



# Temporal dynamics of a *Sabellaria wilsoni* (Sabellariidae: Polychaeta) reef on the Brazilian Amazon Coast

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**ABSTRACT:** Polychaetes of the family Sabellariidae build extensive reefs in many coastal regions worldwide. These structures are dynamic systems that undergo a natural cycle of growth and destruction provoked by fluctuations in hydrodynamic conditions and biological factors. Here, we monitored a *Sabellaria wilsoni* reef over an annual cycle on Algodoal-Maiandeuá Island on the Brazilian Amazon coast. We studied the impact of temporal variations in local environmental characteristics on the structure of the reef and the reef-building polychaete population. Metrics included the local climate (temperature, rainfall, and winds), hydrological variables (suspended particulate matter and salinity), and the output of a numerical model of the local hydrodynamics. There was increased hydrodynamic stress in the dry season due to changes in the direction and intensity of the wind and stronger waves. This in turn led to an accentuated decrease in sabellariid density, and the eventual erosion of the reef, which lost >80% of its original area. The reduction in the hydrodynamic energy at the end of the rainy season favoured the mass recruitment of sabellariids as well as the subsequent growth and recuperation of the reef. Oligohaline conditions also contributed to a reduction in worm density, but not to any loss in reef structure. These findings provide important insights into the thresholds of energy and salinity tolerated by the reef-building polychaete *S. wilsoni* and offer a useful baseline for future research on the ecology of this species and the monitoring of this important marine habitat.

**KEY WORDS:** Ecosystem engineer · Biogenic habitat · Natural disturbance · Amazon beach · Tropical region

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## 1. INTRODUCTION

Polychaetes of the family Sabellariidae are tubiculous marine worms that inhabit both shallow and deep waters. These animals construct their tubes by gluing grains of sand with cement containing proteins and high levels of phosphate, calcium, and

magnesium (Gruet 1972, Stewart et al. 2004). The tubes are fixed to rocks or other hard substrate such as algae, mollusc shells, plant roots (Kirtley 1994, Pohler, 2004), and soft sediments, if stable (van der Reijden et al. 2021). Some gregarious sabellariid species, in particular those of the genera *Sabellaria* and *Phragmatopoma*, build extensive reefs in intertidal

and shallow subtidal areas (Kirtley 1994, van der Reijden et al. 2021). Sabellariid reefs have been recorded in coastal areas of many regions around the world, including in the north-eastern Atlantic in Europe (Wilson 1970a, 1971, Dubois et al. 2002), North Sea (van der Reijden et al. 2021), Mediterranean (Gravina et al. 2018), the Americas (McCarthy et al. 2003, Sepúlveda et al. 2003, Aviz et al. 2018), Asia (Achary 1969, Pohler 2004), and Australia (Shepherd & Thomas 1982). These structures provide microhabitats for a variety of benthic organisms and contribute to coastal biodiversity (Achary 1969, Dubois et al. 2002, Jones et al. 2018, Aviz et al. 2019, Bonifazi et al. 2019). In addition to their biological role, sabellariid reefs can modify the morphology of substrates, stabilize beach sediments, and protect the coastline from wave action (Kirtley 1967, Bruschetti 2019).

Sabellariid reefs experience major morphological changes over time, beginning with the initial settlement phase and leading to extensive structures, which are in turn eventually destroyed (Gruet 1972, Curd et al. 2019, Lisco et al. 2021). The structural cycle of the intertidal reefs of *S. alveolata* (Linnaeus, 1767) can be classified into 4 principal phases based on long-term studies (Gruet 1972, 1986): (1) the settlement phase is based on the aggregation of larvae and the initiation of the construction of overlapping tubes that lie at an acute angle to the substratum ('veneer-type reef'); (2) the growth phase is when the structure becomes increasingly dense and interlinked, thus forming a tapestry of regular mushroom-shaped mounds ('hummock-type reef'), which may aggregate to form barriers and even extensive platforms; (3) the stagnation phase occurs when the structure stops growing both in terms of height and width; and (4) the destruction phase is when the worms suffer mass mortality and the structure is eroded by wind and waves; it may disappear either partially or completely (Gruet 1972, 1986, Gravina et al. 2018, Bonifazi et al. 2019). Other classifications and new terminologies have been proposed to describe the physical appearance and phases of these bioconstructions including describing the reef morphology at the macro- and/or microscale (Curd et al. 2019, Griffin et al. 2020, Lisco et al. 2021, Ventura et al. 2021). Others have attempted to link these physical criteria to the physiological state of the tube-building polychaetes (Curd et al. 2019).

Once destroyed, the reef may eventually be reconstructed depending on the availability of larvae and favourability of the local hydrodynamic conditions. While these 4 phases are typical of the process, they are not always demarcated clearly, and thus erosion

may occur during the growth phase, and the reef may be destroyed well before the stagnation phase (Gruet 1986, Lecornu et al. 2016, Lisco et al. 2021). A number of different factors have been implicated in the destruction of sabellariid reefs, including hydrodynamics, i.e. waves, currents, and storms (Gruet 1971, Wilson 1971, Gravina et al. 2018, Jackson-Bué et al. 2021), silting by sand or mud (Gruet 1971, Wilson 1971, Desroy et al. 2011, Eeo et al. 2017), low temperatures (Hommeril & Larssonneur 1963), anthropogenic impacts such as trampling or fishing (Vorberg 2000, Dubois et al. 2002, Plicanti et al. 2016, Bonifazi et al. 2019, van der Reijden et al. 2019), overgrowth of epibionts (Dubois et al. 2006), and inadequate settlement and recruitment (Wilson 1971, Gruet 1972).

The potential longevity of a sabellariid reef is still unclear, and temporal stability may occur at either the reef (small patches) or habitat scale, i.e. thousands of square metres (Jackson-Bué et al. 2021). In intertidal areas, sabellariid reefs are naturally short-lived and strongly influenced by seasonal shifts in environmental conditions, whereas reefs on more stable substrates and in more sheltered locations with less intense hydrodynamics are more long-lasting (Holt et al. 1998, Hendrick & Foster-Smith 2006, Ingrosso et al. 2018). Well-developed reefs are the result of the colonization of the site by successive generations of worms and are typically much older than the current resident population (Wilson 1971, Gruet 1986).

On the French coast, the complete morphological cycle of *S. alveolata* reefs may take 10 yr at some sites (Gruet 1986), and multi-year stability has been recorded at other sites (Lecornu et al. 2016, Jackson-Bué et al. 2021). Ages of more of 60 yr have been documented for some Mediterranean reefs of *S. alveolata* (Ingrosso et al. 2018). *S. vulgaris* Verrill, 1873 reefs in Delaware Bay (USA) are thought to undergo decadal cycles of growth and decline (H. Wells 1970), but other observations have shown that *S. vulgaris* reefs may be established and decline within a few years (Brown & Miller 2011). Reefs of *S. spinulosa* (Leuckart, 1849) are invariably short-lived or seasonal; they typically last only 1 or 2 yr, depending on the prevailing physical and biological conditions (Hendrick & Foster-Smith 2006, Gravina et al. 2018, Lisco et al. 2021).

The ecology of sabellariid reefs is still poorly known in the tropics. In Brazil, at least 3 sabellariid species (*Phragmatopoma caudata* Krøyer in Mörch, 1863, *S. nanella* Chamberlin, 1919, and *S. wilsoni* Lana & Gruet, 1989) are known to build reefs, but no data are

available on their colonization cycle. *S. wilsoni* is endemic to the Atlantic coast of South America, from French Guiana to Argentina, where it is found on beaches (Lomônaco et al. 2012, Ataíde et al. 2014, Aviz et al. 2018) and on the inner continental shelf (Lana & Gruet 1989, Lana & Bremec 1994, Santos et al. 2010). On the Amazon coast, *S. wilsoni* builds extensive reefs on sandy beaches (Ataíde et al. 2014, Aviz et al. 2019) that in turn undergo major and systematic temporal changes in structure (Aviz et al. 2018). These initial findings led to the present study that was based on the monitoring of an *S. wilsoni* reef off Algodual-Maiandeuá Island in northern Brazil over 1 yr. The objectives of the study were to (1) describe the changes in the structure of the reef and the polychaete population over the course of the year, (2) describe the temporal fluctuations in the climate,

salinity, and hydrodynamics of the study area, and (3) identify the relationship between these fluctuations in environmental parameters and the morphological changes in the reef and the structure of the local polychaete population.

