

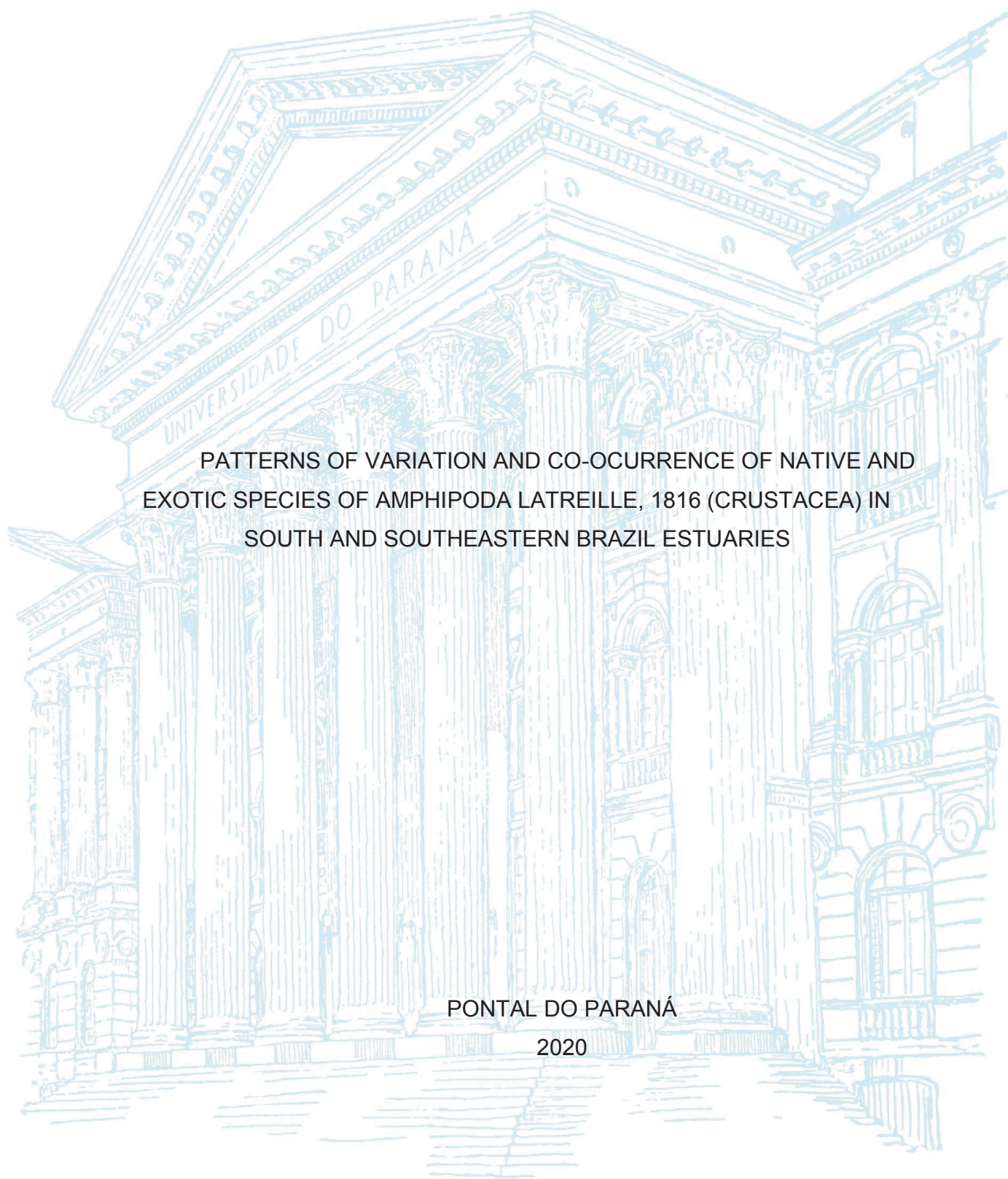
UNIVERSIDADE FEDERAL DO PARANÁ

JOÃO PAULO BOZINA PINE

PATTERNS OF VARIATION AND CO-OCCURRENCE OF NATIVE AND  
EXOTIC SPECIES OF AMPHIPODA LATREILLE, 1816 (CRUSTACEA) IN  
SOUTH AND SOUTHEASTERN BRAZIL ESTUARIES

PONTAL DO PARANÁ

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Orientador: Dr. Leonardo Sandrini Neto

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## ATA DE SESSÃO PÚBLICA DE DEFESA DE MESTRADO PARA A OBTENÇÃO DO GRAU DE MESTRE EM SISTEMAS COSTEIROS E OCEÂNICOS

No dia vinte e seis de março de dois mil e vinte às 13:30 horas, na sala Anfiteatro, Campus Pontal do Paraná - Centro de Estudos do Mar da UFPR. Avenida Beira Mar s/n, 83255-000, Balneário Pontal do Sul, Pontal do Paraná (PR), foram instaladas as atividades pertinentes ao rito de defesa de dissertação do mestrando **JOÃO PAULO BOZINA PINE**, intitulada: **PATTERNS OF VARIATION AND CO-OCCURRENCE OF NATIVE AND EXOTIC SPECIES OF AMPHIPODA LATREILLE, 1816 (CRUSTACEA) IN SOUTH AND SOUTHEASTERN BRAZIL ESTUARIES**, sob orientação do Prof. Dr. LEONARDO SANDRINI NETO. A Banca Examinadora, designada pelo Colegiado do Programa de Pós-Graduação da Universidade Federal do Paraná em SISTEMAS COSTEIROS E OCEÂNICOS, foi constituída pelos seguintes Membros: LEONARDO SANDRINI NETO (UNIVERSIDADE FEDERAL DO PARANÁ), SILVANA GOMES LEITE SIQUEIRA (UNIVERSIDADE ESTADUAL DE CAMPINAS), MAIKON DI DOMENICO (UNIVERSIDADE FEDERAL DO PARANÁ). A presidência iniciou os ritos definidos pelo Colegiado do Programa e, após exarados os pareceres dos membros do comitê examinador e da respectiva contra argumentação, ocorreu a leitura do parecer final da banca examinadora, que decidiu pela APROVAÇÃO. Este resultado deverá ser homologado pelo Colegiado do programa, mediante o atendimento de todas as indicações e correções solicitadas pela banca dentro dos prazos regimentais definidos pelo programa. A outorga de título de mestre está condicionada ao atendimento de todos os requisitos e prazos determinados no regimento do Programa de Pós-Graduação. Nada mais havendo a tratar a presidência deu por encerrada a sessão, da qual eu, LEONARDO SANDRINI NETO, lavrei a presente ata, que vai assinada por mim e pelos demais membros da Comissão Examinadora.

Pontal do Paraná, 26 de Março de 2020.

Assinatura Eletrônica

08/04/2020 18:24:33.0

LEONARDO SANDRINI NETO

Presidente da Banca Examinadora (UNIVERSIDADE FEDERAL DO PARANÁ)

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SILVANA GOMES LEITE SIQUEIRA

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## TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em SISTEMAS COSTEÍROS E OCEÂNICOS da Universidade Federal do Paraná foram convocados para realizar a arguição da Dissertação de Mestrado de **JOÃO PAULO BOZINA PINE** intitulada: **PATTERNS OF VARIATION AND CO-OCCURRENCE OF NATIVE AND EXOTIC SPECIES OF AMPHIPODA LATREILLE, 1816 (CRUSTACEA) IN SOUTH AND SOUTHEASTERN BRAZIL ESTUARIES**, sob orientação do Prof. Dr. LEONARDO SANDRINI NETO, que após terem inquirido o aluno e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de mestre está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

Pontal do Paraná, 26 de Março de 2020.

Assinatura Eletrônica

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## **AGRADECIMENTOS**

Primeiramente gostaria de agradecer aos meus pais Luiz Carlos Pine e Maria de Lourdes Bozina Pine, por desde pequeno incentivar meu interesse pela natureza, e por terem me fornecido todo o apoio e incentivo para chegar onde cheguei.

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## RESUMO

O agrupamento de organismos sésseis em substratos consolidados, conhecido como bioincrustação, fornece espaço adequado para animais epibiontes, como os anfípodos. A crescente substituição de habitat natural por construções portuárias fornece um ambiente homogêneo com baixa diversidade, e os navios internacionais que trafegam servem como vetores para espécies exóticas e oportunistas de Amphipoda. Existem estudos com Amphipoda nas costas sul e sudoeste do Brasil, mas eles se concentram principalmente em substratos naturais, e trabalhos anteriores nessa região com espécies exóticas em áreas portuárias não relataram ocorrência de Amphipoda. Portanto, as áreas afetadas pelos portos podem abrigar espécies introduzidas desconhecidas. Deste modo, este estudo teve como objetivo avaliar padrões de distribuição e abundância de anfípodos nativos e exóticos/criptogênicos, coletados utilizando placas de assentamento durante as estações seca e chuvosa entre 2017 e 2018. As coletas foram realizadas em quatro baías distintas: Paranaguá e Babitonga com a presença de portos internacionais, e Cananéia e Guaratuba que não possuem portos. Entre as espécies nativas investigadas, *Paracaprella pusilla* foi a única presente em todas as baías e estações. *Monocorophium acherusicum* estava ausente na baía de Babitonga, mas presente no restante das baías, enquanto *Stenothoe valida* teve baixa ocorrência em todas as amostras. A abundância de anfípodos exóticos/criptogênicos foi positivamente relacionada às baías com portos internacionais, e a presença de machos, fêmeas, fêmeas ovígeras e juvenis de *Elasmopus* sp., *S. gallensis* e *L. baconi* sugere que essas espécies têm populações bem estruturadas, estabelecidas e reproduzindo em baías portuárias. Isso pode indicar que esses anfípodos introduzidos têm potencial invasivo para se espalhar ainda mais se não forem controlados. As baías de referência não apresentaram um número significativo de espécies exóticas, mas alguns indivíduos de *S. gallensis* e *Apocorophium acutum* encontrados nessas baías podem sinalizar o início de seu processo de introdução. Sugerimos que os esforços de manejo se concentrem nas baías mais afetadas e sejam observados os regulamentos para evitar dispersão para as áreas próximas.

