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Research Article

Molluscan assemblages on artificial structures: a bioinvasion perspective from Northeast Brazilian ports

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Abstract

As the impact of coastal development impinge on our natural ecosystem, we are increasingly compelled to study the effects of artificial habitats on the distribution and abundance of marine species. In particular, understanding how physical factors can influence distributional patterns of benthic communities along artificial structures built in ports that create possibilities for a variety of non-indigenous species (NIS) occur. This paper aims to compare the distribution of mollusc's assemblage along environmental factors known to influence the distribution of epibenthic species: depth, shading and locality features such as distance from shore and period of submersion of artificial structures. Molluscan assemblages were examined over a depth gradient extending from middle intertidal (0 m) to shallow subtidal (5 m). We also assessed and compared the distribution of *Eualetes tulipa* (established) and *Isognomon bicolor* (invasive) in two port locations at Northeast coast of Brazil. A total of 33 native species, 7 cryptogenic and two NIS were found. The most abundant was a native species, *Crassostrea brasiliiana*, followed by the NIS *I. bicolor* and *E. tulipa*, respectively. Using PERMANOVA: depth gradient, locality and interaction between these fixed factors showed significant effects on the vertical distribution along the artificial structures sampled. Results suggest that recent substrata availability supports the colonization of NIS species and that these, in areas with more stable communities, cohabit with and are regulated by native species. Furthermore, this is the first study discussing the distribution of the established NIS vermetid *E. tulipa* in Northeast Brazilian coast.

Key words: invasive species, *Eualetes tulipa*, *Isognomon bicolor*, vertical distribution, biofouling, depth gradients, molluscs

Introduction

The fast-growing expansion and impact of artificial structures in marine and coastal environments compel researchers to study and understand the role exerted by new hard substrata on the patterns of biological invasions (Bishop et al. 2017; Bugnot et al. 2021). Invasive epibiota may be able to opportunistically exploit these artificial structures more effectively than native species (Dafforn et al. 2009). In addition, these novel habitats are subject to a variety of environmental gradients that can drive the survival,

abundance and distribution of benthic organisms since their early life history stages (Doropoulos et al. 2016).

Numerous physical factors can shape native and non-indigenous species (hereafter NIS) distributions on artificial structures such as depth, shading and locality features such as distance from shore and time of submersion (Perkol-Finkel et al. 2005; Rule and Smith 2007; van der Stap et al. 2016). Vertical zonation of sessile organisms, for example, may vary with depth gradients (Walker et al. 2007), driven by different larval supply along the water column (Grosberg 1982), consequently affecting settlement rates. Distance from shore can determine community composition influenced by adjacent native communities and abiotic local conditions (van der Stap et al. 2016). Shading regulates the degree of desiccation suffered by biofouling organisms as well as low sunlight levels may decrease algal cover and augment invertebrate colonization (Miller and Etter 2008; Dafforn et al. 2012).

Time of submersion has direct effects on fouling communities' composition (Vaz-Pinto et al. 2014). Most of studies analyse from early benthic succession trajectories to mid-term effects (3 months–2 years) shaping epibenthic community's cover (Herbert et al. 2017; Lezzi et al. 2018; Toledo et al. 2020). However, there are evidences that even after 10 years, epibenthic communities still varies in composition in a response to long-term effects triggered by phenological processes and anthropogenic impacts (Whomersley and Picken 2003; van der Stap et al. 2016). Therefore, opportunities to compare biofouling composition from artificial structures of old and young ages under different environmental circumstances is necessary and may provide insights in the long-term ecological effects of artificial structures.

Habitat complexity is another important physical factor that can determine benthic species distribution (Kovalenko et al. 2012). Given that artificial structures provide lessen structural complexity comparing to natural surfaces, such habitat homogenization can play a major role boosting marine invasions (Airoldi and Bulleri 2011). Global and local experimental studies have been conducted in an attempt to understand the ecological value of artificial structures, simultaneously, reducing the risk of marine species invasion (Dafforn 2017). Furthermore, effects of patch-scale habitat complexity can vary greatly among sites, functional groups and taxa (Sedano et al. 2020; Strain et al. 2021).

Ports can be significant hotspots of NIS due global shipping traffic (Carlton 1996). Researchers predict that this growing trade will far outweigh climate change as driver of bioinvasions over the next decades (Sardain et al. 2019). Yet there is a little understanding about distribution of new detections, established and invasive species in many port areas (Lopes et al. 2009; Teixeira and Creed 2020; Tempesti et al. 2020). Some mollusc species, for example, are identified as successful global invader of ports (Carlton 1999; Ardura et al. 2015). Biological traits such as high tolerance to abiotic stressors and facility for active and passive dispersal are

some of the triggers of their success (Alonso and Castro-Díez 2008; Weir and Salice 2012).

A relevant NIS introduced to the Brazilian coast is the purse oyster *Isognomon bicolor* (C.B. Adams, 1845). Studies suggest that this bivalve first colonized Brazilian coast between 1970s and 1980s, potentially through petroleum platforms, ballast water and/or ship fouling (Domaneschi and Martins 2002; Breves-Ramos et al. 2010). During the 1990s, dense populations were observed occupying a wide range of the intertidal zone of rocky shores in Rio de Janeiro, Brazil, where the bivalves *Perna perna* (Linnaeus, 1758), *Brachidontes solisianus* (Orbigny, 1846) and *Crassostrea brasiliiana*, as well as the cirriped *Tetraclita stalactifera* (Lamarck, 1818) were previously found (Junqueira et al. 2009; López et al. 2010, 2014; Amaral and Simone 2014). Currently, *I. bicolor* is classified as an invasive species (Teixeira and Creed 2020) along the rocky shores and artificial structures across Northeast, Southeast and South Brazilian coast (Agostini and Ozorio 2016; Barroso et al. 2018; Breves-Ramos et al. 2010).

Investigations demonstrated that *I. bicolor* can be found on empty shells of the barnacles *Tetraclita stalactifera* and *Megabalanus* spp. (Martinez 2012), associated with geniculate coralline algae (López and Coutinho 2010) and crevices such as the ones created by the presence of the native vermetid species *Petalococonchus varians* (d'Orbigny, 1839) (Breves and Junqueira 2017). Therefore, the physical structure of these (micro) habitats potentially exerts a critical role in the success of *I. bicolor* settlement and colonization. Moreover, this species has no commercial value but competes for space with the main marine bivalve (*Perna perna*) commercialized in Brazil (Valenti et al. 2021).