## 2. MATERIALS AND METHODS

### 2.1. Study area

Algodual-Maiandeuá Island (00° 36' S, 47° 34' W) is located in the northeast of the state of Pará, on the Brazilian Amazon coast. The island is surrounded on 3 sides by rivers and estuarine channels, with its northern portion facing the Atlantic Ocean (Fig. 1). The region is dominated by semidiurnal

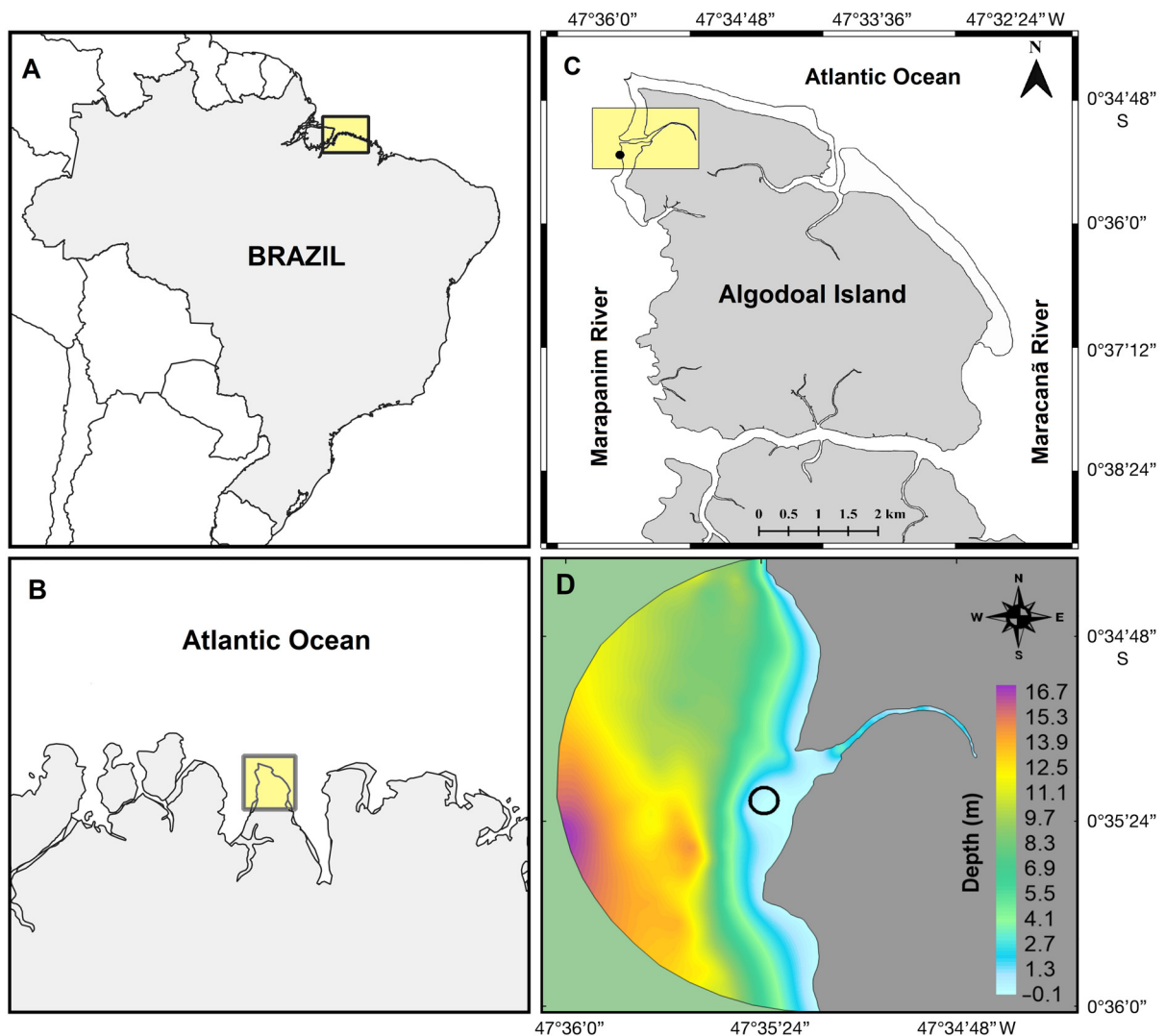


Fig. 1. (A–C) Location of the *Sabellaria wilsoni* reef monitored in the present study off Algodual-Maiandeuá Island in Pará, northern Brazil. (D) Area modelled and the bathymetry (m) of the grid domain used in the hydrodynamic model

macrotides with an amplitude of 4–7 m (Silva et al. 2011). Beaches on the island have a broad mid-littoral zone of 200–400 m (Rosa Filho et al. 2011), and are covered by fine sand, with outcrops of lateritized sandstone that are often colonized by *Sabellaria wilsoni*. As the reefs are established on large rocky outcrops, they are typically composed of cohesive clusters of hummocks. The *S. wilsoni* reef monitored in the present study was a formation of the platform type, with a total area of 1101 m<sup>2</sup> (da Silva 2015). This reef was located in the lower mid-littoral zone of Caixa D'Água beach (Fig. 1), in the northeastern extreme of the island, on the margin of the Marapanim River.

The climate on the Amazon coast is driven by seasonal shifts in the position of the Inter-Tropical Convergence Zone (ITCZ) and instability lines (Marengo 1995, Souza-Filho et al. 2009). In this region, the rainy season (January–June) occurs when the ITCZ shifts to the Southern Hemisphere, resulting in slightly lower air temperatures. During the dry season (July–December), the ITCZ shifts to the Northern Hemisphere, creating higher air temperatures and lower rainfall rates, due primarily to the influence of the instability lines associated with the local sea breezes (Marengo 1995, Pereira et al. 2012). This seasonal dynamic causes well-marked fluctuations in salinity (Dittmar & Lara 2001), sediment load (Jaeger & Nittrouer 1995), and hydrodynamic conditions (Pereira et al. 2012). Trade winds are also an important atmospheric force in the equatorial region, and their seasonal fluctuations are also associated with the migration of the ITCZ (Geyer et al. 1996). These winds shift from predominantly southeast–easterly in the dry season, to northeasterly in the rainy season, when their velocity is lower, in general (Souza-Filho et al. 2009).

The mean annual temperature on the Amazon coast fluctuates from 24 to 27°C (Nobre et al. 2013), and annual precipitation (based on 30 yr of monitoring) is 2200–2800 mm (Moraes et al. 2005). Total precipitation in the rainy season is approximately 1700 mm, while in the dry season it is around 500 mm (Moraes et al. 2005).

## 2.2. Monitoring of the reef

Samples were collected at the reef on Caixa D'Água Beach once a month on the spring tide between May 2008 and April 2009. The samples were collected along 2 transects established perpendicular to the coastline. Two areas on each transect were delimited for sampling, one of which was located at

the low tide line, and the other 50 m further inshore, to ensure the sampling of the full extension of the reef (the complete sampling designs are illustrated in Ataíde et al. 2014). Four samples were collected per month in each area with a cylindrical core (10 cm diameter, 40 cm depth). The volume (measured by the water displacement method) and height (relative to the rocky substrate on which the reef was fixed) of each sample were recorded during collection. The samples were fixed in 5% saline formalin.

The percentage cover (coverage) of the reef in relation to the substrate was also recorded each month in 4 quadrats (1 m<sup>2</sup>) placed randomly within each area. The condition of the reef was also recorded each month, with the reefs being allocated to different phases, based on the percentage cover of consolidated tubes and the visual evaluation of erosive patches (see Aviz et al. 2018).

In the laboratory, the animals present in each sample were extracted from the tubes and counted. The length of the thorax plus abdomen (the caudal appendix was excluded because it is easily lost) was measured in 10 individuals selected randomly from each sample, with the aid of a stereoscopic microscope. Although the opercular crown is considered to be a good proxy of body size in other sabellariids (Gruet 1984, Faroni-Perez 2014), no significant relationship was found between the diameter of the opercular crown and body length (thorax plus abdomen) in fixed (10% formaldehyde) *S. wilsoni* specimens (Aviz et al. 2018).

## 2.3. Sampling of environmental variables

Samples of surface water were collected each month during the ebb and flood tides to determine salinity (with an optical refractometer) and the concentration of suspended particulate matter (using a 0.45 µm porosity filter). Data on air temperature, rainfall, and wind speed and direction were obtained from the meteorological station in Salinópolis (approximately 30 km east of the study site) and were provided by the Brazilian National Meteorological Institute (INMET). Daily tide ranges were obtained from the Directorate of Hydrography and Navigation (DHN-Brasil 2008).