Palavras-chave: Anfípoda. Espécie exótica. Invasão. Substrato artificial. Placas de assentamento.

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## ABSTRACT

The assemblage of sessile organisms in marine hard substrate is known as biofouling, these organisms provide suitable space for epibiont animals such as Amphipods. The increasing replacement of natural habitat by port constructions offers a homogeneous environment with low diversity, and international ships passing serve as vectors for exotic and opportunistic Amphipoda species. There have been studies with Amphipoda on the south and southwestern coasts of Brazil, but they mainly focus on natural substrates, and previous work in this region with exotic species in port areas has not reported any Amphipoda. So port-affected areas could be harbouring unknown introduced species. Thus, this study aimed to assess the abundance and population structure of native and exotic/cryptogenic amphipods collected with settlement plates during the dry and rainy seasons between 2017 and 2018. Specimen collection was performed in four different bays: Paranaguá and Babitonga with the presence of international ports and Cananéia and Guaratuba without ports. Among the native species investigated, *Paracaprella pusilla* was the only one present in all bays and seasons, *Monocorophium acherusicum* was absent from Babitonga port bay, but present in the rest of the bays, and *Stenothoe valida* had very low presence across all samples. The high abundance of exotic/cryptogenic amphipods was positively correlated to bays with international ports, and the presence of males, females, ovigerous females and juveniles of *Elasmopus* sp., *S. gallensis* and *L. baconi*, suggests these species have well-structured populations currently established and reproducing in port bays. This could mean these introduced amphipods have invasive potential to spread even further if left unchecked. The reference bays did not have a significant number of exotic species, but the initial findings of some individuals of *S. gallensis* and *Apocorophium acutum* may signal the beginning of their introduction process. We suggest management efforts should focus on the more affected bays, and enforcing regulations to prevent further dispersal to nearby areas.

Keywords: Amphipods. Exotic species. Invasion. Artificial substrate. Settlement plates.

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## **1 INTRODUCTION**

In marine hard substrate, the community of sessile organisms is commonly known as biofouling, which is typically composed of macrophytes and invertebrates like hydroids, bryozoans, mussels and barnacles (Bulleri 2005; Floerl and Inglis 2005). Besides colonizing natural habitats, these organisms are capable of attaching to artificial structures such as ship's hulls, buoys, pontoons and other submerged buildings (Ashton et al. 2006a; Ros et al. 2013a).

Assemblage of sessile organisms increase the structural complexity of the substrate and the branches, stems or shells of biofouling individuals offer habitat and resources to a wide variety of associated mobile epibiont animals such as amphipods, isopods and gastropods (Ros et al. 2013b). Amphipods are adapted to cling on these fouling organisms, or build tubes upon them, thus getting access to food, whilst also having protection from predators (Cunha et al. 2017).

Amphipoda Latreille, 1816 (Crustacea, Peracarida) is a very diverse group, with 10192 species described spread across 223 families and 1618 genera. Amphipods are small crustaceans, which can colonize a wide variety of habitats (Lowry and Myers 2017; Horton et al. 2020). Amphipod females, like other Peracarids, have a marsupium, where they hold the eggs until the hatching, they have direct development, so there are no larvae and there's lack of a free swimming stage. Despite this low dispersal capacity, there are many amphipod species considered cosmopolitan (Ros et al. 2015).

Most amphipods are benthic, usually found in the sediment, or hard substrata associated with biofouling; many amphipods are detritivores, and they are an important part of the food chain and nutrient cycling (Chapman 2007; Lowry and Myers 2017). Amphipod diversity is often greater in less disturbed coastal environments as opposed to places with high anthropic influence (Mottaghi et al. 2017). Surprisingly, artificial substrates can support higher abundances than natural ones, but they are usually dominated by opportunistic and exotic species. While the species richness and native amphipod abundance are usually higher in rocky shores and coral reefs than on man-made structures (Paz-Ríos et al. 2018).

Furthermore, replacement of available natural habitat with artificial structures for human use, such as pontoons and docks provide a new space to the formation of a less diverse biofouling community and associated epifauna (Glasby et al. 2006; Heldt et al. 2018). The homogenous artificial substrate found in ports and marinas, along with high levels of pollution and shipping traffic, favor the colonization of tolerant species. These environments usually have low diversity and a high abundance of exotic and cryptogenic amphipods (Bulleri 2005; Gartner et al. 2016).

Introduced amphipods can remain undetected for long periods of time in biofouling on artificial substrates, and there are many species with uncertain origins, known as cryptogenic, that can be overlooked due to incomplete knowledge, and researchers may fail to report them (Marchini and Cardeccia 2017). There are records of exotic amphipods in estuaries all over the world, however the real number of introduced species might be greater than reported in

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the literature; in places where monitoring is not conducted regularly, early detections are rare (Ricciardi 2015; Ros et al. 2015; Marchini and Cardeccia 2017). Live trade of marine organisms and aquaculture facilities can bring along unwanted species associated with equipment fouling and species of economic importance (Ricciardi 2015; Fernandez-Gonzalez and Sanchez-Jerez 2017). Still the most important vectors of exotic species in marine habitats are international ships that can carry animals in the ballast water or attached to the ship's hull fouling (Ros et al. 2013b). There are regulations to prevent dispersal of exotic species by ship's ballast water; which prevents the entry of swimming animals or animals with a planktonic larval stage (IMO 2014). The cleaning of the hull outside the water helps prevent dispersal of sessile species and associated epifauna, but that control is not always observed (Minchin et al. 2006; Lacoursière-Roussel et al. 2016).

The settlement and consequent dispersal of exotic species is primarily dependent on the number of introduction events and the amount of individuals released in each event, known as propagule pressure (Lacoursière-Roussel et al. 2016). Locations with high shipping activity, like marinas and ports, may facilitate invasions of exotic species due to their high propagule pressure (Lockwood et al. 2009). These places have been pointed as important environments for the entry and dispersal of exotic species given the traffic of vectors and the habitat promptly provided by ship hull and artificial structure biofouling (Ros et al. 2013b; Rumbold et al. 2016). These factors coupled with exotic species tolerance to human disturbances, are likely the reason for their high abundance in many port areas (Murray et al. 2014; Gartner et al. 2016).

It is important to assess if an exotic species is newly introduced or already established where they are found, since populations in distinct stages may cause different impacts in the local ecosystem (Truhlar and Aldridge 2014; Molnar et al. 2008). Apart from high abundances, the presence of amphipod males, females, ovigerous females and juveniles are signs of well-established populations that are successfully reproducing (Peters and Robinson 2017; Lo Brutto et al. 2016).

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Some exotic amphipods may reproduce all year long in their introduced range, which accelerates their spread even further; and can be an indicative of their invasive potential (Rumbold et al 2016; Peters and Robinson 2017). In some extreme cases, if left unchecked introduced amphipods can reach densities up to 750000 individuals per square meter and eliminate native species in the most affected areas (van den Brink et al. 1993).

Each exotic species may have different impacts on the local ecosystem, and their invasive potential depends on the rate of their spread (Molnar et al 2008). When non-native species successfully establish and spread in a new region to the point of causing damage to the local ecosystem, they are classified as invaders (Ricciardi 2015).

Biological invasions in marine habitats are a growing problem in a globalized world (Mack et al. 2000; Floerl and Inglis 2005; Ricciardi 2015). Invaders may cause damage through predation and competition, and displace or even remove native species, causing changes in the food chain and nutrient cycling, leading to a biodiversity loss (Mack et al. 2000; Jänes et al. 2015).

Management actions towards exotic species are usually taken when their populations are well-established and start causing economic and environmental damage; at this point, actions are scarcely successful in eliminating the invader (Iacarella et al. 2015; Jänes et al. 2015; Ricciardi 2015). For this reason, research on exotic amphipods is important to identify the presence of potentially invasive species before they become a problem, and recognize which places are most vulnerable and need management.

Potential invaders usually have a well-documented history in other places where they have established, and comparing that information with new data might help us identifying which places have conditions that could facilitate their invasion process (Ricciardi et al. 2012; Iacarella et al. 2015; Ricciardi 2015). Still, many coastal locations remain poorly-studied, and there is still much to research on introduced amphipods in artificial substrates (Lacoursière-Roussel et al. 2016; Marraffini et al. 2017).

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To the extent of our knowledge, there have been a few studies with amphipods in Brazil's Southern coast. The literature is scarce and most of the current knowledge is on a few families like Aoridae, Dexaminidae, Ampithoidae, Hyalidae and Caprellidae in association with a variety of sessile organisms in natural substrate (Jacobi 1987; Dubiaski-Silva and Masunari 1995; Serejo and Licínio 2002; Valério-Berardo and Flynn 2002; Alegretti et al. 2016; Mauro and Serejo 2015; Cunha et al. 2017; Garcia et al. 2019). Most of these studies are focused on the occurrence of amphipods on natural habitats.

In our study region there were some works on artificial substrate biofouling in ports and marinas, and the occurrence of exotic species, however there is little mention of amphipods, and the species reported are either native, cryptogenic or unclassified (Ignacio et al. 2010; Bumbeer and Rocha 2016; Neves et al. 2007; Neves and Rocha 2008; Rocha et al. 2010) therefore exotic/cryptogenic amphipods might have been present in this area but were not reported.

In this sense, the main goal of this study was to analyze the spatio-temporal distribution, population structure and co-occurrence patterns of some common native and exotic amphipods associated with artificial substrate fouling in estuaries of the southern and southeastern coasts of Brazil. We expected amphipod abundance to significantly vary in relation to different seasons and levels of stress in each bay. We predicted higher abundances of exotic and cryptogenic species in impacted bays associated with the presence of international ports compared to reference bays. Where there is co-occurrence of native and exotic amphipods, if they are competing for food and space we presume to find a greater number of exotics than natives in the locations they are well-established.