An expressive recent introduction to the Brazilian coast is the vermetid species *Eualetes tulipa* (Rousseau in Chenu, 1843) (Spotorno-Oliveira et al. 2018). This gastropod has been documented as an invasive species in Hawaii, Venezuela, Panama and India (Jebakumar et al. 2015; Miloslavich 2018). The most recent record of *E. tulipa* has been in Southeast Asia (Tan et al. 2021). In Brazil, it was first collected at the offshore Pecém Port in 2005 (03°31'53.3"S; 38°47'36.6"W) located at Ceará State in Northeast Brazil (Spotorno-Oliveira et al. 2018). Over the last decade, *E. tulipa* has been reported in natural rocky shores and artificial structures along Southeast coast of Brazil (Spotorno et al. 2012; Breves et al. 2017; Barroso et al. 2018; Spotorno-Oliveira et al. 2018); and the current status of this NIS is established in Brazil (Teixeira and Creed 2020). There are no studies reporting *E. tulipa* distribution at the Northeast Brazilian coast, only its occurrence. Information about impacts and interspecific interactions of *E. tulipa* with native and non-indigenous benthic species are scarce, however, it has been recorded co-occurring with *P. varians* creating novel interactions with native species in Southeast Brazilian waters (Spotorno-Oliveira et al. 2018; Areias et al. 2020).

The increasingly presence of new source pools contributing to further invasions requires an ongoing vigilance regarding detected, established and invasive species (Simberloff et al. 2013; Grosholz 2018; Seebens et al. 2018). Therefore, the need of further and more detailed investigations of marine species introductions, particularly in the Brazilian coastal context, should be addressed (Robinson et al. 2017; Rocha et al. 2013).

In the present study, a comparative approach investigating molluscan assemblages from two ports in Northeast Brazil was conducted. We compared the distribution and density of mollusc's assemblage along environmental gradients known to influence the distribution of epibenthic species: depth, shading (light exposure) and locality features. Additionally, we assessed and compared the distribution of the NIS *E. tulipa* and *I. bicolor* between ports.

These relatively approximated port areas along with their known ages provide a great opportunity to compare and investigate native and NIS assemblages occupying artificial structures with different time of submersion and distance from the shore. Thus, we hypothesize that community descriptors between sites will be distinct based on their locality features. Additionally, given the long operation time of Mucuripe port, it is predicted a greater occurrence of NIS.

Materials and methods

Study area

Located in Northeastern Brazil, the two port areas surveyed occupy a strategic geographical position for transatlantic traffic and many international trades with Europe, Mediterranean and United States.

The first site sampled was at Pecém Port (38°47'51.56"W; 3°32'4.73"S), which is in an industrial complex, approximately 40.6 km from the second site. Pecém Port commercial operations began in 2001, so it was relatively new when this study was conducted. Pecém offshore port terminal is connected to the coast by a pier, which is erected on numerous pillars. This pier extends approximately 2000 m distant from the coast, towards Northeast. The terminal has a rubble mound breakwater in an L shape 1.7 km, built parallel to the access pier to protect the mooring areas (Figure 1) (Chagas 2000). The tidal range in the pillars varies vertically around 2.5 m, which the middle of tidal zone is submerged and exposed for equal amounts of time.

The second location sampled was at Mucuripe Port (38°28'38.71"W; 3°42'54.11"S) situated in the metropolitan area of Fortaleza. This inshore port facility has been operating for more than 50 years and is protected by two breakwaters of irregular vertical arrangement of granitic rocks built perpendicular to the coast (Figure 1) (Maia et al. 1998). The annual mean water temperature for both sites was around 28 degrees Celsius, and salinity was 35.9.

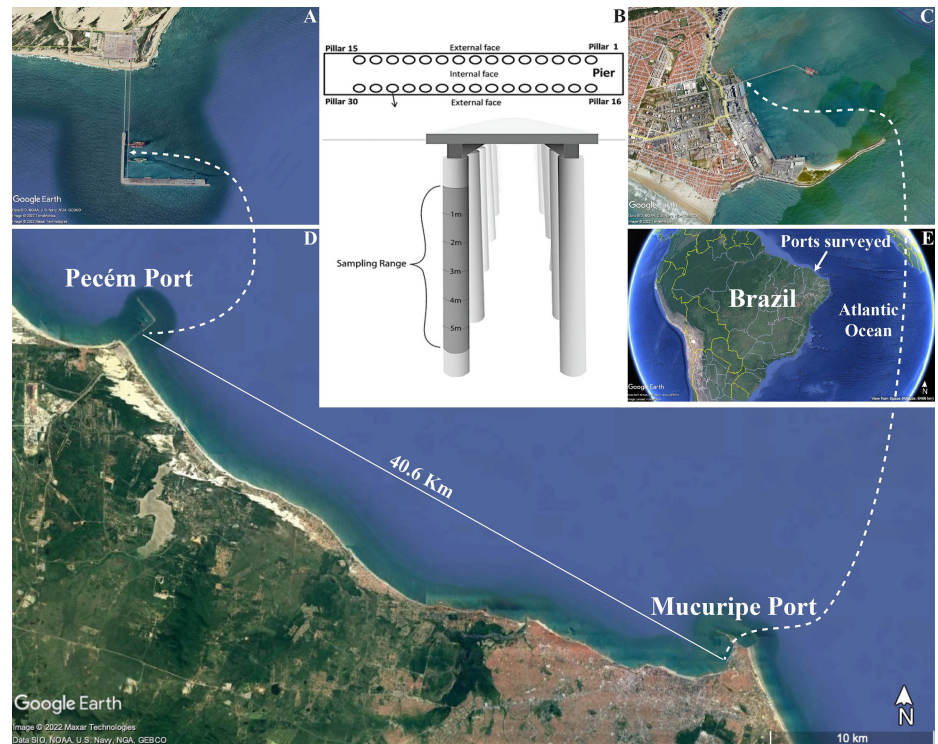


Figure 1. A) Location of samples collection at Pecém Port; B) Schematic representation of the concrete pillar demonstrating the depth-range sampling (Credits: Jason Bell); C) Location of samples collection at Mucuripe Port; D) Map of the coastal state of Ceará highlighting the distance between the studied ports and E) Map of Brazil highlighting the location of the surveyed ports. Source: Google Earth Pro through Image Maxar Technologies.

Experimental design

Given complex logistics and restricted permissions to access these ports areas, a pilot survey was conducted evaluating the adequacy of the sample design and optimizing our sample effort. Species accumulation curves were used to estimate the required sample sufficiency that represents the local marine epibenthic fauna to address our study objective.

A destructive method was applied, fouling organisms were scraped and sampled from the concrete pillars in Pecém and Mucuripe Port between January and February 2009. Through SCUBA diving and quadrat method, samples were taken from a depth range of 0–5 meters within 1 meter interval. The zero meter was delimited by the middle tide zone, therefore, the sampling range was comprised by the lower intertidal zone and the subtidal. At each port, 0.15×0.15 m quadrats were positioned and 40 samples were randomly collected among 30 pillars, which were evenly distributed across depths (8 samples per depth). Pillar’s maintenance has not been done at least in the last ten years previous the timepoint of our sample collection on both ports.