The SisBaHiA<sup>®</sup> wave generation module (Rosman 2018) was used to model the local wind waves. These wind-driven waves are generated locally within a specific area, in which they are energized by the overlying wind, and are related strongly to the local wind field (Rosman 2018). Using domain geometry

and wind data, this modelling permits the calculation of the temporal variation in 3 wave parameters: (1) significant height = height of the highest third of the waves measured during the monitoring period; (2) orbital velocity = oscillatory velocity of the water on the sea bed provoked by the wave action; and (3) bottom shear stress = short-term oscillatory stress on the sea bed, which has a direct influence on the resuspension of the sediment and the remobilization of the organisms it contains. We modelled the whole domain of Caixa D'Água beach (Fig. 1c), an area of approximately 3000 km<sup>2</sup>, resulting in a network with 375 nodes. The wind data analyzed in the present study were provided by INMET and covered a standard area, while the data on the bathymetry and rugosity of the study area were provided by the Physical Oceanography Laboratory at the Federal University of Pará in Belém. The simulation covered a 2 yr period (2008 and 2009), with a 40 s time interval. The model was validated using the *in situ* hydrodynamic data collected at Caixa D'Água beach by Borba (2011). The results were filtered for the target period and area (Fig. 1D).

#### 2.4. Data analysis

The density, both by volume (ind. l<sup>-1</sup>) and area (ind. m<sup>-2</sup>), and length of the *S. wilsoni* worms, and the height and coverage of the reef were compared among the different phases of the cycle using a 1-way ANOVA, with the Student-Newman-Keuls test being applied for *a posteriori* comparisons of the means. Prior to these analyses, the data were examined for normality (Shapiro-Wilk test) and homoscedasticity of variance (Cochran's test), and when necessary, the density (ind. l<sup>-1</sup>) of *S. wilsoni* was fourth-root transformed and reef coverage was arcsine transformed. A 5% significance level was considered in all analyses. The tests were run in the R software (version 3.3.0).

Multiple regression was used to identify the environmental variables that best explain the temporal variability observed in the sabellariid population parameters (density and body size of the worms) and reef conditions (height and coverage). A stepwise forward procedure was used to determine the subset of environmental variables that best explained the observed variation (Tabachnick & Fidell 1996). Prior to the regressions, the degree of collinearity between environmental variables was estimated using Pearson's correlation coefficient, and any variables that were strongly correlated ( $r \geq 0.8$ ) were excluded from all subsequent analyses.

### 3. RESULTS

#### 3.1. Reef conditions

The morphological changes on the reef were classified into 3 phases: (1) preserved (May–August 2008), when the reef has a compact, continuous mass, with a mean cover of at least 70%, (2) eroded (September–December 2008), when many open spaces appear within the reef (mean cover = 10–60%), and blocks have been detached or are becoming dislodged, and (3) recuperation (January–April 2009), when the reef is still low-lying and limited in extent (mean cover = 50–60%).

During the preserved phase, the reef grew both vertically and horizontally (Table 1, Fig. 2). Throughout the eroded phase, however, intense erosion occurred, resulting in the almost complete disappearance of the aggregates (Fig. 2B,C). The recuperation of the reef began in January, at the onset of the rainy season, through the mass recruitment of juveniles, which colonized the rocks (Fig. 2D) and abandoned worm tubes (Fig. 2E). The reef continued to grow in February and March, forming mushroom-shaped hummocks (Fig. 2F,G), which coalesced to form a new platform (Fig. 2H,I). Coverage was significantly greater in the preserved phase, whereas height did not vary significantly among the phases (Table 1).

#### 3.2. *Sabellaria wilsoni* population structure

The density of the sabellariids varied significantly among the different structural phases (Table 1), with 2 peaks. The first and most intense peak occurred during the preserved phase (June and August 2008), while the second, less intense peak was recorded in January and February 2009, in the recuperation phase (Fig. 3). There was a significant reduction in the number of worms during the eroded phase, in particular in December 2008 (Table 1, Fig. 3).

The distribution of *S. wilsoni* by size class (Fig. 4) indicates that the original reef platform, in May 2008, was formed by individuals of varying sizes, with body lengths of 1–21 mm. The presence of smaller classes indicates that a number of recruitment events occurred during the subsequent months, most notably in June and October–January. In December 2008 and January 2009, the population was formed predominantly by small individuals, with a body length of less than 7.5 mm. In the following months, there was an increase in the frequency of individuals in larger size classes (Fig. 4).

Table 1. Characteristics of the *Sabellaria wilsoni* reef of Caixa D'Água beach (Algodual-Maiandeuá Island, Brazilian Amazon Coast) monitored in the present study between May 2008 and April 2009. Results of ANOVA and Student-Newman-Keuls (SNK) test, for comparison among the different structural phases. Values are given as mean  $\pm$  SE; asterisks indicate significant results (\*\* $p < 0.01$ ). Data on the proportion of mature worms are from Aviz et al. (2016)

Phase	Month	Coverage (%)	Height (cm)	Worm density		Worm size (mm)	Proportion of mature worms (%)
				(ind. l <sup>-1</sup> )	(ind. m <sup>-2</sup> )		
<b>Preserved (P)</b>	May-2008	75.0 $\pm$ 3.5	9.8 $\pm$ 0.7	324.9 $\pm$ 58.1	29573 $\pm$ 9551	7.5 $\pm$ 0.3	13
	Jun-2008	71.9 $\pm$ 2.3	13.3 $\pm$ 1.3	1590.9 $\pm$ 159.7	201377 $\pm$ 8132	9.2 $\pm$ 0.3	53
	Jul-2008	80.0 $\pm$ 1.9	12.7 $\pm$ 1.3	2002.8 $\pm$ 153.7	253513 $\pm$ 20218	7.7 $\pm$ 0.2	69
	Aug-2008	81.9 $\pm$ 2.3	17.0 $\pm$ 1.2	1908.6 $\pm$ 195.2	241598 $\pm$ 19453	8.6 $\pm$ 0.2	40
<b>Eroded (E)</b>	Sep-2008	60.0 $\pm$ 3.3	16.6 $\pm$ 1.3	643.5 $\pm$ 125.5	79375 $\pm$ 24713	9.8 $\pm$ 0.2	72
	Oct-2008	26.9 $\pm$ 7.1	14.6 $\pm$ 1.3	541.0 $\pm$ 181.1	68481 $\pm$ 16431	10.4 $\pm$ 0.2	100
	Nov-2008	10.0 $\pm$ 3.3	12.1 $\pm$ 0.7	297.0 $\pm$ 320.6	37595 $\pm$ 22918	10.3 $\pm$ 0.2	90
	Dec-2008	10.0 $\pm$ 3.8	11.7 $\pm$ 0.7	112.2 $\pm$ 49.1	11487 $\pm$ 58905	6.5 $\pm$ 0.2	34
<b>Recuperation (R)</b>	Jan-2009	50.0 $\pm$ 5.3	11.8 $\pm$ 1.1	1245.8 $\pm$ 50.9	190562 $\pm$ 5559	6.3 $\pm$ 0.2	48
	Feb-2009	62.5 $\pm$ 3.7	12.6 $\pm$ 1.1	1814.8 $\pm$ 256	213188 $\pm$ 6443	6.9 $\pm$ 0.1	75
	Mar-2009	60.0 $\pm$ 3.0	12.3 $\pm$ 1.2	858.8 $\pm$ 195.1	101305 $\pm$ 35306	8.6 $\pm$ 0.2	85
	Apr-2009	50.0 $\pm$ 5.3	12.5 $\pm$ 1.1	223.3 $\pm$ 46.0	28259 $\pm$ 25968	12.1 $\pm$ 0.2	65
<b>ANOVA</b>							
$F_{(df)}$		$F_{(2,93)}$ : 80.30**	$F_{(2,189)}$ : 2.06	$F_{(2,189)}$ : 15.81**	$F_{(2,189)}$ : 19.56**	$F_{(2,1917)}$ : 17.19**	
Post hoc (SNK)		P > R > E	P = R = E	P > R > E	P = R > E	E = P > R	