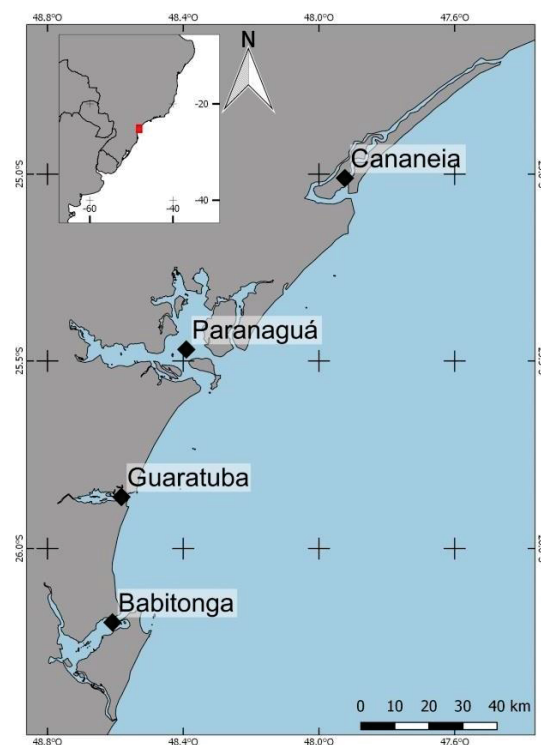
With the results of this study we hope to identify exotic species that are potential invaders and places more vulnerable to invasion, in order to help future management and control efforts.

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## 2 MATERIALS AND METHODS

### 2.1 STUDY AREA

In total, four bays with two different levels of stress were assessed: Babitonga and Paranaguá bays have international ports, whereas Cananéia and Guaratuba bays were considered reference areas (Fig.1).



**Fig. 1** – Study Area, indicating Cananéia, Paranaguá, Guaratuba e Babitonga bays.

Encompassing Cananéia and Paranaguá estuarine complexes, is the Lagamar region, extending from São Paulo to Paraná state. It comprehends many state and national parks and is located inside Brazil's largest continuous rainforest remnant. Moreover, Lagamar is one of the most productive estuarine regions of the world; considered a biodiversity hotspot and, therefore, a priority to conservation efforts (IPeC 2012). This region has a predominant Subtropical climate, with two

defined seasons: a warm and rainy summer and a winter with decline in temperature and precipitation (Lana et al. 2001).

We chose Cananéia and Guaratuba to serve as reference areas for comparison, although these two estuaries are adjacent to the other two, and are affected by human occupation, they do not have the stress associated with the presence of International ports. In contrast, Paranaguá Estuarine Complex (PEC) and Babitonga Bay were chosen as stressed areas in order to study the influence of international ports on native and exotic Amphipoda species.

In 1935 the international port D. Pedro II was built in Paranaguá. The presence of this port turned the region into an important economic center, which caused an increase in human occupation, urbanization and building of artificial structures such as pontoons, pilings and marinas (Caneparo 2000; Lana et al. 2001). Since the port is located further upriver, the two channels in the mouth region of this estuary have to be constantly dredged to allow for the constant traffic of international cargo ships (Angulo et al. 2006; Lamour et al. 2007).

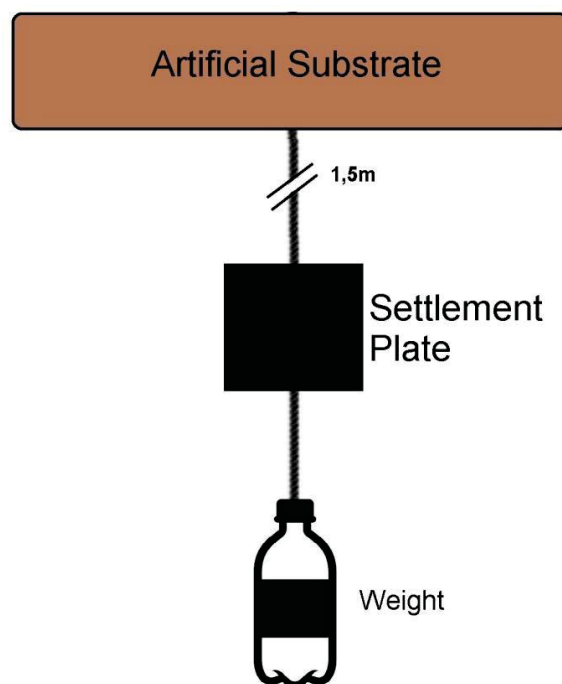
Similarly, further south in the state of Santa Catarina, in Babitonga Bay, we find disturbed conditions associated with human occupation, port buildings, dredging and international ship traffic (Angulo et al. 2006; Goularti-Filho 2008; Mazzer and Gonçalves 2012; Martins Junior and Martins 2019). In this bay there are two international ports, one in São Francisco do Sul built in 1955 and another port recently built in Itapoá in 2011.

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## 2.2 SAMPLE COLLECTION

In studies with biofouling and introduced species, settlement plates are a commonly used artifact, and are considered an important tool for the detection of exotic species present in an estuary. These plates are submerged and overtime allow the development of a biofouling community and associated mobile fauna. The species that colonize the plate are a reflex of those present in the surrounding area that are adapted to live in artificial substrate (Cribb and Marshall 2005; Palardy and Witman 2014; Gartner et al. 2016; Marraffini et al. 2017; Wijnhoven et al. 2017; Gestoso et al. 2018).

Settlement plates can have a variety of designs, in the case of our study each settlement plate consisted of a 12x12 cm black sanded polyethylene square, vertically clamped to a rope with a weight in order to maintain the plate submerged at about 1.5 m deep. These plates were hung to available floating substrates and artificial structures (Fig. 2).



**Fig. 2** – Scheme of the Settlement Plates installed for collection of native and exotic/cryptogenic amphipods associated with artificial substrate biofouling.

To evaluate the effects of different seasons on native and introduced amphipods, in each of the four bays settlement plates were installed in two different seasons: Dry (June/2017) and Rainy (December/2017). In order to cover more time scales and different periods of each season, two time treatments were carried out: plates that were underwater for 90 days and plates that were underwater for 180 days. This allowed us to verify if the amount of time the plates remained submerged had any effect on the amphipods abundance.

For each Season and Time treatment five replicates were installed in Cananéia, Guaratuba and Babitonga, and 10 replicates in Paranaguá Estuarine Complex to encompass the mouth of the estuary and the near-port areas, since this estuary is larger and the Port is located further upriver. To better cover each area the plates were installed with at least 10 m distance between replicates.

At the end of each colonization time, the plates were wrapped in plastic bags still inside the water in order to avoid mobile fauna escape, then removed and afterwards put in 96% alcohol and taken to the lab. The mobile macrofauna was separated by washing the plates over a 500 µm sieve. The specimens were identified to the lowest possible taxa, with the help of experts and relevant literature (e.g. Lecroy 2000, 2002, 2004, 2007, 2011; Mauro and Serejo 2015; Krapp-Schickel 2015). The identified material was added to the Zoology Department collection at Universidade Federal do Paraná.

For this study, we selected some native and exotic/cryptogenic Amphipoda amongst the collected material; the species of interest were common amphipods that could be used for comparison. The chosen species were the natives: *Stenothoe valida* Dana, 1852, *Monocorophium acherusicum* (Costa 1853) and *Paracaprella pusilla* Mayer, 1890, and the exotic/cryptogenic: *Stenothoe gallensis* Walker, 1904, *Elasmopus* sp. Costa, 1853, *Apocorophium acutum* (Chevreux, 1908) and *Laticorophium baconi* (Shoemaker, 1934).

The abundance data was collected by counting the number of individuals per plate, and the population structure was assessed by looking at the number of individuals divided in four sex/age groups: males, females, ovigerous females (those with fully formed marsupium with at least one egg) and juveniles (individuals

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with no distinguishable sexual traits), in order to assess species structure, and if each species is well established and/or reproducing.

Three of the species selected in this study are amphipods from the Corophiidae family: *M. acherusicum*, *L. baconi* and *A. acutum*. Here we consider *M. acherusicum* as the only native species, and the other two as exotic. These Corophiids are tube-building species, so could be competing for space in the substrate.

Two of the selected species are from the genus *Stenothoe*: *S. gallensis* is an exotic amphipod that has a group of very alike congeners worldwide, whilst *S. valida* is native to the Brazilian coast, and although it doesn't belong to the *S. gallensis* species group, it is still very similar to them (Krapp-Schickel, 2015). These two species have minor morphological differences so they might occupy the same niche in the ecosystem and thus compete directly.

One of the chosen species, *Paracaprella pusilla*, is a Caprellid that was proposed as native to the western Atlantic coast (Cabezas et al. 2019). This amphipod has spread beyond its native range and reached other parts of the world including Europe where it is considered an invader, so *P. pusilla* could be a tolerant and opportunistic species potentially able to colonize artificial substrate biofouling (Wakabara et al. 1991; Mauro and Serejo 2015; Ros et al. 2016; Machado et al. 2019).

The last species chosen is *Elasmopus* sp., a cryptogenic amphipod found in our samples that still needs more research on its exact origins. Our identification matches those of the "*Elasmopus pecteniscrus*" species complex (Krapp-Schickel and Ruffo 1990) and it could be a member of this cosmopolitan group.

## 2.3 STATISTICAL ANALYSIS

The abundance data of each species was used for the univariate analyses, and the structure of the sex/age groups was used for the multivariate analyses. Both analyses were performed using the fixed factors: Stress (two levels: Port and Reference) and Season (two levels: Dry and Rainy, crossed with Stress), and the

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random factors: Bay (four levels: BB Babitonga and PEC - Paranaguá Estuarine Complex nested within level Port of Stress factor and CN – Cananéia and GT - Guaratuba nested within level Reference of Stress) and Time (four levels: 90 and 180 days, nested in each Season).

The effects of the fixed and random factors on the abundance of each Amphipoda species were tested by Generalized Linear Mixed Models (GLMMs), which is a good approach for analyzing nonnormal data and can also include random effects (Bolker et al. 2009).

First we checked which probability distribution family best fitted each species' abundance numbers (Poisson, Negative Binomial 1, Negative Binomial 2, with and without adjustment for zero-inflation), and selected the best fit using the Akaike Information Criteria (AIC) as parameter for choosing, then made sure the data had no overdispersion. Second we contrasted a Generalized Linear Mixed Model containing all of the fixed and random factors against different models with only one random factor, or no random factors and based on AIC values, chose the model that best explained each species abundance data. Significance of the fixed factors in the model was assessed and non-significant terms (at  $\alpha = 0.05$ ) were removed. The final model was refitted using restricted maximum likelihood (REML) estimation. Finally, post-hoc pairwise tests were conducted on those factors of the final model that had significant effect on a species' abundance. Normality of residuals and homogeneity assumptions were conducted according to Zuur et al. (2009).

