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Brachyuran crab diversity across spatial and temporal scales in a mangrove ecosystem from the western Atlantic

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ABSTRACT

Brachyuran crabs are considered ecosystem engineers which greatly impact energy flow and are an important link between the base and higher trophic levels in mangrove forests. Thus, their richness and abundance configure a potential ecological indicator of habitat disturbance. Herein, we spatially and seasonally investigated the crab diversity throughout an eight-year time span in a subtropical mangrove. Sampling was performed seasonally from 2011 to 2019 in five sites located in the Babitonga bay mangrove ecosystem. Our results indicate significant differences in the richness, diversity, and abundance among years and among the sites, as well as significant associations and interactions between the abundance and distribution of the crabs' assemblage across temporal and spatial scales. Sites 3 and 2 showed the highest richness, followed by sites 5, 4 and 1, respectively. Temporal analysis showed small fluctuations among the years, with 2011–2012 showing higher richness than the other periods. Ocypodidae was the most dominant family. The fiddler crab *Leptuca thayeri* was the most abundant in all sites, except site 3, which presented *L. leptodactyla* as the most abundant, indicating ecosystem disturbances for sites 2 and 3 as they were the closest to anthropized areas. All results indicate the importance of the brachyuran crab assemblage for characterizing and evaluating the mangrove ecosystem of Babitonga bay, making them fundamental for monitoring and developing plans aimed at reducing the impacts of adjacent anthropized areas.

1. Introduction

Coastal wetlands like mangrove and estuaries are recognized as critical transition zones between freshwater environments and the sea and have several ecological functions that range from nutrient cycling to maintaining biodiversity (Levin et al., 2001; Junk et al., 2014). Found in intertidal zones along tropical and subtropical latitudes, mangroves are very important for both aquatic and terrestrial organisms (Beger et al., 2010). Mangrove vegetation directly impacts its associated fauna, contributing to its diversity and habitat complexity (Lee, 1999).

There are numerous services that ecosystems such as mangroves provide across coastal areas, e.g., flood control, storm protection, pollution control, breeding and nursery habitats, shoreline stabilization and erosion control and carbon sequestration (Barbier, 2017). Mangrove ecosystems have higher primary productivity rates than any other type of ecosystem, with higher carbon cycling (Chmura et al., 2003). In addition to its importance for coastal populations, mangrove forests can make coastal communities more resilient to extreme events and climate change, while improving their livelihoods as well (Duarte et al., 2020).

One of the best ways to characterize and evaluate mangrove ecosystems is through their relationship with the species that inhabit them in both the marine and terrestrial realms (Rog et al., 2017). Mangroves form a habitat for many taxa, with brachyuran crabs and mollusks being the most numerous components of their benthic macrofauna (Nagelkerken et al., 2008). Crabs and mollusks are the dominant macrofauna considering the high number of species and their abundances (Nagelkerken et al., 2008). Crabs are considered ecosystem engineers that have important impacts on energy flow and in the structure and chemistry of sediment (Kristensen, 2008), and form an important link between the base and higher trophic levels of the mangrove food web, including fish species to birds and other taxa (Macintosh et al., 2002).

Considering the importance of crabs for the ecological functioning of the mangrove ecosystem and that their diversity and abundance can reflect the functioning and environmental conditions of the ecosystem (Lee, 1999; Macintosh et al., 2002), information about their ecological parameters is fundamental and

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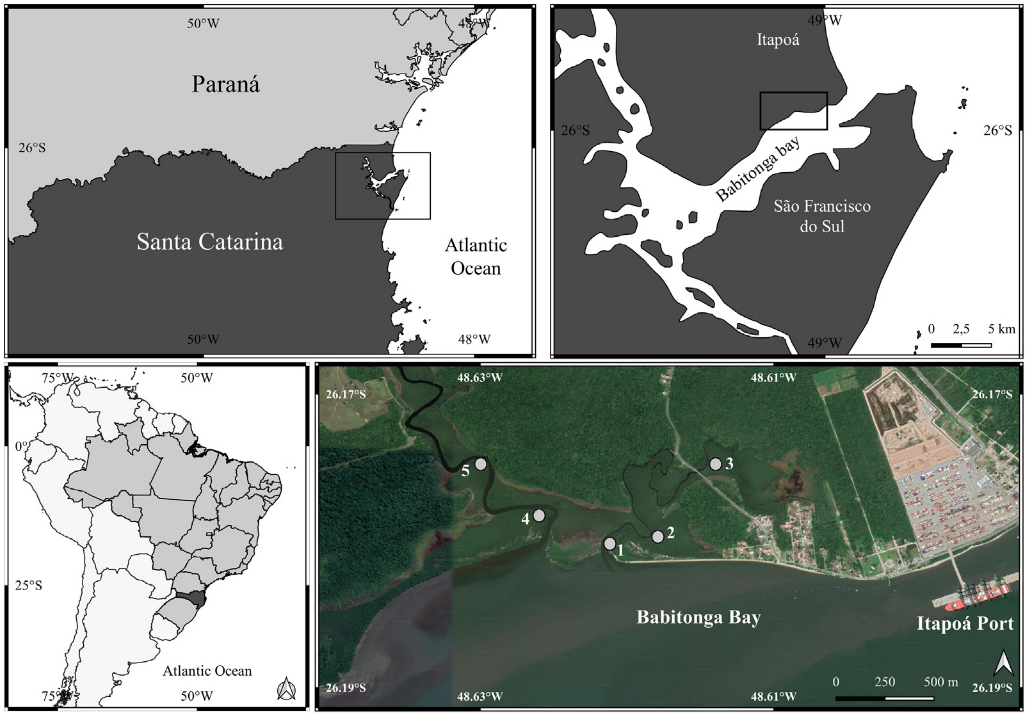

