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Article

Assessment of distribution of two sympatric mud crab species – *Panopeus americanus* and *Panopeus austrobesus* – in a Western Atlantic estuarine intertidal zone

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Abstract: Sympatric mud crab species *Panopeus americanus* and *Panopeus austrobesus* are found in intertidal environments associated with muddy and rocky habitats in the Western Atlantic coast. Therefore, they are a suitable model system to be used in studies focused on investigating biological coexistence aspects between close species, such as population structure and habitat. The aims of the current study are to describe and compare the distribution of two sympatric mud crab species – *P. americanus* and *P. austrobesus* – based on their spatial and temporal distribution, in a low human impact estuarine complex area. The hypothesis that these two species show similar distribution, although one species is more abundant than the other, was herein tested. Sampling was carried out in the intertidal zone of a specific area in Cananeia estuarine complex, São Paulo State, Southeastern Brazil, in different periods of time for two years. Both species presented similar pattern distribution and frequency, with predominance in the middle and high intertidal zones, including all demographic categories. However, *Panopeus americanus* was more abundant and presented smaller mean size in all sampling zones. The pronounced disparity in size between the species suggests divergent dietary preferences, potentially related to prey size allowing the coexistence of these sympatric and syntopic species. The predominance of these two species in the upper intertidal zones was understood as a strategy for avoiding competition with the intertidal alpheid shrimps.
Keywords**:** *Brachyura; coexisting species; microhabitat distribution; Panopeidae.*

Avaliação da distribuição de duas espécies simpátricas de caranguejo-da-lama – *Panopeus americanus* e *Panopeus austrobesus* – em uma zona intertidal estuarina do Atlântico Ocidental

Resumo: As espécies simpátricas de caranguejo-da-lama *Panopeus americanus* e *Panopeus austrobesus* são encontradas em ambientes entremarés associados a habitats lamacentos e rochosos, bem como em simpatria na costa do Atlântico Ocidental. Portanto, constituem um sistema modelo adequado para ser utilizado em estudos focados na investigação de aspectos de coexistência biológica entre espécies semelhantes, como estrutura populacional e habitat. Os objetivos do presente estudo são descrever e comparar a microdistribuição de duas espécies simpátricas de caranguejo-da-lama – *P. americanus* e *P. austrobesus* – com base na avaliação de sua distribuição espacial e temporal, em uma área estuarina complexa e com baixo impacto antrópico. A hipótese de que estas duas espécies apresentam microdistribuição semelhante, embora uma espécie seja mais abundante que a outra, foi testada. A amostragem foi realizada na zona entremarés de uma área específica do complexo estuarino de Cananeia, Estado de São Paulo, Sudeste do Brasil, em diferentes períodos durante dois anos. Ambas as espécies apresentaram microdistribuição e frequência semelhantes, principalmente nas zonas entremarés média e alta. Entretanto, *Panopeus americanus* foi mais abundante e apresentou menor tamanho médio em todas as zonas amostrais. A pronunciada disparidade de tamanho entre as espécies sugere preferências alimentares divergentes, potencialmente relacionadas ao tamanho

das presas possibilitando a coexistência dessas espécies simpátricas. A predominância dessas duas espécies nas zonas intermareais superiores também indica uma estratégia para evitar a competição com os camarões alfeídeos.
Palavras-chave: *Brachyura; espécies coexistentes; distribuição de microhabitat; Panopeidae.*

Introduction

Species interactions in a given community are of major importance to gather information about the function and dynamics of ecosystems. This knowledge is essential to support decision-making for conservation, biodiversity management and overall health of natural systems (Neylan et al. 2019). Coexistence among congeneric species is a key aspect to help better understanding their influence on communities' spatial and temporal distribution. Biological processes capable of interfering with this coexistence process are scale-dependent (Hart et al. 2017). Divergence among niches is a factor capable of explaining species interaction at local scale (Kneitel and Chase 2004). Traits, such as selecting different habitats and consuming food deriving from different sources, may avoid competition between species and enable their coexistence (Stearns 1976). Investigating the coexistence of species living in mangroves, as well as their habitats, can be a fruitful environmental assessment aspect given their richness, specificity and diversity (Amaral et al. 2010). Analyzing ecological roles played by crabs and their impact on crab abundance, diversity, distribution and coexistence, at both spatial and temporal scale, as well as assessing mangrove features, can provide information on habitat quality and indicate likely changes in mangroves (Lee et al. 1999, Krausman 1999, Macintosh et al. 2002, Freitas et al. 2021).

Estuarine complex areas encompass mangroves that, in their turn, form habitats typical of coastal wetlands found in intertidal zones along tropical and subtropical latitudes (Tomlinson 1986, Beger et al. 2010). These environments are essential to both aquatic and terrestrial organisms, since they are one of the most productive ecosystems in the world (Goessens et al. 2019, Hamilton 2020). This ecosystem is acknowledged for providing several ecosystem services, such as biodiversity maintenance, nutrient cycling, breeding and nursery habitat, flood control, shoreline stabilization and erosion control, storm protection and pollution control filter (Junk et al. 2014, Barbier 2017).