To include shading treatment, sampling was divided across the external and internal faces of pillars (4 samples for each face). The inclusion of external and internal faces of the pillars aims to evaluate possible influence of current (Judge and Craig 1997) and solar incidence, taking into account

levels of exposure in each pillar's side. The external face is more subject to desiccation and the internal face more shaded by the access bridge's cover.

Molluscs collected were fixed in 4% formaldehyde saline solution, preserved in ethanol 70% and identified down to the lowest taxonomic level using WORMS (World Register of Marine Species), Rios (2009) and based in the most updated literature including recent published papers, which updated the taxonomy of some molluscs species (Amaral and Simone 2014; Spotorno-Oliveira et al. 2018).

The specimens identified in this study were deposited in the Malacology Collection Professor Henry Ramos Matthews of LABOMAR/ Federal University of Ceara (UFC) – register number: CMPHRM3946A to CMPHRM4061A and in the Malacology Collection of the Museum and Zoology of Sao Paulo University (USP) – register number: MZSP 107786 and 107787.

Data analyses

Quantitative molluscan community descriptors

Molluscan community descriptors such as Shannon-Wiener diversity (H'), Margalef richness (d) and Pielou evenness (J') were calculated by means of the software PRIMER (Plymouth Routines In Multivariate Ecological Research) version 6.0 (Clarke and Gorley 2006). Mean density of molluscs along depth gradients were calculated using individuals by square meters considering the area of 0.0225 m^2 per sample.

The relative abundance (RA) of each species was calculated following (Rilov and Benayahu 2000) by: $RA = P_i/P_{total} \times 100$. P_i is the total number of individuals of i species from each port and P_{total} is the total number of all individuals. The resulting values were then transformed into abundance categories as follows: not recorded (0); rare ($0 < RA < 0.01$); uncommon (RA between 0.01 and 0.1), common (RA between 0.1 and 10), abundant (RA between 10 and 20); and dominant ($RA > 20$).

Statistical analyses

Molluscan assemblage composition on the vertical surfaces of artificial structures was compared using univariate analysis non-parametric analysis of means by the STATISTICA V. 7.0 program. Data visualization was made in R program 2021.09.2 (Rstudio 2020) using package ggplot2 (Wickham 2016). Standard error and means were calculated using function summarySE from the package Rmisc (Hope 2013).

Data were transformed in square root and assumptions of normality were verified but they did not meet for parametric analysis. The Kruskal Wallis H test was used to verify whether there were differences in molluscan assemblages and invasive mollusc species density along depth gradients. Likewise, these densities were tested regarding exposure. The vertical

distributions of molluscs considering depth effects were compared between Pecém (newer port) and Mucuripe (older port) using two-way ANOVA.

The permutational analysis of variance (PERMANOVA) were also performed comparing ports (location), depths and exposures using PRIMER (Plymouth Routines in Multivariate Ecological Research) program for windows v. 5.2.4. Location, depth, and exposure were treated as fixed factor, while density as a random factor. NIS and molluscan assemblage density were analysed separately with PERMANOVA. The non-parametric Spearman rank-order correlation coefficient were conducted aiming to measure the strength and direct association that can exist between native x NIS and NIS x NIS species interactions.

The population structure of *I. bicolor* was analysed through Kruskal Wallis test H considering individuals size frequency and depth distribution. Measure of the hinge from the left valve were obtained and used as a proxy of size (Breves-Ramos et al. 2010). Empty shells were not counted, only individuals with the soft tissue.

Results

A total of 3738 molluscs were sampled with representatives from 42 species identified. Of those 18 species were common to both ports and the most abundant species (Table 1). At Pecém Port, 1064 individuals were sampled, which 818 were bivalves, 244 gastropods and 2 chitons. The most abundant species were *E. tulipa*, *Leiosolenus bisulcatus* (d'Orbigny, 1853), *I. bicolor*, *Chama* cf. *congregata* (Conrad, 1833) and *Crassostrea brasiliiana* (Lamarck, 1819) representing 19.26%; 18.60%; 15.41%; 13.72% and 11.37% of the molluscan assemblage, respectively.

At Mucuripe Port were gathered 2674 individuals, which 2426 were bivalves, 244 gastropods and 4 chitons. The most abundant species were *C. brasiliiana*, *Sphenia fragilis* (H. Adams & A. Adams, 1854), *I. bicolor*, *L. bisulcatus* and *E. tulipa* representing 52.05%; 11.48%; 9.46%, 8.26% and 6.5%, respectively (Table 1).

The dominant native oyster *C. brasiliiana* predominated within massive aggregations of 1,547 ind/m² and the highest record of NIS *I. bicolor* was 73 individuals (15 cm⁻²) at Mucuripe Port. In addition, we found *I. bicolor* mean densities of 182 ind.m⁻² at Mucuripe Port and 281 ind.m⁻² at Pecém Port. The invasive *E. tulipa* recorded its highest density in Pecém Port at 2m in depth with 19 individuals (15 cm⁻²).

Comparing molluscan assemblages along depth gradients between ports

Mollusc's density at Mucuripe Port was more than twofold comparing to Pecém Port. This result was mainly driven by the massive number of dominant native species *C. brasiliiana* (Table 1), determining the statistically significant difference of molluscan assemblages along depth gradients and

Table 1. Relative abundance of mollusc species sampled considering their contribution to the total molluscan assemblage for each port surveyed.