Fig. 1. Location of the study area in the Babitonga Bay mangrove ecosystem on the southern Brazilian coast. Sites 1, 2 and 3 are located in the Rio Pequeno mangrove and sites 4, 5 are in the Jaguaruna mangrove.

could indicate possible habitat changes in mangroves (Macintosh et al., 2002). All these ecological roles characterize brachyuran crabs as keystone species in mangroves (Smith et al., 1991; Sen et al., 2014).

Several factors drive the spatial and temporal distribution of species, including climatic factors on regional to global scales, resource availability, and biotic interactions on smaller scales (Compton et al., 2010; Wisz et al., 2013). Therefore, distribution across spatial and temporal scales could reveal important information about habitat quality, that is intrinsically related to environmental conditions (Krausman, 1999) and could be used to assess possible changes in natural ecosystems. Understanding biotic interactions across spatial–temporal scales is also important for predicting future species assemblages (Wisz et al., 2013).

Considering the representativeness and importance of the brachyuran crab assemblage in mangrove ecosystems and that information about their richness and abundance is the first step towards elaborating conservation strategies for these ecosystems, the present study aimed to analyze the diversity of crabs in a mangrove ecosystem on the southern Brazilian coast across space and time for eight years.

2. Materials and methods

2.1. Study area

Sampling was carried out in five sites from an intertidal zone of the mangrove ecosystem of Babitonga Bay, near the Itapoá Port on the southern Brazilian coast (26°10'55.4"S 48°37'27.9"W) (Fig. 1). The mangrove ecosystem of Babitonga Bay is the largest and most important mangrove area in State of Santa Catarina. The Babitonga Bay receives water from several rivers and several economic activities are carried out in this estuarine complex, including port activities, fishing and the cultivation of marine organisms (Vieira et al., 2008).

2.2. Sampling and data analysis

Collections were carried out in five sites in the vicinity of the Itapoá Port: three in the Rio Pequeno mangrove (sites 1, 2 and 3), and two in the Jaguaruna mangrove (sites 4 and 5) (Fig. 1). Samplings were executed in eight periods (2011–2012 to 2018–2019), each period consists of four samplings, one in each season (spring, summer, autumn, and winter). Thus, a total of 32 samples were collected at each site over the eight years. At each site, two 20 m diameter circles were randomly delimited in the intertidal zone. In each circle, crabs were manually collected by one person for 15 min, which is a technique adapted from Branco (1991).

Specimens were collected from burrows, roots, trunks, and branches of the mangrove trees, and kept in coolers with crushed ice. Next, crabs were transported to the laboratory, where they were identified. Specimens were identified based on Melo (1996) and classified according to Shih et al. (2016).

The sampling effort in each site was evaluated using accumulated curves. To analyze the structure (composition and abundance) of the crabs' assemblage on a spatial and temporal scale, the mean number, richness, diversity, dominance and equitability were estimated across sampling dates within each site.

Homoscedasticity (Levene) and normality (Shapiro–Wilk) tests were first performed as prerequisites for statistical tests (Zar, 1996). The Shannon–Wiener index (H') was used to estimate assemblage diversity. The factorial ANOVA ($P = 0.05$) with Holm–Sidak post-hoc tests was used to evaluate spatial and temporal differences in species richness (number of species), diversity and abundance (number of individuals) and the interaction between periods and sites for all factors. A generalized linear model (GLM) was used to analyze the effect of period (2011–2012 to 2018–2019), sites (1–5), and seasons (spring = October–December; summer = January–March; autumn = April–June; winter = July–September) on mean abundance of crabs' assemblage, as well as the interactions among these factors.

Table 1
Brachyuran crab assemblage, diversity, dominance and equitability in five sites from the mangrove ecosystem of Babitonga Bay, southern Brazilian coast from October 2011 to May 2019.

