis 1, but they were weakly correlated

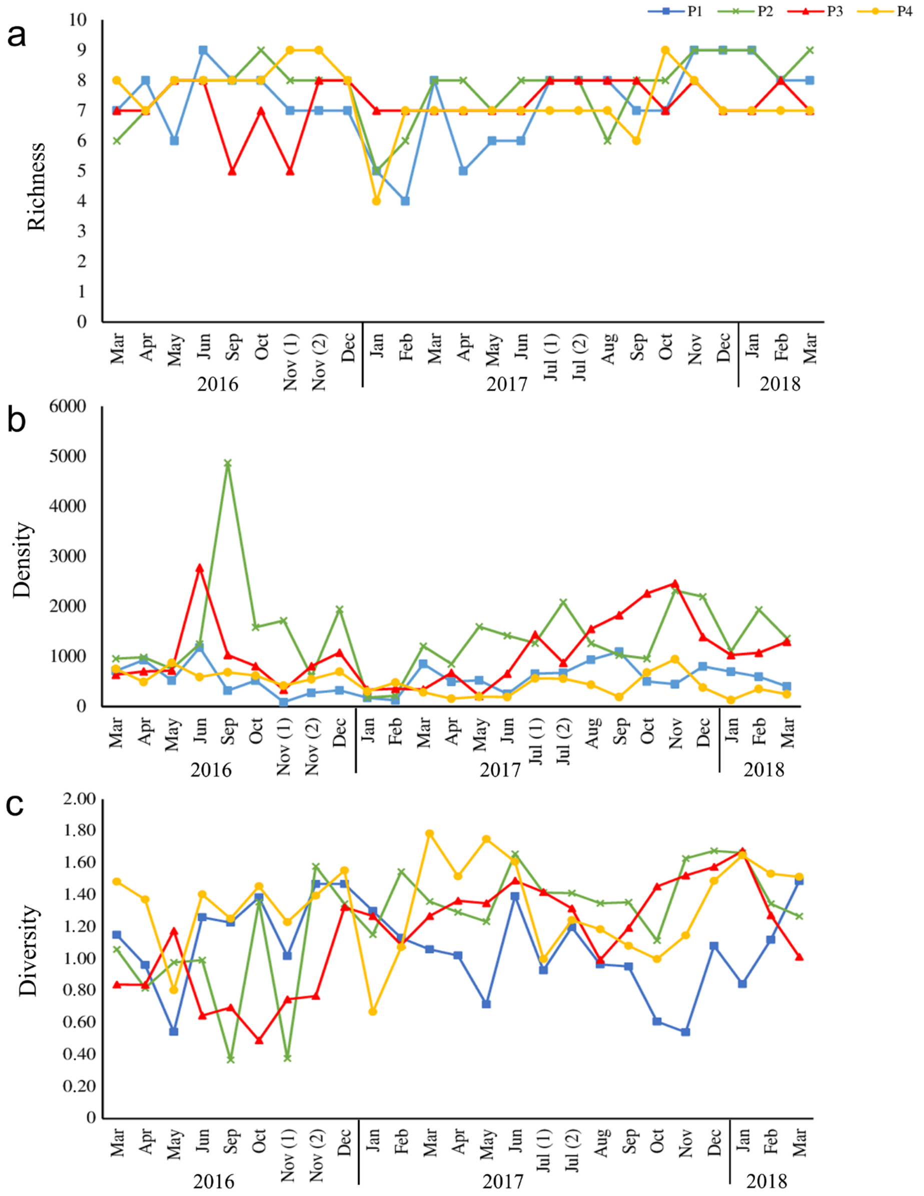

**Figure 3.** Temporal variation of total richness (a), mean density (b) and diversity (c) of the associated benthic macrofauna associated to *Mytilopsis leucophaeata* per sampling site, between March 2016–March 2018.

with this axis. *Melita mangrovi* was positively and highly correlated to RDA axis 2, and thus with increased values of pH and decreased values of temperature, contrasting with the opposite pattern found for *Amphibalanus* spp., and secondarily, *B. darwinianus* (Fig. 7). After controlling for possible autocorrelation effects, temporal patterns were weak and limited to few species, such as the apparently higher densities of *Amphibalanus* spp. and *B. darwinianus* between September-March of the second sampling year.

