



# Brachyuran crab diversity and the population biology of *Panopeus americanus* on a tropical Sabellariidae (Polychaeta: Annelida) reef

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## ABSTRACT

This paper describes the species composition, abundance, and diversity of brachyuran crabs and the population structure of *Panopeus americanus* on a *Sabellaria wilsoni* reef on Caixa D'Água beach, a macrotidal sandy beach on the Amazon coast. Samples were collected monthly throughout a single natural growth–destruction cycle of the reef. Ten crab species were recorded, of which the most abundant were *Panopeus americanus* (83% of the individuals collected), *Panopeus occidentalis* (6.8%), and *Menippe nodifrons* (5.3%). The highest crab species richness was recorded during the eroded reef phase, reflecting the increase in habitat complexity, whereas the highest crab density was recorded during the reef recuperation period, reflecting an intense recruitment process. Juveniles and adults (including ovigerous females) of *P. americanus* and *P. occidentalis* were found at certain times on the reef, while for *M. nodifrons*, the largest species, most of the captured individuals were juveniles, and no ovigerous females were captured. These findings reflect the importance of the biogenic substrate provided by the *S. wilsoni* reef to the population biology of the crabs on the Amazon coast, with some species using the reef more permanently, including as breeding and nursery grounds. The results also showed that the structural cycle of bioconstructions determines changes in the crab assemblages.

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## 1. Introduction

Decapod crustaceans are among the most diverse and abundant animal groups in marine environments (Ng et al., 2008). The infraorder Brachyura Latreille, 1802, which includes crabs, is a large group including over 6800 species worldwide, equivalent to approximately 46% of the known decapod diversity (Ng et al., 2008; Davie et al., 2015). Brachyuran crabs play a key role as predators and prey or consumers of detritus in the complex food webs of coastal ecosystems, such as mangrove forests, seagrass beds, and biogenic reefs (Suraci et al., 2016). Many crabs are also economically important resources for both commercial and artisanal fisheries (Calado et al., 2003).

Some gregarious species of the family Sabellariidae (Annelida, Polychaeta) are known for their capacity to build cemented tubes

of sand and form extensive reefs, particularly in shallow coastal environments. Sabellariid reefs are inhabited by a range of benthic species and are generally more species-rich and productive than adjacent unconsolidated substrates (Mettam, 1992; Gherardi and Cassidy, 1994; Jones et al., 2018; Aviz et al., 2019) or rocky bottoms with no reefs (George and Warwick, 1985; Lane-Medeiros et al., 2021). The macrofauna associated with sabellariid reefs has been investigated amply, particularly in temperate areas of Europe (Gruet, 1971; Porras et al., 1996; Dias and Paula, 2001; Dubois et al., 2002; Gravina et al., 2018; Jones et al., 2018; Bonifazi et al., 2019), although some studies are available for tropical regions (Eeo et al., 2017; Aviz et al., 2019; Lane-Medeiros et al., 2021). Brachyuran crabs are a prominent group associated with sabellariid reefs (Gore et al., 1978; Bosa and Masunari, 2002), and the influence of the structure of these reefs on the crab population biology has been evaluated in some species, such as *Pilumnus hirtellus* (Almaça, 1987) and *Menippe nodifrons* (Rodrigues-Alves et al., 2013).

Extensive reefs of the polychete *Sabellaria wilsoni* Lana & Gruet, 1989 have recently been reported on the Brazilian Amazon

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coast (Ataide et al., 2014; Aviz et al., 2019). These reefs, which support extremely diverse benthic assemblages, undergo major structural modifications over time due to the natural growth–destruction cycle of polychetes (Aviz et al., 2016), typical of those found in other sabellariid species (Gruet, 1986; Brown and Miller, 2011). Studies on sabellariid aggregates in temperate European waters have recorded shifts in the structure of the associated macrofauna assemblages among the different structural phases of the reef (Gruet, 1971; Porras et al., 1996; Dias and Paula, 2001; Dubois et al., 2002, 2006; La Porta and Nicoletti, 2009; Jones et al., 2018; Bonifazi et al., 2019). Up to now, however, the influence of the structural cycle of the reef on the associated fauna has not been evaluated in *S. wilsoni* bioconstructions.

Some aspects of the biology of sabellariid reefs have been studied on the Brazilian Amazon coast, including the reproductive biology of the reef-building polychetes (Aviz et al., 2016) and the effects of reef construction on the associated meiofauna (Ataide et al., 2014) and benthic macrofauna structures (Aviz et al., 2019). While sabellariid reefs play an important role to the life cycle of some crustaceans (Gore et al., 1978; Bosa and Masunari, 2002), to date only the population structure of one species, *Clibanarius symmetricus* (Randall, 1840), has been studied on the reefs of *S. wilsoni* (Aviz et al., 2021). *Panopeus americanus* is one of the most abundant crab species associated with *S. wilsoni* reefs (Aviz et al., 2019). This species is distributed along the eastern coast of the Americas, where it may typically be found in the intertidal zone of muddy estuarine beaches, although it may also be found under rocks and on sandy and biogenic substrates (Melo, 1996; Sánchez and Raz-Guzman, 1997). Despite its extensive distribution, this species has been poorly studied (Vergamini and Mantelatto, 2008a,b; Carvalho-Batista et al., 2015), and ecological data from tropical areas are scarce, in particular for biogenic substrates such as sabellariid reefs.

Our study investigated the association between brachyuran crabs and tropical polychete reefs. This paper describes the structure of the crab assemblages (species composition, richness, and abundance) and the population biology of *P. americanus* on a *S. wilsoni* reef in an Amazon macrotidal beach (the Caixa D'Água beach, Algodual-Maiandeuá Island). We tested the hypothesis that crab species richness and abundance vary significantly among the different phases of the natural growth–destruction cycle of the reef.

## 2. Materials and methods

### 2.1. Study area

The Algodual-Maiandeuá Island is located on the Brazilian Amazon coast (00°36'S, 47°34'W) and is surrounded on three sides by rivers and estuarine channels, with its northern portion facing the Atlantic Ocean (Fig. 1). The local climate is humid tropical, with a mean annual temperature of  $27.7 \pm 1.1^\circ\text{C}$  (Martorano et al., 1993) and a mean annual precipitation ranging from 2300 mm to 2800 mm (Moraes et al., 2005). The precipitation varies considerably throughout the year, with a well-marked rainy season from January to July, when the total rainfall is approximately 1700 mm, and a dry season from August to December, with a total rainfall of around 500 mm (Moraes et al., 2005). The region is dominated by semidiurnal macrotides with an amplitude of 4 m to 6 m (Silva et al., 2011a). The island has a 35 km-long coastline formed by fine sand beaches that vary considerably in extension, width, slope, and exposure to wave action (Rosa Filho et al., 2011). The studied beach, Caixa D'Água, is located on the western margin of the island, which is bathed by the Marapanim River and is a low-tide, sheltered terrace beach with a wide intertidal zone (400 m to 500 m) composed mainly

of fine sand (Rosa Filho et al., 2011). The beach has several rocky outcrops of lateralized sandstone often colonized by *Sabellaria wilsoni* (Aviz et al., 2016).