Species	Family	Site 1	Site 2	Site 3	Site 4	Site 5	Total
Aratus pisonii	**Sesarmidae**	140	162	116	163	179	**760**
Eurytium limosum	**Panopeidae**	329	141	77	155	92	**794**
Goniopsis cruentata	**Grapsidae**	140	58	24	148	121	**491**
Leptuca cumulanta	**Ocypodidae**	10	76	990	36	24	**1,136**
Leptuca leptodactyla	–	600	782	1,362	638	637	**4,019**
Leptuca thayeri	–	1,147	1,480	471	1,432	1,419	**5,949**
Leptuca uruguayensis	–	29	42	45	44	44	**204**
Minuca mordax	–	0	3	44	5	5	**57**
Minuca rapax	–	1	5	16	2	1	**25**
Minuca vocator	–	0	3	8	0	1	**12**
Neohelice granulata	**Varunidae**	0	3	4	0	0	**7**
Pachygrapsus gracilis	**Grapsidae**	24	3	5	17	3	**52**
Sesarma rectum	**Sesarmidae**	10	18	171	17	18	**234**
Ucides cordadus	**Ocypodidae**	4	3	1	12	3	**23**
Total		**2,434**	**2,779**	**3,334**	**2,669**	**2,547**	**13,763**
Richness		11	14	14	12	13	**14**
Shannon's diversity index		1.45	1.33	1.57	1.40	1.31	**1.57**
Dominance		0.31	0.37	0.28	0.36	0.38	**0.29**
Equitability _ J		0.61	0.50	0.59	0.56	0.51	**0.60**

Table 2
Factorial analysis of variance (ANOVA). Comparison of richness, diversity and abundance among periods (2011–2012 to 2018–2019), sites (1-5) and their interaction (period*site).

Factors	*df*	Richness		Diversity		Abundance	
		F	*P*	F	*P*	F	*P*
Main test							
Period	7	2.38	**0.026**[a]	13.16	**0.000**[a]	267.3	**0.000**[a]
Site	4	9.12	**0.001**[a]	6.46	**0.000**[a]	86.4	**0.000**[a]
Interaction							
Period*Site	28	1.41	0.107	1.13	0.321	7.7	**0.016**[a]

[a]Values in bold are significant $P < 0.05$.
df = degrees of freedom; F = test value; *P* = significance.

Similarity throughout space and time was analyzed with a cluster analysis (CA) using Bray–Curtis coefficient and overlapping clusters were visualized using a non-metric multidimensional scaling analysis (NMDS). A canonical correspondence analysis (CCA) was used to analyze crabs' assemblage structure at the sites, period (years) and seasons, and to describe the effects of these factors on crab species.

3. Results

3.1. Species composition

During the study, 14 crab species of five families were sampled (Table 1) and a total of 13,763 specimens were collected. The Ocypodidae Rafinesque, 1815 family showed the highest richness with seven species. Sites 2 and 3 had the highest richness and abundance, while site 1 had the lowest richness and abundance. The species with the highest abundances in all study sites were *Leptuca thayeri* (Rathbun, 1900) (N = 5,949), *Leptuca leptodactyla* (Rathbun, in Rankin, 1898) (N = 4,019) and *L. cumulanta* (Crane, 1943) (N = 1,136). Sites 1 and 3 had lower dominance compared to 2,4 and 5 (Table 1).

3.2. Spatial and temporal species richness, diversity, abundance, and similarity

The stabilization of the number of species occurred in different periods for the sampled sites. Sites 5 and 4 were the first to reach the maximum number of species during the fifth and sixth samplings, respectively. Sites 1, 2 and 3 reached the presented 10, 12 and 14, respectively, as the maximum number of species (Fig. 2).

Mean richness, diversity and abundance varied by years and sites (Fig. 3). The factorial ANOVA showed significant difference in the richness, diversity and abundance among years and among sites ($P < 0.05$). The interaction (period*site) was only significant for mean abundance, while there was no significant interaction between period and site in relation to richness and diversity (Table 2). Holm–Sidak post-hoc tests showed that the richness and diversity were higher in the first period sampled (2011–2012), differing from the other periods ($P < 0.05$), and the lowest richness occurred in the period 2015–2016 (Fig. 3 A). Mean richness and diversity were higher in sites 1, 3 and 4, differing from 2 and 5 (Holm–Sidak, $P < 0.05$) (Fig. 3A–D). Temporal analysis of the data showed a gradual and constant increase in the mean abundance of crabs captured from 2011–2012 to 2015–2016, when the abundance of the collected crabs decreased. After this period, there was an increase in abundance again until the end of collections (Fig. 3E). Mean abundance was the highest at site 3, differing from the other sites (Fig. 3F).

The generalized linear model (GLM) revealed a significant association and interaction between the mean abundance and distribution of crabs' assemblage on a temporal and spatial scale, including a difference among the seasons (Fig. 4). The highest and lowest accumulated abundance were observed in the summer 3,880 and winter 3,006 respectively. In the summer, site 3 showed a higher mean abundance for seven of the eight years sampled, with mean abundance higher than 100 individuals (Fig. 4).