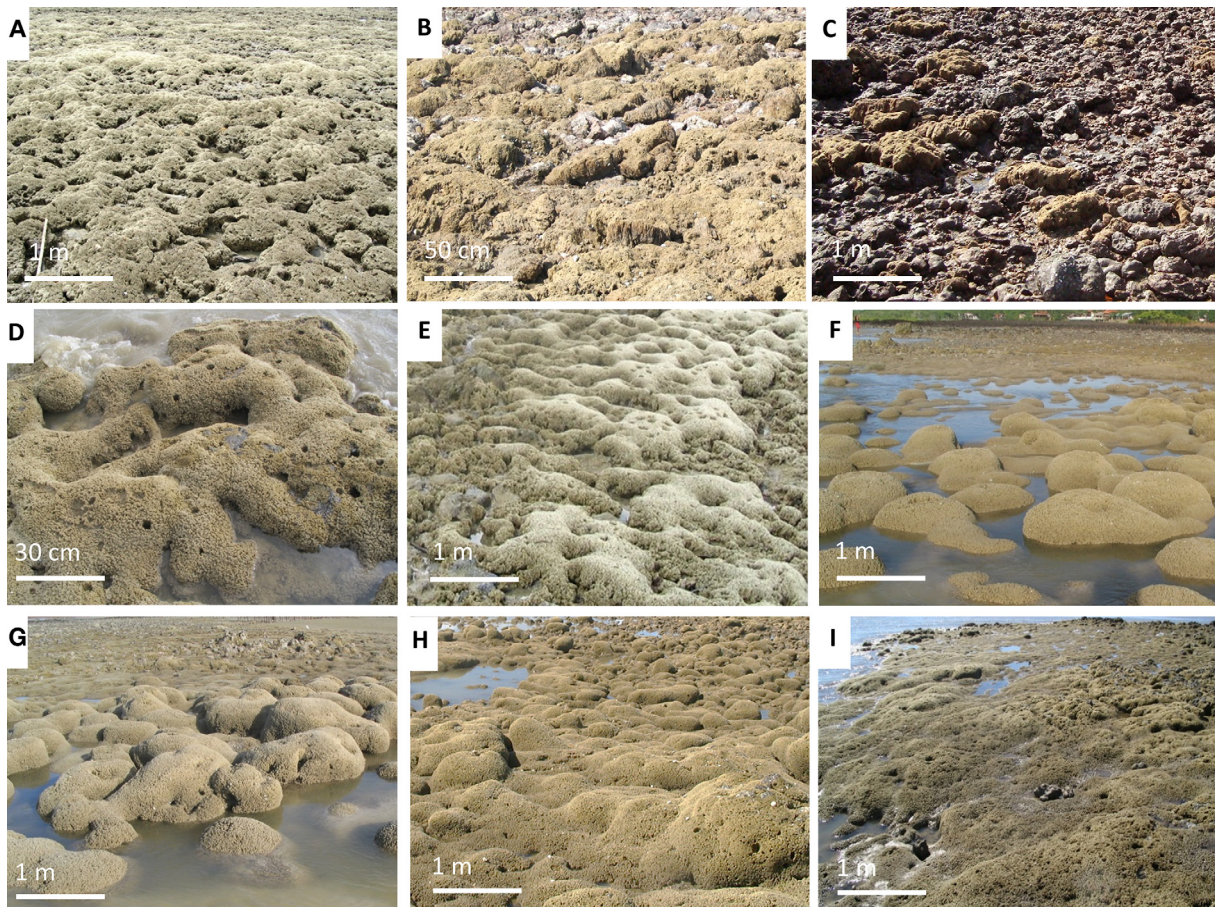


Fig. 2. Principal structural changes in the *Sabellaria wilsoni* reef monitored between May 2008 and April 2009 off Caixa D'Água Beach (Algodual-Maiandeuá Island, Brazilian Amazon Coast). (A) Preserved phase: July 2008 – well-developed platform; (B,C) Eroded phase: September 2008 – initial destruction (B) and December 2008 – mass destruction of the reef (C); (D–I) Recuperation phase: January 2009 – resettlement on rocky substrate (D); January 2009 – resettlement on destroyed reef (E); February 2009 – formation of mushroom-shaped hummocks (F); March 2009 – coalescence of mushroom-shaped hummocks (G,H); March 2009 – new reef platform (I)

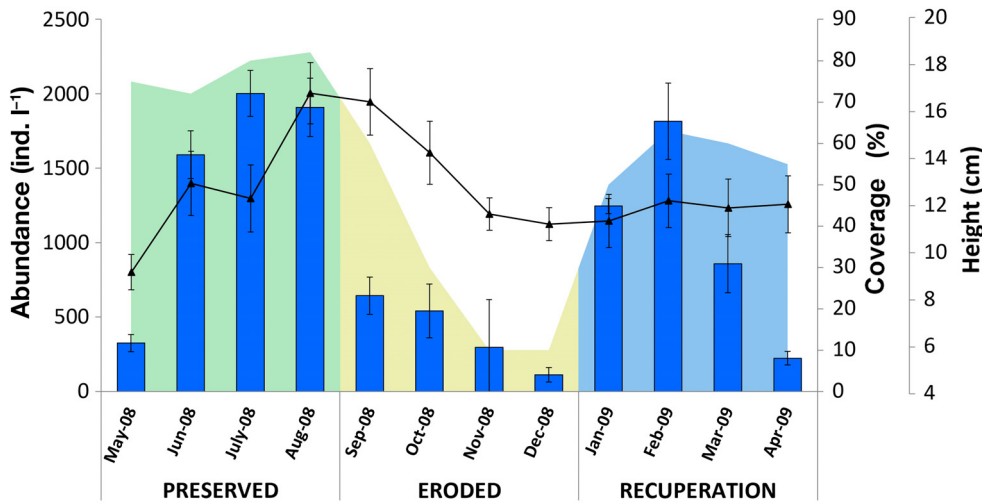


Fig. 3. Monthly variation (mean  $\pm$  SE) in the abundance of *Sabellaria wilsoni* (bars), reef coverage (shaded area), and height (line) on the reef off Caixa D'Água beach on Algodual-Maiandeuá Island, on the Brazilian Amazon Coast

### 3.3. Environmental characteristics of the study area

The highest rainfall rates were recorded January through July (rainy season), together with the lowest temperatures and salinity (Fig. 5A,B). Two peaks were recorded in the concentration of suspended particulate matter, the first in July–August and a second, higher peak in December–January (Fig. 5B). The highest tidal ranges were recorded during the equinoctial spring tides, in March (height: 5.5 m) and September (5.4 m), while the lowest (3.5 m) occurred in neap tide, between August and October (Fig. 5C). In the rainy season, the winds blew predominantly from the northeast and were less intense than during the dry season (Fig. 5D), resulting in milder hydrodynamic conditions (Figs. 5E,F & 6). During the dry season (reef-erosion phase), the winds were more intense, primarily easterly and east–northeasterly (Fig. 5D), provoking more energetic waves (Figs. 5E & 6) and greater bottom shear stress (Fig. 5F).

The best-fitting regression models were found for reef coverage ( $R^2 = 0.68$ ) and *S. wilsoni* density ( $R^2 = 0.46$ ). Wave height was the variable that best explained sabellariid density and body size and reef height, while salinity best explained reef coverage (Table 2, Fig. 7). A negative relationship was observed between wave height and polychaete density, as well as between wave height and reef coverage (Fig. 7A,D). By contrast, salinity was related positively to reef coverage (Fig. 7D), as well as to density and size of the worms (Table 2, Fig. 7A,B). There was a tendency for the height of the reef to increase as wave height increased, and for coverage to increase with tidal range (Table 2, Fig. 7C,E).

### 4. DISCUSSION

Sabellariid reefs occur in a delicate balance between the phases of growth, stagnation, and erosion, which are driven by physical and biological processes (Gruet 1986, Brown & Miller 2011, Eeo et al. 2017, Gravina et al. 2018, Lisco et al. 2021). Local hydrodynamics are undoubtedly among the principal factors affecting the distribution and development of sabellariid reefs. Up to a certain point, the sabellariid mode of life depends on the movement of the water, which is essential to resuspend the grains of sand and food particles required by these organisms (Vovelle 1965, R. Wells 1970, Brown & Miller 2011). However, extreme hydrodynamic conditions may have a negative effect on reef development due to erosion or silting with mud or sand (Wilson 1971, Gruet 1972, Eeo et al. 2017, Lisco et al. 2021). Extreme conditions may also affect the capacity of the worms to capture grains of sand (Vovelle 1965, Wilson 1971) or of the larvae to settle on the reef (Wilson 1970b, Pawlik & Butman 1993, Lisco et al. 2021).