Each month over one year, the phases of the reef were identified, based on the percentage cover of consolidated tubes within the total area of the reef, the height of the aggregate, and on the visual assessment of patches of erosion. Based on this attributes, the reef was classified as follows: (i) preserved (Fig. 1B), with a compact appearance, well-consolidated height (6 cm to 28 cm), and continuous construction (coverage of approximately 70%); (ii) eroded (Fig. 1C), with open spaces within the reef (coverage ranging from 10% to 60%) and detached blocks; (iii) under recuperation (Fig. 1D), with small patches of low reef (height from 4 cm to 16 cm) and coverage of at least 50% (see Silva, 2015; Aviz et al., 2016).

### 2.2. Sampling procedures

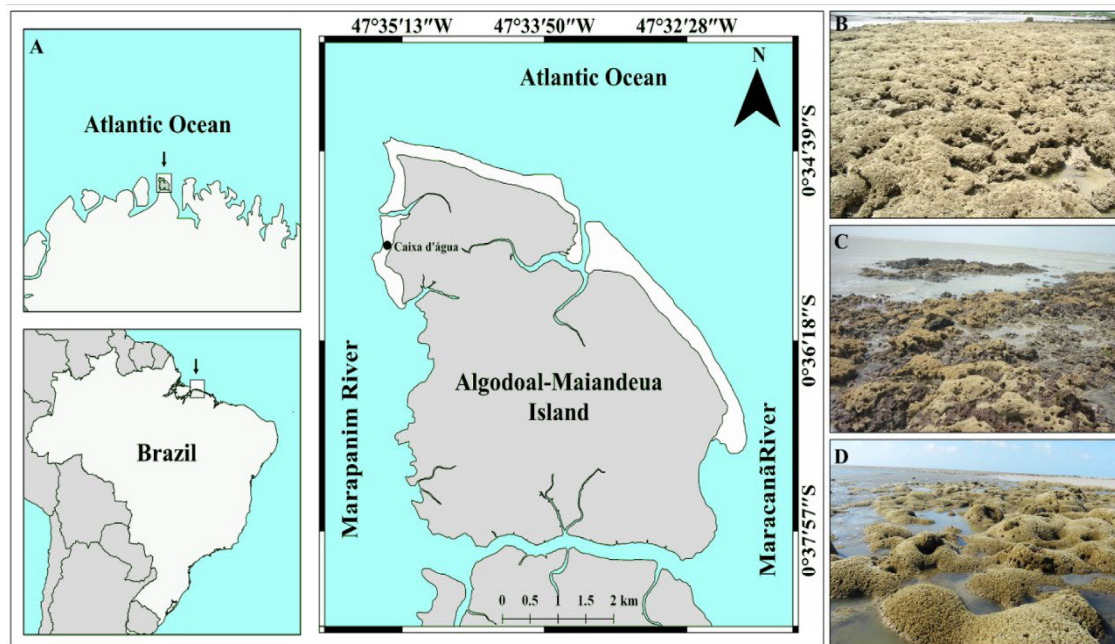
Samples were collected monthly from May 2008 to April 2009 from the *Sabellaria wilsoni* reef on Caixa D'Água beach (Fig. 1A). This reef is located on a large rocky outcrop and is composed of a cohesive cluster of hummocks (area  $\approx 1000\text{ m}^2$ ) surrounded by sandy substrates. The samples were collected during the spring low tide along two transects established perpendicular to the coastline. Two areas were delimited within each transect to ensure the sampling of the full extension of the reef, one located at the low tide line and the other 50 m further inshore (see Ataide et al., 2014). Each month, four samples were collected per area with a metallic core sampler (10 cm in diameter), which was inserted into the substrate until it reached the rocky layer (adapted from Dubois et al., 2002). The volume (measured by the displacement of water in a graduated cylinder) of each sample was recorded in the field, and each sample was then fixed in 5% saline formalin buffered with sodium tetraborate. In addition to the collection of the fauna, samples of surface water were collected each month during the ebb tide to determine salinity. Data on air temperatures and precipitation levels were obtained from the meteorological station in the city of Salinópolis (approximately 30 km east of the study site), with data provided by the Brazilian National Institute of Meteorology (INMET).

### 2.3. Laboratory procedures

Reef fragments were disaggregated over a sieve (0.3 mm mesh), and all the crabs found were identified and counted. The sex and development stage (undetermined juvenile, male, and ovigerous or non-ovigerous female) of each crab were determined, and its carapace width (CW) was measured with a caliper (0.1 mm precision). The smallest individuals were measured under a compound light microscope. In *P. americanus*, individuals smaller than the smallest ovigerous female captured during the study (CW < 2.1 mm) were classified as immature, while all the larger specimens were classified as mature. After the analysis, the specimens were preserved in 70% ethyl alcohol, and vouchers were deposited in the Museum of Zoology of the University of São Paulo (catalog numbers MZUSP 28469–28481) and the Emílio Goeldi Museum in Belém (catalog numbers MPEG 3218–3236).

### 2.4. Statistical analysis

The Relative Abundance (RA—the number of individuals of the species divided by the total number of individuals captured), density (ind.L<sup>-1</sup> of sample), and the Frequency of Occurrence (FO—the number of samples containing the species divided by the total number of samples) were calculated for each crab species. Crab species richness was expressed as the total number of species



**Fig. 1.** Map of the Algodual-Maiandeuá Island (Brazil) showing the studied beach (A) and the different phases of the *Sabellaria wilsoni* reef monitored in this study (B = preserved; C = eroded; D = recuperation).

present in a given sample. The species richness and density were evaluated using a one-factor Analysis of Variance (ANOVA) to test for differences between the structural phases of the reef, followed by Tukey's test for a *posteriori* pairwise comparisons. ANOVA was also applied to compare *P. americanus* densities (total, immature, and mature) between the reef phases and the variation in body size (CW) between the sexes. Prior to the application of the ANOVA, the data were tested for normality (Shapiro-Wilk test) and the homoscedasticity of variance (Cochran's test), and, whenever required, the values were  $\log(x+1)$  transformed. Deviations in the sex ratio of *P. americanus* were evaluated using Chi-square, considering the entire study period, each month, and each body length class (1.1 mm intervals). The relationships between biological (crab species richness and abundance) and abiotic variables (rainfall, salinity, and temperature) were evaluated using Spearman's rank correlation coefficient.

### 3. Results

#### 3.1. Environmental data

During the study period, the rainfall was highest in the months corresponding to the preserved and recuperation phases of the reef, which coincided with the rainy season (January to June). The erosion phase (September to December) coincided with the dry season, when rainfall rates were lower and salinity was higher (Fig. 2). The mean temperatures were slightly higher during the dry season (27.0 °C to 29.6 °C) than in the rainy season (26.3 °C to 27.8 °C).

#### 3.2. Crab assemblages: composition and temporal distribution

A total of 1631 crab specimens was collected during this study (Table 1) and distributed into ten species and four families: Menippidae (two species), Panopeidae (five species), Pinnotheridae (one species), and Sesamidae (two species). *Panopeus americanus* was the most abundant and frequent species overall (RA = 82.7%; FO = 72%), followed by *Panopeus occidentalis* (RA = 6.8%; FO = 22%), and *Menippe nodifrons* (RA = 5.3%; FO = 25%). All

the other species were abundant but infrequently recorded on the reef (Table 1).