Cluster analysis (CA) and a Non-metric multidimensional scaling ordination (NMDS) resulted in similar clusters both in time and space (Fig. 5). Similarity among sites 1, 2, 4 and 5 was higher than 80%, increasing to values above 90% when considering only sites 2, 4 and 5, and almost 100% between sites 4 and 5, while site 3 showed low similarity with the others (below 50%) (Fig. 5 A). The NMDS showed higher similarity of sites 1, 2, 4 and 5, with overlapping clusters, excluding site 3 (Fig. 5B). Temporal cluster analysis revealed highest similarity among the periods 2014–2015 to 2018–2019, higher than 80%. The first sampled period (2011–2012) showed low similarity, below 50% (Fig. 5C). As for spatial scale, the NMDS showed overlapping clusters, excluding the periods 2011–2012 and 2012–2013 (Fig. 5D).

Canonical Correspondence Analysis (CCA) across spatial scale showed that axis F1 contributed to 99.1% of variation. *Goniopsis cruentata* (Latreille, 1803), *Aratus pisonii* (H. Milne Edwards, 1837) and *Pachygrapsus gracilis* (de Saussure, 1857) were highly correlated with sites 4 and 5, whereas *Eurytium limosum* (Say, 1818) and *Sesarma rectum* Randall, 1840 were highly correlated with sites 1 and 3, respectively (Fig. 6).

Canonical Correspondence Analysis (CCA) across temporal scale showed a low correlation in which axis F1 and F2 contributed to 55% and 39%, respectively, of variation throughout the years (Fig. 7). The crabs *G. cruentata*, *S. rectum*, and *E. limosum* were correlated to the first sampled period (2011–2012), while *L. thayeri*, *L. cumulanta*, *L. leptodactyla*, *P. gracilis* and *A. pisonii* were correlated to 2016–2017 to 2018–2019 samples (Fig. 7).

4. Discussion

The present study provides the first detailed spatial and temporal analysis of brachyuran crab diversity over an eight year time period in the mangrove ecosystem of Babitonga Bay, southern Brazil. Our results indicate significant differences in the richness, diversity, and abundance among years and sites, as well as

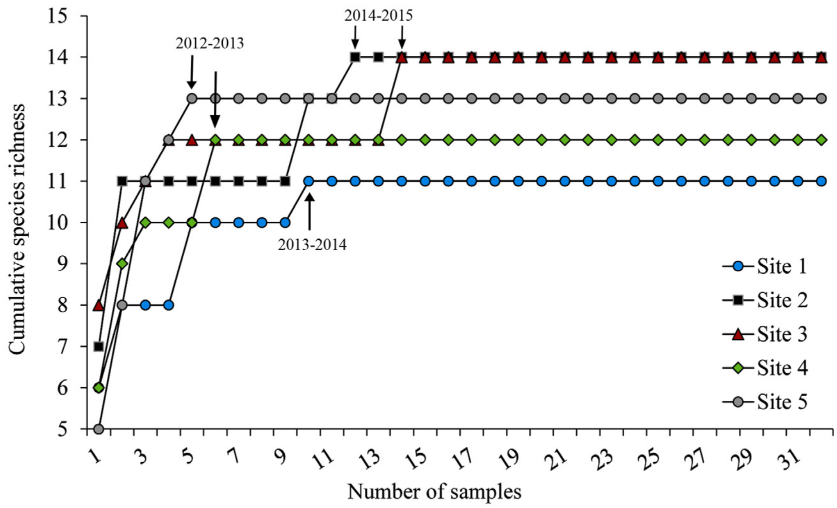

Fig. 2. Cumulated number of brachyuran crab species in five sites from the mangrove ecosystem of Babitonga Bay, southern Brazilian coast from October 2011 to May 2019.