Evidence on the distribution of *Sabellaria wilsoni* indicates that this species prefers low-energy myxohaline to polyhaline environments (Lana & Gruet 1989, Lana & Bremec 1994, Aviz et al. 2018), even though it does appear to be capable of colonizing more exposed coastlines (Dos Santos et al. 2011, Lomônaco et al. 2012). *S. wilsoni* forms small clumps on rocky substrates, where the individual tubes may be associated with stones or with other colonial organisms such as corals and even other sabellariids (Lana & Gruet 1989, Lomônaco et al. 2012). To date, extensive reefs of *S. wilsoni*, with areas of over 1000 m<sup>2</sup>, have only been recorded on Algodual-Maiandeuá Island on the Brazilian Amazon Coast where they are

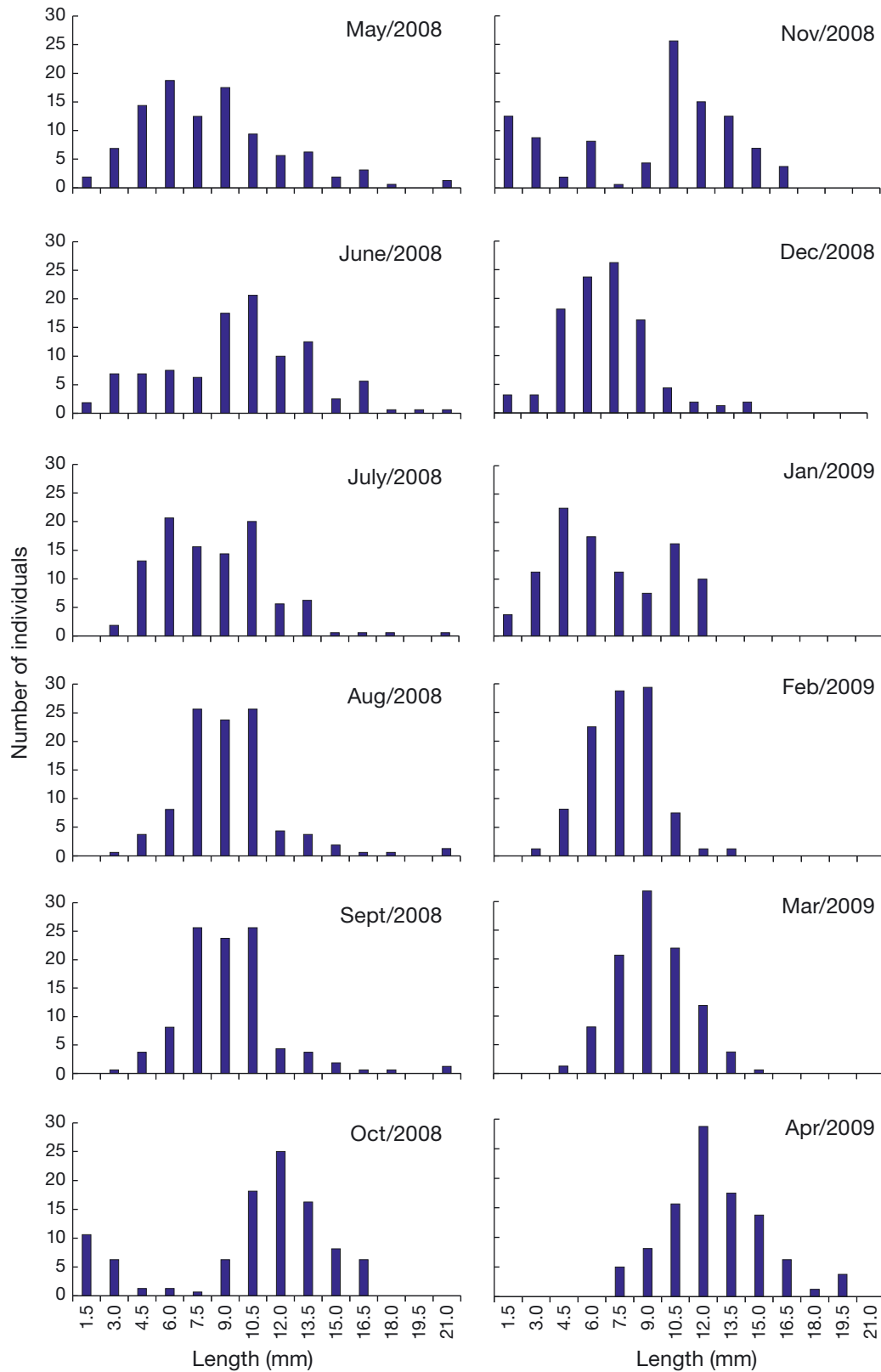


Fig. 4. Monthly variation in the distribution of the body size classes (body length = thorax + abdomen) of the *Sabellaria wilsoni* specimens collected each month between May 2008 and April 2009 from the reef off Caixa D'Água beach on Algodão-Maiandeuá Island, on the Brazilian Amazon Coast.  $N = 160 \text{ ind. mo}^{-1}$



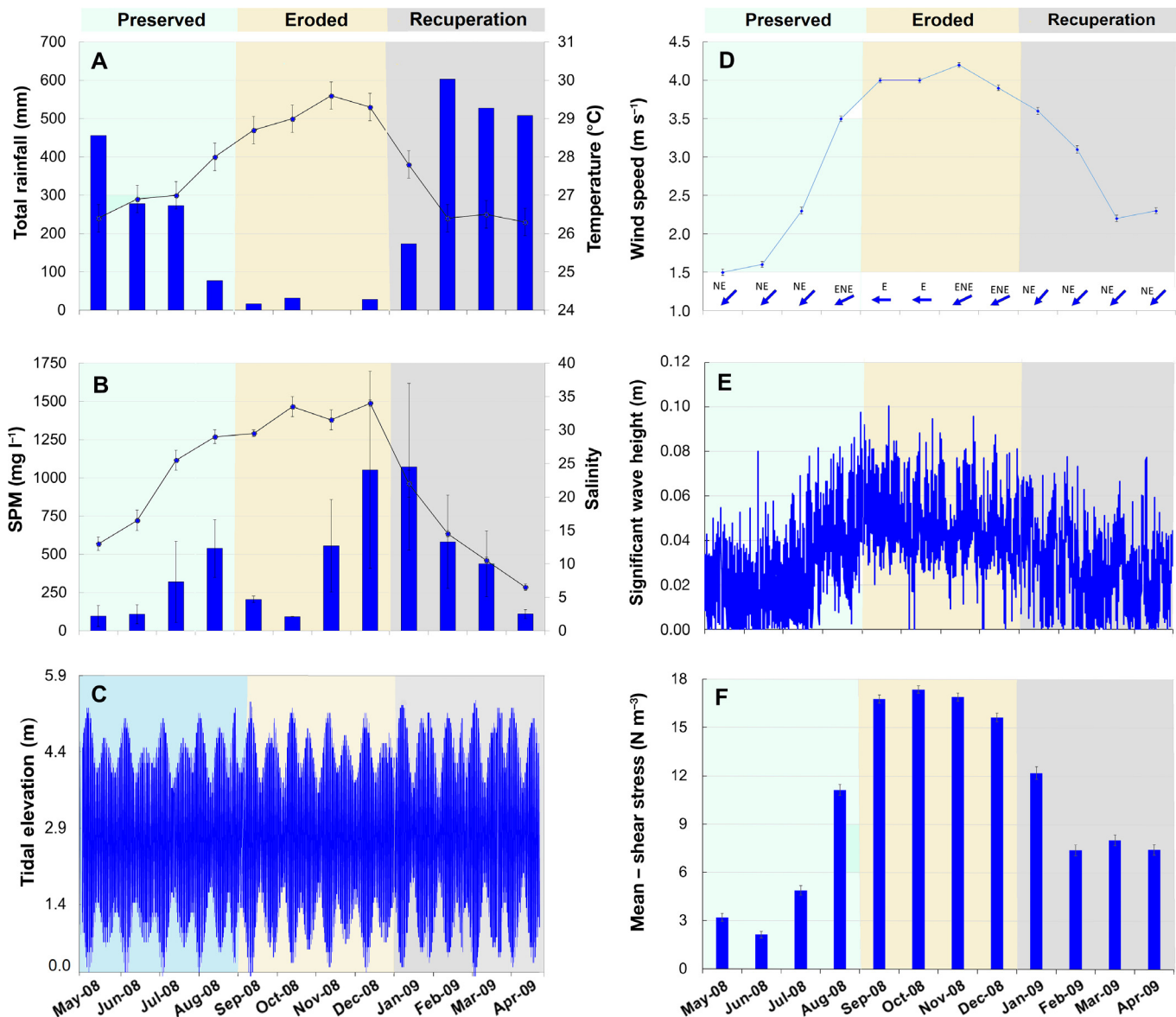


Fig. 5. Monthly variation in the environmental parameters monitored and modelled during the present study at Caixa D'Água beach (Algodual-Maiandea Island, Brazilian Amazon Coast). Parameters: (A) total rainfall (bars) and mean air temperature (line); (B) total suspended particulate matter (SPM; bars) and water salinity (line) (mean); (C) tidal elevation; (D) wind direction (arrows) and intensity (line). Modelling data: (E) significant wave height (range for each hour/day/month); (F) wave-induced bottom shear stress. All error bars are SE

seen on sheltered, sandy estuarine beaches in the lower intertidal to shallow subtidal zones.

