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ORIGINAL PAPER

# Wide tolerance to environmental conditions and substrate colonization mediates the invasion of false mussels (Bivalvia: Dreissenidae) in brackish systems

**Antonio J. S. Rodrigues · Igor C. Miyahira · Nathália Rodrigues · Danielle Ribeiro · Luciano N. Santos · Raquel A. F. Neves**

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**Abstract** False mussels are recognized as the brackish water equivalent of zebra mussels, although the abiotic and habitat conditions that mediate these invaders' success are barely known. In this context, we aimed to evaluate the native and non-native geographical distribution of *Mytilopsis* species worldwide and assess biological traits, environmental condition, and habitat associated with false mussels in native and invaded systems. Our hypothesis is that *Mytilopsis* invasion is driven by species tolerance to environmental conditions and substrate use in brackish systems, where the colonization of non-native populations is favored by great availability of artificial substrates and tolerance to wide ranges of environmental conditions. In addition, this study provides the range and distribution patterns of *Mytilopsis* species within their introduced and native areas and documents the spread of introduced populations worldwide. Considering the five species evaluated, *M. leucophaeata* and *M. sallei* are the most widespread, while *M. adamsi*, *M. trautwineana,* and *M. africana* showed more restricted geographic distribution. In the last decades, *M. leucophaeata* and *M. sallei* consolidated and expanded their distributions. Environmental conditions were significantly different between native and non-native areas, where *Mytilopsis* populations presented significantly higher densities. Non-native populations exhibited remarkable

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A. J. S. Rodrigues · I. C. Miyahira (✉) · N. Rodrigues ·
L. N. Santos · R. A. F. Neves
Graduate Program in Neotropical Biodiversity, Institute of Biosciences, Federal University of the State of Rio de Janeiro (UNIRIO), Avenida Pasteur, 458 - 502, Urca, Rio de Janeiro CEP: 22.290-240, Brazil
e-mail: igor.c.miyahira@unirio.br

A. J. S. Rodrigues
e-mail: antoniojdesrodrigues@gmail.com

N. Rodrigues
e-mail: nathalia.silva@edu.unirio.br

L. N. Santos
e-mail: luciano.santos@unirio.br

R. A. F. Neves
e-mail: raquel.neves@unirio.br

A. J. S. Rodrigues · I. C. Miyahira · N. Rodrigues ·
D. Ribeiro · R. A. F. Neves
Research Group of Experimental and Applied Aquatic Ecology, Federal University of the State of Rio de Janeiro (UNIRIO), Avenida Pasteur, 458 - 307, Urca, Rio de Janeiro CEP: 22.290-240, Brazil
e-mail: danielle.ribeiro1920@edu.unirio.br

L. N. Santos
Laboratory of Theoretical and Applied Ichthyology, Institute of Biosciences, Federal University of the State of Rio de Janeiro (UNIRIO), Avenida Pasteur, 458 - 314A, Urca, Rio de Janeiro CEP: 22.290-240, Brazil

plasticity concerning habitat colonization that was more frequent on artificial substrata. *Mytilopsis* populations presented significant differences in their biological traits, habitat environmental conditions, and substrate use between native and non-native areas. These species seem to adapt to the conditions of invaded systems, changing their preferences, which may reflect plasticity and a potential shift of their realized niches.

**Keywords** *Mytilopsis leucophaeata* · *Mytilopsis sallei* · Invasive species · Biofouling · Environmental conditions

## Introduction

In the last decades, the globalization process has increased the number of biological invasions in marine and brackish environments (Paavola et al. 2005; Hulme 2009; Seebens et al. 2013; Anil and Krishnamurthy 2018; Teixeira and Creed 2020). Currently, the main routes for the dispersal of invasive marine species encompass ports located in the United States of America, Europe, and East Asia, resulting in impacts where these species are introduced (Ruiz et al. 1997; Kaluza et al. 2010; Ojaveer et al. 2018). The most common impact of invasive species is the loss of native biodiversity induced by new-established interactions with the receiving community (e.g. competition, predation), leading to changes in the structure of ecosystems and also possibly modifying their physical and chemical features (Anil 2006; Kalchev et al. 2013; Ojaveer et al. 2018; Neves et al. 2020).

False mussels (Dreissenidae) are among the most notable fresh- and brackish water invaders, including *Dreissena polymorpha* (Pallas 1771), *Dreissena rostriformis bugensis* Andrusov, 1897, *Mytilopsis leucophaeata* (Conrad 1831), and *Mytilopsis sallei* (Récluz 1849) (e.g. Vanderploeg et al. 2002; Verween et al. 2010; McLaughlan et al. 2014; Geda et al. 2018). Members of *Dreissena* and *Mytilopsis* possess a free-swimming larva that allows their dispersal over long distances through ballast water, probably the main vector of their dispersion into new aquatic systems (Chu et al. 1997; Van der Velde et al. 2010; Teixeira and Creed 2020). Moreover, adults attached to hulls can be an important local dispersal agent, carrying reproducing adults to new environments (Minchin et al. 2003; Farrapeira et al. 2007; Richardson and Hammond 2016). The high rates of vessel traffic increase the chance of new introductions of dreissenid species, as evidenced by frequent records of invasions in new geographical locations (Brzana et al. 2017; Zhulidov et al. 2018).

The colonization of invasive dreissenid mussels can drastically alter the functioning of a newly invaded ecosystem, causing economic and ecological problems (e.g. Burlakova et al. 2000; Ward and Ricciardi 2007; Verween et al. 2010; Therriault et al. 2013; Cai et al. 2014). The major ecological consequences include the collapse of native mussel populations (e.g. through space and food competition, and overgrowth), reductions in phytoplankton biomass and changes in water transparency through water filtration, and physical changes in the benthic substrates through biofouling (reviewed in Vanderploeg et al. 2002; Neves et al. 2020). Moreover, dreissenid colonization has implications for the nutrient dynamics in aquatic systems through the removal of nutrients by filtration but also recycling nutrients by mussel excretion, mainly dissolved phosphorus and nitrogen (Arnott and Vanni 1996; James et al. 2001; Conroy et al. 2005; Naddafi et al. 2008). The changes in nutrient dynamics and water transparency can be a trigger to excessive growth of benthic macroalga and macrophytes (Hecky et al. 2004; Wilson et al. 2006; Ozersky et al. 2009). Despite the widely known negative effects, some apparent beneficial impacts, as an improvement in water transparency, have been also described after the dreissenid invasion (Graczyk et al. 2004; Higgins and Vander-Zanden 2010; McLaughlan and Aldridge 2013; Neves et al. 2020).