Univariate analyses were performed using R statistical software (R Core Team 2019) in addition to the packages “glmmTMB” for adjusting the generalized linear mixed models (Brooks et al. 2017), “car” for ANOVA tests (Fox and Weisberg 2019), “bbmle” for AIC values comparison (Bolker and Team 2017) “emmeans” for post-hoc pairwise comparison tests (Lenth et al. 2020) and “ggplot2” for graphical representation of data (Wickham 2011).

For multivariate analyses we used number of males, number of females, number of ovigerous females and number of juveniles and the proportion between these sex/age groups of each species as response variables, to check the effects

of the factors on amphipods population structure, and the contribution of each group to dissimilarity between samples.

A Principal Coordinates Analysis (PCoA) was plotted in order to display variation patterns between amphipod populations from different bays and sampling times. To test the significance of the fixed and random factors, and the interaction between them on amphipods population structure, a permutational multivariate analysis of variance (PERMANOVA) was performed using 9999 permutations and  $n=5$  replicates (except for PEC with  $n=10$ ). Furthermore, a Similarity Percentage (SIMPER) analysis was performed to assess the contribution of each Sex/Age group to the dissimilarity between samples from different levels of Stress and Seasons.

Multivariate analyses were based on a Bray-Curtis Dissimilarity matrix of the number of males, females, ovigerous females and juveniles, which were transformed to  $\ln(x+1)$  prior to the tests. These analyses were performed using the PRIMER v6 software along with PERMANOVA+ add-on (Clarke and Gorley 2006; Anderson et al. 2008).

### 3 RESULTS

#### 3.1. AMPHIPODS

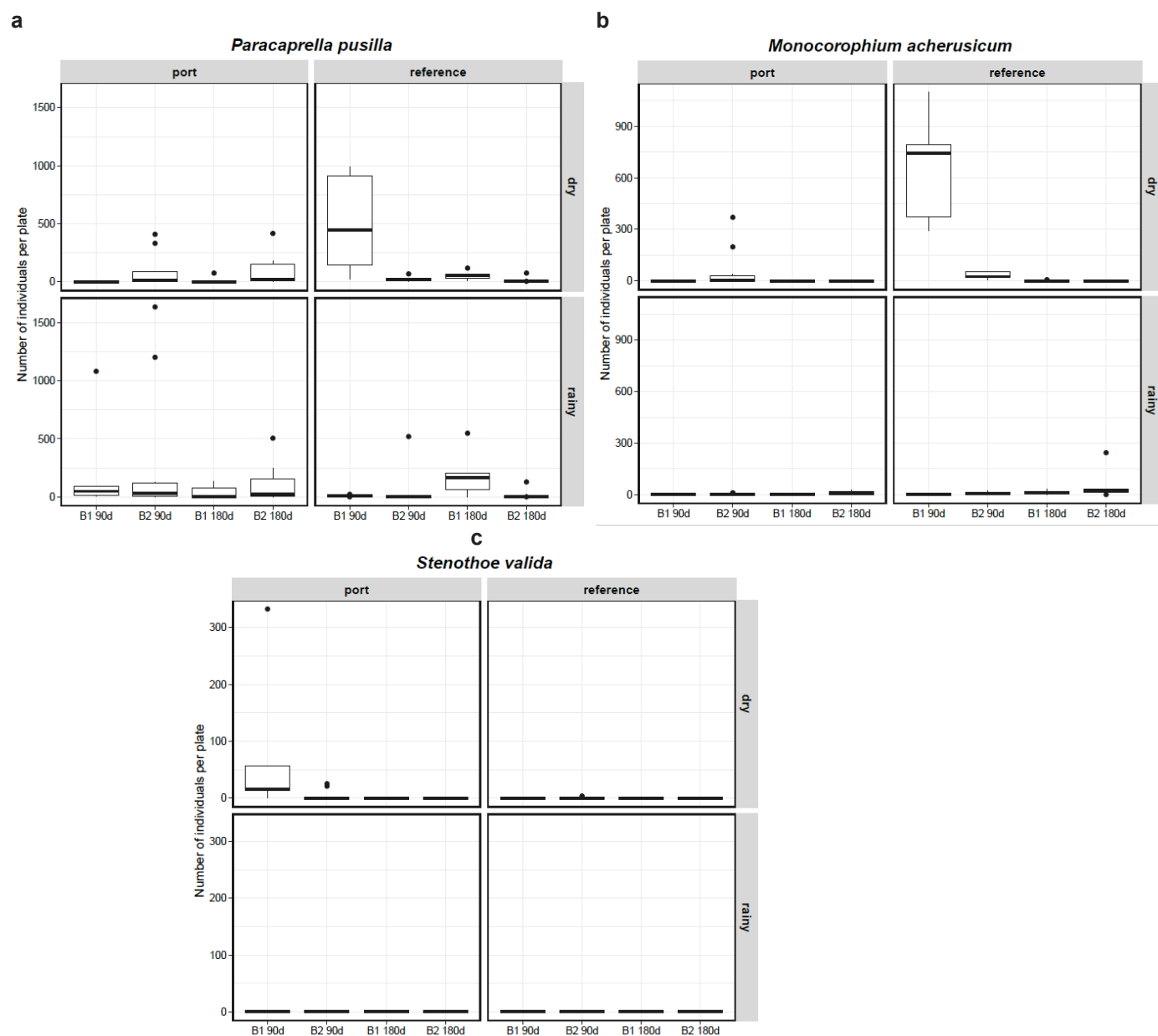
A total of 85623 amphipods were collected, distributed among the seven species. The most abundant species across all the locations was *S. gallensis*, followed by *L. baconi*, *P. pusilla*, *Elasmopus* sp., *M. acherusicum*, *A. acutum* and last *S. valida*. The location with highest total abundance was Babitonga (55% of total), second was Paranaguá (33.2%), then Cananéia (9%) and finally Guaratuba (2.8%).

The abundance of each Amphipoda species in different bays and time treatments is shown in the boxplots of the natives *P. pusilla*, *M. acherusicum* and *S. valida* (Fig. 3) and the exotic/cryptogenic *Elasmopus* sp., *L. baconi*, *S. gallensis* and *A. acutum* (Fig. 4).

The native *P. pusilla* was present in all bays and seasons, only absent in samples from Babitonga 90 days after plates installation in the dry season (Fig. 3a). The native corophiid *M. acherusicum* was absent in Babitonga bay, but present in all other bays in both seasons, with an outlier high abundance in the plates from Cananéia that remained submerged for 90 days in the dry season (Fig. 3b).

*Stenothoe valida* is a common native amphipod, however it was found in very few samples of this study, this species was found in greater numbers in Babitonga (89.5% of total), then PEC (9.6%) and last Guaratuba (0.9%), in Cananéia no individuals of this amphipod appeared in any of the plates (Fig. 3c).

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**Fig. 3** - Number of native amphipod individuals in bays with international ports and reference bays in the dry and rainy seasons (a- *P. pusilla*, b- *M. acherusicum*, c- *S. valida*). In the Port bays, B1 = Babitonga e B2 = Paranaguá and in the Reference bays B1 = Cananéia e B2 = Guaratuba. In all bays plates were recovered after 90 days and 180 days both in the dry and rainy seasons. For each combination between bay and time n=5 plates were deployed, except in Paranaguá where n=10 plates were deployed

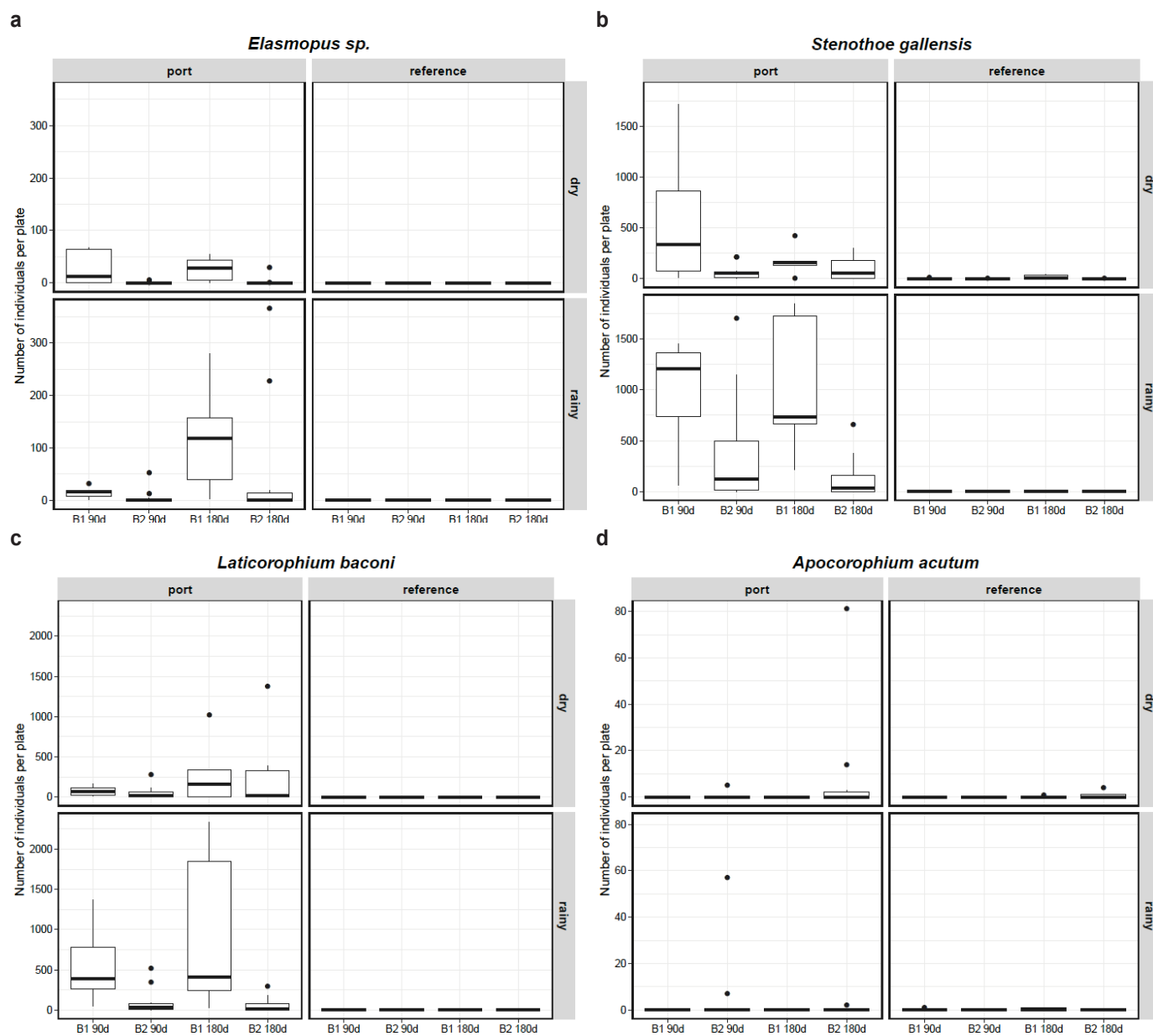
The cryptogenic *Elasmopus* sp. was absent in both reference bays, and had a pronounced presence in Babitonga bay (Fig. 4a). The exotic Stenothoidae *S. gallensis* was found in both port and reference bays, however in the reference bays this species appeared in very few samples only in the dry season, and its numbers were too low to properly serve as comparison between levels of stress. Nearly all individuals (99.7%) of this exotic amphipod were found in bays with international ports (Fig. 4b).