The structural fluctuations observed in the *S. wilsoni* reefs on Algodual-Maiandea Island were influenced primarily by temporal variations in the local hydrodynamics, which, like rainfall, are driven by the shift of the ITCZ (Marengo 1995, Souza-Filho et al. 2009). During the dry season (September–December), the increased hydrodynamic stress resulting from the changes in the direction and inten-

sity of the wind, together with the formation of stronger waves, provoked a marked decrease in worm density and erosion of the reef, which lost more than 80% of its original area. Data from numerical modelling of the waves were consistent with the empirical data from other Amazonian beaches; these data indicate a direct relationship between the wave energy and wind speeds (Geyer et al. 1991, Monteiro et al. 2009). The rainy season offers ideal conditions for reef development, when the hydrodynamic con-

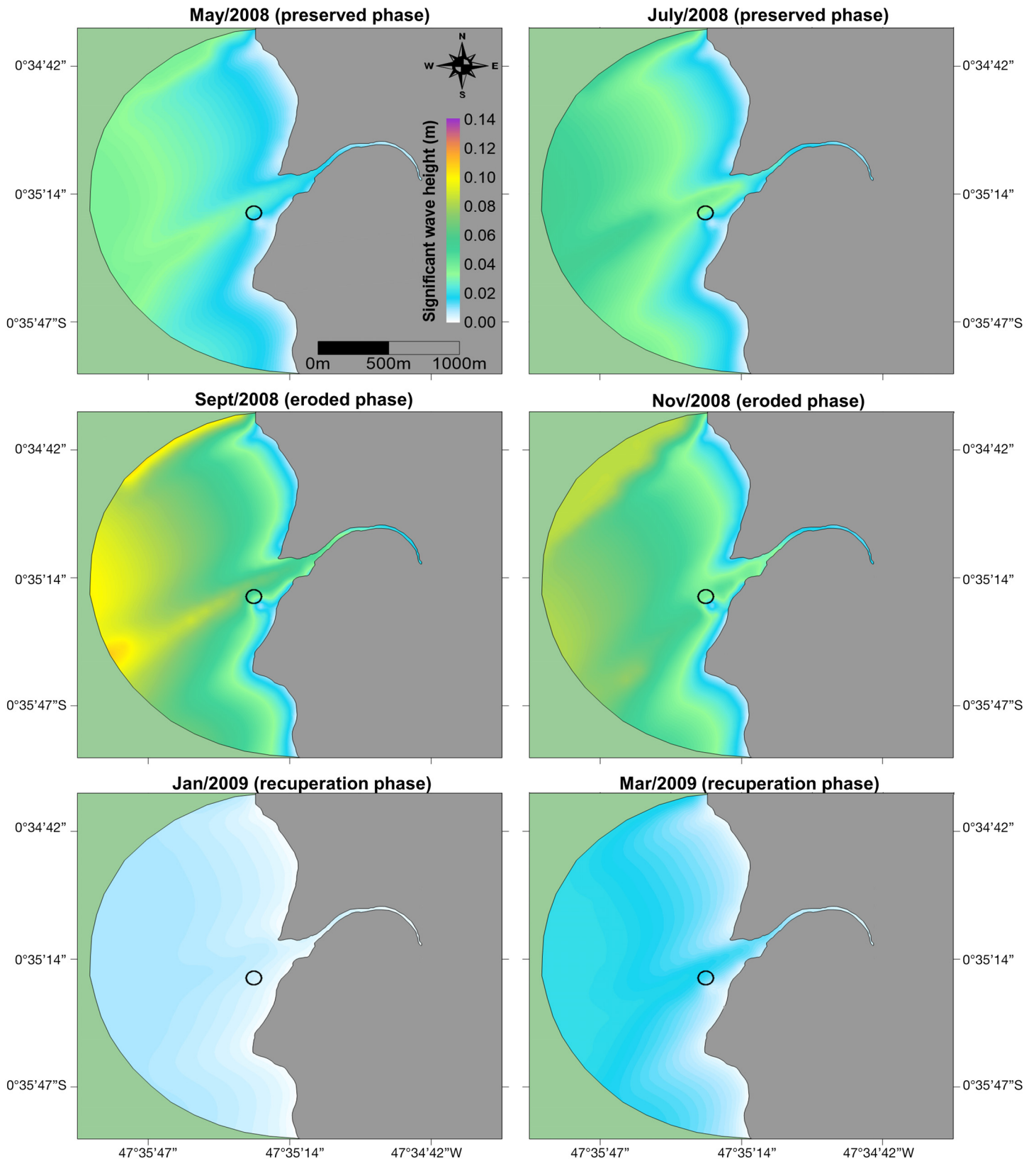


Fig. 6. Significant wave heights (bimonthly scenario) produced by the SisBaHiA<sup>®</sup> hydrodynamic model. The circle indicates the *Sabellaria wilsoni* reef. Data from Caixa D'Água beach (Algoal-Maiandeuá Island, Brazilian Amazon Coast)

Table 2. Best-fit models of the stepwise multiple linear regression of the data on the *Sabellaria wilsoni* population and its reef, and the environmental variables recorded off Caixa D'Água beach (Algodoal-Maiandeuá Island, Brazilian Amazon Coast)

	Beta	SE	<i>t</i>	<i>p</i>
<b>Density:</b> $F = 34.13$ , $p < 0.01$ , adjusted $R^2 = 0.46$				
N = 192				
Intercept			8.54	<0.01
Salinity	1.15	0.15	7.5	<0.01
Wave height	-1.27	0.14	-8.26	<0.01
<b>Body size:</b> $F = 7.28$ , $p < 0.01$ , adjusted $R^2 = 0.30$				
N = 192				
Intercept			13.77	<0.01
Salinity	-0.501	0.129	-3.92	<0.01
Wave height	0.534	0.128	4.18	<0.01
<b>Reef height:</b> $F = 14.61$ , $p < 0.01$ , adjusted $R^2 = 0.17$				
N = 192				
Intercept			10.52	<0.01
Salinity	0.018	0.129	0.14	0.87
Wave height	0.251	0.129	1.95	0.05
<b>Reef coverage:</b> $F = 55.54$ , $p < 0.01$ , adjusted $R^2 = 0.68$				
N = 96				
Intercept			14.36	<0.01
Salinity	2.340	0.144	-16.34	<0.01
Tidal elevation	0.743	0.069	-10.79	<0.01
Wave height	-1.788	0.147	12.18	<0.01

ditions are less intense, despite the increase in rainfall and the related reduction in salinity.

Exposure to tidal action is another important factor in controlling the horizontal extension of the reefs. The study beach has a semi-diurnal macrotidal regime with a tidal range of over 6 m, and most coastal processes are driven by the tide and its seasonal fluctuations (Klein & Short 2016, Pereira et al. 2016). The beginning of the erosive phase in September 2008 coincided with the equinoctial spring tides that can generate exceptionally strong tidal currents on the beaches of Algodoal-Maiandeuá Island (Pereira et al. 2012). The following months (October and November) had the lowest tidal ranges, which implies that the reef located in the lower intertidal zone remained submerged for longer periods. Therefore, it was exposed to more energetic waves and currents that may have contributed to its erosion.

The more intense hydrodynamics of this period not only destroyed the reef, but might have also led to mortality of the reef-building worms while also impacting recruitment of the juveniles that may otherwise have compensated for the impacts caused by the erosion. This conclusion is supported by shifts in the size and density of the worms during the year. There was a significant increase in both the density of

sabellariids and the growth of the reef (horizontal and vertical) following periods of intense recruitment (June 2008 and January 2009). In the eroded phase, while settlement occurred, the number of newly recruited worms may not have been sufficient to ensure the recuperation of the reef. A deficit of sabellariid larvae and juveniles has been associated with both pre-settlement factors (production, survival, dispersion, and behaviour of the larvae in the water column) and post-settlement factors (survival and the interaction between the recruits and physical factors).