Most of the dreissenid studies are focused on the impacts of zebra mussels (*D. polymorpha*), and its congener the quagga mussel (*D. rostriformis bugensis*), in North American lakes and rivers, especially the Laurentian Great Lakes (e.g. Idrisi et al. 2001; reviewed in Vanderploeg et al. 2002; Strayer et al. 2004; Fahnenstiel et al. 2010; Kelly et al. 2010). Invasive dreissenid mussels often filter large volumes of water (e.g. Horgan and Mills 1997; Baldwin et al. 2002; Vanderploeg et al. 2010) and attach to a variety of natural and artificial hard substrata using byssal threads, reaching high densities in invaded areas (Ricciardi et al. 1997; Sousa et al. 2009; Kennedy 2011; Rizzo et al. 2014; Tan and Tay 2018). Dreissenid mussels may also tolerate wide ranges of temperature and salinity (Rajagopal et al. 2005; Verween et al. 2007, 2010; Van der Gaag et al., 2016), which makes them successful aquatic invasive species.

*Mytilopsis* is known as a brackish water equivalent of zebra mussels (Verween et al. 2010), although the optimal abiotic conditions of *Mytilopsis* species and detailed aspects of its invasive process are barely known. The taxonomy of the genus *Mytilopsis* is not well solved, but five recent species are generally recognized (Marelli and Gray 1983, 1985; Nutall 1990a, b; Kennedy 2011): *M. leucophaeata*, *M. sallei*, *Mytilopsis adamsi* Morrison, 1946, *Mytilopsis trautwineana* (Tryon 1866), and *Mytilopsis africana* (Van Beneden 1835). The first four species are known as "invasive species" (e.g. Marelli and Gray 1983; Tan and Morton 2006; Aldridge et al. 2008; Rizzo et al. 2014; Fernandes et al. 2018; Wangkulangkul 2018), and *M. africana* (described upon specimens from African coast) is considered by some authors as a synonymy of *M. sallei*, that was possibly historically introduced into Africa (Morton 1981; Nuttall 1990a, b; Le Loeuff 1999). Regarding the scarcity of ecological information on *Mytilopsis* species within their invaded systems (e.g. Neves et al. 2020; Fernandes et al. 2020; Rodrigues et al. 2021), tracking of environmental and ecological impacts caused by *Mytilopsis* colonization is virtually impossible.

In this context, the present study aims to evaluate the native and non-native geographical distribution of *Mytilopsis* species worldwide and assess biological traits, environmental conditions, and habitat use associated with native and non-native populations of false mussels. More specifically, our goal was i) characterize the abiotic conditions (i.e. physical and chemical variables: salinity, temperature, chlorophyll *a*, dissolved oxygen and transparency) in native and non-native areas, ii) identify and distinguish the environmental conditions and biological traits (such as size, density and biomass) among native and non-native *Mytilopsis* populations, iii) test for differences in the use of substrates for colonization by native and non-native *Mytilopsis* populations, and iv) identify the main sessile epibenthic taxa that co-occur with *Mytilopsis* species. For that, literature data focusing on the geographical occurrence of five extant *Mytilopsis* species (*M. leucophaeata*, *M. sallei*, *M. adamsi*, *M. trautwineana* and *M. africana*) was compiled within their native and invaded brackish systems simultaneously to other biological data (e.g. density and individual size of *Mytilopsis* species, and the occurrence of other sessile epibenthic taxa). The main hypothesis is that *Mytilopsis* invasion is driven by species tolerance to environmental conditions and substrate use in brackish systems, where the colonization of these bivalves is favored by the great availability of artificial substrates and species tolerance to wide ranges of environmental conditions. Besides the disclosure of ecological aspects of these invasive mussels, we describe the range and distribution patterns of *Mytilopsis* species within their native and non-native regions and document the spread of introduced populations around the world.

## Material and methods

### Species selection and data acquisition

Because the specific taxonomy of *Mytilopsis* is inconclusive, we accepted the identifications provided by the author of each work. An electronic survey was performed to compile all published data from the Google Scholar (https://scholar.google.com.br/) database for the five recognized species of the genus using the following keywords: "*Mytilopsis* sp." AND "distribution" OR "occurrence", where the "sp." was replaced by the specific epithet, i.e., *leucophaeata, sallei*, *adamsi, trautwineana,* and *africana*. The search included scientific articles, book chapters, and grey literature (e.g. technical reports and theses). Moreover, references that were cited in retrieved studies for occurrence data not detected in the first survey were also evaluated. Our database included all the retrieved studies that provided geographic records for the assessed *Mytilopsis* species. In seven localities, the false mussel was identified as *M.* cf. *sallei* (see Fernandes et al. 2018 for further information) and considered together with those of *M. sallei* for the purposes of this analysis.

For each study, available data were compiled on the occurrence sites, *Mytilopsis* species (according to author identification), geographical coordinates, population density and biomass, shell length of individuals, the substrate used for attachment, and the presence and identification of co-occurring benthic species. The type of substrate used by false mussel populations was divided into eleven categories: existing benthic fauna (i.e. other fouling animals), mangrove roots, other aquatic or emergent vegetation, rocky substrates, soft substrates where settlement began on a hard object (see Fernandes et al. 2020), human-created concrete structures (e.g. piers, marinas, and others), metals structures, plastic materials (including other petroleum products, such as Styrofoam), vessels, wood fragments (usually experimental plates, with human treatment, not natural), and ropes and meshes (e.g. mooring ropes, fish cages).

A habitat characterization was also performed for each occurrence site (georeferenced) by compiling physical and chemical data from the available literature. For each brackish system where *Mytilopsis* spp. was recorded, data were obtained of area (km$^2$), and mean, minimum, and maximum values of five variables, viz. (1) surface water salinity, (2) surface water temperature (°C), (3) chlorophyll *a* in surface water (mg L$^{-1}$), (4) dissolved oxygen in surface water (mg L$^{-1}$), and (5) water transparency (cm). When abiotic data was not available in the reviewed papers, additional literature searches were performed for the georeferenced localities to obtain all the environmental data. For that, electronic surveys were performed in the Google Scholar (https://scholar.google.com.br/) database applying a combination of keywords with the aquatic system name and the abiotic variable of interest (e.g. "Rodrigo de Freitas Lagoon" AND "water transparency").