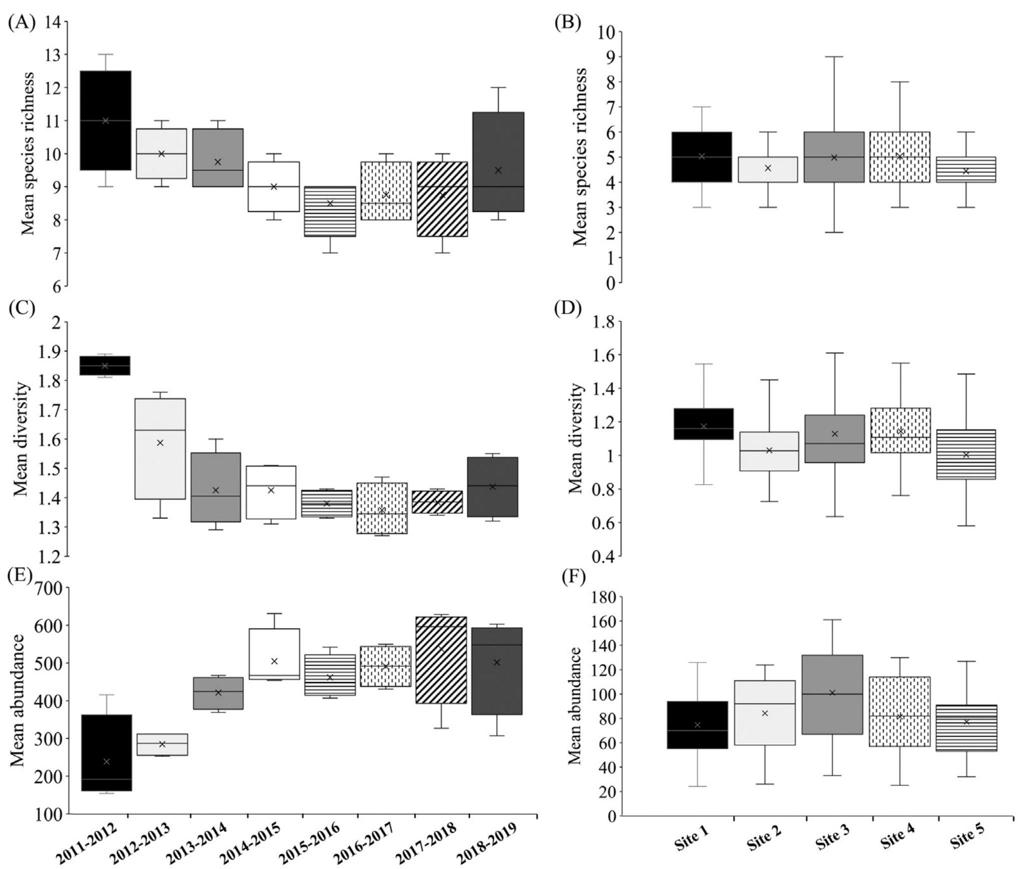

Fig. 3. Mean species richness (A-B), diversity (C-D) and abundance (E-F) of brachyuran crab assemblage on a temporal and spatial scale. Minimum, maximum (whiskers), median (horizontal lines) and mean (x).

significant associations and interactions between the abundance and distribution of the crabs' assemblage throughout time and space, including differences among the seasons. The spatial and temporal analysis of richness and abundance also revealed a possible influence of anthropized areas in the configuration and distribution of the crabs' assemblage.

Mangrove ecosystems are highly productive, presenting high richness and abundance of brachyuran crabs (Smith et al., 1991; Sen et al., 2014). Our study corroborated with the expected results, showing 14 species distributed in five families and high abundance of crabs in the mangrove ecosystem sampled. The family Ocypodidae Rafinesque, 1815 was the most abundant and most representative family, with eight species sampled. This family, as well as the Superfamily Grapsoidea MacLeay, 1838, commonly present the highest diversity of mangrove crabs (Schubart et al., 2002). In a study of brachyuran crab diversity from seven subtropical mangroves in São Paulo state (latitude of 23°S), Colpo