Most *P. americanus* specimens collected were female (51.1%), while roughly equal numbers of males and females were collected for *P. occidentalis* (Table 1). In both species, ovigerous females represented 10% of the total number of individuals collected. In *M. nodifrons*, 50% of the specimens collected were juveniles of undetermined sex (Table 1). In the other species, more males than females were collected in most cases, with some species being represented only by males. However, all *Armases benedicti* and *Pachygrapsus gracilis* specimens were female (Table 1).

The highest mean species richness was recorded during the erosion phase (Fig. 3) when eight species (four exclusive to this phase) were recorded (Fig. 4). Crab density ( $F_{2-189}$ : 3.50;  $p$ : 0.03) and species richness ( $F_{2-189}$ : 3.67;  $p$ : 0.02) varied significantly among the structural phases of the reef. The recuperation phase had the highest crab density (Fig. 3) due to a peak in the abundance of *P. americanus* (Fig. 4). However, some of the other species, such as *P. occidentalis*, had a higher density in the erosion phase (Fig. 4).

#### 3.3. Population structure of *Panopeus americanus*

The abundance of immature ( $F_{2-189}$ : 3.33;  $p$ : 0.04) and mature ( $F_{2-189}$ : 4.49;  $p$ : 0.02) *P. americanus* individuals varied significantly among the structural phases of the reef. Both groups were more abundant in the recuperation phase than in the preserved and eroded phases (Fig. 5A).

The *P. americanus* population was female-biased (1.9:1 females: male) during most months, with significant deviations being recorded during the whole study period ( $\chi^2$ : 112.2;  $p$  < 0.01). Juveniles of undetermined sex (CW = 1.04–1.98 mm; mean =  $1.86 \pm 0.06$  mm) represented 23.1% of the crabs collected (Fig. 5B). Male *P. americanus* (CW = 1.98–10.52 mm; mean =  $5.7 \pm 0.19$  mm) were significantly larger ( $F_{1,2}$ : 63.44;  $p$  < 0.01) than the females (CW = 1.6–7.53 mm; mean =  $4.36 \pm 0.10$  mm). While there was a significant female bias in the 1.5–5 mm CW class, a significant male bias was recorded among individuals

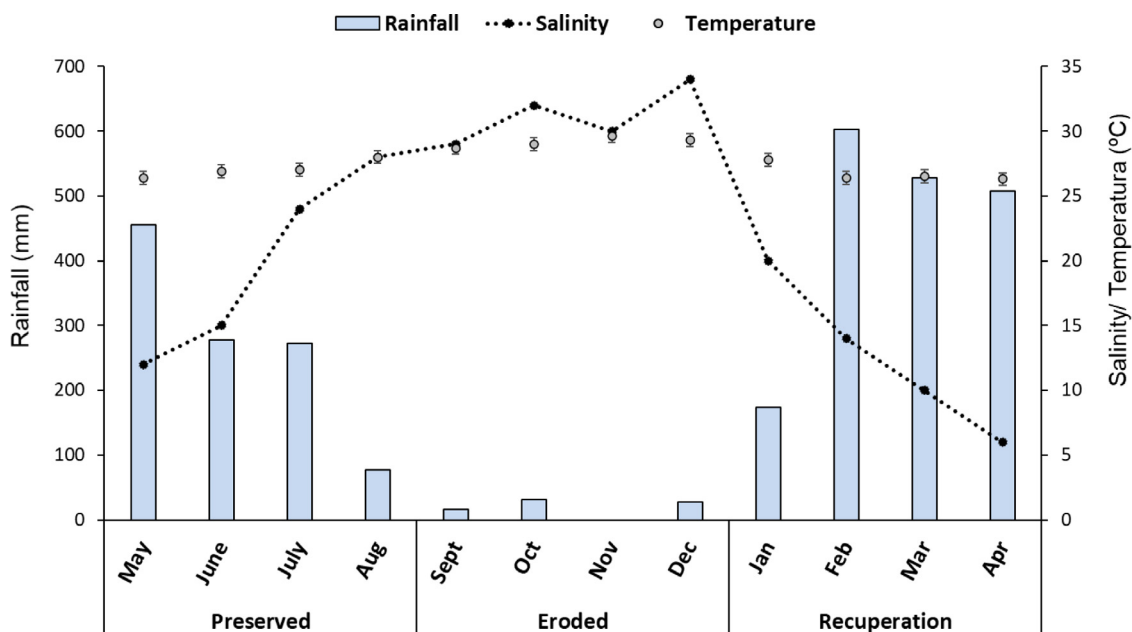


Fig. 2. Rainfall (total monthly precipitation) and monthly mean temperature and salinity recorded from May 2008 to April 2009 on the Algodual-Maiandeuia Island (Brazil).

Table 1

Brachyuran crabs recorded on the *Sabellaria wilsoni* reef monitored on the Algodual-Maiandeuia Island (Brazil). RA = Relative Abundance; FO = Frequency of Occurrence; OF = Oviparous Female; Undet. = Undetermined Sex; CW = Carapace Width; Min. = Minimum CW recorded in this study; CW max. = Maximum CW recorded in this study. Max. lit = Maximum CW recorded in the literature.

TAXA	General participation		Class participation					Size (mm)		
	RA (%)	F.O (%)	Male (%)	Female (%)	O.F (%)	Undet. (%)	Ratio ♂ : ♀	CW min.	CW max.	CW max. lit
<b>PANOPEIDAE</b>										
<i>Eurytium limosum</i> (Say, 1818)	0.5	3.1	100	–	–	–	–	11.1	25.6	43.0 <sup>a</sup>
<i>Hexapanopeus caribbaeus</i> (Stimpson 1871)	2.7	7.3	55	33	–	12.0	1.7:1*	2.0	5.3	14.6 <sup>b</sup>
<i>Panopeus americanus</i> Saussure, 1857	82.7	72.3	25.8	40.8	10.3	23.1	1:1.9*	0.8	10.5	24.3 <sup>c</sup>
<i>Panopeus lacustris</i> Desbonne in Desbonne & Schramm, 1867	0.7	2.1	100	–	–	–	–	13.7	16.6	42.5 <sup>d</sup>
<i>Panopeus occidentalis</i> Saussure, 1857	6.7	32.0	41.5	33.5	10	15.0	1:1	1.3	26.0	40.5 <sup>a</sup>
<b>MENIPPIDAE</b>										
<i>Eurypanopeus dissimilis</i> (Benedict & Rathbun, 1891)	0.4	2.1	100	–	–	–	–	3.1	3.5	14.3 <sup>e</sup>
<i>Menippe nodifrons</i> Stimpson, 1859	5.3	35.0	27	23	–	50.0	1.2:1	1.2	36.5	129.0 <sup>b</sup>
<b>SESARMIDAE</b>										
<i>Armases benedicti</i> (Rathbun, 1897)	0.4	1.0	–	100	–	–	–	3.0	3.8	18.4 <sup>f</sup>
<i>Pachygrapsus gracilis</i> (Saussure, 1857)	0.2	1.0	–	100	–	–	–	7.0	7.0	17.1 <sup>g</sup>
<b>PINNOTHERIDAE</b>										
<i>Austinixa cristata</i> (Rathbun, 1900)	0.2	1.0	100	–	–	–	–	5.1	5.6	10.1 <sup>h</sup>

\*Values with significant deviation from an expected sex ratio of 1:1.