### Data analysis

The densities of *Mytilopsis* were plotted on a distribution map, using 1 as density value for the records without a density value. Considering species record limitations for the other three species of the genus, only the occurrence data of *M. leucophaeata* and *M. sallei* were plotted on the distribution map.

A Principal Component Analysis (PCA) was performed on the abiotic matrix to assess the relationship among environmental variables and how they were associated with the native and non-native sites in which *Mytilopsis* species were recorded. A Hellinger transformation was used to control for the different scaling measures and unities among variables, and the broken-stick model was applied to select which principal components were significant for explaining sample distribution. PCA was performed using the PC-ORD v 6.0 software. A Canonical Analyses of Principal Coordinates (CAP) were performed to test for differences in environmental conditions and substrate types among native and non-native populations of *Mytilopsis* species. Hellinger distance and 9,999 permutations were applied in CAP, following Anderson and Willis (2003). Finally, Generalized Additive Models (GAMs) were applied to assess the smooth terms of the pairwise relationships between biological descriptors (log10-transformed density and shell-length of *Mytilopsis* species) and the environmental variables which could affect the distribution of false dark mussels. GAMs are an extension of generalized linear models that, unlike more conventional regression methods, do not assume a functional relationship between the response variable and the predictors (Lepš and Šmilauer 2003). Model complexity of GAMs was chosen by the stepwise selection procedure using the Akaike Information Criterion (AICc) corrected for small sampling size ($N \leq 30$), and normal data distribution and identity as linkage function were chosen to broaden the selection of either linear as non-linear responses. GAMs were performed using the software CANOCO 4.5.

Considering data limitation for the five species distinguished, statistical analyses were applied for the genus *Mytilopsis* (all species together), but considering the difference in geographical distribution, i.e., native and non-native populations. Student t-test was applied to test for differences in the density of native and non-native *Mytilopsis* populations (without addressing differences for each species separately), to test for differences in shell length between *M. leucophaeata* and *M. sallei* (the two most widespread species), and to test for differences in the proportion of occurring taxa with *Mytilopsis* populations in native and non-native areas.

## Results

### Geographic distribution of *Mytilopsis* species

In total, 158 occurrences of *Mytilopsis* species were obtained from the literature survey ($n = 50$ for native and $n = 108$ for introduced areas). *Mytilopsis* records by specific locality are fully presented in Supplementary Material S1. Among the five *Mytilopsis* species, *M. leucophaeata* and *M. sallei* are most widespread, while *M. adamsi*, *M. trautwineana,* and *M. africana* were reported to be geographically more restricted in distribution. *Mytilopsis adamsi* were reported in few localities on its historical native range, while its introduced range varied from North America (Mexico) to the south of Africa (Mauritius), and Asia (Philippines and Thailand), with an overall latitudinal variation from 23°N to 20°S (*n* = 11 locations). *Mytilopsis trautwineana* (*n* = 3 locations) was reported as associated with shrimp farms in Cartagena, Colombia, a non-native area for this species, despite other unprecise records, as a generically mention for to the eastern Pacific coast of Colombia and Ecuador (Aldridge et al. 2008), within its native area. *Mytilopsis africana* were generically reported to the west coast of Africa, from Ivory Coast to Gabon, from 5°N to 0°, on the native range (Le Loeuff 1999).

The native range of *M. leucophaeata* has been reported as brackish systems in the Chesapeake Bay (USA) and Gulf of Mexico (latitudinal variation from 39°N to 18°N), while its invaded range extends from South America (Brazil), Eurasia (from Spain to Iran), and north of Africa, following a latitudinal variation from 60°N to 23°S (Fig. 1; *n* = 88 occurrence records). The longitudinal range was from 96°W to 76°W for its native range, and from 74°W to 49°E for invaded range. The native range of *M. sallei* has been reported as portions of the Gulf of Mexico, Caribbean Islands, and the North of South America, with a latitudinal variation from 28°N to 10°N. However, its invaded range included the North of Africa (Egypt), Asia (from India to Japan), Oceania (Australia), and Pacific Islands (Fiji), following a latitudinal range from 35°N to 18°S (Fig. 1; *n* = 46 occurrence records). The longitudinal variation was from 88 to 61 W, and the introduced range was almost all the globe around, from 30E to 34 W (considering the records for *M.* cf. *sallei*, *n* = 7).

## Habitat environmental conditions in native and non-native areas

Characterization of environmental conditions associated with the native and non-native geographical distribution range of *Mytilopsis* species is presented as Supplementary Material S2. The multivariate analysis (PCA) applied on the environmental dataset (i.e. latitude, longitude, water temperature, dissolved oxygen, chlorophyll *a*, salinity, and transparency) evidenced preferential conditions for native and non-native *Mytilopsis* populations (Fig. 2). The first two PCA axes were selected by broken-stick