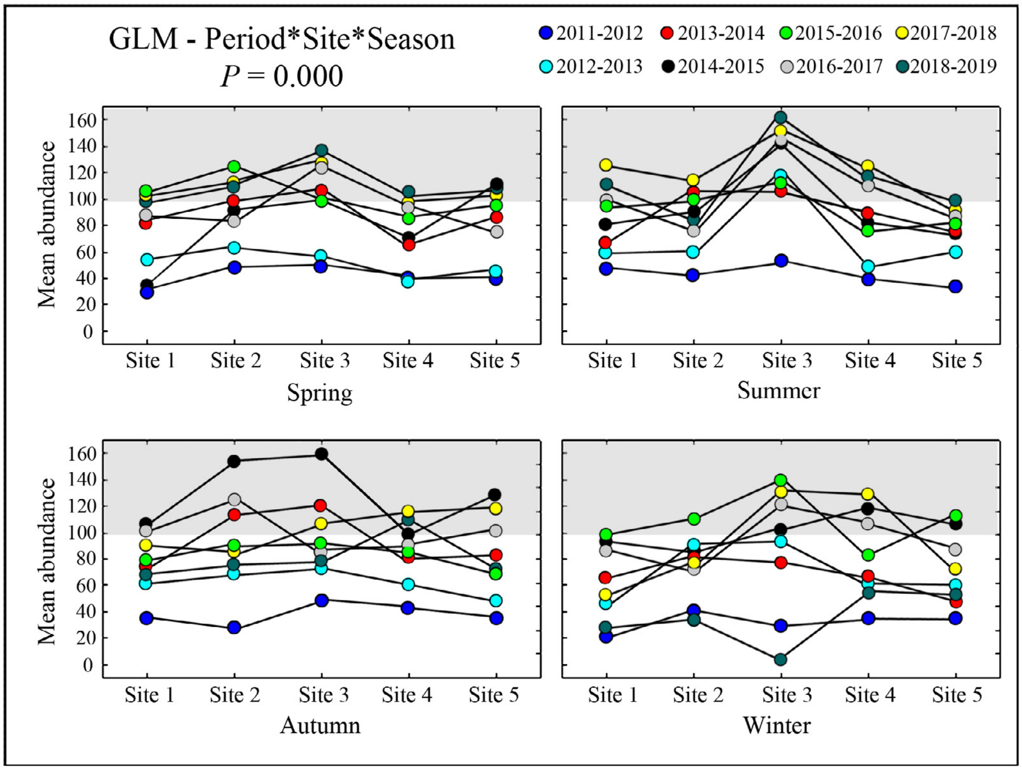

Fig. 4. Generalized linear models (GLM) showing the relationship between the mean abundance of brachyuran crab assemblage on temporal (years and seasons) and spatial (sites) scales, according to the set of environmental factors (Period*Site*Season). Gray area represents mean values greater than 100 individuals.

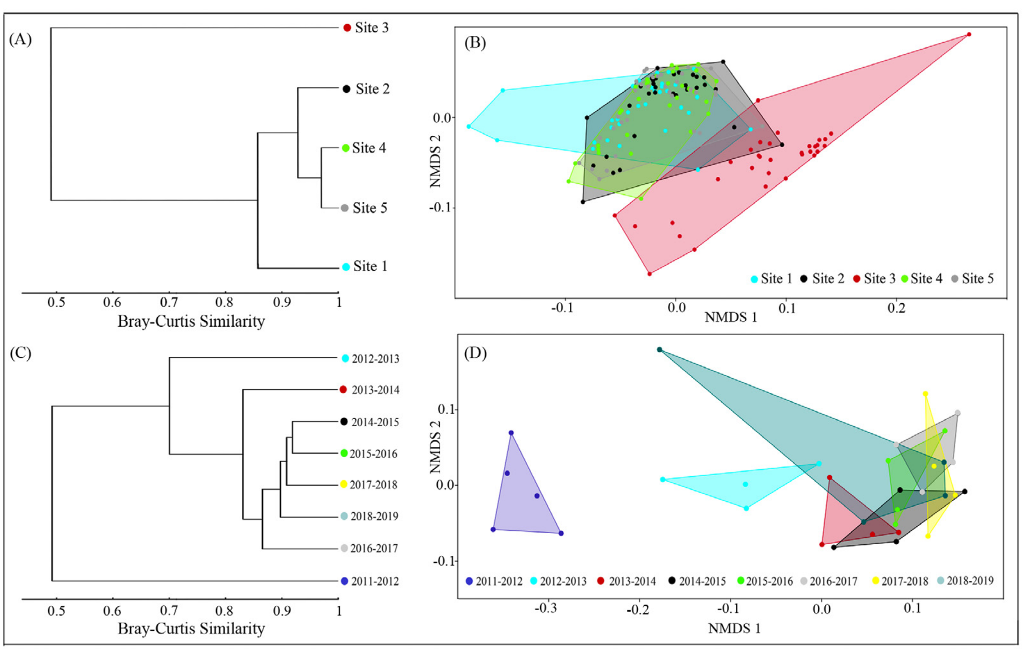

Fig. 5. Cluster analysis (CA) with Bray–Curtis coefficient and non-metric multidimensional scaling (NMDS) showing the similarity of brachyuran crab assemblage on spatial (A-B) and temporal (C-D) scales.

et al. (2011) found from 15 to 19 species depending on the mangrove sampled. Considering that the species richness of mangrove crabs can decrease towards higher latitudes (Sharifian et al., 2020), and that Babitonga Bay is located at 26°S, the richness observed throughout the eight years is expressive and reveals the importance of this ecosystem for maintaining the crabs' assemblage. The richness found in the present study is even more expressive when compared to the crab richness in the Itacorubi mangrove, which is also found in of Santa Catarina. Therein, Branco (1991) recorded 15 brachyuran species from infralittoral to supralittoral zone. Of the 15 species recorded by Branco (1991), 5 species were collected in the infralittoral and 10 in meso and supralittoral, which is lower than the species richness (14 species) found in the mangrove of Babitonga Bay.

