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Marine bioinvasions: Differences in tropical copepod communities between inside and outside a port

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A R T I C L E I N F O

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A B S T R A C T

The difficulty of detecting non-indigenous species (NIS) in marine environments is an "invisible problem" in areas where plankton monitoring does not occur. In this study, we investigated the dominance of the NIS *Temora turbinata* and copepod community structure in two tropical marine habitats: inside an offshore port, which had turbid and calm waters, and outside the port, which was more hydrodynamic. Our study area was on the northeast coast of Brazil. We found 17 taxa of Copepoda, which were dominated by *T. turbinata* and the congener, *T. stylifera*. The high average density of the NIS (21.03 ind./m^3) was in stark contrast with that of the native copepods (0.01–3.27 ind./m^3). The NIS density was negatively correlated with the species richness and evenness of the native community, was significantly higher inside the port than outside, and was positively correlated with phytoplankton density. A multivariate analysis revealed that there was a significant difference in copepod community structure between inside and outside the port; outside the port, the community was more diverse, and the native *T. stylifera* was more abundant. We found that tropical copepod communities inside an offshore port have low diversity, and probably have little biotic resistance against NIS invasions. Our results, combined with those previously obtained, highlight the need to study the spatial distributions of NIS and native species in pelagic environments.

Regional index terms

South Atlantic
Brazil
Port of Pecém

1. Introduction

Invasive species have complex multilevel effects on affected ecosystems (Liu et al., 2014; Ojaveer et al., 2014). Despite their ecological and socioeconomic relevance, it is alarming how little is known about marine biological invasions, particularly those driven by small invertebrates and microscopic organisms (Marques, 2011). Among these mostly ignored organisms, zooplankton are an important, although neglected, component of biological invasions, and their effects on the trophic ecology and community equilibrium of marine systems are poorly understood (Svetlichny and Hubareva, 2014).

Copepods are a major component of marine zooplankton in terms of biomass, diversity, and abundance (Miyashita et al., 2009; Atkinson et al., 2012). These organisms constitute a link in the food chain (in water column and benthic-pelagic coupling processes), participate in nutrient cycling, and include species that act as ecological indicators (McCollin et al., 2008; Campos et al., 2017). Marine bioinvasion research has focused on macroorganisms such as benthic invertebrates (Boets et al., 2011; Marques et al., 2013; Çinar and Bakir, 2014; Evans et al., 2017) and gelatinous macrozooplankton (Van Walraven et al., 2013; Augustine et al., 2014; Vansteenbrugge et al., 2015; Malej et al., 2017), but copepods, as important trophic and biogeochemical links, require further study.

Studies describing mesozooplankton bioinvasions in marine ecosystems have been conducted in the Indo-Pacific and North Atlantic Oceans, and in the Black and Mediterranean Seas (Delpy et al., 2012; Gubanova et al., 2014; Svetlichny and Hubareva, 2014; Meier et al., 2015). Tropical studies are few in number, and some locations are

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virtually undiscovered or underrepresented when NIS are monitored and studied. The lack of scientific knowledge, and the difficulty of detecting and managing invasive species, results in bioinvasion by microscopic organisms becoming an "invisible problem" in marine environments. The plankton of the South Atlantic Ocean seems to be a particularly neglected subject of inquiry (Farrapeira et al., 2011; Rocha et al., 2013). This area has seen significant transoceanic ship traffic, but the consequences of maritime transport, including the introduction of benthic NIS into marine ecosystems, have only recently begun to receive appropriate academic and governmental attention (Rocha et al., 2013; Castro et al., 2017).

Along the western coast of the Atlantic, three species of planktonic copepod of the genus *Temora* (*T. longicornis*, *T stylifera*, and *T. turbinata*) have been recorded (Bradford-Grieve et al., 1999), and *T. turbinata* Dana, 1849 is a non-indigenous species (NIS) on the Brazilian coast. *T. turbinata* did not occur in the tropical Southwestern Atlantic Ocean before 1993 (Araújo and Montú, 1993), and may have been introduced with ballast water from ships (Ferreira et al., 2009). Before the establishment of *T. turbinata*, the only representative of the genus on the Brazilian coast was *T. stylifera* (Ferreira et al., 2009). The NIS *T. turbinata* is a widespread coastal and oceanic species (Björnberg, 1981; Bradford-Grieve et al., 1999), and is tolerant of a wide range of conditions (Bradford, 1977; Campos et al., 2017).