Mollusc Species	Pecém Port	Mucuripe Port	Documented distribution
<i>Eualetes tulipa</i> (Rousseau in Chenu, 1843)	****	***	Florida, Costa Rica, Panama, Hawaii, Venezuelan Caribbean, Brazil (Ceará, Rio Grande do Norte, and Rio de Janeiro); India. a
<i>Leiosolenus bisulcatus</i> (d'Orbigny, 1853)	****	***	N. Carolina and Bermuda to Santa Catarina, Brazil. b
<i>Isognomon bicolor</i> (C. B. Adams, 1845)	****	***	Bermuda, Florida to Texas, Caribbean, Venezuela, Brazil (Piauí to Santa Catarina; Atol das Rocas) c, e
<i>Chama</i> cf. <i>congregate</i> Conrad, 1833	****	**	Cryptogenic
<i>Crassostrea brasiliiana</i> (Lamarck, 1819)	****	*****	Brazil (Ceará to Santa Catarina) d
<i>Arca imbricata</i> Bruguière, 1789	***	***	N. Carolina to Florida, Texas, Caribbean, Venezuela, Surinam, Brazil (Pará to Santa Catarina, Fernando de Noronha) e
<i>Ostrea</i> sp.	***	***	Cryptogenic
<i>Sphenia fragilis</i> (H. Adams & A. Adams, 1854)	***	****	Texas, Puerto Rico, Surinam, Brazil (Ceará to Santa Catarina) e
<i>Brachidontes exustus</i> (Linnaeus, 1758)	***	***	Atlantic coast of North America, ranging from Cape Hatteras to the West Indies and Brazil f
<i>Musculus lateralis</i> (Say, 1822)	***	**	N. Carolina to Florida, Texas, Mexico, Caribbean to Brazil (Ceará, Pernambuco to Santa Catarina; Trindade Is.) e
<i>Rocellaria dubia</i> (Pennant, 1777)	***	**	USA: North Carolina, Florida, Texas; Mexico: Quintana Roo; Bermuda, Brazil: Ceara, Abrolhos Islands, Rio de Janeiro, Sao Paulo; Uruguay. g
<i>Diodora cayenensis</i> (Lamarck, 1822)	**	*	New Jersey south through the West Indies to Brazil; in the Gulf of Mexico and in the Caribbean Sea; off the Canary Islands. e
<i>Lasaea adansonii</i> (Gmelin, 1791)	**	***	Europe; California to Mexico; Bermuda, Florida, Fernando de Noronha Is., Brazilian coast to Patagonia, Ascension Is., Sta. Helena and E. Atlantic. e
<i>Seila adamsi</i> (H.C. Lea, 1845)	**	–	N. Carolina to Florida, Texas, W. Indies, Venezuela, Brazil to Uruguay. h
<i>Anachis isabellei</i> (d'Orbigny, 1839)	**	*	Brazil (NE Brazil and Rio Grande do Sul) to Argentina (Golfo S. Matias) e
<i>Pinctada imbricata</i> Röding, 1798	**	–	Bermuda, N. Carolina to Florida, Texas, W. Indies, Venezuela, Brazil (Para to Santa Catarina). e
<i>Bittium varium</i> (Pfeiffer, 1840)	**	–	N. Carolina to Florida, Texas, Caribbean, all Brazilian coast. e
<i>Serratina aequistriata</i> Say, 1824	**	***	N. Carolina to Florida, Texas, Brazil (Fernando de Noronha, Ceará to Santa Catarina). i
<i>Macromphalina</i> sp.	**	–	Cryptogenic
<i>Anachis lyrata</i> (G.B. Sowerby I, 1832)	**	–	Costa Rica to Panamá, Cuba, Central America to Brazil (Ceará to Santa Catarina) e
<i>Ostrea equestris</i> (Say, 1834)	**	**	N. Carolina to Florida, Texas, W. Indies, Venezuela, Brazil to Golfo San Matias, Argentina. f
<i>Ischnochiton striolatus</i> (Gray, 1828)	*	–	N. Carolina, Brazil (Amapá to Santa Catarina; Fernando de Noronha). j
<i>Puncturella pauper</i> Dall, 1927	*	–	off Guantánamo (Cuba), Abrolhos Is., São Pedro and São Paulo Is. (Brazil) e
<i>Annulobalcis</i> sp.	*	–	Cryptogenic
<i>Arcopsis adamsi</i> (Dall, 1886)	*	–	N. Carolina to Florida, Texas, W. Indies, Venezuela, Brazil (Fernando de Noronha, Amapá to Santa Catarina). e
<i>Rhyssoplax janeirensis</i> (Gray, 1828)	*	**	Florida, W. Indies, Brazil (Ceará to Santa Catarina) e
<i>Littoraria flava</i> (P.P. King, 1832)	*	**	Florida, Bermuda, Texas, W. Indies, E. Colombia, Venezuela, Suriname to Brazil (Maranhão to Torres, AS). e
<i>Echinolittorina ziczac</i> (Gmelin, 1791)	*	–	Florida, W. Indies, Bermuda, E. Colombia, Venezuela, Brazil to Uruguay. Introduced to Pacific Panama (by the Canal). e
<i>Mitrella pusilla</i> (Sowerby, 1844)	*	–	Bermuda, N. Carolina to Florida, Texas, Caribbean, Brazil (Ceará to Santa Catarina, Abrolhos Is., Vitória Seamount) e

Table 1. (continued).

<i>Boonea jadisi</i> (Olsson & McGinty, 1958)	*	–	Florida to Uruguay. In Brazil, from northeast to Rio de Janeiro. k
<i>Turbonilla abrupta</i> Bush, 1899	*	–	West Indies (type locality), Mexico (Yucatan Peninsula), Brazil (Pernambuco to Santa Catarina), Argentina. e
<i>Marshallora nigrocincta</i> (C.B. Adams, 1839)	*	–	N. Carolina to Florida, Texas, W. Indies, Venezuela, Brazil (Ceará to Santa Catarina). e
<i>Crepidula</i> sp.	–	***	Cryptogenic
<i>Petricola bicolor</i> G. B. Sowerby II, 1854	–	**	N. Carolina to Florida, Texas, W. Indies, Brazil (Fernando de Noronha Is; Rio Grande do Norte to Santa Catarina). e
<i>Fissurela clenchi</i> Farfante, 1943	–	**	French Guiana to Brazil (Fernando de Noronha, Pará to Torres, AS). e
<i>Entodesma brasiliense</i> (Gould, 1850)	–	*	Bermuda, N. Carolina to Florida, W. Indies, Brazil (Amapá to Rio de Janeiro). e
<i>Siphonaria</i> sp.	–	*	Cryptogenic
<i>Lottia subrugosa</i> (d'Orbigny, 1846)	–	*	Brazilian coast (Ceará to Rio Grande do Sul) and Uruguay. e
<i>Pusula pediculus</i> (Linnaeus, 1758)	–	*	Bermuda, N. Carolina to Florida, W. Indies, E. Colombia, Venezuela, Brazil (Amapá to São Paulo, Fernando de Noronha Is.). e
<i>Caecum ryssotitum</i> de Folin, 1867	–	*	Texas, Flórida, Antilhas, Venezuela, northeast Brazil. l
<i>Martesia</i> sp.	–	*	Cryptogenic
<i>Transennella stimpsoni</i> Dall, 1902	–	*	N. Carolina to Florida, Bahamas, Brazil (Ceará to Santa Catarina; Abrolhos Is.). e

Species are listed with the following categories of relative abundance (%): –, not recorded; *, rare ($0 < RA < 0.01$); **, uncommon ($RA 0.01-0.1$); ***, common ($RA 1-10$); ****, abundant ($RA 10-20$); *****, dominant ($RA > 20$). References: **a** (Spotorno-Oliveira et al. 2018); **b** (Scott 1988); **c** (Dias et al. 2013; Domaneschi and Martins 2002; Dullinger et al. 2009; Franklin-Junior et al. 2005; Loebmann et al. 2010); **d** (Amaral and Simone 2014); **e** (Rios 2009); **f** (WORMS, 2022a); **g** (Carter 1978; Valentich-Scott and Dinesen 2004); **h** (Rolan and Fernandes 1990); **i** (WORMS 2022b); **j** (Lyons and Moretzsohn 2009); **k** (Pimenta et al. 2009); **l** (Mello and Maestrati 1986). NIS are indicated in bold.

between ports (Table 2). In addition, molluscan assemblage differed between the first meter, represented by the lower intertidal range, when comparing with the rest of the sampled zone of the pillars (Table 2).