Long-term monitoring of *S. alveolata* reefs has indicated that hydrodynamic conditions and a decline in settlement are the principal factors responsible for the onset of the destruction phase (Gruet 1972, 1986, Lisco et al. 2021). Sabellariid reefs are found in environments with high hydrodynamic stress such as beach surf zones, and thus they are subject to constant erosion (Wilson 1971). Individual worms are constantly harvesting sand to rebuild their tubes (Vovelle 1965), and the damage caused by the appearance of cracks and breaks in the reef blocks may only be minimized by the successive recruitment of larvae in the deteriorated areas (Wilson 1971, Gruet 1972, Ventura et al. 2021). Secondary settlement may thus play a fundamental role in the vertical and horizontal growth of the reef (Gruet 1986, Ventura et al. 2021).

In the reef monitored here, *S. wilsoni* reproduces continually and reaches a reproductive peak when 100% of the individuals are either mature or spawning. This is approximately 1 mo after the onset of the erosive phase (Aviz et al. 2018). It is likely that the numbers of larvae sufficient for the settlement and recuperation of the reef will only become available after this period. The duration of the planktonic larval stage of *S. wilsoni* is unknown, but in *S. alveolata*, this period lasts between 4 and 10 wk (Dubois et al. 2007). In this case, the December/January recruits would have been produced during the preceding October–November spawning peak. The occurrence of these reproductive peaks may, in fact, represent a strategy that guarantees the persistence of the reef following its destruction. On the coast of Florida (USA), studies on *Phragmatopoma californica* (Barry 1989) and *P. lapidosa* (McCarthy et al. 2003) showed reproductive peaks in response to severe, but sub-lethal, damage from major storms. In the Mediterranean, the annual reefs of *S. spinulosa*, a semelparous species, grow from the spring and early summer through to the fall after spawning events in the winter and early spring. There is a destructive phase during the winter (Gravina et al. 2018). In contrast,

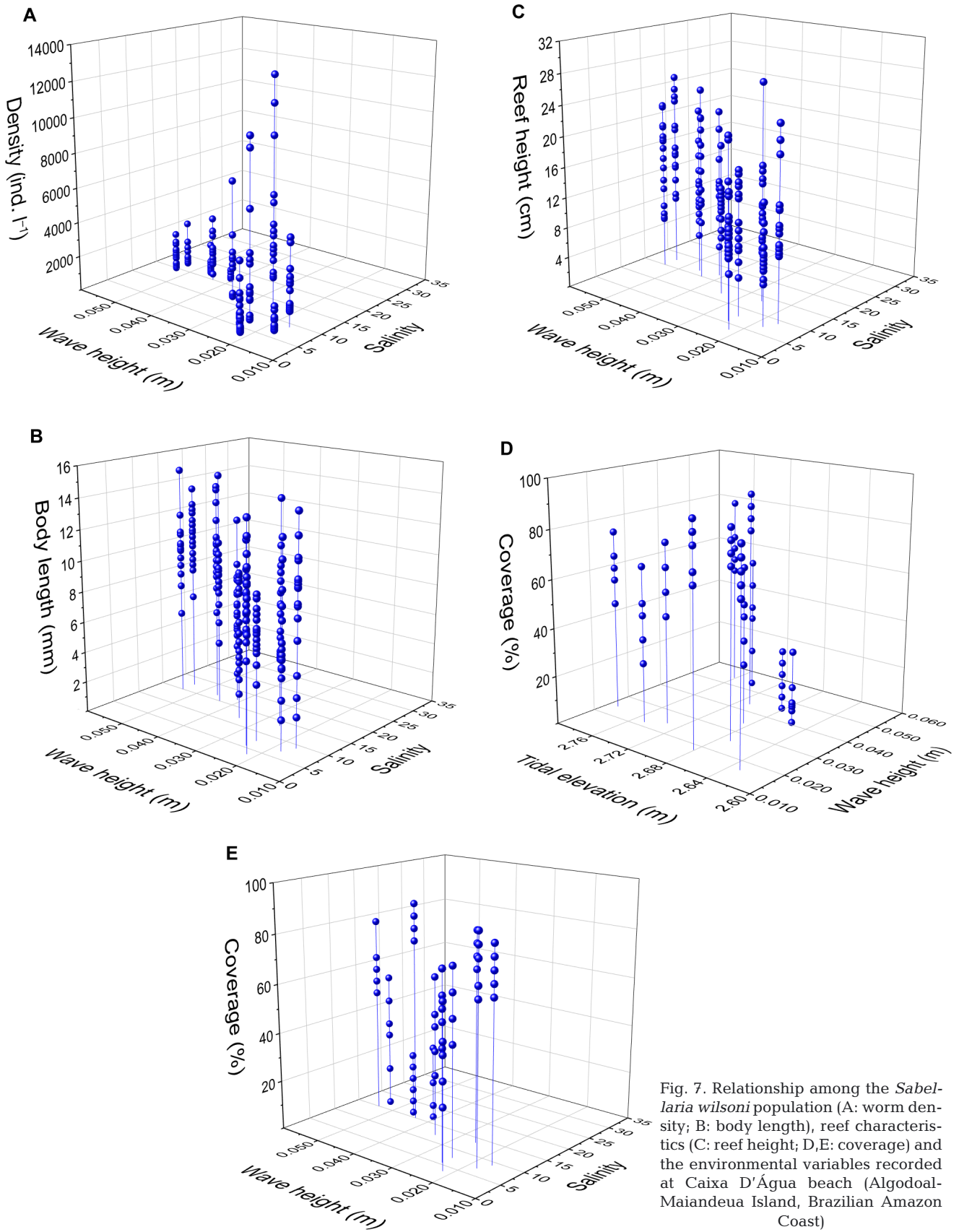


Fig. 7. Relationship among the *Sabelaria wilsoni* population (A: worm density; B: body length), reef characteristics (C: reef height; D,E: coverage) and the environmental variables recorded at Caixa D'Água beach (Algodoal-Maiandeuá Island, Brazilian Amazon Coast)

*S. alveolata* has a retrograde phase that was evident at the beginning of autumn after the destructive phase in summer. This matches the beginning of recruitment; similarly, the growth phase continues from spring to early summer (Bonifazi et al. 2019).

Studies have suggested that changes in wind intensity and direction as well as changes in coastal circulation patterns can lead to the dispersal of *S. alveolata* larvae to areas relatively far away from reefs. This may also cause a recruitment deficit and a decline in the reefs (Dubois et al. 2007, Ayata et al. 2009). This phenomenon is conceivable for *S. wilsoni* larvae. While no specific data are available for the Marapanim estuary, the seasonal variation in the fluvial input and in the direction and intensity of the prevailing winds, and the position of the ITCZ are all known to have a significant influence on coastal circulation patterns in other sectors of the Amazon coast (Nittrouer & DeMaster 1996, da Silva et al. 2009).

Another possibility may be that under extreme hydrodynamic conditions, most *S. wilsoni* larvae may be unable to settle. Those that are recruited may be unable to survive and are washed away by waves and currents or killed by the impact of the waves. These negative effects on recruitment have been linked to the decline of the *S. alveolata* reefs (Wilson 1974). There is some evidence that reef-forming sabellariid larvae can recognize adequate substrates during the settlement process, likely responding to either chemical (the presence of adults or dead reefs) or physical (hydrodynamic conditions) cues (Wilson 1968, Pawlik 1986, Pawlik et al. 1991, Pawlik & Butman 1993). Laboratory experiments also indicate that *P. californica* larvae respond first to water flow conditions and only subsequently to the chemical stimuli that induce metamorphosis (Pawlik et al. 1991, Pawlik & Butman 1993). These results suggest that *P. californica* larvae avoid settling in areas with slow-flowing water and prefer faster currents, but only when the hydraulic energy levels permit adequate contact and physical fixation.

It is important to note that the *S. wilsoni* platform monitored here was not completely eroded. At the end of the destructive phase, small clumps of the original platform still persisted. This resulted in only minor variations in the height of the reef during its cycle. Debris from the old platform is important for the establishment of the new reef given that sabellariid larvae settle and metamorphose preferentially on the cemented tubes of conspecific adults (Pawlik 1986, 1988). 3D mapping of an *S. alveolata* reef showed that the erosive process is spatially random beyond the 4 m colony scales. It alternates between

groups of rapidly-accreting, short-lived colonies of sediment tubes and slowly-accreting, long-lived colonies (Jackson-Bué et al. 2021). These dynamic, reef-scale structural changes may cancel each other out and result in an apparently stable reef structure over larger spatial and temporal scales (Jackson-Bué et al. 2021, Ventura et al. 2021).