In this study, we investigated the dominance of *T. turbinata* and copepod community structure in two tropical marine habitats: inside an offshore port, which had turbid and calm waters, and outside the port, which was more hydrodynamic. This sampling design can elucidate the ecology of invasive planktonic organisms in tropical marine ecosystems. By means of comparison two copepod assemblages, this study indicated the clear impact of oceanographic regime (circulation pattern and flows) on the zooplankton communities and the dominance of the NIS in the region. The main objectives were to (1) analyze the distribution patterns of this NIS inside and outside an offshore port, and (2) to provide a baseline assessment of copepod assemblages and the dominance of *T. turbinata* and the native *T. stylifera*.

2. Materials and methods

2.1. Study area

The tropical coast of Brazil (tropical Southwestern Atlantic Coast) extends from the Maranhense Gulf (2°00′S) to the Paraíba do Sul coastal plain (21°50′S). It comprises three sectors: northern (2–5°S), northeastern (5–12°S), and eastern (12–21°S). Our study area was on the northern coast near the equator, which can be classified as tropical semiarid. This coast contains vast areas of active and stabilized sand dunes, as is typical for semiarid coastal areas. The sea temperature stays within a narrow range of 27 to 29 °C, without any significant seasonal variation (Tsoar et al., 2009). The continental shelf region is characterized by a western boundary current, strong winds, mesotidal regimes, and estuarine discharges. This is a dynamic region, and the origin of many unique features of Atlantic Ocean circulation. One of these is the eastward-flowing equatorial undercurrent, which is fed by the North Brazil Current as it flows along the southwestern coast near the equator (Dias et al., 2013).

Operating since 2002, the Port of Pecém (3°32′S; 38°47′W) is a major port in Latin America because of its geographical location, being relatively close to both Africa and Europe. It is in Northeast Brazil (56 km west of Fortaleza, the capital city of Ceará State), and its offshore terminal is a technologically advanced site that is about 1 km from the shoreline and connected to the land by a bridge.

2.2. Methodology

Samples of the copepod community were taken at 20 stations in both internal (P14 to P20) and external (P1 to P13) areas of the port (Fig. 1). Oceanographic sampling was conducted in the dry season, in October of 2013. The samples were obtained using subsurface plankton nets in 5-min tows, with a conical-cylindrical net (mesh size, 200 μm and mouth diameter, 0.5 m) equipped with a mechanical flow meter. The samples were immediately fixed in 4% formaldehyde buffered with sodium tetraborate (5 g/L).

In addition, physical parameters of the water, such as temperature, pH, dissolved oxygen, and salinity, were measured with a multiparameter probe. Water samples were also analyzed for phosphate, total phosphorus, nitrite, nitrate, ammonia nitrogen, phytoplankton density, and total organic carbon (Strickland and Parsons, 1972; Valderrama, 1981; Edler and Elbrächter, 2010).

Each sample was fractionated in a Motoda box splitter (Omori and Ikeda, 1984) before being divided into subsamples of 1/8 (P1 and P8), 1/16 (P2-P6 and P18-P20), 1/32 (P7, P8, P15, and P16), and 1/512 (P17) of the original. The organisms present were then counted under a stereomicroscope. The species were identified to the lowest taxonomic level possible according to Tregouboff and Rose (1957), Boltovskoy (1981, 1999), and Omori and Ikeda (1984).

The data were analyzed based on the absolute density, relative abundance (%), and frequency of occurrence across stations. The density of copepod species was expressed as the number of individuals per cubic meter of filtered water (ind./m^{-3}). Zooplankton occurrence was classified as very frequent ($>$ 70%), frequent (70–30%), infrequent (30–10%), or sporadic ($\leq$10%). Copepods were analyzed according to the Shannon-Wiener diversity index (H′, $\log_{10}$), Margalef's richness index (d), and Pielou's evenness index (J′).