Community descriptors showed greater richness index values at the first meter comparing to the deeper zones on both studied areas. Mucuripe Port presented a lower mean diversity H' but a great mean density (Table 3). Further, there was a greater mean density of mollusc species at Mucuripe Port comparing to all depths, apart from the second meter depth, which showed a lower density but a relatively high mean diversity H' (1.64) (Table 3). Evenness values demonstrated a similar pattern along the depths at Pecém Port showing a slightly increase as much it becomes deeper. Yet Mucuripe Port, evenness index values J' at 1m depth had a lower value.

In our study, light exposure was used as proxy for shading. However, there were no significant difference in density between exposed and no-exposed side of the pillars. The non-parametric Spearman rank-order correlation coefficient results also did not show any significant correlation between *C. brasiliiana* and the whole molluscan assemblage density and NIS. Similarly, correlations were not found between NIS \times NIS interactions. Even analyses between *C. brasiliiana* and *I. bicolor*, which showed a similar distribution and high densities, did not present statistically significant correlation.

Table 2. PERMANOVA results comparing molluscan assemblage densities, the most dominant native species, and NIS species between ports (location) along depth gradients and light exposure.

Molluscan assemblage (total density)						<i>Crassostrea brasiliiana</i> (native)			
Source	Df	SS	MS	Pseudo-F	P(perm)	SS	MS	Pseudo-F	P(perm)
Location	1	21.09	21.09	22.45	0.001	13.13	13.13	27.19	0.001
Depth	4	104.72	26.17	27.86	0.001	60.88	15.22	31.52	0.001
Exposure	1	0.34	0.34	0.37	0.56	6.58	6.58	1.36	0.965
LoxDe	4	58.61	14.65	15.59	0.001	58.92	14.73	30.50	0.001
LoxEx	1	0.94	0.94	1.00	0.327	5.93	5.93	1.23	0.904
DexEx	4	11.93	0.29	0.31	0.885	4.12	1.03	2.14	0.999
LoxDexEx	4	0.98	0.24	0.26	0.894	1.55	3.87	8.02	1
<i>Eualetes tulipa</i> (NIS)						<i>Isognomon bicolor</i> (NIS)			
Source	Df	SS	MS	Pseudo-F	P(perm)	SS	MS	Pseudo-F	P(perm)
Location	1	7.81	7.81	0.65	0.42	6.44	6.44	10.02	0.331
Depth	4	0.13	3.33	28.09	0.036	17.30	0.43	6.73	0.001
Exposure	1	8.13	8.13	6.85	0.98	1.19	1.19	1.85	0.197
LoxDe	4	2.16	5.39	0.45	0.75	0.14	3.58	0.55	0.715
LoxEx	1	2.35	2.35	0.19	0.67	6.15	6.15	0.95	0.36
DexEx	4	7.64	1.91	1.60	0.19	0.18	4.60	0.71	0.623
LoxDexEx	4	1.57	3.91	0.33	0.83	8.45	2.11	0.32	0.9

Significant results ($p < 0.05$) are indicated in bold.

Table 3. Quantitative molluscan community descriptors calculated comparing Pecém and Mucuripe Port.

Depth (Meters)	Diversity	Mean (H')	Richness	Mean (S)	Evenness	Mean (J')	Mean Density
Pecém Port	1m	0.63–1.76	1.54	2.0–13.0	7.75	0.71–0.91	71.5
	2m	1.34–1.98	1.71	6.0–10.0	7.5	0.69–0.97	53.94
	3m	0.70–2.16	1.43	3.0–10.0	5.87	0.64–0.94	26.88
	4m	1.29–1.84	1.39	1.0–7.0	5.37	0.80–0.94	20.6
	5m	1.01–2.20	1.66	3.0–10.0	6.37	0.86–1.0	17.74
Mucuripe Port	1m	0.42–1.36	0.95	6.0–12.0	8.38	0.22–0.76	353.17
	2m	1.39–1.90	1.64	5.0–10.0	6.63	0.78–0.94	36.7
	3m	1.33–1.96	1.74	4.0–11.0	7.88	0.77–0.96	51.38
	4m	1.15–2.09	1.64	4.0–11.0	7.63	0.69–0.88	42.65
	5m	0.79–1.97	1.49	4.0–10.0	6.75	0.57–0.94	46.62

Mean density (unit: individuals per square meter).

Non-indigenous × *native species*

The whole molluscan assemblage, the dominant native species *C. brasiliiana* and NIS were analysed separately using PERMANOVA and Kruskal Wallis test. The NIS *I. bicolor* and *E. tulipa* showed significant difference among depths ($p < 0.001$, $p < 0.036$; respectively). Whereas *E. tulipa* demonstrated a slightly density decrease along deeper zones, *I. bicolor* had a well-defined distribution with high densities at the first meter and similar distribution on the other depths at both ports (Figure 2, Table 2). Overall, the greatest abundance of NIS and richness of native species occurred in the shallowest zone on both ports (Figure 2).

The rank based non-parametric Kruskal Wallis H test also showed density depth dissimilarities within the molluscan assemblages. On both ports, *I. bicolor* and molluscan assemblage densities differed when considering densities. Pecém Port: molluscan assemblages ($H(4, N = 40) = 19.55$ $p = 0.0006$); *I. bicolor* ($H = 20.22$ $p = 0.0005$). However, density of *E. tulipa* was