The Akaike information criterion (AIC) selected significant ($F \geq 7.25$; $p < 0.01$ for all) and negative linear responses for the densities of seven macrofauna benthic species with the unconstrained scores of the environmental axis 1 from RDA (Fig. 8a). However, the densities of Chironomidae larvae, *S. stanfordi*, and *Heleobia* sp. decreased more sharply with oxygen and

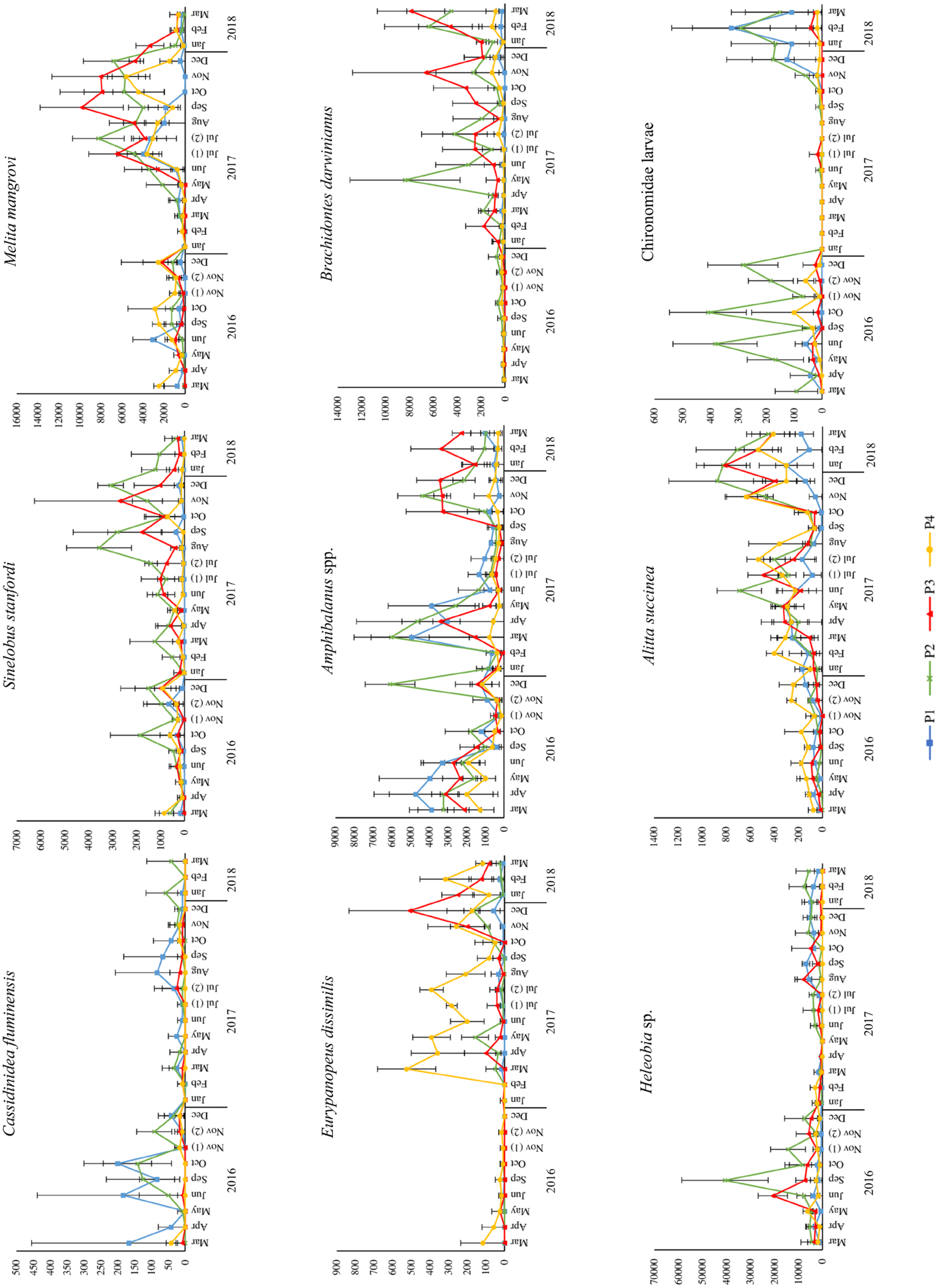

**Figure 4.** Temporal variation of the mean density (with standard deviation) for each species of the benthic macrofauna associated to *Mytilopsis leucophaeata* per sampling site, between March 2016–March 2018.