To elucidate the effects of biological invasions on community structure, we used Spearman's ranked correlations to analyze the relationships between the NIS (*T. turbinata*) density and the community descriptors (H′, d, and J′). We also tested for possible correlations between the abiotic data and NIS density using Spearman's rank coefficient. The Mann-Whitney *U* test was used to compare NIS species density and Shannon-Wiener diversity index values inside the port and outside the port (on the continental shelf), and to assess differences in abiotic variables inside and outside the port.

We conducted a permutational multivariate analysis of variance (PERMANOVA) to ascertain whether copepod community distributions were significantly different between inside and outside the port. The significance level of all the statistical analyses was set to $\alpha = 0.05$ in the software packages Primer 6.0, PAST, and Statistica.

3. Results

3.1. Environmental variables

Temperature, pH, and salinity varied across the stations (27.8–28.0 °C, 7.7–8.1, and 37.5–37.9, respectively). Levels of nitrate (0.13 ± 0.04 mg/L; mean ± standard deviation), nitrite (0.02 ± 0.05 mg/L), ammonia nitrogen (0.03 ± 0.01 mg/L), phosphate (0.03 ± 0.01 mg/L), phosphorus (0.06 ± 0.04 mg/L), phytoplankton density (93,150 ± 35,559 ind./L^{-1}), and total organic carbon (14.99 ± 6.41 mg/L) did not significantly differ between stations inside and outside the port (Mann–Whitney *U* test, $p > 0.05$). Values for the 11 environmental variables measured at each site are shown in Supplementary material 1.

3.2. Copepod community

Individuals from three orders were detected in the study area: Calanoida, Cyclopoida, and Harpacticoida, which collectively comprised 17 species. *Temora turbinata* (NIS) had the highest density among the taxa (Table 1) and the highest relative abundance (78%) among the Copepoda, including its native congener, *Temora stylifera*. *Temora turbinata* was abundant at P15-P19 (inside the port) and was present at all stations, except P14 (Fig. 2A), and was dominant inside the port