<sup>a</sup>Williams (1984).

<sup>b</sup>Alves et al. (2012).

<sup>c</sup>Carvalho-Batista et al. (2015).

<sup>d</sup>Santos Filho et al. (2017).

<sup>e</sup>Marochi and Masunari (2011).

<sup>f</sup>Abele (1992).

<sup>g</sup>Nóbrega and Martinelli-Lemos (2016).

<sup>h</sup>Manning and Felder (1989).

larger than 7.1 mm (Fig. 5B). Oviparous females (CW = 2.10–7.53 mm; mean = 5.06 ± 0.21 mm) were more abundant from August to November 2008 and were absent from January to March 2009 (Fig. 5C).

Overall, immature individuals (CW < 2.1 mm) represented approximately 40% of the crab specimens collected during the study (Fig. 5B). The monthly variation in the distribution of the size classes (Fig. 6) indicates the recruitment of juveniles throughout the year and fluctuations in the size structure of the population. Nevertheless, the recruitment of juveniles appeared to slow down from May to July (the preserved phase) before increasing markedly from August onward (Fig. 6).

### 3.4. Relationship between crab diversity parameters and environmental variables

The total abundance of brachyuran did not vary significantly in relation to the environmental variables (Table 2), while crab species richness was positively correlated with salinity and temperature, and negatively correlated with rainfall. The abundance of *P. occidentalis* and of oviparous females (including *P. americanus*) were also positively correlated with salinity and negatively with rainfall. In contrast, the abundance of immature *P. americanus* was positively correlated with rainfall and negatively with salinity (Table 2).

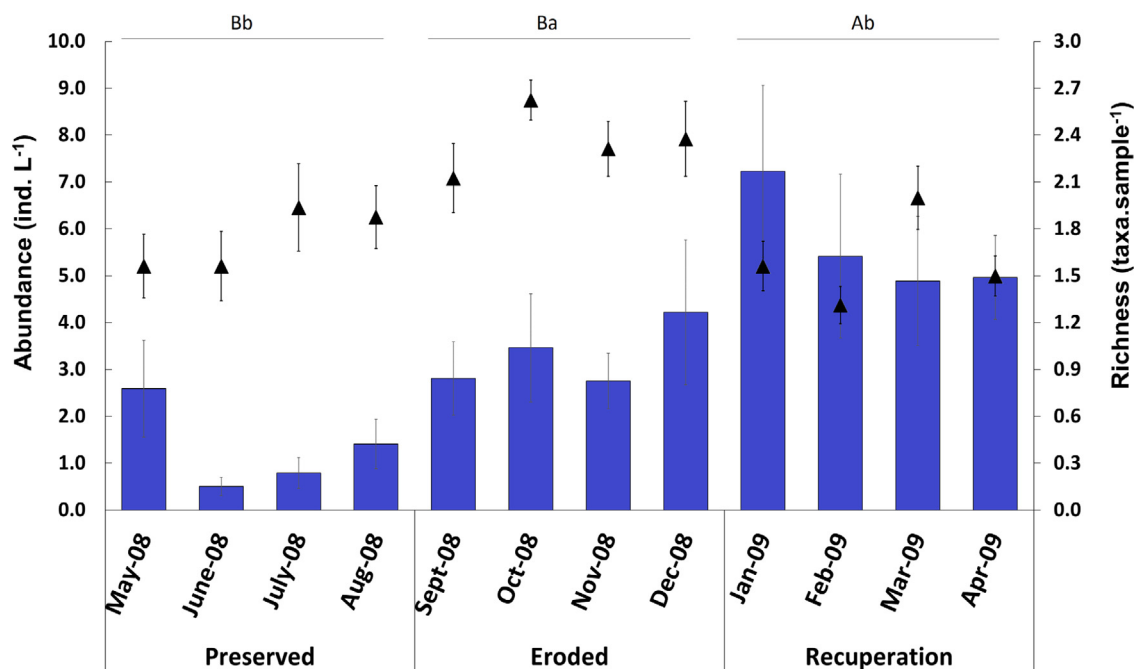


Fig. 3. Mean abundance (bars) and species richness (triangles) of brachyurans recorded during the different structural phases of the studied *Sabellaria wilsoni* reef on the Algodual-Maiandeuá Island (Brazil). Different letters in the same case above the columns indicate significant ( $p < 0.05$ ) differences between reef phases (A, B = for species richness; a, b = for density). The vertical lines represent the standard error.

Table 2

Spearman's correlation coefficients for the comparisons between crab biological parameters and environmental variables. The coefficients in bold type are significant ( $p < 0.05$ ).

	Rainfall	Salinity	Air temperature
<b>Brachyura</b>			
Richness	<b>-0.75</b>	<b>0.79</b>	<b>0.84</b>
Abundance	0.20	-0.12	-0.10
<b>Panopeus americanus</b>			
Abundance of immature individuals	<b>0.59</b>	<b>-0.53</b>	-0.54
Abundance of mature individuals	-0.19	0.15	0.20
Abundance of ovigerous females	<b>-0.69</b>	<b>0.64</b>	0.60
<b>Other species</b>			
Abundance of <i>Panopeus occidentalis</i>	<b>-0.70</b>	<b>0.65</b>	0.51
Abundance of <i>Menippe nodifrons</i>	-0.34	0.38	0.05
Abundance of all ovigerous females	<b>-0.69</b>	<b>0.64</b>	0.45
Abundance of all other species	-0.14	0.26	-0.34