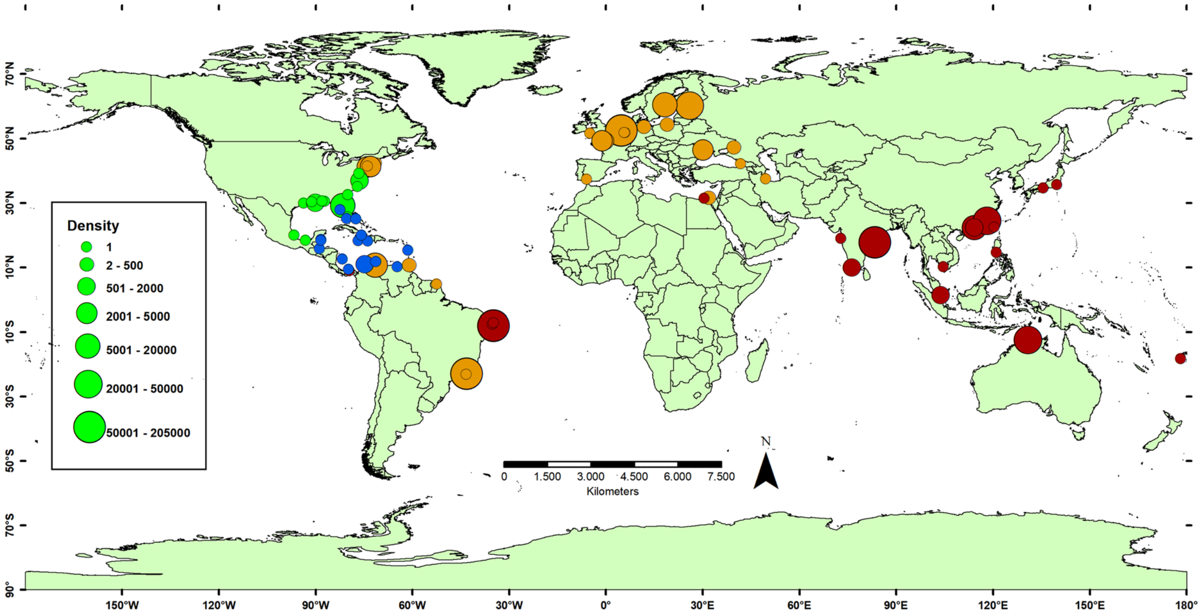

**Fig. 1** World map indicating the distributions of *Mytilopsis leucophaeata* (*n* = 88) and *M. sallei* (*n* = 53, including *M.* cf. *sallei*) in native (green and blue circles, respectively) and non-native (orange and red circles, respectively) areas. Differences in population density are expressed by distinct circle sizes

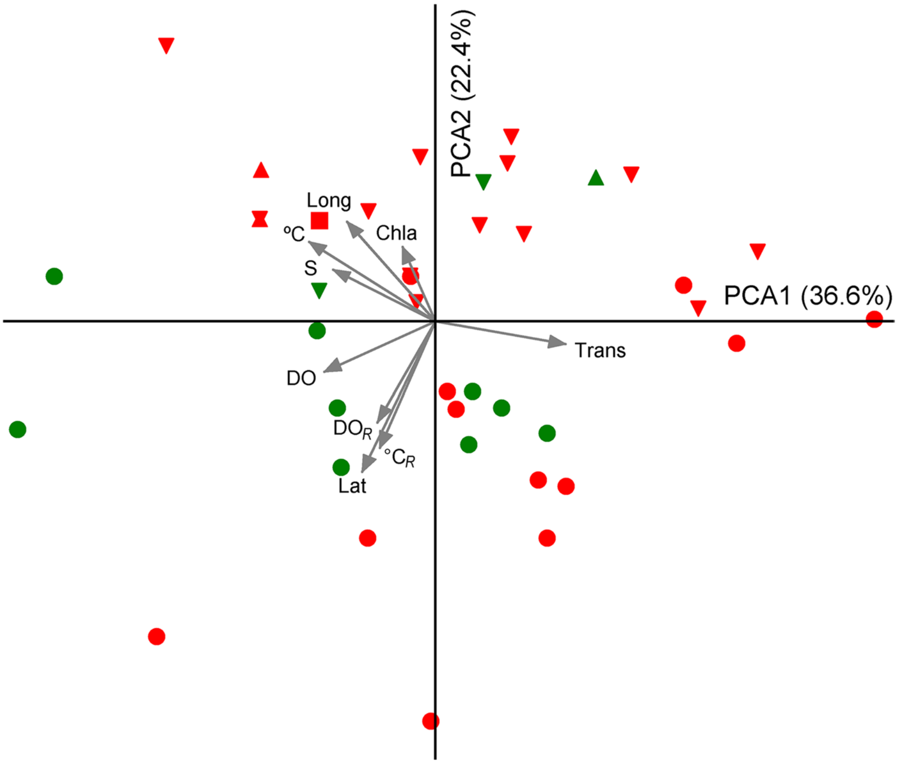

**Fig. 2** PCA biplot ordination diagram of environmental conditions for *Mytilopsis* species within its native (green color) and non-native (red color) geographical range of distribution. Environmental dataset of geographical distribution of four *Mytilopsis* species were considered: *M. leucophaeata* (●), *M. sallei* (▼), *M. adamsi* (▲), and *M. trautwineana* (■). Environmental variables analyzed were: latitude (Lat), longitude (Long), water temperature (°C), salinity (S), chlorophyll *a* (Chla), dissolved oxygen (DO), and transparency (Trans). Values of data range (i.e. maximum-minimum values) were only used for temperature and dissolved oxygen since no significant correlation was found between mean and range data (Pearson *p*-value > 0.05)

(BS) method, with axis 1 and 2 explaining, respectively 36.6% (BS eigenvalue = 2.829) and 22.4% (BS eigenvalue = 1.829) of total variance. PCA axis 1 accounted for most of the differences between native and non-native geographical locations. Most of the samples from non-native populations (i.e. red color in Fig. 2) were located at the right side of the biplot and correlated with high values of water transparency (r = 0.856). This difference in environmental conditions between samples from native and non-native systems was overall supported by canonical analysis of principal coordinates (CAP trace statistics, $p = 0.035$). Moreover, PCA axis 2 accounted for the sample's separation among *Mytilopsis* species. Most of the samples from *M. leucophaeata* distribution were located at the lower side of biplot and correlated with higher values of dissolved oxygen, both for mean (r = − 0.260) and range (r = − 0.520) values, latitude (r = − 0.774) and temperature range (r = − 0.649); while samples from the other three *Mytilopsis* species (i.e. *M. sallei*, *M. adamsi*, and *M. trautwineana*) were exclusively located at the upper side of biplot and correlated with higher values of salinity (r = 0.269), mean temperature (r = 0.407), longitude (r = 0.513), and chlorophyll *a* (r = 0.383). These differences in the environmental conditions between samples of *M. leucophaeata* distribution and samples from the other *Mytilopsis* species were statistically significant (CAP trace statistics, $p < 0.0001$).

## Populational traits of *Mytilopsis* within native and introduced systems

The maximum values found for the populational traits (i.e. density and shell length) of *Mytilopsis* species are presented in Table 1. Moreover, all the compiled values (mean, minimum and maximum) of population traits for four *Mytilopsis* species (except by *M. africana* for which no data was found) are presented in Supplementary Material S1.

