

Diversity of Bivalve Mollusks Associated with Macroalgae on the Continental Shelf in the States of Alagoas, Sergipe and Bahia, Northeastern Brazil

Lucas Santos¹, J. Weverton S. Souza^{1,2}, Silvio Lima^{3,4}, and Carmen Guimarães^{1,*}

¹Federal University of Sergipe, Center for Biological and Health Sciences, Department of Biology, Coastal Ecosystems Laboratory, Avenida Marechal Rondon, Rosa Elze, São Cristóvão 49100-000, Sergipe, Brazil. E-mail: carmenparisotto@gmail.com (Santos)

²State University of Campinas, Institute of Biology, Post-Graduate Program in Ecology, Avenida Bertrand Russel, Cidade Universitária Zeferino Vaz - Barão Geraldo 13083-865, Campinas, São Paulo, Brazil. E-mail: souza.jws@gmail.com (Soutza)

³Federal University of Campina Grande, Teacher Training Center, Academic Unit of Exact and Natural Sciences, Rua Sérgio Moreira de Figueiredo, Casas Populares, Cajazeiras 58900-000, Paraíba, Brazil. E-mail: sfblima@gmail.com (Lima)

⁴Federal University of Paraíba - Campus I, Exact and Natural Sciences Center, Department of Systematics and Ecology, Post-Graduate Program in Biological Sciences (Zoology), Cidade Universitária, João Pessoa 58051-900, Paraíba, Brazil.

*Correspondence: E-mail: carmenparisotto@gmail.com (Guimarães). Tel: +55 (79) 31946695

Received 7 May 2020 / Accepted 6 September 2020 / Published 19 November 2020
Communicated by Yoko Nozawa

The phytal environment is a complex system that involves the association between marine organisms and macroalgae. In this paper, we investigate the diversity of bivalves associated with macroalgae on the continental shelf between the states of Alagoas and Bahia, including Sergipe, in northeastern Brazil. Macroalgae and associated fauna were collected during two sampling campaigns under the MARSEAL project (February and July 2011 [dry and rainy seasons, respectively]), covering 24 stations and three isobaths (10, 25 and 50 m). The following ecological descriptors were calculated: abundance (N), richness (S), diversity (H') and evenness (J). A total of 1384 individuals from 20 families, 28 genera and 44 species were obtained. Arcidae was the most abundant group, followed by the families Pteriidae and Mytilidae. The most abundant species were *Arca zebra*, *Anadara* sp. 1 and *Pinctada imbricata*, representing 71% of the total abundance. The families Arcidae, Corbulidae and Mytilidae were considered constant, as they occurred in more than 50% of the samples. A higher abundance was recorded during the rainy season. No seasonal differences were found regarding S, H' or J. Richness increased with increasing depth, whereas the other indices (N, H' and J) were not influenced by bathymetry. This reveals that the 50 m isobath has a greater support capacity and houses richer, more diverse fauna. Bivalve richness and composition data from this study expand the information on mollusk biodiversity associated with the phytal environment on the continental shelf off northeastern Brazil.

Key words: Mollusca, Bivalvia, Phytal, Marine macrophytes, Coastal zone.

BACKGROUND

The coastal zone is a dynamic, productive, complex ecosystem composed of a wide variety of habitats and high faunistic and floristic diversity (Ray 1991; Rodrigues 2001; Ruttenberg and Granek 2011;

Balasuriya 2018). Among the habitats in the photic zone of the continental shelf, the phytal environment is dominated by macroalgae and phanerogams (Nascimento and Rosso 2007). This is a complex system of reciprocal ecological associations between marine organisms and macrophytes (Masunari and Forneris

1981; Flynn et al. 1996; Nascimento and Rosso 2007). Marine macrophytes have considerable importance to the epibenthic fauna, serving as substrate, protection, food sources, breeding grounds and nursery as well as attenuating luminosity and hydrodynamic factors (Brawley 1992; Viejo 1999; Nakaoka et al. 2001; Chavanichi and Harris 2002).