## 4. Discussion

### 4.1. Crab assemblages

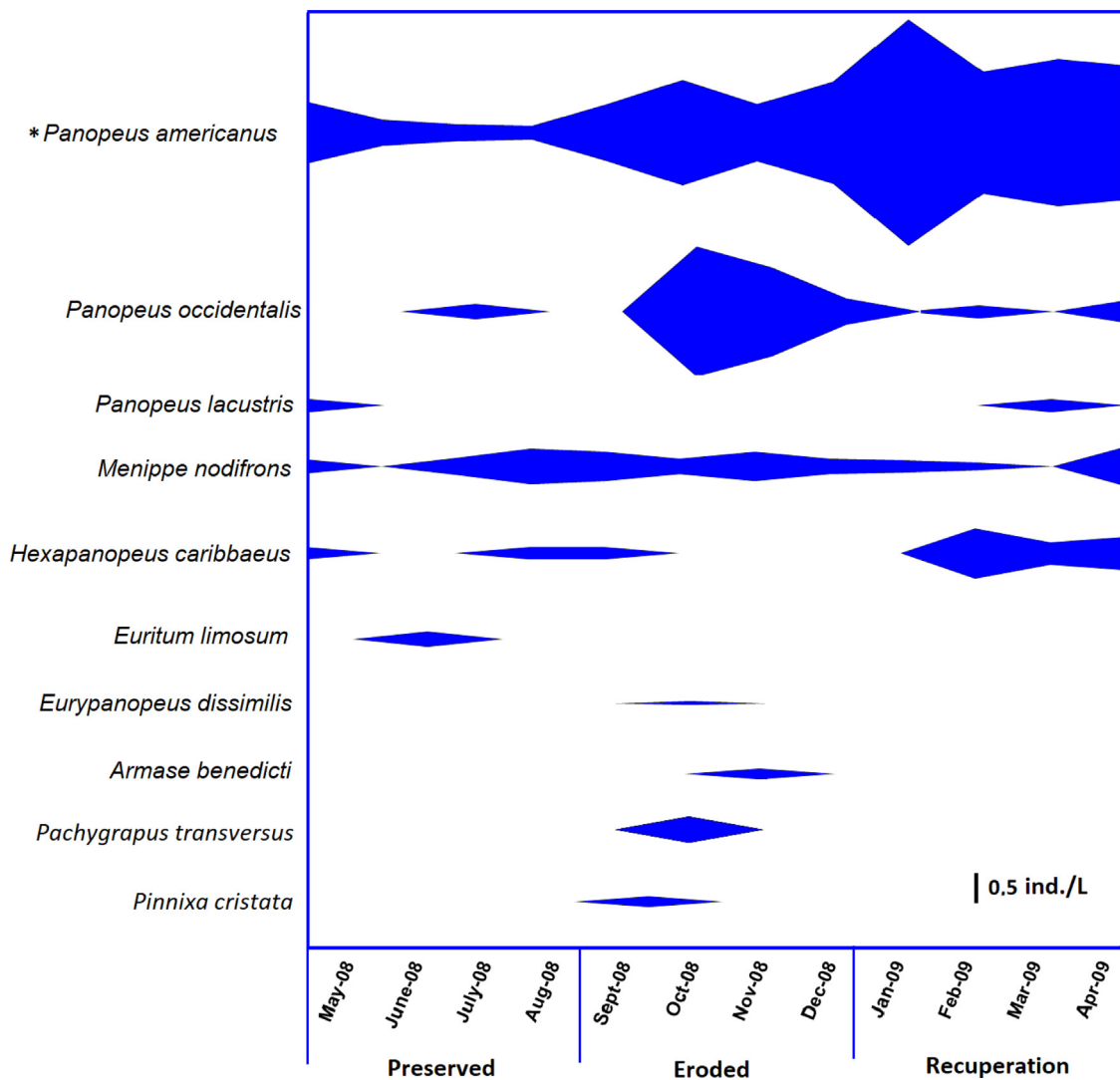
The results of this study indicate that the *S. wilsoni* reef provides a permanent habitat for at least three crab species (*P. americanus*, *M. nodifrons*, and *P. occidentalis*), while other crabs were encountered more sporadically. The crab assemblage was made up of species of small size, in general, and the juveniles of large species. Biological reefs are known to provide small-scale refuges at a millimetric to centimetric scale (Jackson-Bué et al., 2021; Ventura et al., 2021) that may be occupied either permanently or temporarily for the settlement of crabs that will eventually grow to larger sizes (Gore et al., 1978; Dubois et al., 2002). Motile crabs from adjacent substrates may also use these biological formations as an occasional refuge against predation and adverse environmental conditions as well as feeding areas and/or a breeding and nursery ground (Gore et al., 1978; González-Gómez et al., 2018).

Panopeids were the most common brachyuran crabs found on the studied reef, with *P. americanus* being the most abundant

and permanent species, as observed on *Phragmatopoma caudata* reefs in southeastern Brazil (Bosa and Masunari, 2002). These results highlight the importance of this biogenic substrate for the maintenance of crab species that use sabellariid reefs as permanent habitats. Reefs are a favorable habitat for *P. americanus*, which avoids abiotic stress in rocky environments by seeking refuge in crevices between rocks and, frequently, by burying itself in the sand or mud found in such indentations (Masunari and Dubiaski-Silva, 1998).

*Menippe nodifrons* is a large crab with a carapace width of up to 130 mm (Williams, 1984) that appears to use *S. wilsoni* reefs as a breeding ground, given the predominance of juveniles (specimens of undetermined sex with a carapace length < 4 mm) and the absence of ovigerous females. A predominance of juvenile *M. nodifrons* was also recorded on *P. caudata* reefs in southeastern Brazil (Pinheiro et al., 1997; Bosa and Masunari, 2002). However, both juvenile and mature *M. nodifrons* are widespread on *P. caudata* reefs in Florida, United States (Gore et al., 1978). Previous studies have indicated that the availability of biogenic substrates is fundamental to the development of *M. nodifrons* juveniles, while the adults typically inhabit rocky substrates (Rodrigues-Alves et al., 2013; Alves et al., 2013). This may be because rocky substrates provide a greater diversity of potential refuges for larger crabs but much fewer micro-scale refuges for smaller crabs (Rodrigues-Alves et al., 2013). Another suggested hypothesis is that, on rocks, a higher number of adults may increase competition and cannibalism (Rodrigues-Alves et al., 2013). The use of distinct microhabitats during different the life cycle phases has been reported in many crab species (Moksnes, 2002; Werner and Gilliam, 1984; Moksnes and Heck Jr., 2006).

The crab species that occur occasionally on the reefs of the Algodual-Maiandeuá Island are relatively common in the rocky outcrops found on the Amazon coast (Morais and Lee, 2013; Nóbrega and Martinelli-Lemos, 2016); until now, none of them had been recorded on *S. wilsoni* reefs (Aviz et al., 2019). Despite the sporadic nature of this occurrence, further research will be necessary to attribute habitat preferences to these species. There is increasing evidence of the importance of the role of