**Table 1** Maximum values of density and individual size (shell length) found for *Mytilopsis* species on native (N) and introduced (I) areas

| Species | Density (ind. m$^{-2}$) | | Size (mm) | |
|---|---|---|---|---|
| | N | I | N | I |
| *M. leucophaeata* | 14,150 | 204,000 | 22.0 | 31.7 |
| *M. sallei* | 900 | 83,000 | 25.6 | 35.0 |
| *M. adamsi* | – | 569,000 | – | 32.0 |
| *M. trautwineana* | – | – | – | 24.0 |

No information was found for *M. africana*. A fully detailed compilation of populational traits is shown in Supplementary Material S1

(–) No data available

The density of *Mytilopsis* species in introduced aquatic systems was significantly higher than in native ones (Table 1; t-test, $p=0.012$). Significant relationships between the density of native and invasive populations and environmental data were only found for two variables: values of longitude (Linear AIC = 44.26; F = 8.11, $p<0.01$) and temperature range (Non-linear AIC = 47.88; F = 6.56, $p=0.017$) (Fig. 3). A non-linear model for *Mytilopsis* density in relation to the range in water temperature was selected by AIC, where invasive populations (red color) showed higher densities, but was more restricted to a lower temperature range (i.e. lower variation), with a tendency to decrease after a range of 15 °C (Fig. 3b). A linear model was chosen by AIC

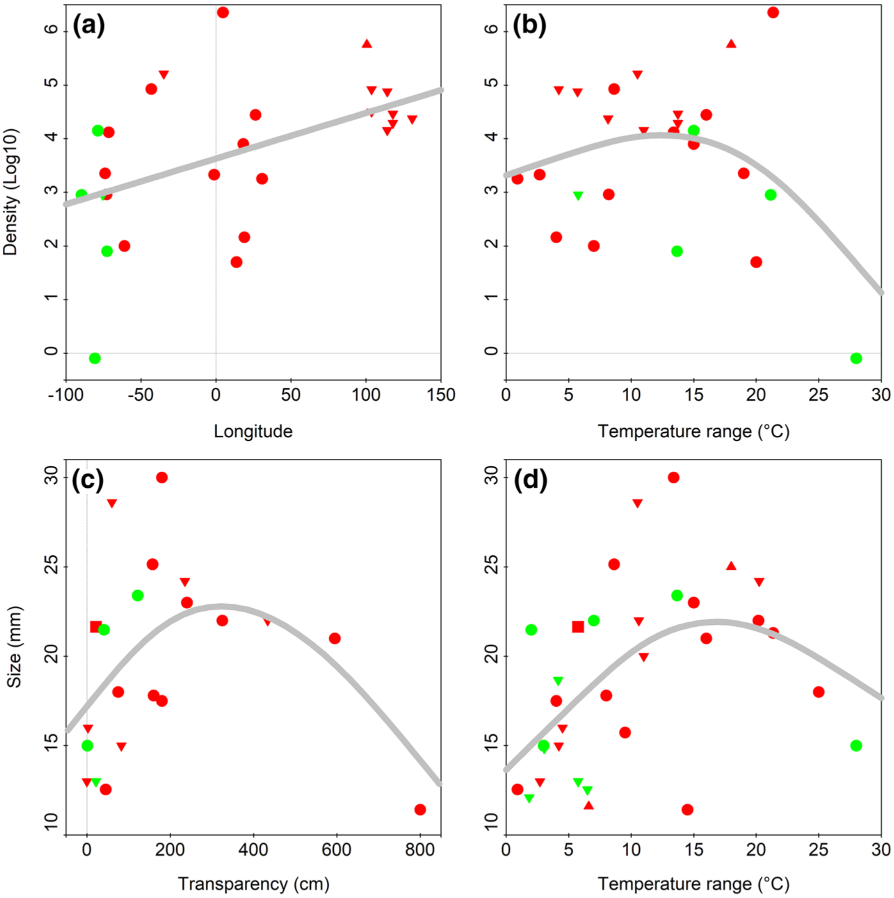

**Fig. 3** Generalized Additive Models (GAMs) selected for Akaike Information Criterion (AIC) for biological traits of invasive (red color) and native (green color) *Mytilopsis* populations to environmental variables. Relationships of the population density (Log$_{10}$-transformed) to longitude of georeferenced species distribution (a) and temperature range (°C; b); and of the false mussel size (in shell length, mm) to water transparency (c) and temperature range (d) were presented. Samples were coded by species: *M. leucophaeata* (●), *M. sallei* (▼), *M. adamsi* (▲), and *M. trautwineana* (■)

for *Mytilopsis* species density in relation to the longitude of the sampling site, where *M. leucophaeata* was more restricted to lower longitudinal areas and lower density within its native range and extended its longitudinal distribution and density on the introduced range (Fig. 3a). In contrast, the distribution of *M. sallei* was more restricted to higher longitudinal areas, where this species is invasive, with higher densities (Fig. 3a). Independently of the distribution range, populations of *M. sallei* showed significantly higher densities than *M. leucophaeata* (t-test, $p = 0.025$).

No significant difference was found for false mussel size (in shell length) between the most widespread species, *M. leucophaeata* and *M. sallei* (t-test, $p = 0.207$). However, significant relationships (GAMs) between size and environmental data were found for two variables: water transparency range (Non-linear AIC = 480.18; F = 9.87, $p < 0.01$) and temperature range (Non-linear AIC = 641.34; F = 8.75, $p < 0.01$) (Fig. 3). A unimodal response was found for the relationship of mussel size and with the range of temperature (Fig. 3d) and transparency (Fig. 3c), in which a maximum shell length was reached close to 15 °C of temperature variation and 200 cm of water transparency, and then decreasing towards higher temperature range (i.e. broader variation) and water transparency.

### Taxa co-occurring with native and invasive populations of *Mytilopsis* spp.

Information on the epibenthic taxa that co-occur with *Mytilopsis* populations in native and invaded systems was restricted to four species: *M. adamsi* ($n = 3$), *M. leucophaeata* ($n = 25$), *M. sallei* ($n = 30$), and *M. trautwineana* ($n = 1$). No information about co-occurring species with *M. africana* was found in the literature. A significant difference was found in the proportion of epibenthic taxa that co-occur with *Mytilopsis* populations between native and invaded areas (t-test, $p < 0.0001$). *Mytilopsis* has been recorded occurring with the greatest variety of epibenthic taxa in non-native areas. Seventeen epibenthic groups of ten different phyla were found to co-occur with *Mytilopsis* populations (Fig. 4), in which four groups have co-occurred exclusively with non-native false mussels (Nematoda, Nemertea, Platyhelminthes and Porifera). Bivalvia was the most frequent taxa associated with *Mytilopsis* populations, regardless of the origin of the false mussel populations (i.e. native or non-native) and considering all the co-occurring groups, followed by Gastropoda for native populations and Cirripedia for non-native ones (Fig. 4).