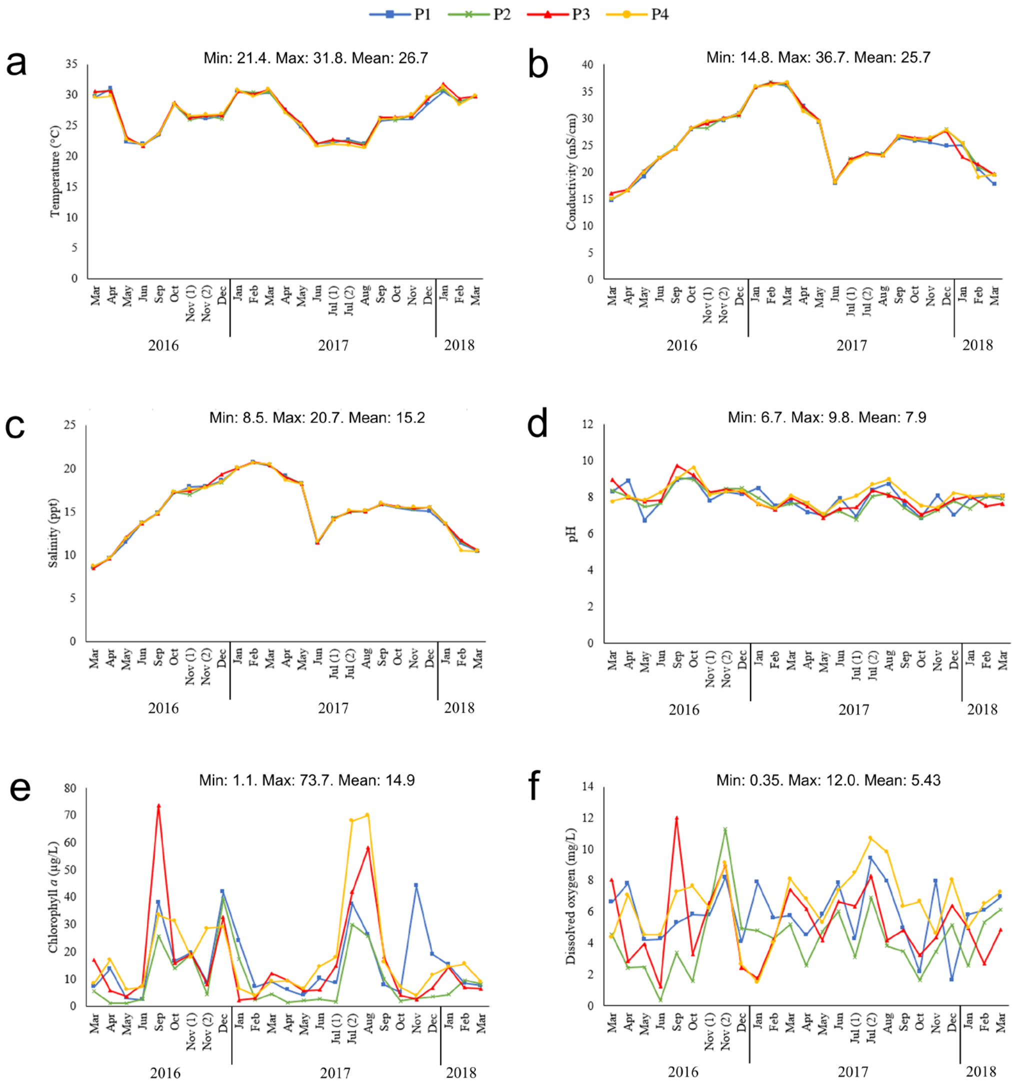

**Figure 5. Temporal variation of mean temperature (a), conductivity (b), salinity (c), pH (d), chlorophyll *a* (e) and dissolved oxygen (f) per sampling site, between March 2016–March 2018.**