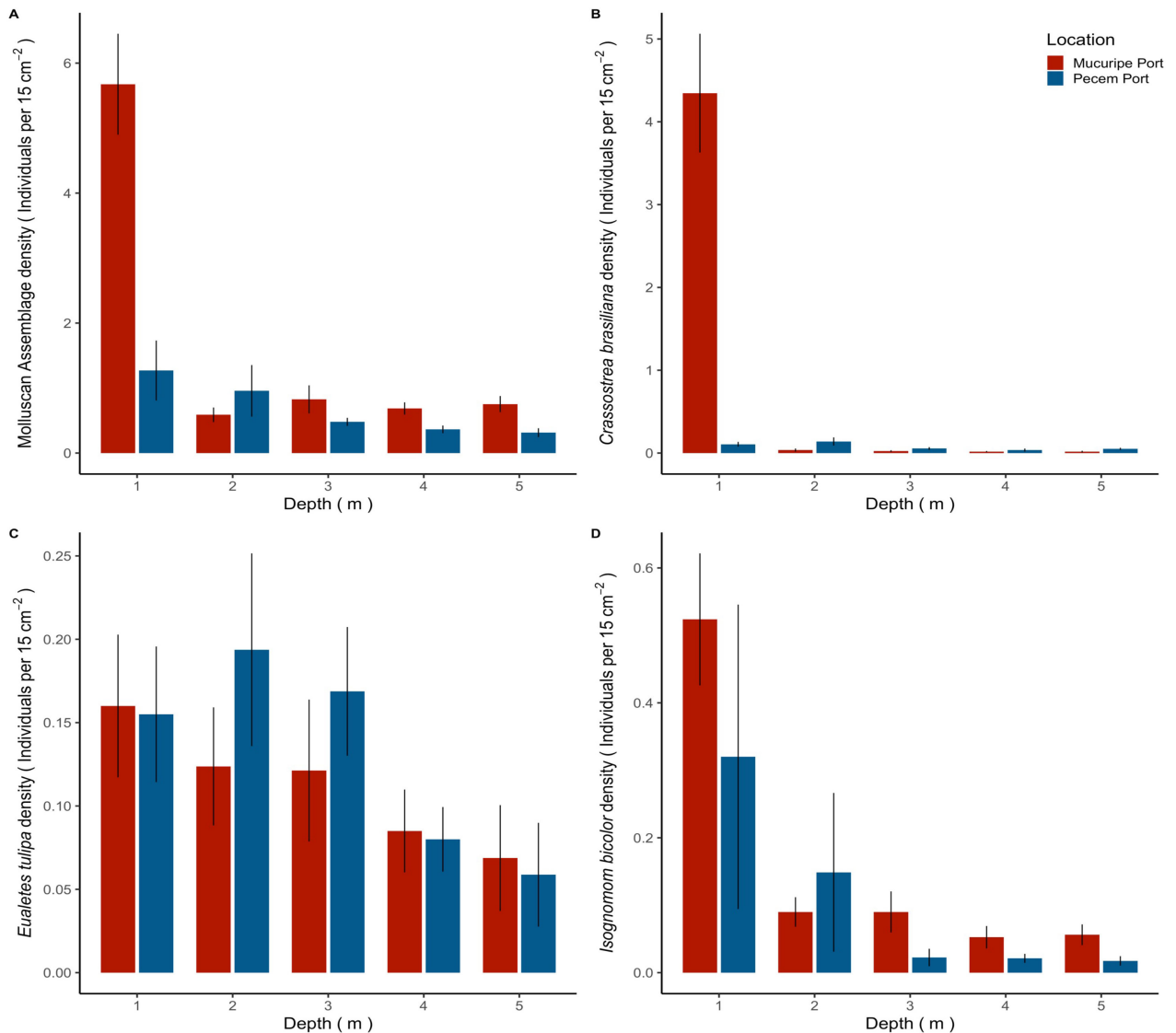


Figure 2. Comparison between ports of molluscan assemblages' distribution along depth gradients sampled from pillars. a) the whole molluscan assemblage density; b) *Crassostrea brasiliana* density; c) *Eualetes tulipa* density and d) *Isognomon bicolor* density. The mean values with the respective Standard Errors (SE).

not affected by depth ($H = 5.45$ $p = 0.2434$). Mucuripe Port: molluscan community ($H = 19.55824$ $p = 0.0006$); *I. bicolor* ($H = 20,22849$, $p = 0.0005$) and *E. tulipa* ($H = 5.45$, $p = 0.2434$).

Isognomon bicolor size frequency distribution along depth gradients

At Pecém Port, shell size ranged from 1.75 to 13.67 mm, with an average size of 7.3 mm, whilst on the older port, it ranged from 1.86 to 18.55 mm presenting 6.85 mm as an average size. Despite this difference among shell sizes, it was not statistically significant between ports. At Pecém Port, average shell size increased with depth (Table 4), where the smaller individuals occupied the first meter, while the larger individuals, although fewer, were found in the third and fifth meters (Figure 3). In general, both ports showed a slightly increase of size frequency of *I. bicolor* as it becomes deeper.

Table 4. Size frequency of *Isognomon bicolor* along depth gradient and Kruskal Wallis test results for each port.

Depth	Pecém Port		Mucuripe Port	
	Mean size (mm)	Range size	Mean size (mm)	Range size
1 m.	6.39	1.96–11.2	6.4	1.35–14.7
2 m.	7.69	1.75–13.67	6.13	2.1–13.9
3 m.	9.07	5.7–12.5	6.73	2.0–16.4
4 m.	5.8	2.16–8.85	7.43	3.7–12.0
5 m.	7.89	6.45–8.8	7.58	5.1–9.8
	H	<i>p</i>	H	<i>p</i>
Size × Depth	12.03	0.017	6.19	0.18

Significant results ($p < 0.05$) are indicated in bold.

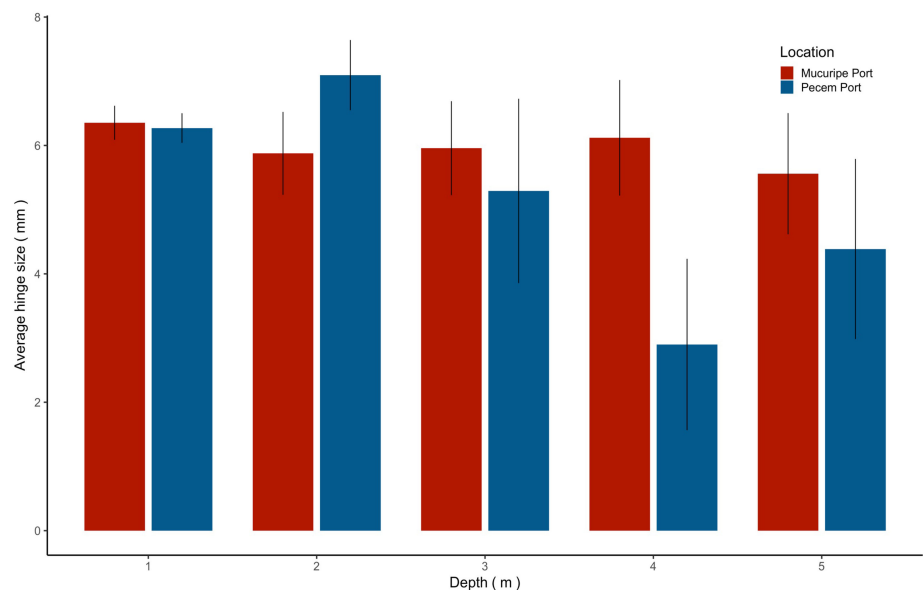


Figure 3. Average hinge size of *Isognomon bicolor* along depth gradient in each port. The mean values with the respective Standard Errors (SE).