Information on species richness and interaction are essential to help featuring and assessing this ecosystem, given its high diversity level (Rog et al. 2017). Crabs play essential ecological role in mangroves due to their large number of species and abundance (Nagelkerken et al. 2008, Mokhtari et al. 2015). In addition, they are seen as ecosystem engineers in mangroves because they can affect energy flow, as well as sediment structure and chemistry (Kristensen 2008). Furthermore, crabs form an important link between the basal food web components and the highest trophic levels, consequently, they are capable of affecting different fish and bird species, among other taxa (Macintosh et al. 2002).

Sympatric crab species like *Panopeus americanus* de Saussure, 1857 and *Panopeus austrobesus* Williams, 1983 are widely distributed in intertidal enviroments throughout the Western Atlantic (Melo 1996, 2008), including São Paulo State coast (Mantelatto et al. 2020). Oliveira-Rogeri et al. (2023) recently performed an integrative study focused on explaining the taxonomy and distribution range of mud crab species belonging to genus *Panopeus* in the Southwestern Atlantic zone. Their findings have evidenced six different *Panopeus* species in the investigated region. According to the aforementioned authors, *Panopeus austrobesus* presented wide distribution in almost all Brazilian states and in all marine provinces bordering the country. On the other hand, morphologically similar species, such as *Panopeus occidentalis*, presented a more limited range; its Southern incidence was observed between Southern Pernambuco and Northern Rio de Janeiro states. Consequently, the aforementioned study suggested that previously studies focused on investigating *P. occidentalis* along the Brazilian Southeastern coast likely analyzed *P. austrobesus* populations.

The sympatric crab species *P. americanus* and *P. austrobesus* are suitable to investigate coexistence between similar species, since they inhabit the same ecosystem although they have different reproduction patterns (Peres et al. 2018 and Vergamini and Mantelatto, 2008a,b, both the references as *P. occidentalis*). Habitats occupied by *P. americanus* and *P. austrobesus* comprise algae and roots, and both species can be found under rocks and gravel, or buried in sand (Melo 1996, 2008).

The aims of the current study were to describe and compare the distribution of the sympatric mudcrab species *P. americanus* and *P. austrobesus,* based on assessing their spatial and temporal distribution in an estuarine intertidal zone located in a well-preserved estuarine complex in Western Atlantic coast. We hypothesized that the investigated species show similar distribution in the intertidal zones, although one species is more abundant than the other. Species size and distribution based on demographic categories, juveniles, adults and ovigerous females were also analyzed.

Material and Methods

1. Study site

Sampling was done in the intertidal zone of the intertidal zone in Cananeia estuarine complex, São Paulo State, Southeastern Brazil (25°04'11.2"S, 48°03'08.9"W); this site is a well-preserved area and is considered one of the most productive estuaries in the world (Diegues 1987, Cunha-Lignon et al. 2011) (Figure 1). The substrate of this site is mainly composed of a mixed sediment of sand and mud, on which randomly distributed gravels and boulders are laid. Although these gravels remain exposed to the air during the low tide, small water puddles provide a moisture refuge to *Panopeus americanus* and *P. austrobesus*. The estuarine complex edges hold a dense mangrove forest (Figure 2A-B).

2. Sampling and data analysis

Sampling was carried out in an area of approximately 600 m^2. Collections were performed in June, July, August, October and December 2015, as well as in February 2016, during spring low-tide