### Substrate colonization by native and non-native *Mytilopsis* populations

Non-native *Mytilopsis* populations colonized a wider variety of substrates, including the artificial ones, in their invaded systems compared to individuals within

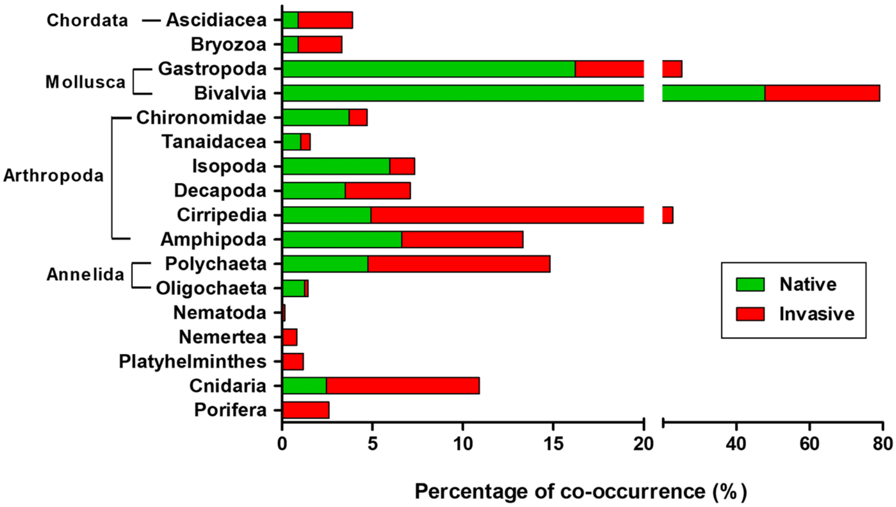

**Fig. 4** Percentage of occurrence of epibenthic taxa with native (green bar, $n = 16$) and invasive (red bar, $n = 43$) populations of *Mytilopsis* in brackish systems. Data are shown as the mean percentage of taxa occurrence

their native geographical distribution (Fig. 5). In the native area, *M. leucophaeata* was found mainly on soft sediment samples (42%), over benthic fauna (31%), and rocks (17%); while in the invaded systems, the most colonized substrates were human constructions (28%), rocks (24%), and plastic materials (13%). In the native range, *M. sallei* was found attached on mangrove roots (56%), rocks (19%), and sediment samples (19%); whereas in the non-native areas, the species occurred mainly on human constructions (35%), wood fragments (13%), and plastic materials (12%). No information regarding substrate colonization was found for *M. adamsi* within its native occurrence, but the species was mostly found attached to plastic materials (34%) within invaded systems. No information about substrate occurrence was found for *M. africana* and only two records for *M.trautwineana*, thus not displayed in Fig. 5.

A significant difference in the colonization of natural and artificial substrates was found between native and non-native populations of *Mytilopsis* (CAP trace statistics, $p < 0.001$; Fig. 6). Non-native populations of *Mytilopsis* used significantly more artificial substrates for colonization in introduced areas. Most samples of substrate colonization within the invaded systems (red color) were located at the left side of CAP axis 1 and highly correlated with artificial substrates: human construction (r = − 0.64), rope and mesh netting (r = − 0.48), plastic material (r = − 0.47), and vessels (r = − 0.37). However, most samples of substrate colonization within the *Mytilopsis* native systems (green color) were located at the right side of CAP axis 1 and highly correlated with natural substrates: soft sediments (r = 0.47) and benthic fauna (r = 0.26).

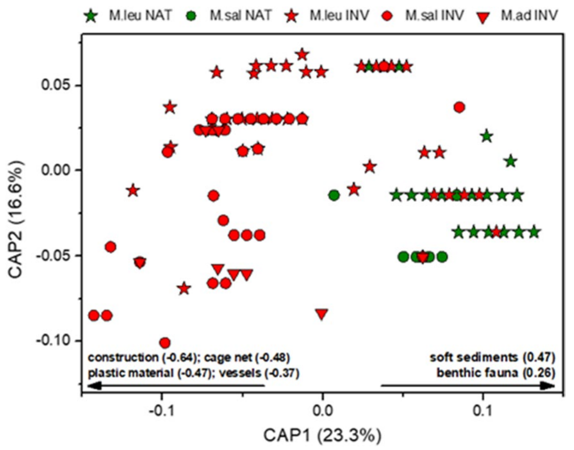

**Fig. 6** Biplot ordination diagram (CAP) of substrate colonization within the *Mytilopsis* native (green color, $n = 31$) and invaded (red color, $n = 72$) systems. Samples were categorized by species: *M. leucophaeata* (M.leu, star symbol), *M. sallei* (M.sal, circle symbol), and *M. adamsi* (M.ad, down triangle symbol)

## Discussion

This study evaluated the worldwide distribution of five *Mytilopsis* species and revealed distinct patterns