salinity than *C. fluminensis*, and especially in relation to those of *Amphibalanus* spp. and *B. darwinianus*. AIC also selected significant (F ≥ 4.16; p < 0.04 for all) linear responses for the densities of six macrofauna benthic species with the unconstrained scores of the environmental axis 2 from RDA, but the patterns varied more with each species (Fig. 8b). The densities of *M. mangrovi*, *E. dissimilis*, and *S. stanfordi*, but particularly of the first two species, were positively associated with increased values of pH and decreased values of temperature. In contrast, the opposite pattern was found for the densities of Chironomidae larvae, *Amphibalanus* spp. and *B. darwinianus*, particularly for the first species.

## DISCUSSION

### Benthic macrofauna of the Rodrigo de Freitas Lagoon

Most knowledge on the benthic estuarine macrofauna in Brazil came from studies performed on the Southeastern and Southern regions (Neves & Valentin 2011, Bernardino et al. 2016). In Rio de Janeiro state, some studies

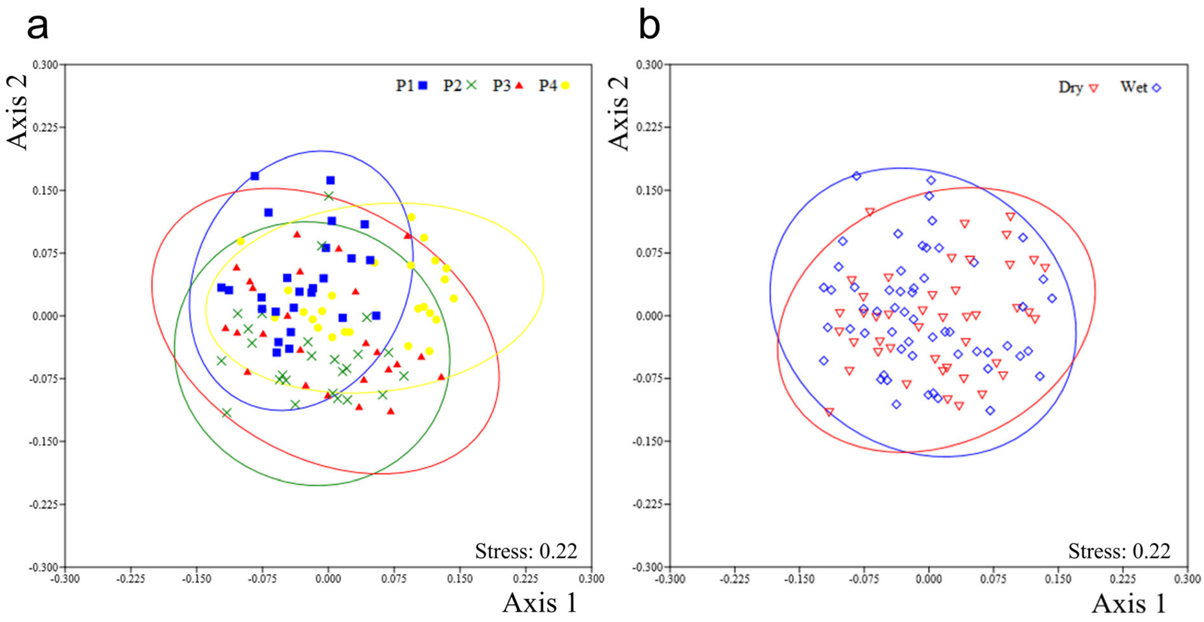

**Figure 6. nMDS of the mean density of species associated to *Mytilopsis leucophaeata* per sampling site (a) and per season (b).**

covered the Imboassica Lagoon (Callisto et al. 1998, Albertoni et al. 2001, Figueiredo-Barros et al. 2006, Henriques-de-Oliveira et al. 2007), Jaconé Lagoon (Mendes & Soares-Gomes 2011), Maricá Lagoon (Oliveira et al. 1955, M.A.K Dominguez, unpublished data *apud* Neves & Valentin 2011), Piratininga-Itaipu lagoon system (Oliveira 1948, Mendes & Soares-Gomes 2013), Marapendi Lagoon (L.V. Carvalheira, unpublished data) and Guanabara Bay (Santi & Tavares 2009, Echeverría et al. 2010, Soares-Gomes et al. 2012, 2016). However, except for a single study addressing benthic assemblages associated with patches of the algae *Chara* spp. (Albertoni et al. 2001), all other ones have targeted soft, unconsolidated, and structurally-simple substrata. Even though, some taxa found in our study, such as *C. fluminensis*, *A. succinea* and *Heleobia* sp. [the most common cited species in the literature is *Heleobia australis* (d'Orbigny, 1835)] were often listed by these studies.