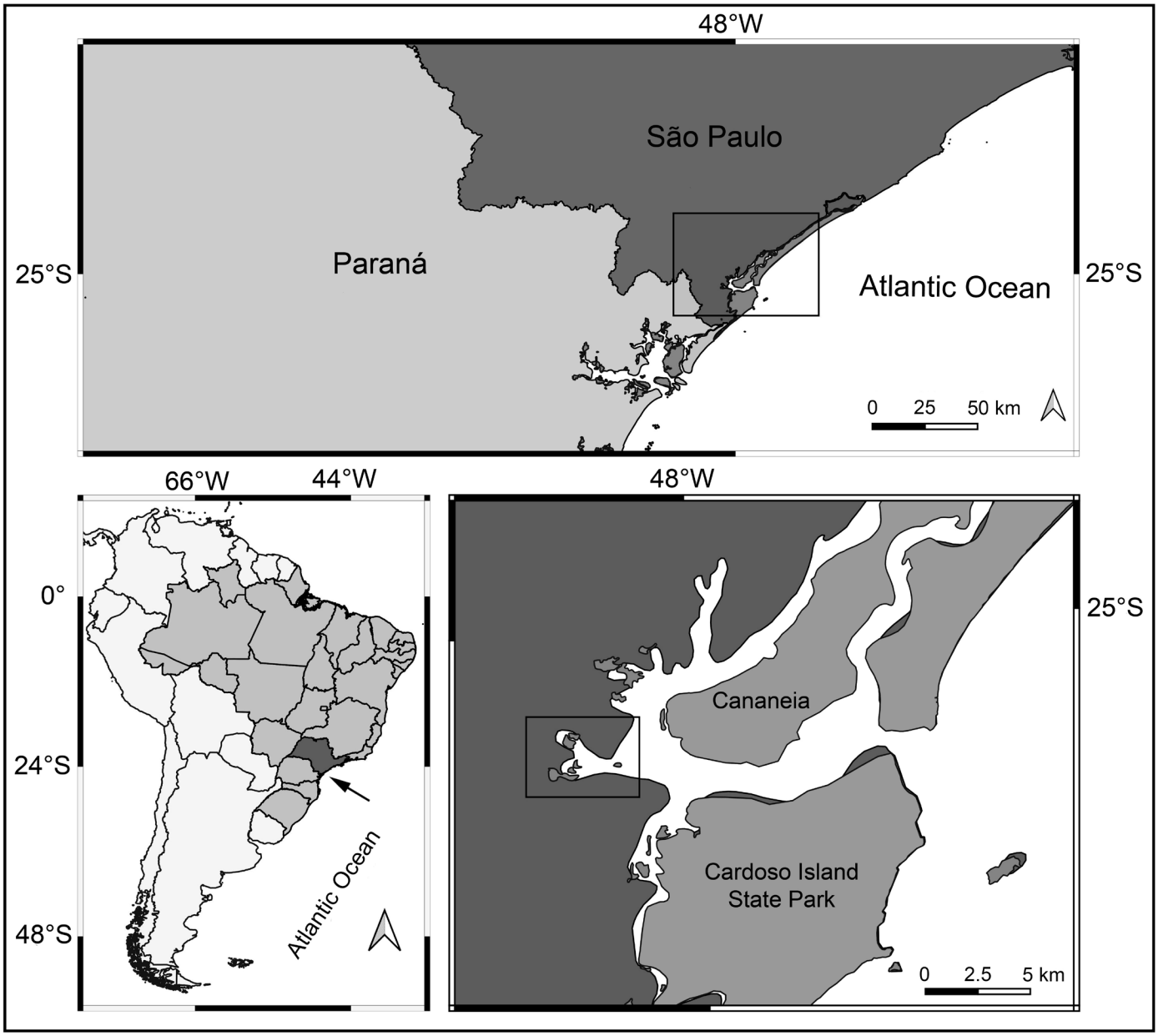

Figure 1. Location of the study area in the intertidal estuarine complex of Cananeia, São Paulo, Southeastern Brazil. Adapted from Pescinelli et al. (2021).

periods. These dates were selected due to good weather conditions, as well as to the ease of access and the longer low tide time during the collection.

The intertidal area was divided into three sub-areas parallel to the waterline, in the following zones according with the position of the sampling area relative to the waterline at high and low tide: low intertidal zone (the nearest to the waterline), middle intertidal zone (that between the low and high zones) and high intertidal zone (the adjacent to the supralittoral zone and the farthest from the waterline). Three 1-m^2 sampling units were established in each sub-area; in total, nine sampling units were obtained per month. Sampling units in each sub-area were equidistant from each other, based on the methodology adapted from Vergamini et al. (2008b) and Costa-Souza et al. (2014) (for further details, see Pescinelli et al. 2017).

Two people have manually collected the crabs in a 2-h catch effort per person (one hour before and one hour after the exact lowest tide time in the day). Gravel, boulders sediments were removed from the collection spot in order to enable capturing the specimens. All *Panopeus americanus* and *P. austrobesus* individuals found in each sampling unit were collected. Then, crabs were placed in coolers filled with crushed ice. All collected individuals were identified in laboratory, according to Melo (1996) and Oliveira-Rogeri et al. (2023). The sex of each crab was identified based on pleon morphology and on paired males'gonopods. Carapace width (CW) was measured with digital caliper (0.01 mm). Crabs were classified into juveniles and adults, based on morphological sexual maturity values estimated by Carvalho-Batista et al. (2015) and Santos et al. (2017).