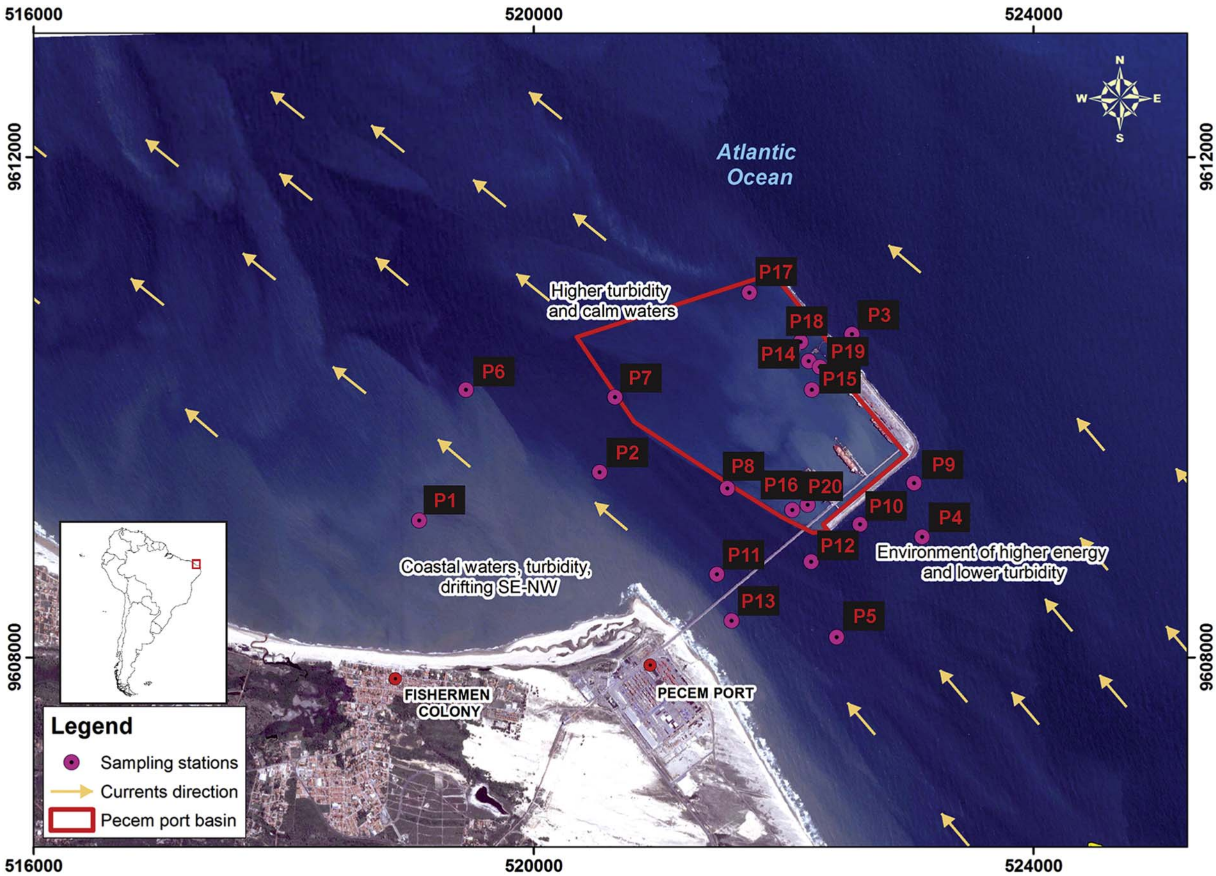

Fig. 1. Sampling stations (P1-P20) on the tropical Southwestern Atlantic Coast (Northeast Brazil). Stations P13 to P20 were in the inner basin of the Port of Pecém (red outline). Arrows indicate the water current direction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fig.2B). The NIS density inside the port was significantly higher ($p < 0.01$) than outside the port. However, the native *T. stylifera* was found at higher densities at a few stations (P14 and P20) inside the port. *Temora stylifera* was abundant at stations outside the port, particularly P1, P7-P10, and P12.

A multivariate analysis (PERMANOVA, $p < 0.037$) revealed that there was a significant difference in copepod community structure between inside and outside the port; outside the port, the community was more diverse (Fig. 2C), and the native *T. stylifera* was more abundant. Inside the port was significantly less diverse ($p = 0.0038$) than outside the port.

The NIS density was significantly, negatively correlated ($p < 0.05$) with the species evenness and richness of the Copepoda community ($r = -0.56$, $p = 0.012$, and $r = -0.70$, $p = 0.0008$, respectively). Shannon-Wiener index values and NIS density were not significantly correlated ($r = -0.40$, $p = 0.08$). Correlations between *T. turbinata* density and abiotic factors were not statistically significant ($p > 0.05$) (Supplementary material 2), except for phytoplankton density ($r = 0.923$, $p < 0.05$). Pielou's evenness (J′) varied from 0.15 to 0.83 (mean 0.55 ± 0.19). Because this metric reflects the relative abundances of different species, the low values (< 0.5) observed at stations P2, P7, P8, and P15 to P19 indicate the strong dominance of a few

Table 1
Frequency of occurrence and mean absolute density (± standard deviation) of copepod taxa at the study site.

Copepoda (Crustacea)	Frequency (%)	Mean density ± standard deviation (ind./m^3)
Acartia (Odontacartia) lilljeborgi Giesbrecht, 1889	55	0.17 ± 0.29
Centropages velificatus (Oliveira, 1947)	75	0.14 ± 0.23
Parvocalanus crassirostris (Dahl F., 1894)	30	0.01 ± 0.02
Paracalanus aculeatus Giesbrecht, 1888	95	1.25 ± 1.57
Temora stylifera (Dana, 1849)	90	0.46 ± 0.43
Temora turbinata (Dana, 1849)	95	21.03 ± 66.75
Undinula vulgaris (Dana, 1849)	25	0.02 ± 0.03
Labidocera spp.	30	0.04 ± 0.11
Calanopia americana (Dahl F., 1894)	60	0.08 ± 0.09
Clausocalanus furcatus (Brady, 1883)	20	0.01 ± 0.04
Pseudodiaptomus acutus (Dahl F., 1894)	15	0.01 ± 0.02
Macrosetella gracilis (Dana, 1847)	20	0.03 ± 0.11
Microsetella rosea (Dana, 1847)	10	0.00 ± 0.01
Euterpina acutifrons (Dana, 1847)	85	0.14 ± 0.23
Corycaeus spp.	100	3.27 ± 3.38
Oithona spp.	85	0.13 ± 0.32
Oncaea sp.	5	0.00 ± 0.01