The corophiid *L. baconi* was an exotic species absent in the Reference bays and with high abundances in the Port bays (Fig. 4c). The third corophiid investigated in this study, the exotic *A. acutum* was absent from Babitonga bay, and had very low numbers in Cananéia (0.3% of total) and Guaratuba (0.3%), the only bay that seems to have a reasonable number of individuals is PEC (99.4%) (Fig. 4d).

Given the very low occurrence of the native *S. valida* and the exotic *A. acutum*, the same analyses performed for the other species could not be applied; however looking at their abundance we can further discuss them in a more descriptive manner. Also, the exotic/cryptogenic *Elasmopus* sp. and *L. baconi* only occurred only in bays with international ports, and *S. gallensis* and *A. acutum* had extremely low numbers in the reference bays, therefore, analyses for these taxa were conducted excluding the factor Stress, since reference areas were not comparable.

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**Fig. 4** - Number of exotic/cryptogenic amphipod individuals in bays with international ports and reference bays in the dry and rainy seasons (a-*Elasmopus sp.*, b- *L. baconi*, c- *S. gallensis*, d- *A. acutum*). In the Port bays, B1 = Babitonga e B2 = Paranaguá and in the Reference bays B1 = Cananéia e B2 = Guaratuba. In all bays plates were recovered after 90 days and 180 days both in the dry and rainy seasons. For each combination between bay and time n=5 plates were deployed, except in Paranaguá where n=10 plates were deployed

### 3.2. EFFECTS OF STRESS AND SEASON ON AMPHIPODS ABUNDANCE

After the selection of the generalized linear mixed model that best explained the abundance of each species, ANOVA tests revealed the significance of the factors and their interaction, and the Post-hoc tests compared the levels of the significant factors (Table 1).

**Table 1** - Analysis of deviance table for the response of amphipod abundance to each factor of the best fitted generalized linear mixed model (GLMM) ( natives: a - *P. pusilla*, b - *M. acherusicum*, exotic/cryptogenic: c - *Elasmopus* sp., d - *S. gallensis*, e - *L. baconi*). The degrees of freedom and p values for each factor are presented and significant terms ( $\alpha = 0.05$ ) are highlighted in bold. Post-hoc analyses between levels of the significant factors are presented below.

a- <i>P. pusilla</i>				Post-hoc tests
Factor	Chisq	Df	Pr (>Chisq)	Stress (Port): Dry<Rainy
Stress	3.929	1	0.0695	Stress (Reference): Dry=Rainy
Season	0.402	1	0.5259	Season (Dry): Port<Reference
Stress x Season	6.159	1	<b>0.0131</b>	Season (Rainy): Port=Reference
b - <i>M. acherusicum</i>				
Factor	Chisq	Df	Pr (>Chisq)	
Stress	0.9035	1	0.3419	
Season	0.0197	1	0.8884	
Stress x Season	0.1986	1	0.6559	
c - <i>Elasmopus</i> sp.				
Factor	Chisq	Df	Pr (>Chisq)	Season: Dry<Rainy
Season	3.752	1	<b>0.0528</b>	
d - <i>Stenothoe gallensis</i>				
Factor	Chisq	Df	Pr (>Chisq)	Season: Dry<Rainy
Season	4.523	1	<b>0.0334</b>	
e - <i>L. baconi</i>				
Factor	Chisq	Df	Pr (>Chisq)	
Season	0.1998	1	0.6549	

The abundance of *P. pusilla* was not influenced by any of the random factors, as for the fixed factors, neither stress nor season alone had an effect on this native amphipod abundance, but ANOVA test showed a significant influence of

the interaction between Stress and Season (Table 1a). Post-hoc tests reveal that when comparing samples from Port and Reference locations over each season, the abundance of *P. pusilla* in the rainy season did not differ between stress levels, however in the dry season this species show a significantly higher abundance in the Reference bays. Furthermore, when comparing samples from the Dry and Rainy seasons for each stress level, the abundance of *P. pusilla* in the reference bays remains somewhat similar across both seasons, on the other hand, in the port bays this native species was significantly more abundant in the rainy season.

The levels of stress and the changes between seasons had no effect on the abundance of *M. acherusicum* (i.e., none of the fixed factors were significant) (Table 1b). The model that best explained this native species abundance included only the random factors Bay and Time.

Because of the absence of *Elasmopus* sp. from the reference bays, the levels of Stress could not be compared, so the best model for explaining this cryptogenic amphipod's abundance included only Season as fixed factor, and had no significant random factor. The ANOVA results show a weak correlation between the season and the abundance of this cryptogenic species (Table 1c), and post-hoc tests show that *Elasmopus* sp. appears to have a marginally significant higher abundance in the rainy season.

The nearly insignificant numbers of the exotic *S. gallensis* in the reference bays could not be used for comparison, so the factor stress was excluded, and the model that best explained this species abundance included only Season as fixed factor and Bay as random factor. The results of ANOVA show that the abundance of this amphipod is significantly affected by the season (Table 1d); and the post-hoc test reveals that *S. gallensis* abundance was significantly higher in the rainy season.

Another amphipod absent from the reference areas is the exotic *L. baconii*; besides excluding the factor stress, the season had no significant effect on the abundance of this species, so the model that best explained the abundance of *L.*

*baconi* had no fixed factors and only included Bay as random factor. The results of ANOVA show no significant factor (Table 1e). The contribution of Bay as an effect may be related to higher abundances found in Babitonga than PEC.

### 3.3. EFFECTS OF STRESS AND SEASON ON AMPHIPODS POPULATION STRUCTURE

Using the proportion between sex/age groups we were able to assess how much each group contributes to the dissimilarity between populations as shown in the SIMPER results (Table 2), in all species tested, females outnumbered males and contribute more to variation between populations from different seasons and stress levels.

The average dissimilarity of the native *P. pusilla* in samples from Port and Reference bays was 67.6%, with females contributing to 27.41% and juveniles 27.25% of the difference in populations, with higher numbers in the reference bays. The average dissimilarity between populations from the dry and rainy seasons was 67.4% and juveniles and females represented 26.62% and 26.11% of the variation respectively, with higher abundances in the rainy season (Table 2a).

The populations of the native *M. acherusicum* had average 85.5% dissimilarity between port and reference mostly due to juveniles and females which contributed to 37.12% and 35.72% respectively, with highest numbers in the reference bays. In regards to seasonality, populations had average 83.5% dissimilarity between dry and rainy seasons, and again juveniles and females were responsible for most of the variation with 45.56% and 32.68%, achieving higher numbers in the dry season (Table 2b). Both native species seem to reproduce better in the reference bays, but with different seasonality patterns.

For the exotic/cryptogenic species, only populations of different seasons were compared, and again juveniles and females were responsible for most of the

variation between samples from dry and rainy season. The average dissimilarity of *Elasmopus* sp. populations between seasons was 85.4%, these differences are mainly explained by the variation in juvenile numbers, responsible for 54.59% of the dissimilarity, with highest numbers in the rainy season (Table 2c).

Populations of the exotic *S. gallensis* had average 50.11% dissimilarity between seasons, with juveniles and females contributing to 27.61% and 27.39% of the variation, with highest abundance in the rainy season (Table 2d).

Similarly for the exotic *L. baconii*, the average dissimilarity between populations from different seasons was 55.4%, juveniles and females, contribute with 28.43% and 27.91% respectively to the variation between seasons, with higher numbers again in the rainy season (Table 2e).

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**Table 2** - Results of Similarity Percentage analysis (SIMPER) with mean values of the variables number of males, number of females, number of juveniles and number of ovigerous females ( natives: a - *P. pusilla*, b - *M. acherusicum*, exotic/cryptogenic: c - *Elasmopus* sp., d - *S. gallensis*, e - *L. baconii*) and the percent and cumulative contribution of the most important variables to the dissimilarity between stress levels "Port" and "Reference" and the "Dry" and "Rainy" seasons.