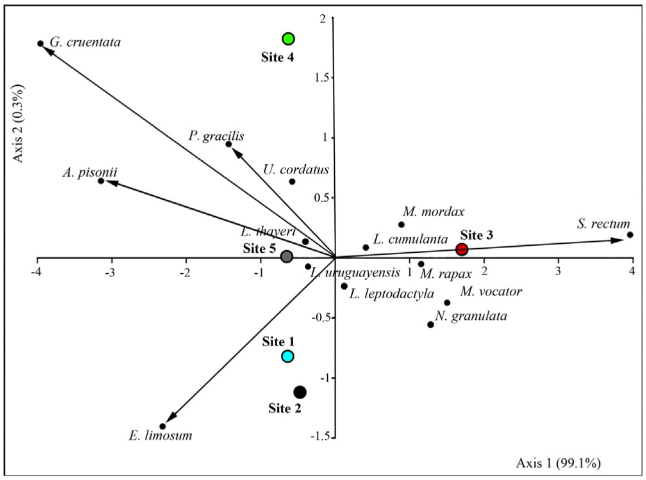

Fig. 6. Canonical Correspondence Analysis (CCA) biplot showing the association of species abundance with the sampled sites. The arrow lengths show the degree of influence of each variable.

The crabs' assemblage structure and diversity patterns differed among the sites. Sites 3 and 2 had the highest richness followed by sites 5, 4 and 1, respectively. The stabilization in the number of species at different periods in the sampled sites followed the opposite order of the observed richness gradient (sites 5, 4, 1, 2, 3). In addition to presenting high richness, site 3 stands out for its high abundance and low dominance. The stabilization in number of species sampled at sites 2 and 3 during the 2014–2015 period only highlights the complexity of mangroves and the importance of long-term studies for accurate estimates of local richness.

Analyzing the data from eight years of sampling, the richness fluctuated slightly among the years, with 2011–2012 showing a higher richness than the other periods. The same trend was observed for diversity and equitability, revealing stability in the crabs' assemblage structure throughout the studied period. However, the pattern of increased mean abundance was not maintained in the 2015–2016 period, when this decreased and presented the lowest average number of species for the eight year collection period. This decrease in richness and abundance was possibly related to the intense storms in the region in early March 2015, with several floods that could have destroyed the burrows of many crab species. In the following periods, the pattern observed before the storms returned, with a gradual increase in the mean richness and mean abundance, showing that the climate events that occurred during the summer of 2015 directly impacted the crabs' assemblage.

The generalized linear model revealed an interaction between the spatial and temporal factors, including the seasons and mean abundance of crabs. Considering that mangrove species show physiological, morphological and behavioral adaptations that allow them to tolerate wide fluctuations in environmental factors, e.g., salinity and tides (Lee, 1999; Macintosh et al., 2002), the differences in richness and abundance across space and time observed herein could be a result of biotic factors as competition for resources and predation. In intertidal zones, it has been often reported that species distribution is limited by biotic factors, such as competition for food, refuges and predation pressure (Somero, 2002). The heterogeneity of the substrate and the degree of environmental impacts are other factors that should be considered to evaluate the distribution and abundance of crabs (Ashton et al., 2003).

The cluster analysis (CA) and Non-metric multidimensional scaling ordination (NMDS) showed high similarity between sites 4 and 5 and between sites 1 and 2. However, site 3 showed low similarity with the others. These results reveal that site 3 has specific characteristics such as high richness and abundance. In addition, the greater proximity of site 3 to urban groupings in relation to the other sites probably contributed to its uniqueness. An hypothesis that could explain the higher diversity and abundance of crabs in site 3 is that the habitat heterogeneity found at this site, ranging from a mix of sand and mud to completely muddy sediment, provides more diverse habitats occupied by different species. Among the factors modulating the distribution of fiddler crabs, the substrate-dependent spatial distribution resulting from morphological specializations to deposit-feeding must be considered (Bezerra et al., 2006).

The brachyuran assemblage composition at a site could be an important indicator of habit status (Macintosh et al., 2002). Its diversity and abundance in an area reflect the status and dynamic of the mangrove ecosystem and also act as indicators of habitat changes (Macintosh et al., 2002). Since site 3 is close to urban groupings, roads, and construction of an access bridge to the Itapoá Port, this area could be more impacted than more distant ones.

By analyzing the brachyuran crabs' assemblage, it was possible to observe a dominance of Ocypodidae species in all sites monitored. The fiddler crab *L. thayeri* was the most abundant at all sites, except site 3, which showed *L. leptodactyla* as most

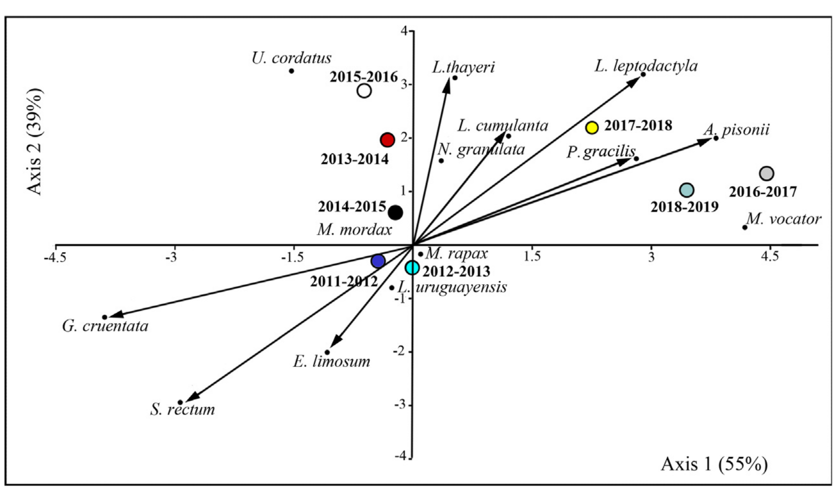

Fig. 7. Canonical Correspondence Analysis (CCA) biplot showing the association of species abundance and years. The arrow lengths show the degree of influence of each variable.