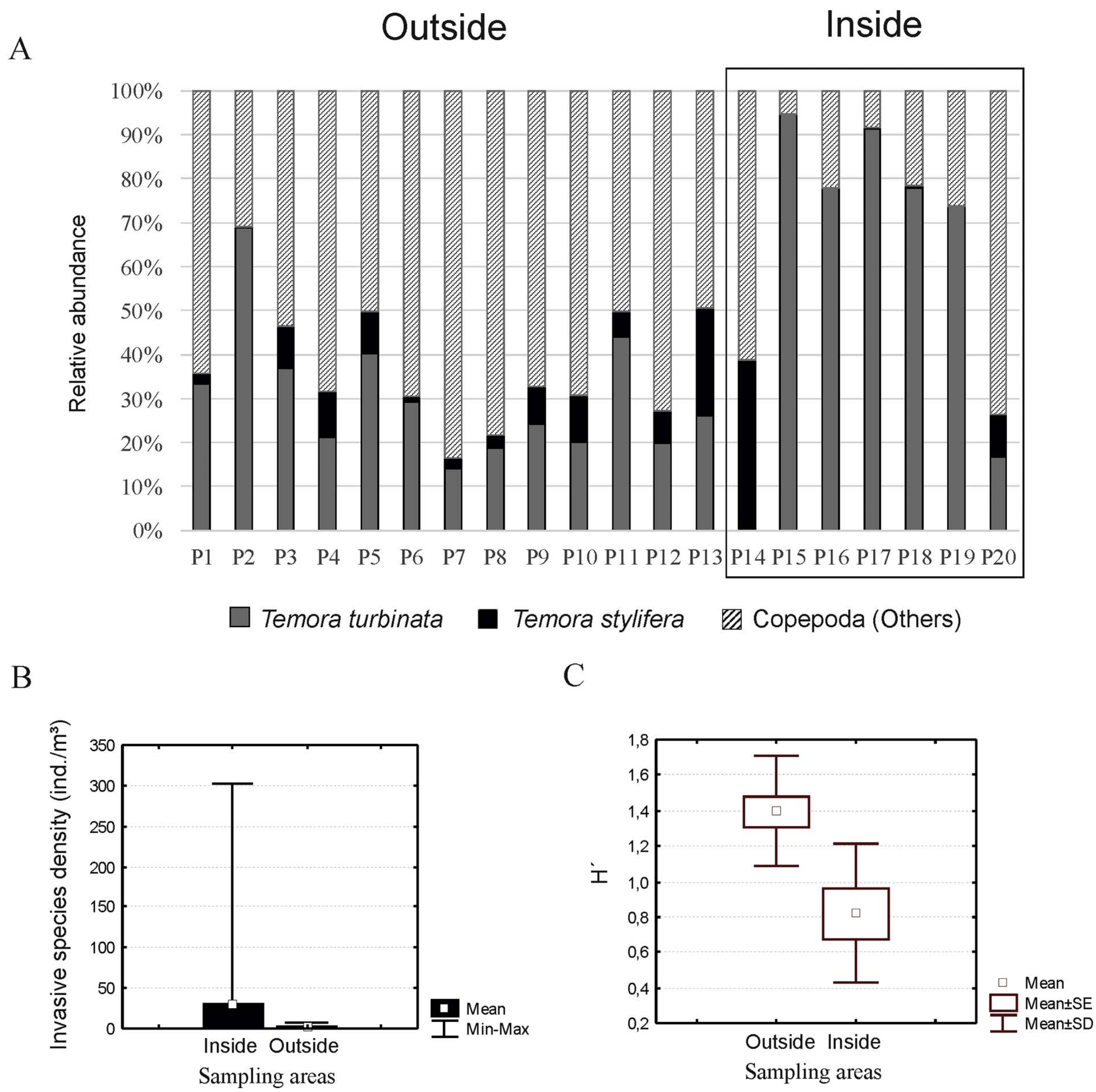

Fig. 2. (A) Relative abundances of two *Temora* species (NIS and native) and other Copepoda by station; (B) Mean *Temora turbinata* density outside and inside the port. The difference was significant (Mann-Whitney *U* test, $p = 0.0032$); (C) Shannon-Wiener index (H′) values outside and inside the port. The difference was significant (Mann-Whitney U test, $p = 0.0038$).