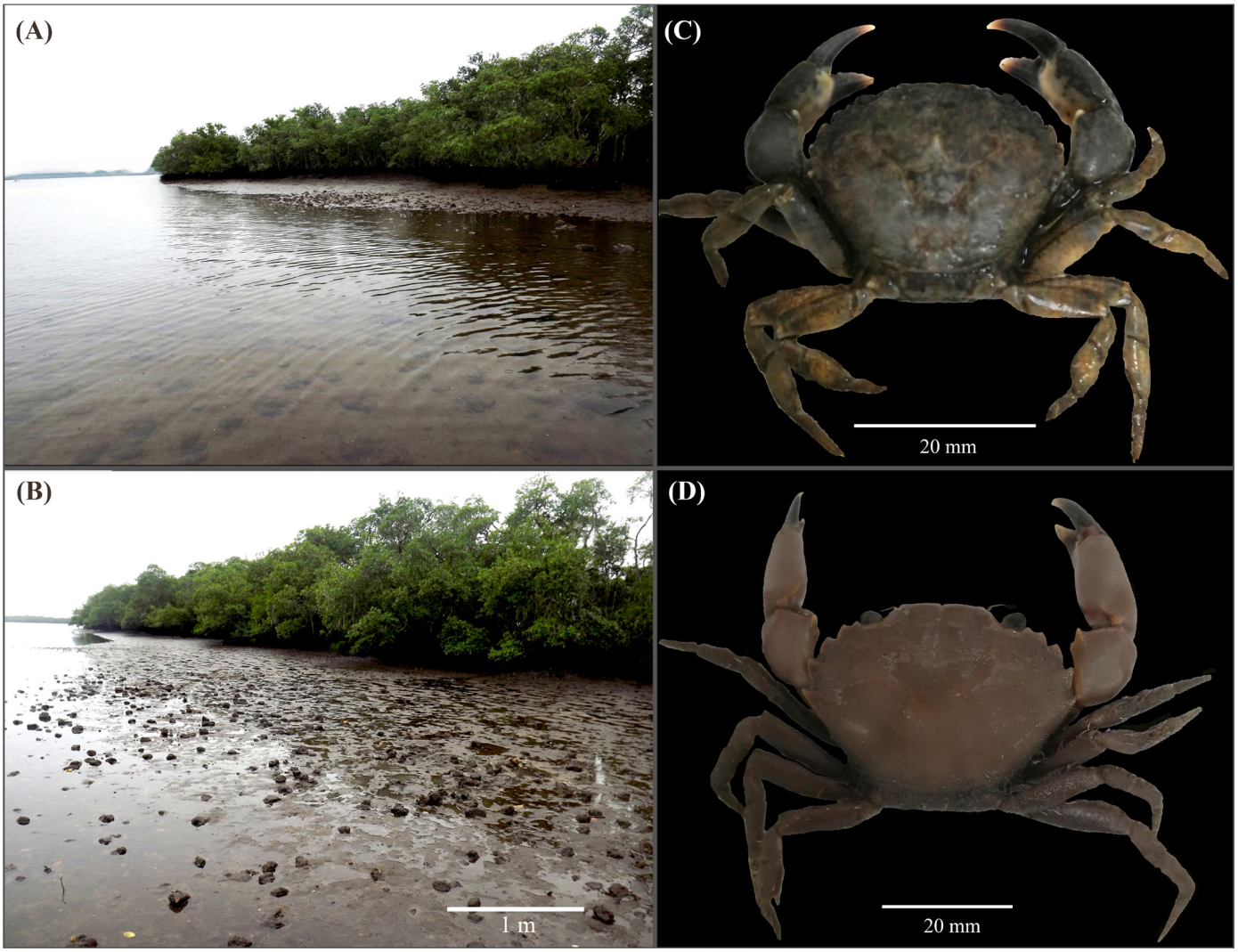

Figure 2. (A-B) view of the sampling area, intertidal zone of the estuary of Cananeia, São Paulo, South-eastern Brazil. (C) dorsal view of a male of *Panopeus americanus* and (D) *Panopeus austrobesus*. Photograph by Pescinelli RA.

Homoscedasticity (Levene) and normality (Shapiro–Wilk) tests were carried out as statistical analysis prerequisites (Zar 1996). Temporal distribution was analyzed based on species' incidence in the sampled months. Mann-Whitney test ($\alpha = 0.05$) was used to investigate differences in CW mean (mm) between *Panopeus americanus* and *P. austrobesus*, in each intertidal zone. Generalized linear model (GLM) was used to analyze the effect of zones (low, middle and high) on crabs' mean abundance value. Similarity in spatial distribution (intertidal zones) was analyzed through non-metric multidimensional scaling analysis (NMDS). ANOSIM test was used to compare the separation degree between intertidal zones.

Results

In total, 211 crabs were collected: 133 *Panopeus americanus* (63%) and 78 *P. austrobesus* (37%). Although crabs of both species were collected in all monthly-sampling and in the three intertidal zones, *P. americanus* was the most abundant both in the collection months and in those zones (Figure 3). Abundance data did not present normal distribution (Shapiro-Wilk, $P < 0.05$). However, both species showed similar spatial distribution and frequency (%) rates: presence in all intertidal zones with gradual increase of abundance towards the intertidal high zone (Table 1, Figure 4A). Moreover, ovigerous females were only collected in the middle and high intertidal zones (Figure 4A).

There was a significant difference in the mean CW between *P. americanus* and *P. austrobesus* (Mann-Whitney test $P < 0.05$). Despite its higher abundance, *P. americanus* presented smaller mean CW in all sampled zones (Figure 4B).