abundant. High abundances of ocypodid crabs are commonly found in semi-open mangrove habitats with periods of direct solar radiation (Ashton et al., 2003), which are the exact characteristic of site 3. Since grapsid crabs are more frequently found in mature ecosystems (Ashton et al., 2003), the low abundance of these crabs in site 3 also indicates the possible impacts of human activities in this area.

Analyzing the results of the canonical correspondence analysis (CCA), it was possible to observe an association of *E. limosum* with site I, as well as *G. cruentata* and *S. rectum* with sites 4 and 3, respectively. Regarding the dominant species, there was also a positive correlation among *L. thayeri* and sites 1, 2, 4 and 5, while *L. leptodactyla* and *L. cumulanta* were dominant in and positively correlated to site 3. All these results could indicate the habit status of the mangrove ecosystem studied. Considering the dominance of fiddler crabs in the sites studied, understanding their distribution may be the key to assessing and monitoring this important ecosystem on the southern coast of Brazil. The dominance of *L. thayeri* in almost all sites is attributed to the muddy sediment present therein. Sediment grain size is considered the main factor affecting the spatial distribution of fiddler crabs (Bezerra et al., 2006; Colpo and Negreiros-Fransozo, 2011, 2013), with *L. thayeri* showing affinity for very fine and very fine sand sediments (Bezerra et al., 2006). Thus, this species is commonly found in shaded areas (Bezerra et al., 2006), which coincides with our results since the sites where this species was abundant are vegetated habitats. *Leptuca leptodactyla* was dominant in site 3 and has an affinity for sediments composed of medium sand and is found living in sunny areas (Coelho, 1965; Warner, 1969; Bezerra et al., 2006).

Temporal analysis throughout the eight years revealed an association of *G. cruentata* and *S. rectum* with the first collection periods. Such association is due to a continuous decrease in abundance, mainly for *G. cruentata*. The dominant species *L. thayeri* and *L. leptodactyla*, as well as *L. cumulanta* and *A. pisonii,* showed a constant increase in abundance and an association with collection periods from 2014 to 2019. These results confirm stable abundances for the dominant crab species (Ocypodidae) in the mangrove swamps throughout the whole study period. This high ocypodid crab abundance is characteristic of areas with disturbances or those in the process of regeneration (Macintosh et al., 2002; Ashton et al., 2003).

The significant decrease in *G. cruentata* in sites 4 and 5, which are considered those with less anthropic impact, points to possible disturbances in these areas of the mangrove. Considering that grapsid crabs are associated with mature forests in more preserved mangrove areas (Macintosh et al., 2002), the constant decrease in the abundance of *G. cruentata* throughout the eight years reaffirms the importance of monitoring crabs' assemblage in order to detect possible disturbances in mangrove ecosystems. The monitoring of crabs' assemblage is fundamental for understanding the structure, dynamics and resilience of mangrove ecosystems (Macintosh et al., 2002; Ashton et al., 2003).

5. Conclusions

Our results indicate the importance of the brachyuran crabs' assemblage for characterizing and evaluating the mangrove ecosystem of Babitonga Bay. We observed a significant association and interaction between the abundance and distribution of the crab assemblage throughout space and time. Monitoring for eight years made it possible to characterize the structure of the brachyuran crab assemblage. However, despite the high abundance of crabs in the studied ecosystem, the highest abundances were found for three dominant species in the study area: *L. thayeri*, *L. leptodactyla* and *L. cumulanta*, all of which belong to the family Ocypodidae. Therefore, these species indicate that there are disturbances in the ecosystem, mainly in the sites closest to anthropized areas. Overall, all the results presented here are fundamental for monitoring and developing measures aimed at reducing the impacts of adjacent anthropized areas on the biodiversity of the mangrove ecosystem in Babitonga Bay.

CRediT authorship contribution statement

Felipe Freitas Jr: Methodology. **Régis A. Pescinelli:** Writing - original draft, Writing review & editing, Conceptualization, Investigation, Data curation, Formal analysis. **Rogerio C. Costa:** Visualization, Review & editing. **Juliano C. Hilesheim:** Methodology. **Fernando L. Dieh:** Methodology. **Joaquim O. Branco:** Project administration, Methodology, Review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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