Discussion

This work demonstrated how molluscan assemblages vary along depth gradients and are influenced by locality features found in two ports terminal at Northeastern Brazil, determining distributional patterns of native and NIS in artificial structures. The shallowest zone sampled, where molluscs are subject to tidal variation, presented the greatest richness comprised mainly by invasive and native dominant species. This result may be explained by the larval settlement preference and specific traits exhibited by typical intertidal species, such as the NIS *Isognomon bicolor*, which were found coexisting with massive aggregations of native *Crassostrea brasiliiana*. It highlights the susceptibility of intertidal zones to molluscan invasions compelling targeted programs for monitoring these systems (Minchin et al. 2016; Zwerschke et al. 2018).

Shading treatment did not show any differences in densities of mollusc species on both ports. Even the greater exposure of sunlight faced by molluscan assemblages in intertidal ranges did not show any significant differences. Although we did not explicitly test the effects of Mucuripe and

Pecém Port operation time, some patterns were evidenced. The molluscan community of both ports were quite similar, possibly due to the proximity between them (40.6 km) and the biota surrounded influencing the fouling composition of these areas. Effects of period of submersion of pillars and specific features of each port may be elucidated by an increased species richness index caused by the prevalence of dominant species at the older port. The long period of submersion of pillars from Mucuripe Port (50 years) suggests a late successional species composition depicted by native and invasive dominant species regulating the whole molluscan assemblage. *Crassostrea brasiliiana*, *I. bicolor* and *E. tulipa* can act as pioneer species as they were found colonizing settlement plates submersed at Pecém Port (Barroso et al. 2018). Thus, given that *C. brasiliiana* and NIS are well-established on both ports, our results suggest that invasive mollusc species can colonize, persist, and cohabit within the community regardless the successional recipient community stage. This is significant as it is critical to demonstrate the effects of physical features such as depth regulating epibenthic communities under different community succession stages. Such information can provide insights into NIS establishment, survival, persistence and/or range-expansion. Studies using long-term data (> 10 years) aiming to understand and compare the successional trajectory of epibenthic communities in artificial structures (Vaz-Pinto et al. 2014) such as port areas still scarce and should be addressed.

Another factor that possibly favoured the massive densities of *C. brasiliiana* is larval supply due to the distance from the shore. This species is commonly found in adjacent artificial breakwaters substrata, therefore, propagule supply at Mucuripe Port may be greater comparing to Pecém Port, which is around 2 km away from the shore. This dominant native oyster prevailed within massive aggregations of 1,547 ind/m² regulating *I. bicolor*' establishment, providing shelter to young individuals among crevices in intertidal ranges. Even if *I. bicolor* may act as a pioneer species colonizing bare substrata, it typically succeed settling among other epibenthic organisms or new recruiting conspecific individuals (Breves-Ramos et al. 2010). Therefore, in this present study, *C. brasiliiana* seems cohabit rather than resist to the invasion of *I. bicolor*, which exert a role of opportunistic colonizer.

Despite of forming clusters being a common feature of the native *C. brasiliiana*, massive aggregations such as those recorded in our research, suggests a dominant invasive behaviour (Valéry et al. 2009). In altered environments such as port areas, even native species can massively proliferate and affect local community. Further, the spreading of this species into new localities within and beyond national jurisdictions should be monitored.

The representative abundance of *S. fragilis* and *L. bisulcatus* were related to the presence of *C. brasiliiana* dense aggregations. *Sphenia fragilis* individuals were found occupying empty shells of *C. brasiliiana* and hosting ascidians (Narchi and Domaneschi 1993). Similarly, *L. bisulcatus*, an

endolithic bivalve that colonize boring artificial or natural structures by means of glandular secretions (Devescovi 2009), was encountered inhabiting among *C. brasiliiana* individuals at Mucuripe Port. Noticeably, *C. brasiliiana* was playing a role of ecosystem engineer along the shallowest range providing complex habitat to other organisms as well as limiting others.

We verified a significant prevalence of *I. bicolor* at the first meter surveyed, characterized by smaller shell sizes in this depth, while maximum shell sizes were collected at deeper ranges but in low density. It is likely that individuals settled on the intertidal range may serve as propagule source to the deeper zones. Such populational distribution can be explained by the preferential intertidal settlement pattern, where *I. bicolor* can find habitat heterogeneity and is more physiologically adapted (Zamprogno et al. 2010). In our study, the highest aggregation of this species was 73 individuals (15 cm^{-2}), which corresponds to 3244 ind.m^{-2} . In addition, we found mean densities of 182 ind.m^{-2} and 281 ind.m^{-2} at Mucuripe and Pecém Port, respectively. Breves-Ramos et al. (2010) recorded over 800 individuals per cm^{-2} on intertidal rocky shores from Rio De Janeiro, evidencing that *I. bicolor* can colonize in dense populations on artificial and natural habitats. Most of studies describing *I. bicolor*'s distribution had been carried out on natural rocky shores, and others bioinvasion investigations only mention its occurrence in different locations (Ignacio et al. 2010; Teixeira et al. 2010; Zamprogno et al. 2010; Marques et al. 2013). In artificial structures, occurrence and abundances of *I. bicolor* had been reported colonizing settlement plates (Barroso et al. 2018), marinas (Oricchio et al. 2019), man-made rocky structure (Dias et al. 2013) and pipeline monobuoys (Agostini and Ozorio 2016). Therefore, to our knowledge this is the first study documenting *I. bicolor*'s distribution along depth gradients in artificial structures from Northeast Brazil. As artificial substrata are considered high-risk habitat of introduction and source of invasive species, our results contribute to the understanding of how these species occupy and interact with native species in port systems.

The strength of interactions between native and NIS can reduce or enhance invasibility. Predation and competition are often mentioned as key factors limiting NIS, but these processes can vary between artificial and natural habitat, particularly, considering the specific biological composition and abiotic conditions. On natural rocky shores, experimental manipulations demonstrated that the predator gastropod *Stramonita brasiliensis* Claremont & D. Reid, 2011 rather prey on the invasive *Perna perna* than *I. bicolor* (López et al. 2010). Despite *S. brasiliensis* had not been found in our studies, this species is common on natural sandstone rocky in neighboring areas.

Isognomon bicolor and *C. brasiliiana* are species with similar biological attributes such as gregarious populational structure, typical intertidal settlement and irregular morphology providing high capacity of adaptation to different biophysical environmental conditions underpinning their

co-occurrence. On the other hand, high abundances of *C. brasiliiana* probably limited *E. tulipa* colonization in the first meter at Mucuripe Port associated with desiccation caused by tidal variation. This invasive vermetid prefers to colonize from below the mediolittoral and firmly cement to the substrate being almost impossible to dislodge it without breaking the shell (Usvyatsov and Galil 2012).