The densities recorded here, despite the relatively high maximum values, were within the range of values recorded for most other reef-building sabellariids, e.g. *Idanthyrsus cretus* (72200 ind. m<sup>-2</sup>) in Las Perlas, Panama (Barrios et al. 2009), *P. lapidosa* (44000–84000 tubes m<sup>-2</sup>) in Florida (McCarthy et al. 2003), and *P. caudata* (39420–65090 ind. m<sup>-2</sup>) in São Paulo, Brazil (Faroni-Perez 2014) as well as the congeners *S. alveolata* (13807–60000 ind. m<sup>-2</sup>) in Mont Saint-Michel Bay (Caline et al. 1992, Dubois et al. 2002) and in the Central Tyrrhenian Sea (43100–157100 tubes m<sup>-2</sup>) (Bonifazi et al. 2019), and *S. spinulosa* (18875–36975 tubes m<sup>-2</sup>) in the Italian Mediterranean (Gravina et al. 2018). Reef-building sabellariids are *r*-strategist species, characterized by marked demographic fluctuations, catastrophic mortality, and high rates of recovery (Giangrande 1997). This life history strategy allows the species to survive in highly variable or unpredictable environments; they respond to shifts in environmental conditions with high reproductive rates and rapid development (Krebs 1994, Giangrande 1997).

The body size and density of *S. wilsoni* had a positive relationship with salinity. This pattern was confirmed by the major reduction in density observed during the recuperation phase (March and April 2009) and the low values recorded in March 2008. We believe that this reflects high mortality due to the extremely low salinity (6–11) recorded during these months. Although *S. wilsoni* can survive under highly variable conditions and can tolerate salinity levels ranging from 0.5 to 35 (Lana & Gruet 1989, Bremec & Giberto 2004), low salinity may be a limiting factor in the development of dense populations. Sabellariids are primarily marine species, and few taxa are found in areas subject to extreme fluctuations in salinity (Hutchings 2000). While there are no specific data on *S. wilsoni*, low salinity is known to cause mortality, reduce fecundity, and inhibit reproduction to varying degrees in estuarine polychaetes (Daunys et al. 2000, Pechenik et al. 2000). In Delaware Bay (USA), the distribution of *S. vulgaris* is determined by low salinity (<6), which prevents survival (Curtis 1975). Adult *P. caudata* and *P. californica* can tolerate brackish waters containing up to 30–40‰ seawater (Mauro 1977); these conditions are typical of those in which *S. alveolata* is normally found (Gruet 1972, Dubois et al. 2007).

Another important point is that there is some decoupling between the physiological state of the worms and the actual reef types or phases (Curd et al. 2019). Curd et al. (2019) showed that worms sampled in retrograding reefs (i.e. displaying signs of erosion) were healthy and less physiologically stressed than worms sampled in prograding (growing) bioconstructions, possibly due to lower intra-specific competition and hence greater food availability. In the case of *S. wilsoni* reefs, it is likely that salinity is a key factor underlying the health of the builder-worms and consequently the persistence of their constructions.

Quantifiable and reliable criteria are needed to evaluate the ecological state of Sabellariidae reefs, in order to monitor and protect them (Curd et al. 2019). Here, we added new structural metrics to describe the phases (Fig. 8) of the *S. wilsoni* reef cycle and linked these physical metrics to the populational structure of the tube-building worms. In future studies, we recommend characterizing and monitoring changes in biogenic structures at multiple scales (cm to km) over time, as well as the physiological responses of these worms to environmental stressors (hydrodynamic energy and low salinity).

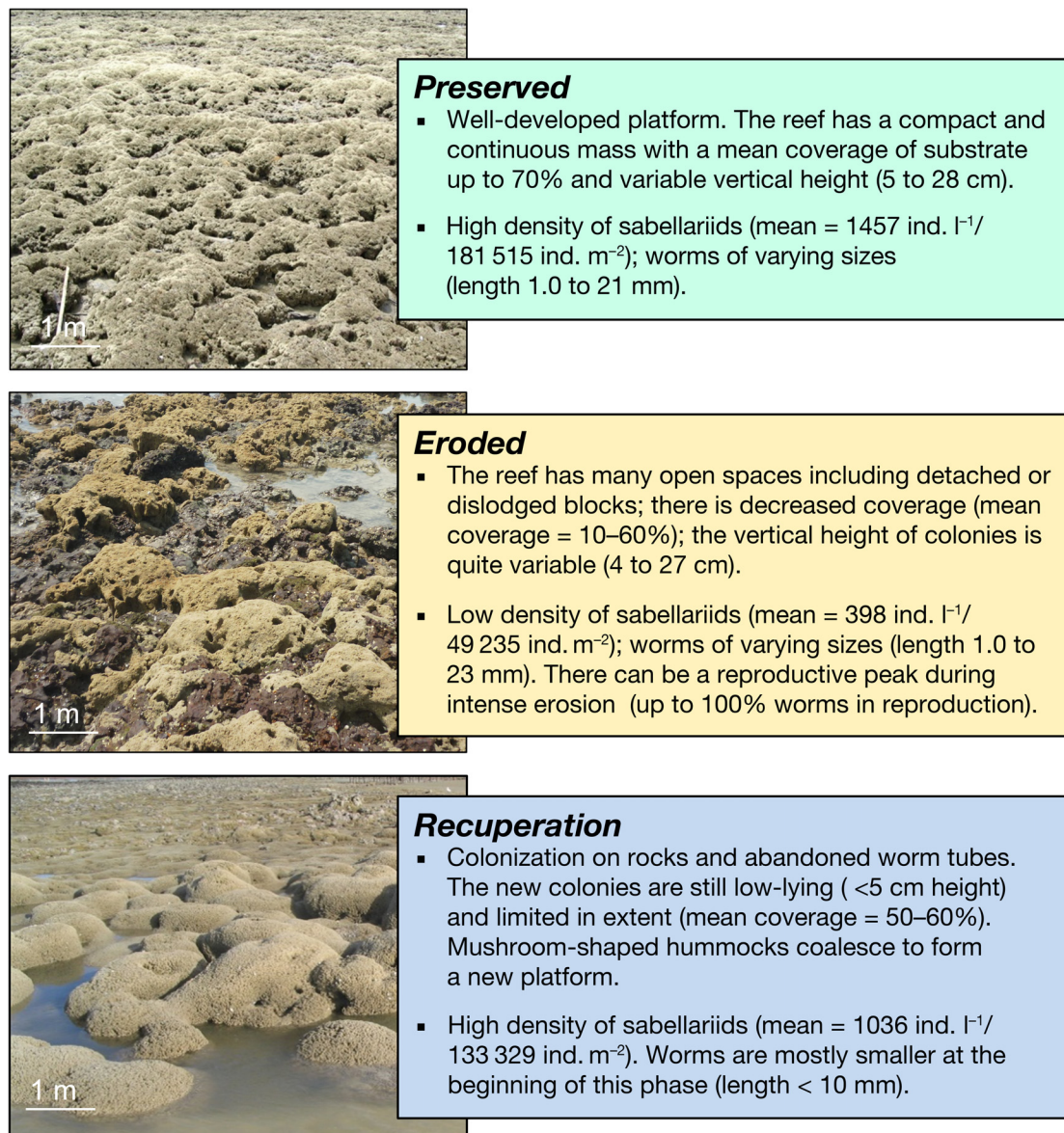


Fig. 8. Summary of phase characteristics in the structural cycle of *Sabellaria wilsoni* reef on Brazilian Amazon Coast: preserved, eroded, and recuperation

## 5. CONCLUSIONS

Empirical data are still required on many specific aspects of the life history of *Sabellaria wilsoni*, including the duration of the larval phase, life expectancy of adults, connectivity between local sub-populations, and oceanographic processes involved in reef development. However, our results do provide important insights into the hydrodynamic energy and salinity levels that can be tolerated by the species. This study offers a systematic baseline for future ecological research and monitoring of this important marine habitat. Our findings are especially important in the context of the impact of climate change on coastal regions, particularly considering likely future scenarios with increased intensity and frequency of sea surges, marine storms, and extreme events.

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