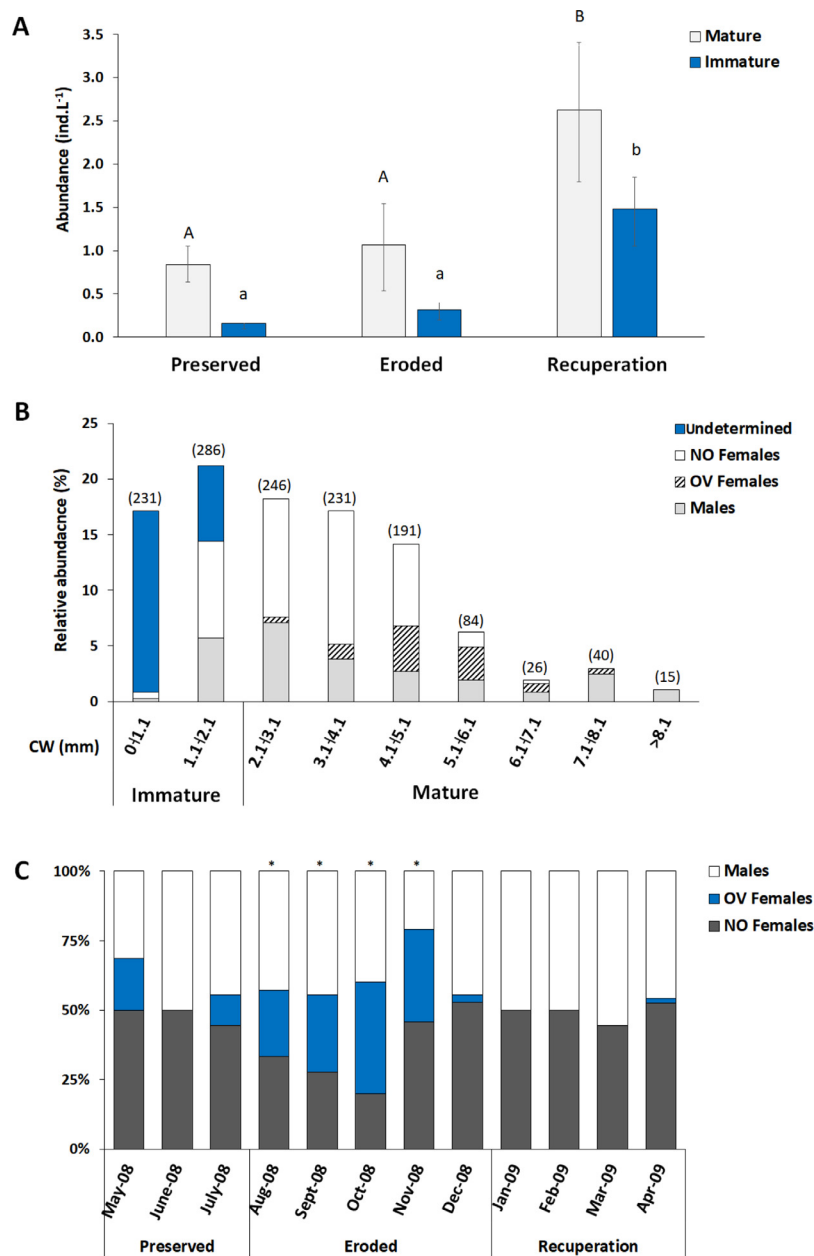
**Fig. 4.** Kite diagram showing the temporal distribution of crab species among the different structural phases of the *Sabellaria wilsoni* reef monitored on the Algodual-Maiandeuá Island (Brazil). The vertical bar represents scale of the crab abundance (\*1.0 ind./L for *Panopeus americanus*).

rare species as in supporting community diversity, given their ability to replace dominant species following disturbance, and the maintenance of ecological functions in the system (Lyons et al., 2005; Angeler et al., 2019).

The brachyuran species richness recorded in the present study (10 species) on the *S. wilsoni* reef is greater than that recorded in most of the previous studies of sabellariid reefs around the world (see Table 3), except for those by Gore et al. (1978) and Lane-Medeiros et al. (2021), who recorded more than twenty crab species on reefs built by *P. caudata*. However, these studies were based on more than double the sampling effort in terms of either the area surveyed and the study period. The number of species increase with the sampling effort, and more extensive studies tend to provide better estimates of species richness (Hoffmann et al., 2019). In particular, studies of longer duration may provide a more reliable diagnosis of diversity, given the greater probability of documenting rare species and changes in the composition of communities (Carballo et al., 2008). This is especially important for interpreting complex patterns of variation in natural systems (Levin, 1992; Carballo et al., 2008). In the specific case of sabellariid reefs, any systematic inventory would need to take the natural growth–destruction cycle into account.

The *S. wilsoni* reefs on the Algodual-Maiandeuá Island undergo regular structural modifications related to natural erosive and reconstructive processes that have been observed in other sabellariid species (Gruet, 1986; Porras et al., 1996; Gravina et al., 2018; Bonifazi et al., 2019). Hydrodynamic processes appear to be the primary factor determining the construction–reconstruction cycle of a reef. The reefs are destroyed during the dry season when the easterly trade winds are more intense and generate higher and more frequent waves (Aviz et al., 2016). During the rainy season, when the winds are weaker and the waves less energetic, the reefs grow or are reconstructed (Aviz et al., 2016).

The erosion of the *S. wilsoni* reef led to a significant increase in brachyuran species richness. In the destruction phase, a reef typically has a greater diversity than a well-preserved reef, given that its fragmentation contributes to an increase in its structural complexity in terms of microhabitats (Gruet, 1971; Porras et al., 1996; Dias and Paula, 2001; Dubois et al., 2002; La Porta and Nicoletti, 2009; Gravina et al., 2018; Jones et al., 2018; Bonifazi et al., 2019). The presence of living and dead reef structures, cracks, crevices, and fissures creates a diversity of cavities that provide shelter for many animal species that inhabit soft- and hard-bottom substrates in the surrounding area (Gruet, 1972;