The generalized linear model (GLM) revealed a significant association between the mean abundance and spatial distribution of both species. The significant association was observed between the zones (GLM $P < 0.05$). As there was no difference in the spatial distribution between the species (GLM $P > 0.05$) (Figure 5A), Non-Metric Dimensional Scaling (NMDS) with the Bray-Curtis index was performed for the grouped species. It revealed a significant difference between the zones low *vs*. middle zones, and between low *vs*. high intertidal zones (ANOSIM $P < 0.05$). The NMDS showed no significant difference between the zones middle *vs*. high intertidal zones (ANOSIM

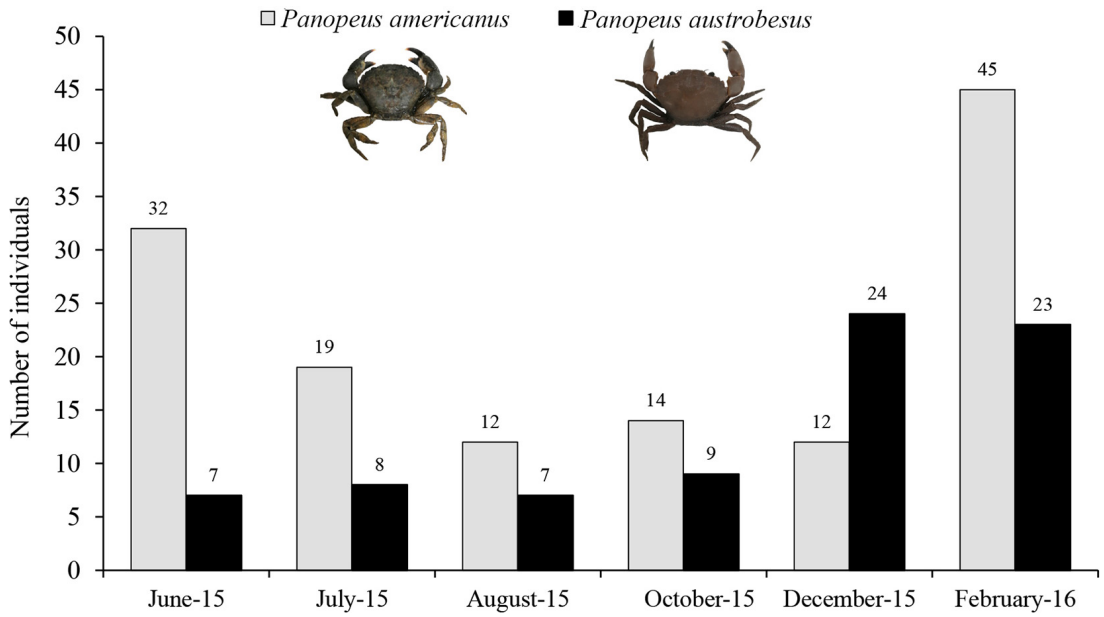

Figure 3. Temporal distribution of *Panopeus americanus* and *Panopeus austrobesus* during the sampling period in the estuarine complex of Cananeia, São Paulo, Southeastern Brazil.

Table 1. Abundance, carapace width (CW) (mm) and frequency (%) of *Panopeus americanus* and *Panopeus austrobesus* according to sampling zones in the estuarine complex of Cananeia, São Paulo, Southeast Brazil.

Zones	*Panopeus americanus*				*Panopeus austrobesus*			
	N	Min–Max	Mean ± SD	%	N	Min–Max	Mean ± SD	%
Low intertidal	28	5.91–18.95	12.94 ± 2.92	21.3	13	5.83–43.67	20.76 ± 11.81	16.6
Middle intertidal	43	7.11–26-44	13.80 ± 4.13	32.4	29	7.84–45.85	21.96 ± 9.71	37.2
High intertidal	62	6.42–26.75	14.33 ± 4.44	46.3	36	5.38–45.71	24.41 ± 11.69	46.2
Total	133	5.91–26.75	13.80 ± 4.07	100	78	5.38–45.85	22.89 ± 10.97	100

$P > 0.05$), revealing a higher similarity of these zones with overlapping clusters (Figure 5B).

Discussion

The current study has comprehensively assessed the distribution patterns of two sympatric mud crab species – *Panopeus americanus* and *P. austrobesus* – in a Western Atlantic estuarine intertidal zone. The present findings substantiated the initial hypothesis and confirmed that both species share the same distribution and coexist within identical intertidal zones (middle and high levels). However, *P. americanus* was more abundant than *P. austrobesus* in all sampled zones. Despite this discrepancy in abundance, the distribution and frequency of both species remained similar in all investigated zones – the highest abundance was observed in the middle and high intertidal zones.

Different demographic categories (juveniles, as well as adult male and female individuals) have also evidenced the preference of both species for middle and high intertidal zones. Assumingly, competition in ecological contexts is higher when species have niche overlapping, i.e., use similar resources in space and time (Rosenfeld 2002). This competition type can lead to likely exclusion of one species from the community. Results in the current study have evidenced that not only both species are present in the intertidal ecosystem, but that they have also same distribution pattern in the intertidal zone (high abundance in middle and high zones). This pattern was also observed for *P. americanus* by Vergamini and Mantelatto (2008b) who analyzed a crab population in the remnant mangrove of Araçá, near São Sebastião Channel, on the Northern coast of São Paulo State, Brazil. Interestingly, although both investigated areas (Araçá and Cananeia), are located along the same São Paulo State coast, they are approximately 400 km away from each other and, present different geomorphological features. However, their mud-crab populations present the same genetic and taxonomic aspects (Oliveira-Rogeri et al. 2023), as well as show similar distribution pattern.