Oliveira et al. (1957) is the single study that previously dealt with the macroinvertebrate fauna of the Rodrigo de Freitas Lagoon. They verified the occurrence of Chironomidae larvae, amphipods *Platorchestia platensis* (Krøyer, 1845), crabs *Neohelice granulata* (Dana, 1851), gastropods *Lymnaea* sp. and barnacles *Balanus* sp. and *Amphibalanus amphitrite* (Darwin, 1854) in this lagoon during a brief period of fish mortality. They sampled soft substrata and water in three sites (all close to the Piraquê Island), with salinity levels measuring 18–20 ppt. Gastropods were found in the soft substratum and in aquatic plants, and named *Lymnaea* sp.; however, *Lymnaea* species usually live in freshwater habitats (Stanisic 1998), and this identification was possibly incorrect [*Heleobia* sp., for example, also has a slight globose shell shape and small dimensions]. Oliveira et al. (1957) also found *P. platensis* in a site dominated by seagrasses, and *A. amphitrite* in an artificial substratum; none of these species (in addition to *N. granulata*) were found in association with *M. leucophaeata* in our study.

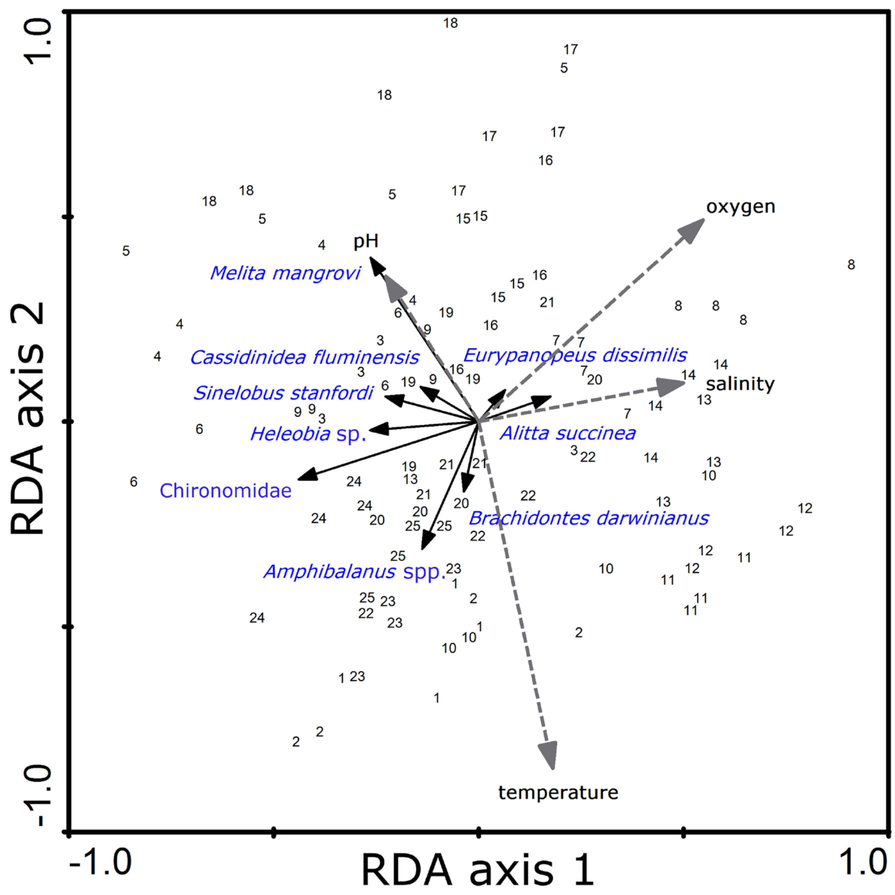

**Figure 7.** Ordinal diagram of the partial Redundancy Analysis (RDA) showing the relationship between the densities of the macrofauna benthic species associated to *Mytilopsis leucophaeata* and water quality variables. Samples were labelled by month, wherein number one represents the first sampling month (i.e. March 2016), and subsequently.