Species	Season				Stress			
	Average dissimilarity = 67.4%				Average dissimilarity = 67.6%			
a - <i>P. pusilla</i>	Sex/Age group	Dry	Rainy	Contrib. %	Cum. %	Port	Reference	Cum. %
	Juveniles	1.97	2.07	26.62	26.62	1.82	2.01	27.41
	Females	1.88	1.92	26.11	52.74	1.9	2.21	54.66
	Males	1.57	1.86	25.64	78.37	1.75	1.67	77.98
b - <i>M. acherusicum</i>	Ovigerous	1.44	1.65	21.63	100	1.49	1.62	100
	Sex/Age group	Dry	Rainy	Contrib. %	Cum. %	Port	Reference	Cum. %
	Juveniles	0.59	1.76	37.12	37.12	1.24	0.88	45.56
	Females	0.41	1.63	35.72	72.83	1.07	0.73	78.24
c - <i>Elasmopus</i> sp.	Males	0.27	1.13	19.66	92.5	0.8	0.42	93.42
	Sex/Age group	Dry	Rainy	Contrib. %	Cum. %	Port	Reference	Cum. %
	Juveniles	0.92	1.61	54.59	54.59	1.24	0.88	45.56
	Females	0.45	1.1	24.57	79.16	1.07	0.73	78.24
d - <i>S. gallensis</i>	Males	0.29	0.59	11.7	90.86	0.8	0.42	93.42
	Sex/Age group	Dry	Rainy	Contrib. %	Cum. %	Port	Reference	Cum. %
	Juveniles	2.92	3.77	27.61	27.61	1.24	0.88	45.56
	Females	2.82	3.8	27.39	55	1.07	0.73	78.24
e - <i>L. baconii</i>	Males	2.33	3.02	23.12	78.11	0.8	0.42	93.42
	Ovigerous	2.11	2.93	21.89	100	0.8	0.42	93.42
	Sex/Age group	Dry	Rainy	Contrib. %	Cum. %	Port	Reference	Cum. %
	Juveniles	2.65	3.09	28.43	28.43	1.24	0.88	45.56
	Females	2.53	2.92	27.91	56.33	1.07	0.73	78.24
	Males	2.24	2.66	24.79	81.12	0.8	0.42	93.42
	Ovigerous	1.59	1.97	18.88	100	0.8	0.42	93.42



Plotting the Bray-curtis dissimilarity matrix in a Principal Coordinate Analysis (PCoA) allow the visualization of similarity between populations from different bays and sampling times (Fig. 5).

Populations of the native *P. pusilla* from each bay are more closely grouped together with the exception of the plates from BB and CN that remained for 90 days in the rainy season, the main axis of the PCoA explained 80.5% while the second axis explained 15.9% of the total variation amongst samples (Fig. 5a).

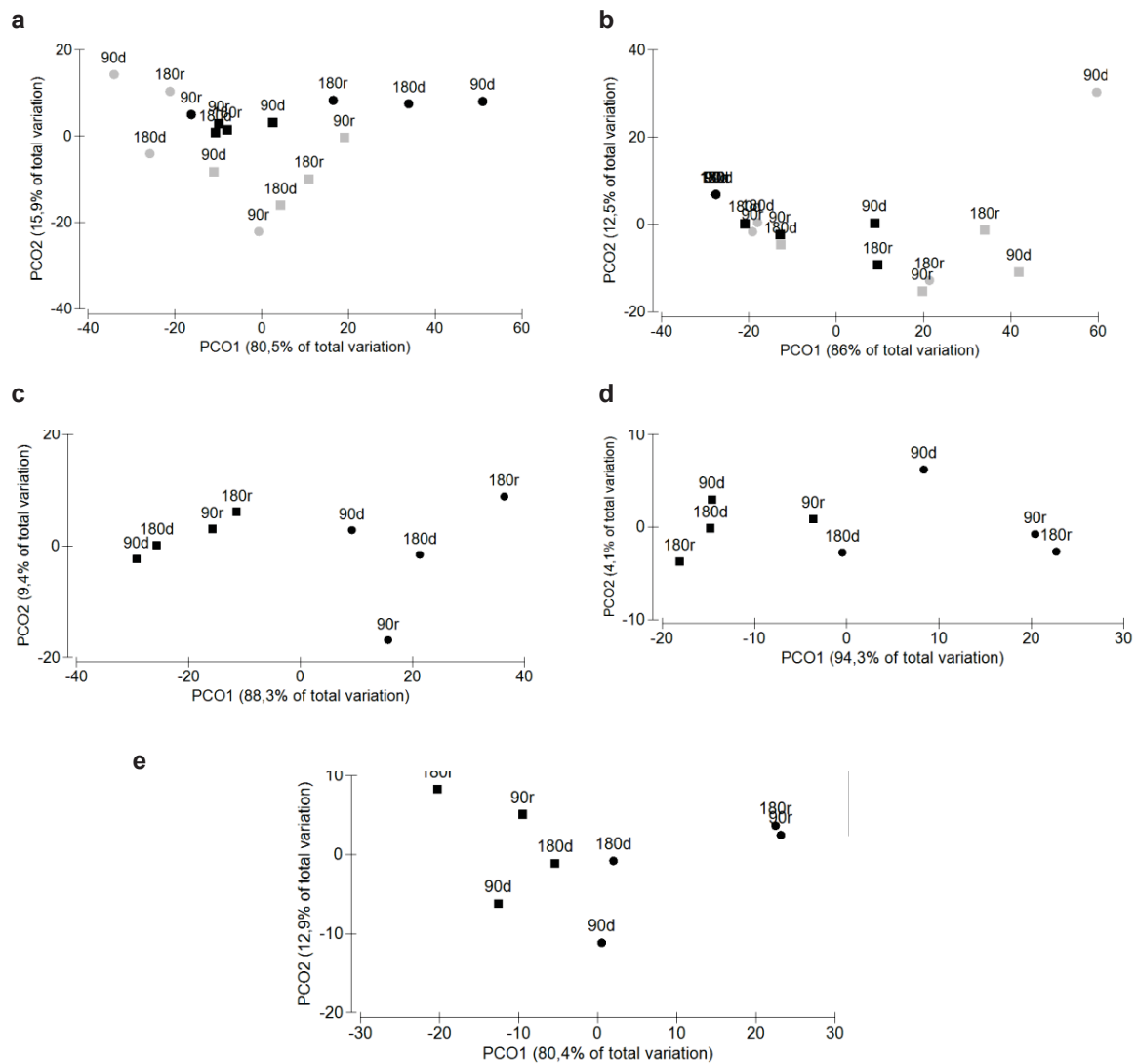
Since the other native *M. acherusicum* was absent from Babitonga the points from this bay are negligible, the rest of the samples from the dry season that remained for 90 days and the ones from the rainy season that remained for 180 days from all bays seem to be more similar, the same grouping is true for the 180 days samples from the dry season and the 90 days samples from the rainy season. The dissimilarity of *M. acherusicum* populations in the PCoA resulted in a main axis explaining 86% of total variation and a second axis explaining 12.5% of total variation (Fig. 5b).

The PCoA for the exotic/cryptogenic amphipods lacks the points from the reference bays, so it mainly shows the differences between populations from Babitonga and Paranaguá. The cryptogenic *Elasmopus* sp. had all sex/age groups present in both seasons in port bays, populations of Babitonga bay are similar amongst themselves, and the same grouping is true for Paranaguá. In Paranaguá the populations of *Elasmopus* sp. seem to be grouped by season, on the other hand Babitonga samples seem to be grouped by the amount of days they spent submerged, for this species the first axis of the PCoA explained 88.3% and the second axis explained 9.4% of the total variation between samples (Fig. 5c).

For the exotic *S. gallensis*, a clear difference between populations from Babitonga and Paranaguá can be seen, as the points of each bay are grouped together, and the first axis of the PCoA explained 94.3% of the variation and the second axis explained 4.1% of the total variation between bays and time treatments (Fig. 5d).

The exotic *L. baconi* shows different population structure in the two port bays, there is a clear separation in the samples from Babitonga to those of Paranaguá, besides that in Babitonga the plates from the Rainy season are more similar to each other and the same goes for those from the Dry season. The main axis of the PCoA explained 80.4% of the variation between samples while the second axis explained 12.9% of the variation (Fig. 5e).

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**Fig. 5** - Principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarity matrix of the variables number of males, number of females, number of juveniles and number of ovigerous females. Data was transformed to  $\ln(x+1)$  prior to analysis. Points represent distances between centroids for each Bay (Babitonga = ●, Paranaguá = ■, Cananéia = ●, Guaratuba = ■) for 90 and 180 days of the dry (90d, 180d) and rainy (90r, 180r) seasons. (a- *P. pusilla*, b- *M. acherusicum*, c- *Elasmopus* sp., d- *S. gallensis*, e- *L. baconi*)

After looking at the influence of the fixed and random factors to Amphipoda abundance, we analyze the effects of those same factors and their interaction on the population structure of the native and exotic/cryptogenic amphipods through a PERMANOVA test (Table 3).

The population structure of *P. pusilla* seems to be significantly affected by the bay where it is from, as Bay was the significant factor to explain the dissimilarity in populations of this native amphipod (Table 3a).

Populations of the native Corophiid *M. acherusicum* on the other hand are significantly different between time treatments as shown by Permutational analyses, the specific times of the year the samples were retrieved seem to be important for the variations among sex/age groups (Table 3b).

The results from PERMANOVA show a clear difference on populations of the cryptogenic *Elasmopus* sp. from different Bays, populations from Babitonga bay were significantly different from those of Paranaguá (Table 3c).

Similarly, population structure of the exotic *S. gallensis* is significantly different between bays, and Babitonga populations have different numbers and proportions of those from Paranaguá (Table 3d).

For the exotic *L. baconi* the factor bay and the interaction between bay and season had significant effect on this amphipod's population structure, the populations from Paranaguá are different from those of Babitonga, and in Babitonga the populations are different in the dry and rainy seasons (Table 3e).