The temporal distribution also showed the same pattern for both species. Despite the higher abundance of *P. americanus* specimens during all sampling period, *P. austrobesus* increased in abundance in December and February. These results may be correlated to different reproductive periods, especially during December, when *P. austrobesus*' abundance surpassed that of *P. americanus*. According to Peres et al.

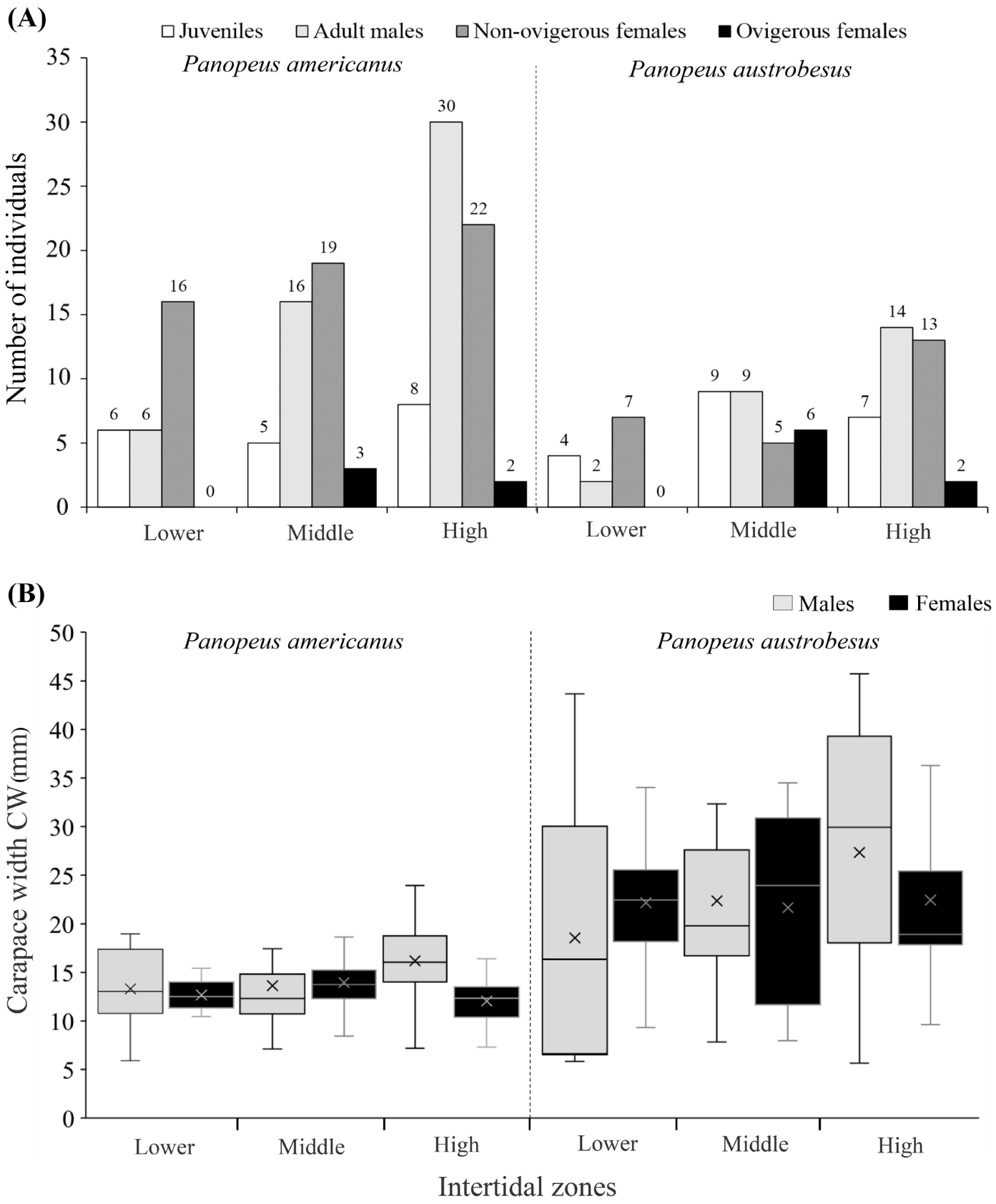

Figure 4. (A) Spatial distribution of juveniles, males, non-ovigerous females and ovigerous females of *Panopeus americanus* and *Panopeus austrobesus* in the intertidal zones in the estuarine complex of Cananeia, São Paulo, Southeastern Brazil. (B) Minimum, maximum (whiskers), median (horizontal lines) and mean (x) of the CW of both species are also plotted.