The composition and structure of the benthic community differed slightly among sites in Rodrigo de Freitas Lagoon, except between sites P2 and P3, which presented highest densities of the associated macrofauna especially due to population peaks of *Heleobia* sp. (influencing the similar composition of these two sites). High abundances of *Heleobia* sp. are possibly related to great accumulation of organic matter (Bemvenuti et al. 2003, 2005, Neves et al. 2011); conversely, dissolved oxygen levels were usually lower in sites P2 and P3 (Fig. 5).

The Rodrigo de Freitas Lagoon has an artificial system of floodgates, which are located near to sites P1 and P2, leading to a cyclical exchange of marine and fresh-water into the lagoon. The opening of the floodgates is usually related to periods of atypical rainstorms or when there is a need to renew the waters of the estuary (RIOÁGUAS 2013). Some water parameters (e.g., salinity and conductivity) seem to be more directly influenced by this man-made control system. Even though, the community composition was quite similar between dry and wet seasons.

Water temperature was inversely related to the density of the amphipod *M. mangrovi* in the Rodrigo de Freitas Lagoon, with maximum densities occurring during winter and spring (Fig. 4), whereas Bemvenuti (1987) *apud* L.G. Angonesi (unpublished data) found most specimens between autumn and winter in Patos Lagoon (southern Brazil). The density of *E. dissimilis* was also inversely related to temperature, in contrast to the supposed ideal temperature ranges of 21ºC–35ºC in a population of this crab

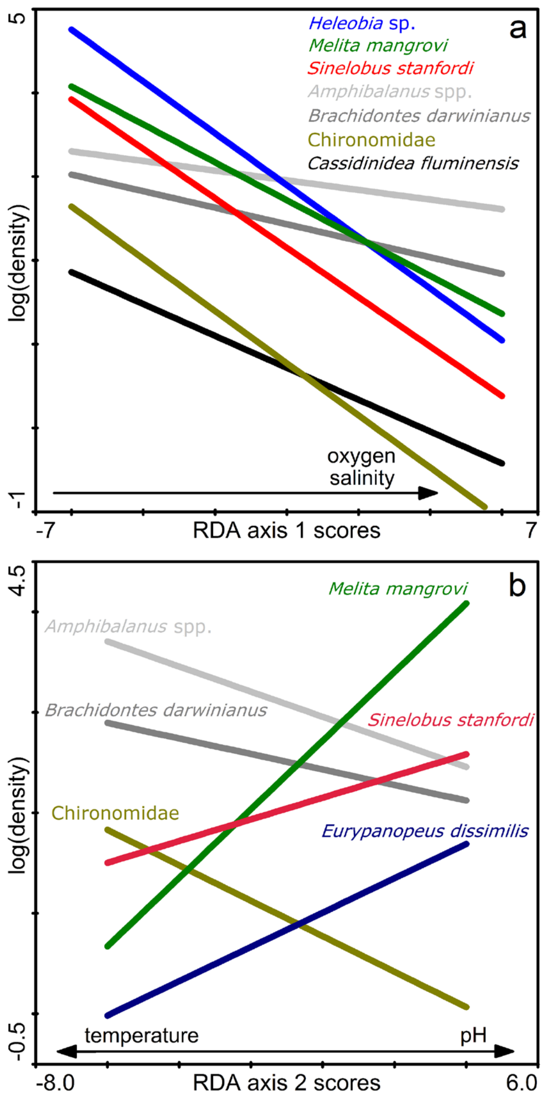

**Figure 8. Relationships of the densities of the macrofauna benthic species associated to *Mytilopsis leucophaeata* and the suite of the environmental variables retrieved from RDA axes one (a) and two (b). Lines represent the generalized linear model (GLM) selected by the AIC.**