species, particularly *T. turbinata* and *Corycaeus* spp. Only stations P1, P5, P13, and P14 had evenness that was > 0.7 (Table 2).

The highest copepod density was observed at station P17, and the lowest at station P1 (Table 2). The diversity of copepod species across stations, according to the Shannon-Wiener index (H′), was 1.19 ± 0.43, and ranged from 0.27 to 1.85 at individual stations. Margalef's richness index (d) values ranged from 1.28 to 20.52 (Table 2). We observed the highest richness value (20.52) at the only station (P14) without the NIS (*T. turbinata*), which was dominated by *T. stylifera*.

4. Discussion

This study had two primary features: (I) we observed differences in species diversity, evenness, and richness in the copepod assemblage that were associated with the construction of an offshore port and the presence of the NIS, *T. turbinata;* and (II) We surveyed the plankton community in a little-studied region of the planet, which increased our knowledge of pelagic diversity and marine bioinvasions in tropical coastal ecosystems. Outside the port, native *T. stylifera* was abundant in many stations, suggesting that there is some degree of biotic resistance by tropical zooplankton communities against NIS invasions. We found that copepod communities inside the port were less diverse than those outside the port, and probably less resistant to NIS invasion.

We found that this NIS was dominant in the dry season, particularly inside the port; it had high average density and relative abundance. NIS density was negatively correlated with the evenness and richness of the copepod community. It is important to note that, although *T. turbinata* dominated *T. stylifera* at most of the inner stations in Pecém Harbor, coexistence between the two species occurred outside the port. The congener and native copepod *T. stylifera* was abundant at many stations outside the port, suggesting that the copepod communities were resilient against the invader away from the environmental conditions created by the construction of the port. *T. stylifera* is abundant in the middle and outer parts of continental shelves (Campos et al., 2017). Campos et al. (2017) suggest that there is a gradient of zooplankton distribution on this continental shelf. The copepod species have different functional traits and distinct cross-shelf distributions, where the

Table 2
Shannon–Wiener diversity index (H′), Pielou's evenness index (J′), and Margalef's richness index (d) values of copepods. Stations P14 to P20 (gray background), were in the port.

	Copepoda density (ind./m³)	H´	J´	d
P1	0.04 ± 0.07	1.73	0.83	-
P2	0.61 ±1.76	0.99	0.43	3.85
P3	0.69 ± 1.39	1.41	0.64	3.26
P4	0.48 ± 0.98	1.50	0.65	4.27
P5	0.31 ± 0.57	1.72	0.75	5.37
P6	0.18 ± 0.37	1.40	0.67	6.18
P7	0.46 ± 1.49	0.79	0.41	2.90
P8	0.43 ± 1.25	1.01	0.46	4.01
P9	0.50 ± 0.99	1.53	0.67	4.22
P10	0.38 ± 0.84	1.41	0.61	4.81
P11	0.29 ± 0.63	1.43	0.65	5.01
P12	0.34 ± 0.77	1.37	0.59	5.14
P13	0.32 ± 0.50	1.85	0.75	6.54
P14	0.08 ± 0.16	1.30	0.73	20.52
P15	2.20 ± 8.58	0.27	0.15	1.38
P16	2.19 ± 6.99	0.80	0.41	1.66
P17	19.38 ± 72.76	0.41	0.18	1.55
P18	1.66 ± 5.31	0.83	0.33	3.29
P19	0.31 ± 0.96	0.84	0.47	2.98
P20	0.63 ± 1.54	1.28	0.55	3.79

alien species (*Temora turbinata*) dominates the tropical coastal waters and probably impact nearshore plankton communities, and *Clausocalanus furcatus* is an indicator of outer-shelf waters.