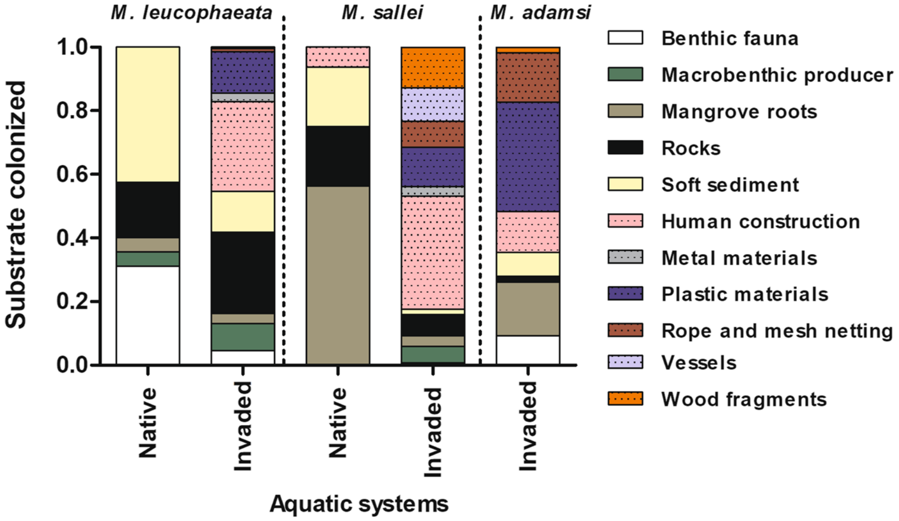

**Fig. 5** Substrate type colonized by *Mytilopsis* species within native and invaded systems. Artificial substrates are distinguished by a dotted pattern. Data are shown as the mean proportion of substrate occurrence by species according to data availability in the literature, in which data for native and invaded systems were: *M. leucophaeata* ($n = 22$ and $n = 35$, respectively), *M. sallei* ($n = 9$ and $n = 29$, respectively), and *M. adamsi* ($n = 8$ for invaded systems)

of environmental conditions and habitat colonization between native and non-native areas. There are some divergences in the theories with respect to the *M. leucophaeata* native distribution range of *M. leucophaeata* (Kennedy 2011); some authors (e.g. Pathy and Mackie 1993; Richardson and Hammond 2016) consider the Hudson River (41°12′49″N; 73°57′50″W) as an invaded area, while Marelli and Gray (1983) indicated based on literature records the Hudson River estuary as a native area. In his historic overview, Kennedy (2011) pointed that the first authors end the distribution of *M. leucophaeata* on Chesapeake Bay, limit range adopted by us, as also by other authors (e.g. Pathy and Mackie 1993; Richardson and Hammond 2016). The introduced ranges of *M. leucophaeata* and *M. sallei* described by us were overall similar to those presented by Marelli and Gray (1983) but updated considering recently published studies. The latitudinal variation of native occurrence is similar between *M. leucophaeata* and *M. sallei* (Δ Lat = 21° and 18°, respectively) but, in the last four decades, both species consolidated and expanded their distributions to non-native areas. Considering our compilation of georeferenced occurrence records for *Mytilopsis* species, the updated distribution of *M. leucophaeata* ranges from almost the polar seas of Finland (Forsström et al. 2016) to the tropical climate of Brazil (Rizzo et al. 2014) (Δ Lat = 83°). In parallel, the updated distribution of *M. sallei* ranges from the temperate climate of Japan (Otani 2002) to the tropical climate of Fiji Island (Marelli and Gray 1983) (Δ Lat = 53°). These latitudinal variations highlight that *M. leucophaeata* has spread more along a latitudinal gradient than *M. sallei*. However, the longitudinal distribution range of *M. sallei* is wider (Δ Long = 296°) than that observed for *M. leucophaeata* (Δ Long = 145°). The updated geographical occurrence of *M. adamsi* extends from Mexico (23°N) to Mauritius (20°S), also a high latitudinal variation (Δ Lat = 43°) but only inside the tropical zone, indicating more limited environmental distribution. *Mytilopsis trautwineana* and *M. africana* were recorded in few native and non-native areas, and this narrow distribution can be related to the lack of available studies for those species, which have reduced our analytical power but may also indicate lower invasiveness potential of these species. The taxonomy of *Mytilopsis* is not well solved and some of these two lineages (*africana* and/or *trautwineana*) may not represent valid species. However, despite some morphological similarities, some studies have shown that may be considerable hidden molecular differences between different lineages of *Mytilopsis* (Fernandes et al. 2020). Another source of debate is the identification of *Mytilopsis* found in the Pacific (e.g. Marelli 2021). A broad morphological and molecular study is desirable to move forward in this question.

The macro-scale perception of *Mytilopsis* distribution patterns indicates a clear geographical spreading of invasive species, especially *M. leucophaeata* and *M. sallei*, across brackish systems of the world. This wide distribution range suggests high species tolerance to a range of environmental factors that varies along latitudinal and longitudinal gradients, such as water temperature. These dreissenids are known to tolerate changes in temperature and salinity (Rajagopal et al. 2005; Verween et al. 2007, 2010; Astudillo et al. 2017; Sa-Nguansil and Wangkulangkul 2020), which reinforces *Mytilopsis* ability to colonize new areas, as evidenced by our geographic distribution map, and reflects their invasiveness potential in aquatic systems worldwide. Moreover, environmental conditions in non-native areas provided beneficial conditions for population establishment and growth, which could be reinforced by significantly higher densities of *Mytilopsis* in non-native areas. Higher density values were reported for *M. leucophaeata* and *M. sallei* on their non-native range (e.g. Pati 2011; Van der Gaag et al. 2017), in addition, high recruitment rates were also observed in these areas (Van der Gaag et al. 2014). As evidenced by our study, invasive populations of *M. sallei* reach significantly higher densities than *M. leucophaeata*. The biomass proved to be difficult to compare considering the different methodologies employed by the authors, which made unfeasible any analysis in the present study. However, high biomass values have been found for *M. leucophaeata* (e.g. Rajagopal et al. 2002) and *M. sallei* (e.g. Shetty et al. 1989) on their introduced range. All the available data of biomass or secondary production for *Mytilopsis* species found in the literature were included in our Supplementary Material S1. There are several theories to explain the success of invasive species, like the release of predators and pathogens, absence of competitors, among others (Fagan et al. 2002; Simberloff et al. 2013). The wide tolerance evidenced here for *Mytilopsis* false mussels, mainly *M. leucophaeata*, are expected to contribute to the successful establishment of this species across non-native ranges, thus increasing its invasiveness potential.