from Florida, U.S.A. (Garcés 1987). In addition to *Heleobia* sp., reduced salinity and oxygen levels favored higher densities of Chironomidae larvae (Fig. 8a), a common trend for this group (Machado et al. 2015), which is also directly related to higher water temperatures (Fig. 8b). Salinity and oxygen levels were inversely related to the density of *S. stanfordi*, contrary to results obtained by N.M. Santos (unpublished data) in a population from Rio Grande do Sul (southern Brazil) and by Ambrosio et al. (2014) in Argentina. In relation to pH, the water of Rodrigo de Freitas Lagoon is usually alkaline (Fig. 5); slight changes in acidification may result in different behavioral and physiological responses between taxa (Courtney & Clements 1998), as observed in the varied relationships with this parameter (Fig. 8b). We also cannot ignore the effects of other constraints on species distribution, such as the concentration of recalcitrant and toxic pollutants in the water and substrate, the composition and spatial distribution of marginal habitats, possible interactions with other species, and synergetic effects.

## Possible impacts of *Mytilopsis leucophaeata* in the benthic macrofauna

Invasive bivalves, such as some species of Dreissenidae, may increase habitat availability and three-dimensionality and alter the trophic dynamics in the associated communities (Sousa et al. 2013), thus affecting native species. Great amount of feces and pseudofeces produced by invasive bivalves may lead to an enrichment of organic matter in the nearby sediments of the bivalve clusters, providing additional feeding resources for depositivorous species (Rodriguez 2006), such as the gastropod *Heleobia* sp. Species of *Heleobia* are able to inhabit diverse types of substrata (e.g., soft sediment, rocks, macrophytes), being also commonly found within bivalve clusters (Mansur et al. 2008). Crustaceans from Rodrigo de Freitas Lagoon might be favored from *M. leucophaeata* or *B. darwinianus* clusters, regarding that the increase of physical complexity may increase the availability of habitat and refuge against predators, also reducing the risk of desiccation and the effects of water turbulence (Palmer &

Ricciardi 2005, Borthagaray & Carranza 2007). *Melita mangrovi* and *C. fluminensis* are often found in macroalgae, feeding preferentially on macro and microalgae (*M. mangrovi*: L.G. Angonesi, unpublished data) or microalgae and detritus (*C. fluminensis*: Seeliger 2001). Clusters of *M. leucophaeata* might be used as substrata for the construction of tubes by *S. stanfordi*, due to the generally high retention level of suspended particles. Although this tanaidacean is usually associated with substrata colonized by macrophytes, it was also observed in clusters of a similar freshwater and invasive mussel *Limnoperna fortunei* (Dunker, 1857) (N.M. Santos, unpublished data, Spaccesi & Capítulo 2012). The usual epibiosis of *Amphibalanus* spp. over *M. leucophaeata* specimens may be related to a higher ecological fitness of barnacles over the invader (Buschbaum 2001), but demands further investigation. Crabs of the genus *Eurypanopeus* seem to be omnivorous, feeding on detritus, algae and a variety of animals, such as amphipods, polychaetes, oysters and mussels [data based on *Eurypanopeus depressus* (Smith, 1869) - Mcdonald 1982, O'Shaughnessy et al. 2014]. The robust increase of *E. dissimilis* in the second year of this study (Fig. 4) may be related to the concomitant increase of some prey(s) (e.g., *A. succinea*, $r = 0.47$, $r^2 = 0.22$, $p = 4.84E\text{-}08$). The nereidid *A. succinea* is favored by the shelter provided by *M. leucophaeata* clusters, as observed for other mobile polychaetes (Borthagaray & Carranza 2007).

The presence of *M. leucophaeata* in the Rodrigo de Freitas Lagoon enhances the availability of biogenic hard substrata to native species. The densities of most associated benthic species were not directly related to that of *M. leucophaeata*, possibly owing to particular species-specific recruitment periods of native macrofauna species, natural variations of abiotic variables and population peaks, and the combination of these factors. However, the lowest density values recorded for *M. leucophaeata* in our study were still high (Maia-Neto et al. 2020), and more robust analysis, particularly using bare hard substrata and sparser clusters of *M. leucophaeata*, should be performed to test the influence of this invasive bivalve on native species (Ricciardi et al. 1997, Sardiña et al. 2008).