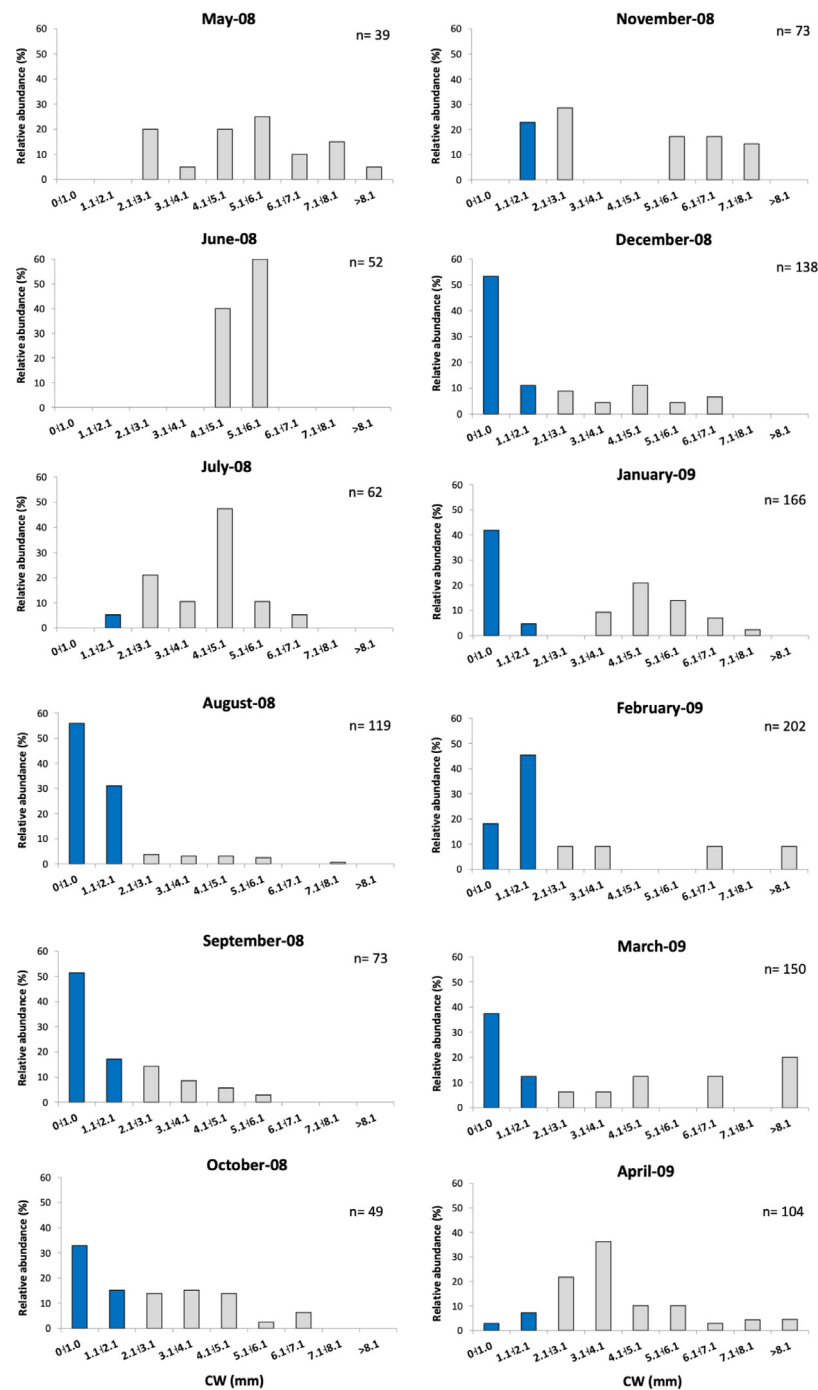


**Fig. 5.** Variation in the *Panopeus americanus* population structure recorded during this study on the Algodual-Maiandeuia Island (Brazil): (A) mean abundance of different age groups. Different letters (uppercase = mature; lowercase = juvenile) above the columns indicate significant (Tukey's test:  $p < 0.05$ ) differences in abundance between reef phases. (B) Variation in the frequency of carapace width (CW) classes in the different sexes and life stages (OV = ovigerous; NO = non-ovigerous). The value above each bar indicates the number of individuals in the respective size class. (C) Monthly variation in the proportion of male and female individuals collected from May 2008 to April 2009. An asterisk above a column indicates a significant ( $p < 0.05$ ) deviation from the expected ratio of 1:1 in that month.

Dubois et al., 2006). The reef erosion phase during the dry period coincides with higher salinity on the Amazon coast, when benthic communities tend to be denser and richer in species (Silva et al., 2011b; Braga et al., 2013) and there is a peak in reproduction and the production of larvae in many crab species (Diele and Koch, 2010; Lima et al., 2019). Some species thus appear to occupy the reef taking advantage of the availability of new spaces and favorable conditions, as they were represented by individuals of all age-sex classes, as in the case of *P. occidentalis*, or only by juveniles, as in the case of *A. benedicti*, *P. gracilis*, and *Austinixa cristata*.

The crab assemblages that occupy sabellariid reefs have similar traits in terms of trophic groups when comparing temperate, tropical, and subtropical reefs (Gore et al., 1978; Pinheiro

et al., 1997; Bosa and Masunari, 2002; Lane-Medeiros et al., 2021). There is a predominance of larger species, particularly large predators such as *M. nodifrons* (on *P. caudata* reefs in the Americas) and *Carcinus maenas* (on *S. alveolata* reefs in Europe), on well-developed and long-lasting reefs that remain stable for several years rather than undergoing an annual destruction cycle (Gruet, 1971; Gore et al., 1978). On less developed reefs and those with shorter cycles, omnivores/predators (such as *Panopeus* and *Pilumnus*) and omnivores/filter-feeders (such as *P. transversus*) tend to be more successful and occupy the reefs more permanently. Gore et al. (1978) suggested that less developed reefs might not be able to support larger carnivorous crabs due to a lack of prey, whereas omnivores face fewer restrictions and encounter a greater variety of potential feeding resources.



**Fig. 6.** Monthly variation in the relative frequency of the different *Panopeus americanus* size classes (carapace width—CW) of the specimens collected from May 2008 to April 2009 on a *Sabellaria wilsoni* reef on the Algodual-Maiandeua Island (Brazil).

#### 4.2. Population structure of *Panopeus americanus*

The overall sex ratio of *P. americanus* recorded in the present study ( $1\sigma:1.9\varphi$ ) was skewed significantly in favor of the females. This pattern is consistent with the female-biased sex ratios recorded previously for several crab species (Wenner, 1972; Johnson, 2003) and in other Panopeidae populations on the Brazilian coast (Camargo et al., 2017; Santos Filho et al., 2017). This female-biased ratio contrasts with the *P. americanus* populations from southeastern Brazil, in which more balanced sex ratios have been recorded (Vergamini and Mantelatto, 2008a,b; Carvalho-Batista et al., 2015). Skewed sex ratios are common and widespread in crustaceans, reflecting the influence of a wide range of factors,

such as differential mortality, behavior, and migration patterns between the sexes (Wenner, 1972; Hartnoll and Gould, 1988; Johnson, 2003). Mature crabs of different sexes are known to have distinct habitat preferences, with the females preferring more protected microhabitats that limit predation and environmental stress, which is necessary for successful egg development and extrusion (Koga, 1995; Andrade et al., 2014).

In the present study, the male *P. americanus* individuals were significantly larger than the females, as reported previously for other populations of this species (Vergamini and Mantelatto, 2008a; Carvalho-Batista et al., 2015) and many other species of marine crabs (Hartnoll, 1985b). This pattern has been attributed to the differential energy requirement of the two sexes, given that

**Table 3**

Species richness and predominant species of brachyuran crabs associated with sabellariid reefs in different regions around the world.

Sabellariidae species	Locality	Organisms sampled	Effort		Brachyura richness	Most abundant species	Source
			Number of months	Sampling total area/volume			
<i>Sabellaria wilsoni</i>	Algodoal-Maiandeuá Island (0°S 47°W), northern Brazil	Brachyura	12 months	1.5 m <sup>2</sup> ; 176 L	10	<i>Panopeus americanus</i>	Present study
<i>Phragmatopoma caudata</i>	Santa Rita beach (5°S 35°W), northeast Brazil	Macrocrustaceans	12 months	<sup>n</sup> 100 m <sup>2</sup>	21	<i>Pilumnus dasypodus</i> , <i>Pilumnus reticulatus</i>	<sup>a</sup>
<i>Sabellaria</i> spp.	Cabo Branco beach (7°S34°W), northeast Brazil	Macrofauna	2 months	0.2 m <sup>2</sup> ; 96 L	1	Decapoda ind.	<sup>b</sup>
<i>Phragmatopoma caudata</i> <sup>m</sup>	Praia Grande (23°S 45°W), southeast Brazil	Decapoda	11 months	247.5 L	5	<i>Pachygrapsus transversus</i>	<sup>c</sup>
<i>Phragmatopoma caudata</i>	Caiobá beach (25°S 48°W), southern Brazil	Decapoda	12 months	3.2 m <sup>2</sup>	6	<i>Panopeus americanus</i>	<sup>d</sup>
<i>Phragmatopoma moerchi</i>	Cocholgüe beach (36°S 72°W), Chile	Macrofauna	2 months	4.2 L	1	<i>Acanthocyclus gayi</i>	<sup>e</sup>
<i>Sabellaria nanella</i>	Monte Hermoso (38°S 61°W), Argentina	Macrofauna	2 months	0.12 m <sup>2</sup> ; 18 L	2	<i>Cyrtograpsus</i> sp.	<sup>f</sup>
<i>Phragmatopoma caudata</i> <sup>m</sup>	Indian River, Florida (28°N 80°W), U.S.A	Decapoda	24 months	27 m <sup>2</sup>	23	<i>Menippe nodifrons</i> , <i>Panopeus bermudensis</i> , <i>Pilumnus dasipodus</i>	<sup>g</sup>
<i>Sabellaria cementarium</i>	Puget Sound (48°N 122°W), U.S.A	Macrofauna	2 months	2.2 m <sup>2</sup>	6	<i>Cancer oregonensis</i>	<sup>h</sup>
<i>Sabellaria alveolata</i>	Central Tyrrhenian Sea (41°N 12°W), Rome	Macrofauna	4 months	1.44 m <sup>2</sup>	8	<i>Pilumnus hirtellus</i>	<sup>i</sup>
	Ria de Vigo, Monteferro (42°N 8°W), Spain	Macrofauna	1 month	0.5 m <sup>2</sup>	6	<i>Pilumnus hirtellus</i> , <i>Perimela denticulata</i>	<sup>j</sup>
	Bay of Mont Saint-Michel (48°N 1°W), France	Macrofauna	1 month	0.7 m <sup>2</sup>	1	<i>Carcinus maenas</i>	<sup>k</sup>
	Bay of Mont Saint-Michel (48°N 1°W), France	Macrofauna	2 months	<sup>o</sup> 1.6 m <sup>2</sup> /30 m <sup>2</sup>	5	<i>Carcinus maenas</i>	<sup>l</sup>