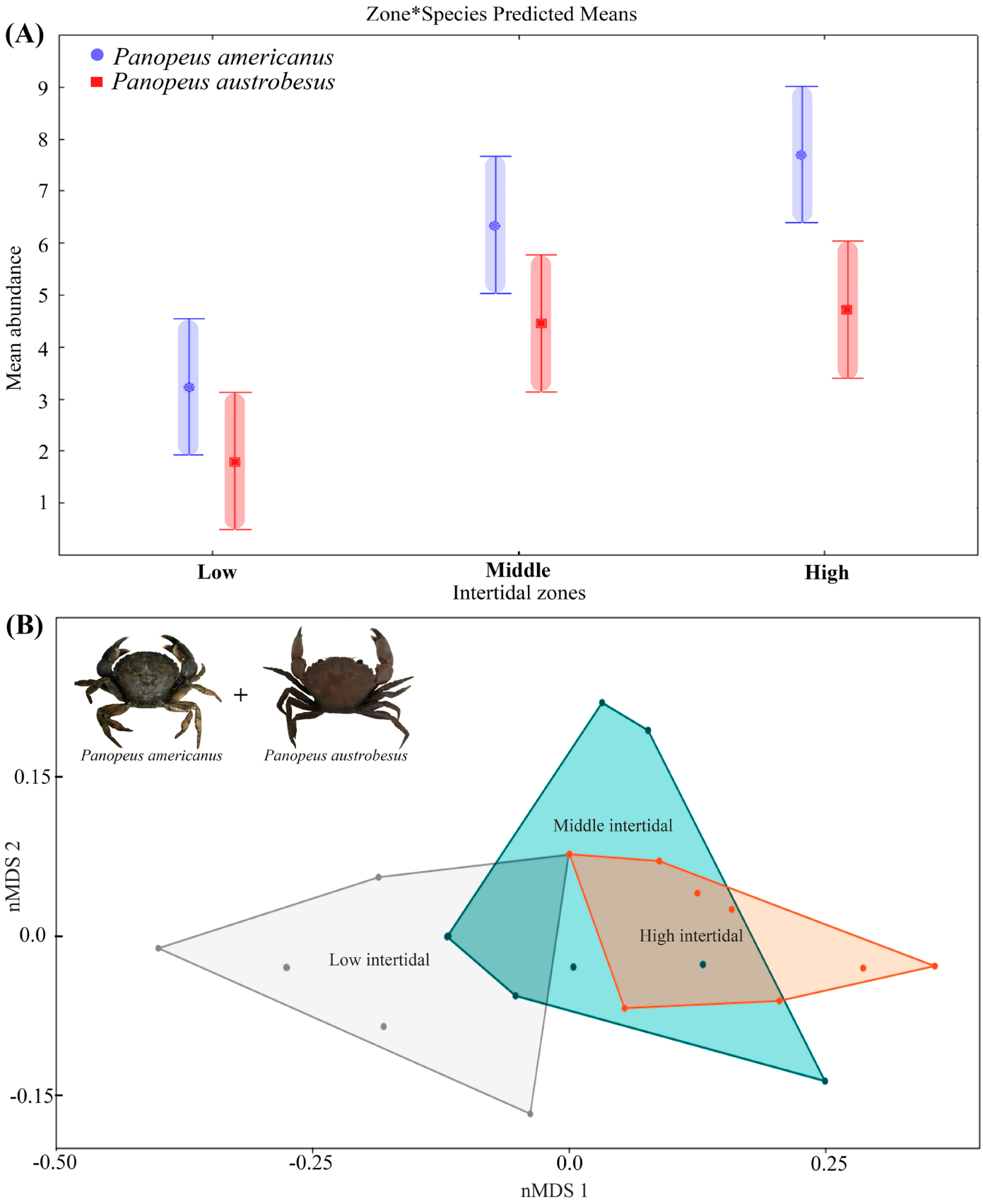

Figure 5. (A) Generalized linear models (GLM) showing the relationship between the mean abundance of *Panopeus americanus* and *Panopeus austrobesus* in the spatial (zones) scale. (B) Non-metric multidimensional scaling (NMDS) showing the distribution of grouped species in the intertidal zones.

(2018), *P. americanus* presents continuous reproduction, whereas *P. austrobesus* (assessed as *P. occidentalis*) presents seasonal reproduction between September and March – our results corroborate these authors' observation. Considering both species have similar spatial distribution, the following question arises: How can one explain their interspecific coexistence? The explanation for this factor may lie on poorly-explored niche features that go beyond temporal and spatial distribution aspects. Niche specializations can happen in the least obvious ways, such as varying activity patterns (Albrecht and Gotelli 2001). Although the diet of other panopeid crabs includes barnacles, oysters, mollusks and other crabs (Guida 1976, Brown and Haight 1992, Milke and Kennedy 2001), unfortunately, no data are available about the natural diet of *P. americanus* nor *P. austrobesus*. Certainly, the pattern of spatial distribution observed in the present study may be associated with different diet and/or food of different sizes, as their body size is quite different.

The pronounced disparity in size of the two species suggests divergent dietary preferences, potentially related to prey size, in this syntopic setting. It is conceivable that *P. americanus* predominantly preys upon smaller organisms, whereas *P. austrobesus*, prey larger items. While direct dietary analysis was not conducted in this study, the observed size variation is indicative of potential dietary specialization based on prey dimensions. The substantial difference in average size between the two species, and consequent consumption of prey of differing sizes, likely contributes significantly to their coexistence within the middle and high intertidal zones. A study on the diet of both species, as well as a morphological analysis on the mouth morphology and size of structures related to feeding habit, could confirm the difference in feeding between the species studied here.