The results of our study (2013, dry season) corroborate those from surveys conducted in 2005 (dry season) and 2006 (dry and wet seasons) (Garcia et al., 2007), indicating that *T. turbinata* dominance inside the port is well-established. The establishment of NIS in ecosystems is the subject of invasion ecology, which focuses on the identification of invasiveness characteristics of species that proliferate in novel habitats, habitat invasibility characteristics (Occhipinti-Ambrogi, 2007), or both. Lee et al. (2008) surveyed native and exotic biodiversity, and found that invasion patterns were related to biotic and abiotic factors.

In this study, we found that *T. turbinata* was only dominant inside the port; outside the port, the congener and native copepod *T. stylifera* was dominant. These findings elucidate NIS dispersion and the resilience of native copepod communities against invaders, and can be explained by (1) competition between the two congeners and (2) the environmental conditions in the offshore port.

The first explanation is based on the observation that the NIS (*T. turbinata*) was at higher densities than the native species (*T. stylifera*) inside the port. Interestingly, *T. stylifera* used to have the greatest density of any copepod present, before being replaced by the invading species inside the port in 2005 and 2006, after the port had started operating in 2002 (Garcia et al., 2007). In the oligotrophic waters of the tropical Southwestern Atlantic Ocean, *T. turbinata* probably has a higher resource acquisition rate than *T. stylifera* at the same resource density. *T. turbinata* differentiates between living and dead organisms, and rejects what it cannot digest (Wu et al., 2010), whereas *T. stylifera* is nonselective in its feeding behavior (Barreiro et al., 2011). The behavior of a filter-feeding copepod such as *T. turbinata*, which is constantly swimming, differs substantially to that of a slowly sinking ambush predator, such as *T. stylifera*, which has the advantage of not being detected until it attacks (Wu et al., 2010).

In a new habitat (e.g., inside a port), an invading species such as *T. turbinata* may have a competitive advantage over native species because it is a filter feeder, which is new to the resident community (Shea and Chesson, 2002). Gubanova et al. (2014) reported that two NIS copepods (*Acartia tonsa* and *Oithona davisae*) became established in the ecosystems of the Black Sea in the 1970s and 2000s, respectively. The success of these species was determined by their biological features, and by the vulnerability of the native copepod community to invasions (Svetlichny and Hubareva, 2014). In the Southwestern Atlantic Ocean, *T. turbinata* has mainly been found in coastal ecosystems (Ara, 2002; Silva et al., 2003, 2004; Sterza and Fernandes, 2006) and on the inner continental shelf (Campos et al., 2017). In the Taiwan Strait, this species is restricted to neritic environments, rather than being limited by temperature or salinity (Lan et al., 2009).

On the tropical coast of Brazil, *T. turbinata* appears to compete with, and exclude (or push further into the ocean), the native copepod *T. stylifera*, which was once common in coastal and estuarine areas of the Southwestern Atlantic Ocean (Campos et al., 2017). Ara (2002) suggested that *T. turbinata*'s has potential for genetic adaptation, and its tolerance to temperature, salinity, and pollution, favor its advance in continental waters. Recent research has revealed contaminants in Pecém Harbor that were produced by harbor activity (Moreira et al., 2017). This species has adapted to the environment near outfall outlets, and may exclude other zooplankton species that are less tolerant to pollution (Tseng et al., 2008).

The second explanation relates to the physical, environmental conditions of equatorial waters. We found no abiotic differences between locations inside and outside the port, and no significant correlations were found between them and the density of the NIS, except for phytoplankton density. In general, these ecosystems are environmentally stable in terms of temperature and salinity, and are oligotrophic because of the low concentrations of dissolved inorganic nutrients present. The hydrodynamic conditions that were created by the construction of the port may explain the dominance of the exotic species. *T. turbinata* had the highest density in the port basin (delimited by the L-shaped structure of the port), and the PERMANOVA analysis revealed that there was a significant difference in copepod community structure between inside and outside the port. The offshore terminal is protected by a rubble-mound breakwater in the shape of the letter L that is 1768 m in length (Fig. 1), the purpose of which is to create an artificial bay along the piers for berthing. This type of breakwater is generally trapezoidal in shape and contains a core of clay and rock fragments of varying sizes, whereas the sides are covered with sloping, larger stones that are designed to absorb wave energy (Buruaem et al., 2012). Because *T. turbinata* is more successful at low-turbulence sites (Wu et al., 2010), its abundance was high in the relatively calm and productive waters inside the port basin. NIS are usually abundant in ports, partly because of the high propagule delivery rate of these environments. An alternative explanation of why invasions are successful in ports and marinas is that the environmental degradation of these marine habitats favors the establishment of NIS (Marins et al., 2010; Ardura et al., 2017).