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**Table 3** - Summary of PERMANOVA (9999 permutations, n=5 plates) based on Bray-Curtis dissimilarity matrix of the variables number of males, number of females, number of juveniles and number of ovigerous females of each amphipod species ( natives: a - *P. pusilla*, b - *M. acherusicum*, exotic/cryptogenic: c - *Elasmopus* sp., d - *S. gallensis*, e - *L. baconi*). Data was transformed to  $\ln(x+1)$  prior to analysis. Significant terms ( $\alpha = 0.05$ ) are highlighted in bold

	df	MS	F	P
<u><i>a-Paracaprella pusilla</i></u>				
Stress = St	1	6937.2	0.664	0.7138
Season = Se	1	214.7	0.372	0.9248
Bay (St)	2	9273.8	8.274	<b>0.0036</b>
Time (Se)	1	763.6	0.678	0.6422
St x Se	1	10276	1.964	0.1583
St x Time (Se)	2	3022.8	2.685	0.0955
Se x Bay (St)	2	2826	2.521	0.1050
Bay (St) x Time (Se)	4	1120.8	0.817	0.5617
Residual	84	1371.2		
<u><i>b-Monocorophium acherusicum</i></u>				
Stress = St	1	23407	2.483	0.1130
Season = Se	1	1231.5	0.201	0.9816
Bay (St)	2	5578.4	3.556	0.0562
Time (Se)	2	11819	7.621	<b>0.0082</b>
St $\square$ Se	1	692	0.340	0.9231
St $\square$ Time (Se)	2	4579.3	2.953	0.0964
Se $\square$ Bay (St)	2	2014.1	1.284	0.3529
Bay (St) $\square$ Time (Se)	4	1568.6	2.232	<b>0.0372</b>
Residual	84	702.8		
<u><i>c-Elasmopus sp.</i></u>				
Season = Se	1	2053.6	1.360	0.4041
Bay	1	22746	27.008	<b>0.0060</b>
Time (Se)	2	1564.8	1.858	0.3175
Se $\square$ Bay	1	564.2	0.670	0.5150
Time (Se) $\square$ Bay	2	842.2	0.815	0.4597
Residual	52	1032.8		
<u><i>d-Stenothoe gallensis</i></u>				
Season = Se	1	1692.6	2.084	0.2720
Bay	1	8725.2	23.108	<b>0.0280</b>
Time (Se)	2	394.2	1.044	0.4704
Se $\square$ Bay	1	598.9	1.586	0.3264
Time (Se) $\square$ Bay	2	377.6	0.284	0.8866
Residual	52	1328.1		
<u><i>e-Laticorophium baconi</i></u>				
Season = Se	1	2195.3	0.733	0.6667
Bay	1	7839.3	32.751	<b>0.0028</b>
Time (Se)	2	551.7	2.305	0.1999
Se $\square$ Bay	1	2768.5	11.566	<b>0.0267</b>
Time (Se) $\square$ Bay	2	239.4	0.182	0.9633
Residual	52	1312.8		

## 4 DISCUSSION

This study provided a first look into some understudied areas which, to the extent of our knowledge, had very few records of exotic amphipods in artificial substrate. We assessed the distribution, population structure and abundance of native and exotic/cryptogenic amphipods in bays with and without ports, given the influence of proximity with shipping vectors and the homogenous habitat provided by artificial substrate.

In our study, almost all species show a female-biased sex ratio, and females contributed more than males to dissimilarities between samples. This ratio is similar to what is found in most studies with amphipods where females outnumber males (Sconfietti and Lupari 1995; Ros et al. 2013a; Alegretti et al. 2016; Rumbold et al. 2016; Velazquez et al. 2017; Ozga et al. 2018). This unbalance is common for brooding crustacean species with low dispersal, where the males are more active, and compete with other males for the chance to reproduce with the females, while the females do not compete amongst each other (Ewers-Saucedo 2019).

Most of the species in this study, except for *S. valida* and *A. acutum* (and *M. acherusicum* in Cananéia), had ovigerous females and juveniles present in both seasons, and no sex/age group was totally absent across sampling times. This is an indicative that these amphipods have well-structured populations in the studied bays and are able to reproduce, although in different rates, throughout the whole year (Ros et al. 2013b; Rumbold et al 2016).

In southeastern Brazil amphipod density may show some seasonal variation, but even though their numbers fluctuate, most species are present throughout the whole year (Valério-Berardo and Flynn 2002; Jacobucci et al. 2009). Amphipod reproduction in the southern Atlantic seem to have less variance between summer (rainy) and winter (dry) seasons where both juveniles and ovigerous females can be found, as opposed to what happens in other parts of the world, where amphipods reproduction show a more clear seasonality pattern (Caine 1987; Navarro-Barranco et al. 2017; Fyttis et al. 2019) and some sex/age groups may not be present for some part of the year.

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The native *P. pusilla* is a very common caprellid from the southwestern Atlantic, first described in Rio de Janeiro by Mayer (Wakabara 1991; Mauro and Serejo 2015; Machado et al. 2019); this species is mainly detritivore, and can be found in a great variety of host organisms, both in natural sheltered habitats and artificial structures in marinas and aquaculture farms (Alarcón-Ortega et al. 2012, 2015). Overall *P. pusilla* seems to be well adapted to live in human-impacted areas, and can be found on artificial and natural substrate (Ros et al. 2016), it can survive in temperate and tropical climates and relatively stable salinities, and is able to colonize impacted places with poor water quality where other amphipods cannot (Alfaro-Montoya and Ramírez-Alvarado 2018).

This caprellid was able to expand beyond the Southwestern Atlantic and reached the Northeastern Pacific, Northeastern Atlantic and entered the Mediterranean, reaching as far as the coast of Israel (Ros et al. 2015; Ros et al. 2013b). The presence of ovigerous females and juveniles in Mexico and Costa Rica indicates well-established populations of this species (Alarcón-Ortega et al. 2015; Alfaro-Montoya and Ramírez-Alvarado 2018).

In our study the abundance of *P. pusilla* was similar between both Stress levels in the rainy season, which is usually warmer and precipitation is much higher, these conditions could favor similar abundance in both Port and Reference areas. On the other hand, in the dry season, when there's less rain and temperatures are lower, the Port-impacted areas had significantly lower abundance, this suggests that despite being adapted to live in impacted environments, *P. pusilla* can still thrive better in less impacted bays when conditions are best. When looking at the seasonality of this species, the abundance seems to remain similar for both seasons in the non-impacted areas, but in the Port areas the rainy season had significantly higher abundance than the dry season. The reference areas seem to offer good conditions for a high abundance of *P. pusilla* throughout the whole year, while in the Port-affected areas conditions are significantly less favorable for this species in the dry colder season and their numbers are lower.

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Populations of *P. pusilla* appear to be different in each bay, indicating contrasting conditions in each bay can support distinct population structures of this amphipod. Juvenile and female *P. pusilla* were the most abundant in our samples and their numbers were the most variable between seasons and stress levels. This kind of variation between populations from different locations was found in other studies, suggesting that although *P. pusilla* has expanded its reach, it still able to achieve highest numbers in its native range especially in wave-protected environments (Ros et al. 2016; Cabezas et al. 2019).

The tube-building Corophiidae *M. acherusicum* is considered a cosmopolitan species, with its total native distribution range still uncertain. This species has a well-known presence in the eastern Atlantic, and early works and reviews of Brazilian amphipod fauna, as well as recent studies, list it as a common species spread across wide latitude and environmental range (Wakabara 1991; Netto et al. 2018). These reports lead us to consider it as native, rather than cryptogenic (Neves and Rocha 2008).

The abundance of *M. acherusicum* does not seem to be affected by the Stress nor the Season; it did not appear in the plates from Babitonga, but in the other three bays it showed two peaks in abundance one from June to September and other from March to June.

Juveniles and females again were the groups with most variation between season and stress levels, in the rainy season no ovigerous females were found in Cananéia and very few in PEC; as opposed to *P. pusilla* this amphipod does not seem to reproduce with the same rate all year long, but appears to be present in the three bays across both seasons. Populations of *M. acherusicum* are more affected by the time of the year when samples were retrieved rather than the season or amount of days the plates remained submerged. Changes in environmental conditions from October to February might be less favorable for *M. acherusicum* reproduction which would explain the differences in this amphipods abundance and population structure.

The native *S. valida* is a common shallow water amphipod in Brazil, found in natural substrates (Jacobucci et al. 2018), however, this native Stenothoid had



very low presence in our samples, and the plates recovered in the period from June to September were the only ones where this species was found.

The very low abundance of this native species in all the samples could mean that *S. valida* is not a good colonizer of artificial substrate, remaining mostly in the natural hard substrata but that goes against reports of *S. valida* successfully inhabiting pillars, buoys, pontoons and aquaculture facilities elsewhere (Agostini and Ozorio 2018; Silvestri et al. 2019). The reference bays might have more availability of natural habitat so they do not have to resort to artificial structures as opposed to the port bays where natural substrate was replaced with less preferred artificial substrate. Another possibility is that it is being outcompeted by another very similar species like the exotic congener *S. gallensis* in the port bays. In the case of the reference bays, it could be just a coincidence that *S. valida* is absent in Cananéia where some amount of *S. gallensis* were found, since their low numbers prevents us from assuring anything.

Natural, less disturbed environments usually have higher amphipod diversity and lower abundance, whereas artificial and impacted places can have a higher total abundance but are mostly dominated by exotic and opportunistic species (Mottaghi et al. 2017; Paz-Ríos et al. 2018). In our study this high density of exotic amphipods was also found, especially in the impacted areas of Babitonga and Paranaguá.

This significantly higher presence of exotic and cryptogenic amphipods in bays with international ports is of particular importance in a globalized world, where there is growing trade and shipping between countries and more ports are built every year (Mack et al. 2000; Floerl and Inglis 2005; Murray et al. 2014). One big concern is the future spread of these exotics to the bays without ports, which could be aided by traffic of commercial and recreational boats between nearby estuaries (Davidson et al. 2010; Ros et al. 2013b; Zabin 2014).

The rate at which exotic/cryptogenic amphipods reproduce and spread out in a new region is an indication of a species invasive potential, and the spread of an introduced species can be accelerated if there is enough propagule pressure

and a well-established population reproducing along the year (Molnar et al 2008; Lockwood et al. 2009; Truhlar and Aldridge 2014; Rumbold et al 2016).

Amongst the non-native species investigated in this study, the cryptogenic *Elasmopus* sp. and the exotics *S. gallensis* and *L. baconi* seem to have well-established populations, reproducing in both port impacted bays, as revealed by the presence of ovigerous females and juveniles all year long. Additionally, these three species are broadly distributed across Babitonga and Paranaguá, so they have some invasive potential, and could proliferate even further if left unchecked (Molnar et al 2008; Lo Brutto et al 2016; Peters and Robinson 2017).