As discriminated by Principal Coordinates Analysis (PCA), native and non-native areas of *Mytilopsis* distribution were modulated by different environmental conditions, overall, statistically supported by Canonical Analysis of Principal Coordinates (CAP). Environmental conditions in non-native areas showed a high correlation with increased values of water transparency, and this significant marked difference between native and non-native areas is known as a consequence of *Mytilopsis* invasion in brackish systems (Vanderploeg et al. 2002; Neves et al. 2020). High populational densities, associated with high biomass, may lead to habitat modifications (e.g. higher water transparency, reductions in chlorophyll *a*, and phytoplankton density) promoted by dark false mussel's filtration (Neves et al. 2020). Moreover, as evidenced by PCA and statistically supported by CAP analysis, the environmental conditions most closely related to *M. leucophaeata* distribution areas were significantly different from the other three species tested (*M. sallei*, *M. adamsi*, and *M. trautwineana*). The similar habitat environmental conditions shared by these three *Mytilopsis* species suggest a higher tendency of co-occurrence in aquatic systems, mostly related to high values of salinity, mean temperature, longitude, and chlorophyll *a*. In contrast, geographic areas of *M. leucophaeata* distribution showed a high correlation with ranges in dissolved oxygen and temperature in surface water, which suggests that this species has great plasticity for extreme values and shifts in these environmental conditions.

Seventeen different taxa were found co-occurring with *Mytilopsis* populations, in which four have occurred exclusively with non-native populations. In invaded systems, Bivalvia (31.28%) and Cirripedia (17.72%) were the most frequent taxa associated with false mussel clusters. These two groups are the commonest sessile invertebrates on the hard substrate of brackish areas around the world (Grzelak and Kuklinski 2010; Oganjan et al. 2017; Sokołowski et al. 2017). Our results presented a snapshot of the distribution and co-occurrence of *Mytilopsis* populations with several epibenthic taxa, but our data is not appropriate to indicate changes in the pattern of epibenthic communities related to false mussels' invasion. However, more detailed effects, on a local scale, have more diverse outputs. Cai et al. (2014) observed a reduction in the density, biomass, and richness of other co-occurring fauna in the presence of *M. sallei*. Rodrigues et al. (2021) have found variations of sympatric populations of *M. leucophaeata* and *Brachidontes darwinianus* (d'Orbigny 1842) (the native ecological equivalent) on a two years follow-up. After two years, neither *M. leucophaeata* nor *B. darwinianus* were excluded. Similarly, *M. sallei* and *Brachidontes variabilis* (Krauss 1848) were found co-occurring in Hong Kong, although the invasive species was dominant (Astudillo et al. 2017). Other species, like gastropods, can take advantage of the clusters created by invasive *Mytilopsis* species (Boltovskoy and Correa 2015; Fernandes et al. 2020), using the clusters as refuge area and hard substrate habitat. More detailed studies are needed for a better comprehension of the ecological impacts of *Mytilopsis* invasion on native epibenthic species, as well as shifts in the ecological interactions of brackish benthic communities after false mussels' invasion.

The availability of suitable colonization substrates is one of the main ecological requirements for epibenthic species, which seems to be crucial for the transport, introduction, and establishment of bivalves in new habitats (Rajagopal and Van der Velde 2012; Zhulidov et al. 2018). Non-native *Mytilopsis* populations exhibited remarkable plasticity concerning habitat colonization. The colonization of non-native *Mytilopsis* populations was significantly more frequent on artificial substrata (e.g. human construction, plastic material, cage net, vessels), but occurred mainly on natural substrata on its native range (e.g. benthic fauna, soft sediments). In anthropogenically modified systems, non-native species may have an advantage over the natives (Tyrrel and Byers 2007; Dafforn et al. 2009; Johnston et al. 2009), as natives are now existing in conditions different than those in which they have evolved. This hypothesis—called selection regime alteration—establishes that an environment becomes more prone to receive invasive species due to man-made modifications, modifying the selection pressures that already exist (Byers 2002; Riquet et al. 2013). One of those human modifications is the creation of new artificial substrata on brackish environments (i.e. human constructions), where the false mussels have been colonizing and performing well. McCarthy et al. (2006) observed a change in substrate use by an invasive crayfish. Similarly, the present study showed that *Mytilopsis* spp. were able to take advantage of the new opportunities in the invaded area, shifting some of their preferences, as substrate use. Invasive species can occur abundantly on artificial substrates, having a preference for these substrates or using them in an opportunistic way (Creed and Paula 2007; Neves et al. 2007; Tyrrel and Byers 2007). *Mytilopsis* can also grow over soft substrata, although a hard nucleus is necessary (Fernandes et al. 2020), potentializing the areas for species distribution, but this strategy was more frequently used in the native area. Another invasive dreissenid, *D. polymorpha* also started to explore soft substrata after colonizing the available hard substrata (Strayer and Malcom 2006). Moreover, several estuaries were naturally poor on hard substrata, thus without (or only with few) native species that explore this new, hard, and artificial substrate, 'leaving the way clear' for the invaders (Tyrrel and Byers 2007). The initial record of *M. leucophaeata* in Rio de Janeiro (Brazil) was done mainly on man-made substrata (Rizzo et al. 2014), therefore the species was also recorded in natural substrata (Maia-Neto 2018; Fernandes et al. 2020), which highlights the wide species plasticity for colonization within invaded systems. Noteworthy that our data were based on available literature records, a systematic sampling effort to investigate the substrate used by native and invasive populations can return a different result.

Invasive species are known to alter their habitats and life histories within native and introduced ranges (Côté and Maljkovic 2010; Petanidou et al. 2012). *Mytilopsis* populations presented significant differences in their biological traits, environmental conditions, and substrate use between native and non-native areas. Moreover, these species seem to easily adapt to the new conditions faced on invaded systems, significantly changing their preferences (e.g. substrate type, environmental conditions), which may reflect wide plasticity and a potential shift in their realized niches (i.e. novel biotic and abiotic conditions) in their non-native ranges. Niche plasticity is certainly a feature that helps species to spread to new habitats, and that was usually related to invasive species (Davidson et al. 2011). Evidence of invasive species success has been related to shifts in the species' realized niche, as opposed to evolutionary shifts in range limiting traits (Tingley et al. 2014; Escobar et al. 2016; Gallego-Tévar et al. 2018). Therefore, we recommend further studies on distribution modelling (e.g. niche modelling) and biological aspects of *Mytilopsis* invasive populations to understand their ecological and economic impacts on introduced brackish systems and to propose measures for the management and control of invasive *Mytilopsis* populations and on comparative and taxonomic studies of all *Mytilopsis* species.

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**Availability of data and material** All the data used in the manuscript are available as supplementary material (S1 and S2).

**Declarations**

**Conflict of interest** The authors declare no conflict of interest.

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