Another aspect to be evaluated would be different reproductive traits. Peres et al. (2018) reported that sympatric congeneric species can adopt life history strategies to avoid competition and to enable coexistence, such as females from the same area that do not share same reproductive features. According to results by Peres et al. (2018), *P. americanus* has shown higher fecundity and reproductive output, as well as smaller embryo size, than *P. austrobesus.* Certainly, these contrasting characteristics allow these two populations from Cananeia estuarine complex to share the same habitat.

Based on the current findings, the different demographic categories followed the same spatial distribution of the species. The coexistence of ovigerous females of both species corroborates the results observed by Peres et al. (2018), according to whom, different reproductive traits may be mainly accountable for avoiding juvenile competition.

The spatial distribution pattern observed in the present study may be also correlated to availability of cracks and refuges amongst boulders and gravels, as well as to the presence of other decapods in the intertidal zone, as shown by Generalized linear models (GLM) and Non-metric multidimensional scaling (NMDS). In the study site, rocks are exposed to the air during low tide periods (See Figure 2A-B), but certainly small water puddles around them provide refuge an immediate water to *Panopeus americanus* and *P. austrobesus*.

Mud crabs are not the only organisms using these habitats throughout the intertidal zone. *Alpheus* snapping shrimps were observed in high abundance during collection procedures in the present study (data not shown), mainly in the low intertidal zone. Previous studies focused on alpheid shrimps in this same area have shown that many of them inhabit the same intertidal zone, but in highest abundance in the low intertidal zone (Pescinelli, pers. obs.). Thus, *Panopeus* predominance in the middle and high intertidal zones may be a strategy to avoid competition for space with alpheid shrimps. *Alpheus brasileiro* (Pescinelli et al. 2017, 2018) and *Alpheus carlae* (Ghizelli-Fraga et al. 2021) were the most abundant snapping shrimp species found in the study site, whereas *Alpheus buckupi*, *Alpheus petronioi* and *Alpheus estuariensis*, the least abundant (Almeida et al. 2018). Pescinelli et al. (2017) conducted a study on social monogamy of *A. brasileiro* in this same area and observed male and female individuals living together in the same space, besides their high territorialism and territorial defense (Mathews 2002). This behavior and the strong weaponry of these shrimps are factors likely influencing *Panopeus* species' distribution in the intertidal zone. In addition, species of the genus *Panopeus*, as *P. americanus* studied by Carvalho-Batista et al. (2015) show evidences of cryptic/non-cryptic color pattern in males and females and relationships to morphological and functional sexual maturity, which is another variable in the life strategy in this complex intertidal system.

Considering that studied populations of *P. americanus* and *P. austrobesus* coming from Cananeia mangrove and from São Sebastião Channel show the same pattern of spatial distribution in the intertidal zone, certainly, biological factors such as competition, reproductive trait and social organization are stronger that physical features in determining such pattern. Cananeia mangrove is one of the five least degraded and most productive estuaries worldwide (Schaeffer-Novelli et al. 1990), and it is supposed that it provides abundant food resources and diverse habitat refuges. In contrast, São Sebastião Channel is in frequent influence of water pollution and urban development.

On top of that, the availability of refuges can also be a decisive factor in the investigated intertidal zone. Rocks distributed throughout the intertidal zone, as well as their use as refuge by crabs and snapping shrimp species, creates a scenario featured by high competition for space, which is essential to enable species survival. This refuge not only provides protection from desiccation, but also from nekton predators during the high tide, as well as from birds and other predators during the low tide.

The hypothesis of species coexistence within intertidal zones, although with different abundance was confirmed. Furthermore, differences in the crabs' mean size were observed. Despite the similarity in space occupied by each species, the current findings have suggested that different activity patterns, such as divergent dietary preferences, allow the same distribution of crabs. Due to the great importance of Cananeia mangrove, data on crab populations living in the intertidal zone are essential to help monitoring this ecosystem. Thus, the current findings on the distribution and abundance of sympatric mud-crab species *P. americanus* and *P. austrobesus* can be used as indicators to help detecting and assessing disturbances in this important ecosystem.

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Associate Editor

Tito Lotufo

Author Contributions

Gabriel L. Saraiva: led the writing and analyzed the data; read and approved the final manuscript.

Leonardo Moreira: led the writing and analyzed the data; read and approved the final manuscript.

Fernando L. Mantelatto: participated in revising of the manuscript; read and approved the final manuscript.

Rogerio C. Costa: conducted the fieldwork sampling; participated in revising of the manuscript; read and approved the final manuscript.

Régis A. Pescinelli: led the writing and analyzed the data; conducted the fieldwork sampling; participated in revising of the manuscript; read and approved the final manuscript.

Conflicts of Interest

The author(s) declare(s) that they have no conflict of interest related to the publication of this manuscript.

Ethics

The present study was conducted in compliance with current Brazilian laws; specimens were obtained under collection permits (permanent license to RCC for the collection of Zoological Material N. 23012-1 MMA/IBAMA/SISBIO and SISGEN AE942E3).

Data Availability

Supporting data are available at <https://doi.org/10.48331/scielodata.T4SALV>.

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