The genus *Elasmopus* Costa, 1853 is the most diverse in the Maeridae family, which has a history of taxonomic confusion, given lost type specimens and dubious descriptions. Individuals identified as one species could actually belong to a complex of many similar species such as happened with *Elasmopus rapax* (Senna and Souza-Filho 2011). There have been more than 18 species of this genus reported occurring in Brazil, with new species being described recently (Senna 2011; Alves et al. 2016), however the description of native species does not match our findings, but morphology indicates that it belongs to the *Elasmopus pecteniscrus* species complex, which is a group of species distinct by the casteloserrate posterior margin of basis of pereopods 6 and 7 (Krapp-Schickel and Ruffo 1990; Senna and Souza-Filho 2011; Alves et al. 2016).

The amphipods from the *E. pecteniscrus* group are notable invaders; they were able to expand from their tropical range to temperate regions, most likely with the help of shipping vectors (Sezgin et al. 2007; Zakhama-Sraieb and Charfi-Cheikhrouha 2010) suggesting they are opportunistic and able to quickly adapt and colonize new habitats.

The cryptogenic *Elasmopus* sp. was only present in the Port-affected bays and absent from the reference bays, so this possibly means that the presence of this species is directly linked to the presence of ports in Babitonga and Paranaguá. The absence of *Elasmopus* sp. in the reference areas could be because the distance between those bays and the International Ports is enough to keep them free from the spread of this amphipod, or because opportunistic species are unable

to survive for long and compete with native amphipods in non-impacted areas (Macneil and Dick 2014; Macneil 2018; Macneil and Campbell 2018).

The abundance of *Elasmopus* sp. was marginally influenced by seasonality, better conditions in the rainy season could be the reason for higher numbers of this amphipod. The difference between seasons was mostly explained by the variation in number of juveniles, the rainy season must be more favorable to a higher reproduction in this species, explaining the increased number of young individuals.

The populations of *Elasmopus* sp. in the two port-affected bays are significantly different, in Babitonga this species is more well-spread and has higher numbers of all sex/age groups across both seasons. We suggest that Babitonga has better environmental conditions for the reproduction, establishment and spread of *Elasmopus* sp. than Paranaguá, as optimal physicochemical conditions increase the chance of success of a potentially invasive species (Iacarella et al. 2015), or that the propagule pressure for this *Elasmopus* sp. is much higher in the ports of Babitonga, and ship hull fouling could accelerate its spread across the bay (Lacoursière-Roussel et al. 2016).

Likewise, the higher abundance of *S. gallensis* in Babitonga and Paranaguá seem to be positively correlated to the presence of the ports and the lack of significant numbers in the reference bays is probably due to the lower introduction pressure in areas without international shipping traffic (Lockwood et al. 2009). This exotic species showed some seasonal variations, as with other amphipods their numbers were higher in the rainy season.

Juveniles and females contribute the most to variation between seasons, probably related to different reproduction and growth rates. Given the presence of ovigerous females and juveniles all year long, *S. gallensis* appears to be well-established and reproducing in both port bays; however Babitonga has a differently structured and more abundant population than Paranaguá which could be related to gradients in environmental conditions and the species tolerance and adaptation to live in each bay (Grabowski et al. 2009).

The exotic corophiid *A. acutum*, is native to the Atlantic coast of Spain, where it is present all year long especially in the warmer months (Gavira-O'Neill et

al. 2016). In our samples this exotic had very low presence and Paranaguá is the only bay that seems to have a reproducing population, with ovigerous females appearing only in the rainy season.

This Corophiidae, like *M. acherusicum*, is absent from Babitonga bay, but a few individuals were able to reach Cananéia and Guaratuba reference bays, although their numbers may appear insignificant now, repeated introductions, or a large introduction event could help this species later achieve a stable population in the non-impacted areas (Lockwood 2009).

Like *M. acherusicum*, the exotic *A. acutum* has tube-building behavior and can colonize marinas and ship hull fouling and coexist with this similar species in European waters, although *A. acutum* is more present across bays, it is not clear the level of competition that goes on between the two species (Gavira-O'Neill et al. 2016; Martínez-Laiz et al. 2019).

The last exotic *L. baconi* is also closely related to the other two corophiids, this species was once considered endemic to the North Pacific (Bousfield and Hoover 1997), and has a positive synanthropic relationship, which allowed it to spread beyond to the north and south Atlantic, Oceania and further into the Mediterranean (Ahyong and Wilkens 2011; Gouillieux and Sauriau 2019).

This amphipod was absent in the reference bays, which suggests its presence is positively correlated to the presence of international ports. The seasons had no significant effect on its abundance. Most of the difference between populations from Dry and Rainy season is due to variation in juvenile and female numbers, possibly because different conditions allow different reproduction and growth rates.

The population structure of *L. baconi* in each of the ports is different; in PEC it coexists with *M. acherusicum* and *A. acutum* and populations are similar between sampling times, whereas in Babitonga there seems to be a seasonal variation in population structure, a higher total abundance increasing especially in the Rainy season and absence of individuals from the other two corophiid species.

Similar species can coexist and one can dominate over another depending on their reproduction, seasonality, temperature and host availability (Costa et al.

2015; Valério-Berardo and Flynn 2002; Ferreira et al. 2018). The patterns of co-existence or exclusion are known to be heavily influenced by abiotic factors, different tolerances to pollution, salinity and oxygen levels can affect the success of one species over another (Macneil and Dick 2014; Macneil and Campbell 2018). In addition to water chemistry, the temperature affects growth and metabolism, and the impacts of a potential invader will be more notable in locations that meet its optimal requirements (Iacarella et al. 2015).

The exact nature of the competitive interactions between the species is beyond the scale of our study, although we cannot quantify the ecological impacts of the exotic/cryptogenic amphipods, their high abundance in relation to very similar natives in bays with international ports show how much these locations are favorable to the establishment success of introduced amphipods (Molnar et al. 2008; Lockwood et al. 2009; Ros et al. 2013b; Gartner et al. 2016; Rumbold et al. 2016).

The two *Stenothoe* congeners investigated here are very similar species; *S. gallensis* was once considered a single cosmopolitan amphipod, later discovered as a complex of many species very slightly distinct with different origins. The native *S. valida* first described in Rio de Janeiro, is not in the “*gallensis*” group for very small morphological differences, in males the article of the third uropod end in a straight tip as opposed to an acute uncinat tip, and in all individuals the merus of pereopods 6 and 7 is much wider and elongated reaching the end of the carpus (Krapp-Shickel 2015). Individuals of both species can be found living together in the Pacific and Atlantic Ocean (Krapp-Shickel 2015), and *S. valida* and *S. gallensis* have also been reported coexisting in India, where they are both invasive (Roy and Nandi 2017) but in our study the exotic *S. gallensis* was significantly more dominant than its native counterpart in the artificial substrate samples.

The anatomical similarity of these two Stenothoids suggests they might have the same feeding habit and could also compete directly for space, but in order to really understand what drives the success of an exotic congener over a native we suggest behavioral studies as a good approach (Dick et al. 1995; Truhlar and Aldridge 2014; Beggel et al. 2016; Bierbach et al. 2016).

The three members of the Corophiidae family found in this study are closely related, their small sizes and the slight morphological differences between them may cause taxonomic confusion. They can be distinguished by the urossome which in *M. acherusicum* lacks the lateral margin ridge the other two have, *L. baconi* has a median notch in the lateral margin of the urossome and gnathopod 2 dactyl with 1 tooth, as opposed to *A. acutum* with an entire urossome lateral margin and 2 to 3 teeth in the gnathopod 2 (Myers and Lowry 2003; Lecroy 2004; Gouillieux and Sauriau 2019).

There have been reports of co-occurrence of these three species in many locations of the North Pacific where they have a positive relationship with human activities (Bousfield and Hover 1997). These corophiidae were successfully introduced to New Zealand and Australia, where they build their tubes on fouling assemblages (Ahyong and Wilkens 2011). In Brazil both *M. acherusicum* and *L. baconi* have been found in natural habitat living in algal hosts and octocorals (Nascimento 2016; Machado et al. 2019), in those studies *L. baconi* was more numerous and more present across samples than *M. acherusicum*.

In our case this was true for the bays with ports, but not in the reference areas, which can have two reasons; one is that *L. baconi* has not yet been introduced to Cananéia or Guaratuba and the distance of those bays to the ports is enough to keep them free from a crustacean with low dispersal (Ewers-Saucedo 2019) the other is that *L. baconi* cannot survive and spread in areas with different water quality, where the native *M. acherusicum* can thrive (Macneil and Dick 2014; Macneil 2018; Macneil and Campbell 2018).

A similar reasoning can be made to understand why *L. baconi* is the only corophiidae present in Babitonga bay; it could be colonizing areas previously devoid of *M. acherusicum* and *A. acutum* and successfully occupying a vacant niche, or it could be a better competitor and displaced them. Differences in abiotic variables could explain why the three species can co-exist in PEC, but in Babitonga conditions could be optimal so that *L. baconi* thrives.

## 5 CONCLUSIONS

This study reports the well-established presence of populations of the exotic/cryptogenic amphipods *Elasmopus* sp., *S. gallensis* and *L. baconi* in bays with international ports, all of which could have invasive potential. Although there are some constraints given the sampling method and time scale, our samples are a good representation of the species present in surrounding areas. Further research in different time scales could build up on this knowledge, by helping understand the dynamics of colonization, migration and introduction rates of these introduced amphipods, and behavioral studies can help determine the nature of their inter-specific interactions with the natives, and the level of impact they cause.

The two estuaries without ports, although adjacent to the others, showed little presence of exotics, and seem especially favorable for natives in the rainy warmer season. This might indicate that the distance from the ports and the absence of international shipping traffic, has kept these places reasonably unaffected by the introductions; or that exotics are unable to establish a population and compete with the natives in the non-impacted environment. Nevertheless a few exotic individuals of *S. gallensis* and *A. acutum* found in the reference areas are worth noting, as they could represent the beginning of the spread of those exotic amphipods to Cananéia and Guaratuba.

Both port-impacted bays seem to be favorable to the establishment and spread of introduced species, however Babitonga bay appears to be significantly more affected by exotic/cryptogenic amphipods than Paranaguá. We suggest that mitigation efforts should consider both the management of exotics in the heavily affected areas of Paranaguá and Babitonga, and also try to enforce control measures to avoid further spread from the ports to the adjacent unaffected areas.

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