Source:

<sup>a</sup>Lane-Medeiros et al. (2021).<sup>b</sup>Lomônaco et al. (2012).<sup>c</sup>Pinheiro et al. (1997).<sup>d</sup>Bosa and Masunari (2002).<sup>e</sup>Septúlveda et al. (2003).<sup>f</sup>Bremec et al. (2013).<sup>g</sup>Gore et al. (1978).<sup>h</sup>Gherardi and Cassidy (1994).<sup>i</sup>Bonifazi et al. (2019).<sup>j</sup>Anádon (1981).<sup>k</sup>Dubois et al. (2006).<sup>l</sup>Jones et al. (2018).<sup>m</sup>As *Phragmatopoma lapidosa*.<sup>n</sup>Qualitative sampling, capture effort.<sup>o</sup>1.6 m<sup>2</sup> = samples of epi-endofauna, 30 m<sup>2</sup> = samples of epifauna.

the metabolic energy is directed toward somatic growth in males and to reproduction (gonad development and egg production) in females (Hartnoll, 1985b; Wenner, 1972). Larger males also have advantages in territorial defense and may compete more successfully for access to breeding partners and the manipulation of females, and, in some cases, they may be better able to protect females during and after copulation (Wenner, 1972; Mantelatto and Fransozo, 1994; Hartnoll, 1985a).

The constant presence of *P. americanus* adults, juveniles, and ovigerous females indicates that *S. wilsoni* reefs are a suitable and permanent habitat for this species. In the studied area, fluctuations in the abundance of *P. americanus* reflect pulses of reproduction and recruitment. Although the year-round presence of ovigerous females and juveniles indicates continuous reproduction, as suggested previously for this species (Vergamini and Mantelatto, 2008a), the population presented well-marked responses to seasonal changes in the environment. Ovigerous females were less frequent in the rainy season, and their abundance was correlated positively with salinity and negatively with

rainfall. Masunari et al. (1998) and Vergamini and Mantelatto (2008a) also reported a positive relationship between the abundance of *P. americanus* and salinity, which is a key environmental factor in the ecology of many coastal brachyurans and may affect larval survival rates and development, as well as growth, dispersal, osmoregulation, and feeding behavior (Charmantier, 1998; Anger, 2003, 2006; Anger et al., 2008). Laboratory experiments indicate that *P. americanus* larvae survive and develop better at higher salinities, i.e., ranging from 30‰ to 35‰ (Negreiros-Fransozo and Fransozo, 1990). On the Algodoal-Maiandeuá island, this would account for the reduced occurrence of ovigerous females in the rainy season, during which salinity ranged from 6‰ to 24‰.

The population density of *P. americanus* in the studied area was correlated positively with rainfall and negatively with salinity and, thus, peaked during the reef recuperation phase, in the rainy season. The density of *P. americanus* was boosted by recruitment peaks at the onset of the rainy season (January to March). Estuarine decapods obviously need to adapt to variations

in salinity, and the larvae typically tolerate a narrower salinity range than the adults (Charmantier, 1998; Anger, 2006). Thus, it is possible that, in the case of *P. americanus*, while most larvae are released as plankton during the dry season when high salinity favors their development, recruits will arrive on the substrate during the rainy season, during which more space and food are available despite low salinity. This strategy is reinforced by data on the zooplankton from the same area that show a peak in the abundance of *P. americanus* larvae at the end of the dry season (November) and an absence of larvae in the rainy season, from January to May (Lima et al., 2019). The absence of the later zoeal stages indicates migratory behavior, with the larvae dispersing from the estuary to open coast areas (Lima et al., 2019).

The preserved reef was inhabited primarily by *P. americanus* adults (mature), whereas juveniles predominated on the eroded and early-recuperating reef. Fluctuations in the size structure, which involved the disappearance and reappearance of the larger size classes, might reflect the dispersal of adults to adjacent rocky substrates. This, together with a high proportion of immature and smaller individuals, much smaller than those found on the rocky substrates, appears to indicate that these reefs represent important nursery grounds. A similar pattern has been observed for the hermit crab *Clibanarius symmetricus* (Aviz et al., 2021). Sabellariid reefs are complex habitats that may provide refuge from severe abiotic (e.g., winds, currents, waves, and desiccation) and biotic factors (e.g., predation), as well as foraging areas (Aviz et al., 2019), and may be especially important for crabs in the more susceptible life cycle phases (Andrade et al., 2014). Polychete colonies may provide nursery habitats, known to enhance the survivorship of other brachyurans (Heck and Hambrook, 1991), and might support very dense aggregations of young individuals (Spivak et al., 1994).

## 5. Conclusions

This study provided important new insights into the characteristics of tropical sabellariid reefs and their associated fauna and added to the existing knowledge provided by previous studies by emphasizing the ecological importance of these habitats and their structural conditions for the associated populations of different invertebrate species. The *S. wilsoni* reefs were a suitable habitat for at least three crab species that remained constant over time: *Panopeus americanus* and *Panopeus occidentalis*, which used the reef at different stages of the life cycle, and *Menippe nodifrons*, which used it essentially as a nursery habitat. Seven other crab species common in rocky substrates on the Amazon coast were also found on the Algodoal-Maiandeuá reef. The structural cycle of the bioconstruction determined changes in the structure of crab assemblages, with the highest species richness occurring during the reef eroded phase, which reflects an increase in habitat complexity. By contrast, the highest density of crabs was recorded during the reef recuperation phase, which is due to intense recruitment.

## 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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