Our results provide a baseline assessment of a little-known tropical environment, because previous data on bioinvasions by zooplankton have mainly been obtained from studies conducted in lacustrine (Dzialowski et al., 2006; Havel and Medley, 2006; Rennie et al., 2011; Kelly et al., 2012; Papa et al., 2012) or temperate marine environments (Gubanova et al., 2014; Svetlichny and Hubareva, 2014).

According to previous studies conducted in the tropical Southwestern Atlantic Ocean (Boltovskoy, 1999; Schwamborn and Bonecker, 1996), the Copepoda is the most prevalent group of holoplankton (Dias et al., 2009; Melo Júnior et al., 2016; Campos et al., 2017). Among the Copepoda, *T. stylifera*, *Paracalanus aculeatus*, and *Corycaeus* spp. dominate in these pelagic ecosystems.

Important species in this tropical community were identified (Table 1). *Acartia (Odontacartia) lilljeborgi* is an estuarine and coastal organism (Björnsen, 1986; Bradford-Grieve et al., 1999) that is commonly found in the mangrove ecosystems of South Atlantic estuaries (Silva et al., 2003; Marcolin et al., 2010). *Centropages velificatus* is an oceanic and coastal species (Björnsen, 1986; Bradford-Grieve et al., 1999). *Clausocalanus furcatus* is one of the most abundant members of the Calanoida in oligotrophic epipelagic waters (Peralba and Mazzocchi, 2004) and coastal eutrophic regions (Mazzocchi and D'Alcalà, 1995). *Euterpina acutifrons* is a neritic organism (Villate, 1997) that is found in ecosystems with a high concentration of suspended particulate matter (Sautour and Castel, 1993), as at our study site. *Calanopia americana* is a vertical migrant that exhibits nocturnal and crepuscular habits at shallow (< 15 m) and deep (> 700 m) locations, and is most abundant in shallow water at night (Turner et al., 1979). *Macrosetella gracilis* and *Microsetella rosea* are found in tropical and subtropical marine regions that are usually poor in nutrients (Eberl et al., 2007), such as our study site (see Supplementary material 1).

The samples were obtained using subsurface plankton nets (200 μm net - mesozooplankton). Skjoldal et al. (2013) suggest that no single net is suitable to sample across the wide size range of zooplankton (microzooplankton to macrozooplankton). More detailed ecological studies, such as nictemeral sampling; and also a temporal data, with additional information from another trophic compartiments (like phytoplankton, microzooplankton and bacterioplankton) are needed to elucidate the role of invasive copepods in pelagic ecosystems.

Oceanographic sampling (copepods and nutrients) were conducted in the dry season. Drainage of estuaries and superficial flow from the continent may modify environmental characteristics of the continental shelf, thereby influencing the composition and distribution of the copepod community. Nonetheless, samples were collected during the dry season, when there is practically no outwelling in most estuaries (Campos et al., 2017). Santos et al. (2016) also indicate the strong influence of rainfall on the zooplankton composition in this tropical coast. To better understand the impacts of invasive species, it is important to conduct long-term monitoring including sampling stations in the oceanic domain and temporal series.

In conclusion, the results of this and previous studies provide evidence of the long-term dominance of a NIS in a tropical copepod community inside an offshore port. The density of the NIS inside the port was significantly higher than that outside the port; outside the port, the native congener *T. stylifera* was abundant and the community was more diverse, suggesting that some degree of biotic resistance by native communities against the invader exists.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2018.01.002.

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