The native estuarine bivalve *B. darwinianus* co-occurs with *M. leucophaeata* in the Rodrigo de Freitas Lagoon. In the first year of samplings, *B. darwinianus* was exclusively found in the core of *M. leucophaeata* clusters, being completely covered by the high densities of this invader. During the second year, a segregated distribution pattern was observed for these bivalves in sites P2 and P3, suggesting a possible spatial competition that should be better investigated by further studies. The increased densities of *B. darwinianus* in the second year were moderately or weakly related to high densities of *M. mangrovi* ($r = 0.36$, $r^2 = 0.13$, $p = 0.0001$), *S. stanfordi* ($r = 0.36$, $r^2 = 0.13$, $p = 0.0001$) and *A. succinea* ($r = 0.52$, $r^2 = 0.27$, $p = 2.66E\text{-}08$). In the Vistula Delta (Poland), *M. leucophaeata* has similar habitat requirements to two other bivalves, the native *Mytilus trossulus* (Gould, 1850) and the invasive *Dreissena polymorpha* (Pallas, 1771), possibly generating interspecific competition (Brzana et al. 2017). Similarly, in northeastern Brazil *M.* cf. *sallei* altered the distribution of the native *Mytella charruana* (d'Orbigny, 1842) in the estuary of the Capibaribe River, Pernambuco (Freitas-Galeão & Souza 2015) and probably competed with *M. charruana* in the estuary of the Paraíba River, Paraíba (Queiroz et al. 2020).

Some studies have dealt with the macroinvertebrate fauna associated to *Mytilopsis* species. Clusters of *M.* cf. *sallei* in Recife (Brazil) harbored 48 taxa, although most of these clusters were located in near-marine sites (G.M.R. Freitas, unpublished data), which probably affected the total amount of species. In the Yundang Lagoon (China), 28 taxa were associated to *M. sallei* in polyhaline sites, with decreased diversity levels in the benthic community after this invasion (Cai et al. 2014). Contrastingly, Magni et al. (2019) recorded higher species richness where *M. sallei* clusters were more abundant, at the same lagoon. *Mytilopsis sallei* apparently lead to a decrement of the macrofauna richness in the Visakhapatnam harbour (India) and competed intensively with *A. amphitrite* in Hong Kong (Morton 1981, 1989). Other barnacles were observed in association with *M. leucophaeata*, e.g., *A. eburneus* in the Caspian Sea (Heiler et al. 2010) and *A. improvisus* in The Netherlands and Poland (Van der Gaag et al. 1998, Brzana et al. 2017). In New Haven, Connecticut (U.S.A.), 10 taxa were associated to *M. leucophaeata* clusters (Richardson & Hammond 2016). All those studies show that clusters of dreissenids can harbor some variety of species, because the associated fauna may take advantage of the new formed habitats and promptly colonizes them. Therefore, the benthic species found in *M. leucophaeata* clusters in the Rodrigo de Freitas Lagoon are found in other substrata, but probably expanded their local distributions after this invasion.

Studies about the interactions between invasive and native species are essential for the comprehension of the impacts caused by invasions. This is the case of the apparent competition between *M. leucophaeata* and *B. darwinianus* in the Rodrigo de Freitas Lagoon. The anthropic pressure in this coastal lagoon may be a major cause for the well-succeeded invasion of that bivalve, because disturbed sites are usually simplified and often have low species richness. A regular monitoring program along estuarine sites in Rio de Janeiro coast is essential to identify possible new records of *M. leucophaeata* and thus limit the spread of this invader. Studies of the native benthic macrofauna, particularly those obtained from sites prior to the invasion of *M. leucophaeata*, are therefore crucial to assess the impacts of this invader over native species and ecosystem.

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M.R. Fernandes, I.C. Miyahira and C.H.S. Caetano designed the work. Data acquisition and laboratory procedures were conducted by A.J.S. Rodrigues, M.R. Fernandes, I.C. Miyahira and C.H.S. Caetano. Statistical procedures were performed by L.N. Santos and I.C. Miyahira. The original draft of the manuscript was written by A.J.S. Rodrigues and M.R. Fernandes. All authors considerably improved the manuscript and approved the final version.