While the invasive bivalve *I. bicolor* is commonly found and studied along the Brazilian coast, this is the first study documenting the distribution of the recently introduced vermetid *E. tulipa* along depth gradients from Northeast Brazil. Currently, *E. tulipa* can be encountered at Ceará and Rio Grande do Norte State situated at Northeastern Brazilian waters, and Rio de Janeiro in the Southeast Brazil (Spotorno-Oliveira et al. 2018). Despite of the same marine jurisdiction, Northeastern and Southeaster coastal areas of Brazil are biogeographically distinct (Spalding et al. 2007), hence, these distribution demonstrate how *E. tulipa* can thrive under different biotic/abiotic conditions once introduced from Northeast to Southeast of Brazilian coast (Skinner et al. 2019).

In 2005, it was first gathered at depths of up to 16m in Pecém Port, but surveys of its density and distributions were only published recently (Skinner et al. 2019; Spotorno-Oliveira et al. 2018). Densities of up to 24 ind.100cm⁻² were found attached to the breakwaters at Southeast coast of Brazil (Forno Port, Arraial do Cabo, Rio de Janeiro State) (Spotorno-Oliveira et al. 2018). On our studied areas, *E. tulipa* showed a relatively uniform vertical distribution pattern along the 5 meter sampled, although it presented slightly higher densities in the shallower two meters at both ports, being consistent with previous studies in Venezuela, India, Hawaii and Panama (Jebakumar et al. 2015; Spotorno-Oliveira et al. 2018). The highest density recorded was in Pecém Port at 2 m in depth with 19 individuals (15 cm⁻²) which is equivalent to 844 ind.m⁻². These numbers are among the highest densities ever recorded for this species in Brazil and can generate concerns considering *E. tulipa* short period of introduction. One of the most likely reasons for these high aggregations is related to protected environments provided by ports (Hadfield et al. 1972; Osman 1987), influencing settlement rates and post-settlement survival. Furthermore, the presence of crustose coralline algae (CCA) substrates can induce settlement of vermetids, as reported for Atlantic vermetid reefs (Spotorno-Oliveira et al. 2015). Future investigations assessing whether CCA induce settlement of the NIS *E. tulipa* along Brazilian ports, can provide insights to understand its invasive colonization process.

The presence of this species commonly occur at shallow ranges in high water temperatures between 23 °C and 30 °C (Miloslavich and Penchaszadeh 1992; Jebakumar et al. 2015) as found in Mucuripe and Pecém Port waters (26 °C–29 °C). However, a recent survey conducted in artificial substrata under upwelling conditions (19.5 °C–25 °C) recorded larger shell aperture

sizes and greater densities of 4.0 ind.m⁻² at deeper ranges (6–8 meter) (Skinner et al. 2019). Even though, these densities were quite lower comparing to our results.

Eualetes tulipa is well-established among live epibenthic subtidal organisms to intertidal habitats and sometimes can live in empty shells create microhabitats providing shelter to other epibenthic organisms (Jebakumar et al. 2015). The vermetid *P. varians*, which can cohabit with *E. tulipa* (Spotorno-Oliveira et al. 2018), has been reported to provide shelter to invasive bivalve species such as *I. bicolor* and *Leiosolenus aristatus* (Breves and Junqueira 2017). Thus, further studies investigating *E. tulipa* competition, predation, provision of habitat and other interactions between native and NIS should be investigated.

High tolerance to stresses such as exposition to poor quality water and low levels of food, ability to co-occur with other epibenthic species, diverse reproductive strategies and capability to occupy substrata at a wide depth range make *E. tulipa* a high potential invader (Miloslavich and Penchaszadeh 1992; Strathmann and Strathmann 2005; Jebakumar et al. 2015; Spotorno-Oliveira et al. 2018). In our study, we found high densities of *E. tulipa* represented by large numbers of juvenile and adult individuals, indicating that its population is well established and can further spread changing the composition and structure of local communities.

Among 42 species of molluscs surveyed, 7 were cryptogenic and 2 non-indigenous. At Mucuripe Port, we found 44 specimens of the cryptogenic *Crepidula* sp. The taxonomy of this slipper limpet is particularly difficult to identify by means of shell characters alone, being necessary to analyze anatomically and, in this case, the reproductive apparatus. The morphotype *Crepidula* sp. differ from *Crepidula plana* and *Crepidula aculeata* commonly found in the surrounding areas (Simone 2006). The Calyptraeidae genus has a well-known invader example, the *Crepidula fornicata*, which competes with commercially important mollusc species and can modify substantially local marine benthos (Martin et al. 2007). Thus, *Crepidula* sp. and the others cryptogenic species found in this study require further taxonomic and genetic investigation.

Given that artificial structures provide a reduced structural complexity, the range of trophic categories and feeding guilds found at both ports, were remarkably robust. 19 bivalves, 21 gastropods and 2 chitons species were sampled in such narrow vertical zone, represented mainly by carnivores, herbivores, parasitic, filter feeders and grazers. Even though our results were based on a limited number of samples, these data reveal rich and diversified mollusc assemblages on artificial structures, which can sustain complex systems. Data presented in this study describe the role exerted by depth gradients and locality features structuring native and NIS mollusc composition and how NIS can coexist and/or compete with dominant native species.

Conclusions

Our work highlights that depth can play an essential role shaping the assemblages of molluscs, and dominant species can change greatly its distribution with relatively slight variations in depth. Moreover, the NIS *E. tulipa* seems to be well-established in artificial structures at Northeast Brazilian ports, therefore, monitoring and feasible measures of control averting their further expansion are recommended.

While our findings report specific patterns in species' distribution, we highlight the value of periodic research in providing early detection and assessment of newly settled and well-established NIS. In our study, molluscan assemblages exhibited a rich diversity in a narrow depth range of artificial structures. However, the presence of native dominant species such as *C. brasiliiana* may interfere local community descriptors, concomitantly, cohabiting with NIS. Furthermore, despite of the confirmed distinct abundance and distribution of molluscs between ports, the hypothesis that an older port would demonstrate greater occurrence of NIS was refuted.

It is expected an expansion of port areas in Brazilian coastal zones along with the construction of more breakwaters intercepting longshore currents. Ecological principles should be incorporated when designing and implementing new intertidal and subtidal artificial structures, and existing infrastructures may be adapted to mimic natural reefs and promote native biodiversity. Adding context specific experimental projects providing novel habitats to marine species within human-made marine constructions could ameliorate its negative effects, elucidate the best solutions and lead to conservation gains.

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Authors' contribution

D.F.B. conceived, designed and conducted the field experiment, performed data analysis, and wrote the manuscript; C.R-B. conceived, designed, performed data analysis, edited the manuscript and supervision; W.F.J. conceived, designed, edited the manuscript and assisted with the fieldwork. P.S.O. reviewed and edited the manuscript. All authors wrote, read, and approve the manuscript.

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