Phytoplankton communities composed of marine invertebrates associated with macrophytes are abundant and diversified (Johnson and Scheibling 1987; Taylor and Cole 1994; Jacobucci and Leite 2002; Leite and Turra 2003). Members of the phylum Mollusca are among the most representative marine invertebrates in these communities (Chemello and Milazzo 2002; Jacobucci and Leite 2002; Jacobucci et al. 2006; Nascimento and Rosso 2007; Leite et al. 2009). Gastropods and bivalves are the main groups of mollusks and marine organisms in the metazoan community of the phytoplankton environment (Tararan and Wakabara 1981; Viejo 1999; Jacobucci and Leite 2002; Lacerda et al. 2009; Barros and Rocha-Barreira 2010).

Mollusks in the class Bivalvia are commonly representative components of phytoplankton communities (Masunari 1983; Leite and Turra 2003; Jacobucci et al. 2006; Nascimento and Rosso 2007; Lacerda et al. 2009). A number of studies have demonstrated the ecological importance of bivalves as numerous, frequent metazoans in phytoplankton environments (Masunari 1983; Leite and Turra 2003; Jacobucci et al. 2006; Lacerda et al. 2009; Miloslavich and Huck 2009; Rosenfeld et al. 2017), the abundance and density of which vary significantly among macroalgal species (Johnson and Scheibling 1987).

More research is needed on the bivalve communities associated with macrophytes on the continental shelf off northeastern Brazil in view of the ecological importance of the group and to help protect and manage coastal biodiversity.

The aim of the present study was to investigate the diversity of bivalves associated with macroalgae on the continental shelf from the southern portion of the state of Alagoas to the northern portion of the state of Bahia in northeastern Brazil.

MATERIALS AND METHODS

Study area

The continental shelf off the state of Alagoas is approximately 220 km long and 20 to 40 km wide. It is delimited to the south (state of Sergipe) by the mouth of the São Francisco River. The continental slope of Alagoas begins between 60 and 80 m in depth. The shelf

is characterized by an uneven, irregular relief involving several environments formed by fluvial sedimentation, Holocene and Pleistocene marine terraces, carbonate sediments, calcareous and chalky sands, sand, mud, algae, coral and sandstone reefs (Araújo et al. 2006; Fontes et al. 2017).

The coast of the state of Sergipe (10°30'–11°40'S, 37°25'–36°10'W) is 168 km long (Guimarães 2010; Lemos Júnior 2011) and passes through the continental shelf and the beginning of the continental slope (Guimarães and Landim 2017). It is a depositional environment with a smooth declivity, small width (12 to 35 km) and variable depths (mean: 41 m) at the limit between the continental shelf and the slope (Guimarães 2010; Lemos Júnior et al. 2014; Fontes et al. 2017; Guimarães and Landim 2017). The shelf is strongly influenced by the intense river inputs, especially the estuaries of the São Francisco River to the north and the Japarutuba, Sergipe and Vaza-Barris Rivers and the Piauí-Fundo-Real river complex to the south (Guimarães 2010; Lemos Júnior 2011; Knopper et al. 2018), which give rise to five submarine canyons (Guimarães 2010; Lemos Júnior et al. 2014; Oliveira Junior et al. 2017). This environment is dominated by fine terrigenous sediment, a sandy bottom in the coastal region and a gravel bottom in deeper regions (Guimarães 2010; Fontes et al. 2017; Guimarães and Landim 2017).

The continental shelf off the state of Bahia is the narrowest in the country, with an average width of 14 km, and includes the beginning of the continental slope (next to the city of Salvador) at a depth of about 50 m. The transition from the inner to the outer continental shelf has a marked gradient. The inner continental shelf reaches the 20 m isobath, while the outer continental shelf falls between the 30 m and 50 m isobaths. The shelf has rocky outcrops and hard substrates at the edge, enabling the formation of reef constructions, siliciclastic and bioclast components, with a predominance of fragments of coral algae, mollusks, foraminifera and bryozoans in some areas. There is essentially carbonate sedimentation covering part of the consolidated substrate and recesses in the margin, where a sharp retreat is found with the deposition of thin sediments (Dominguez et al. 2011).

Sampling design

The bivalve fauna associated with macroalgae considered in this study were collected during oceanographic sampling campaigns carried out in February and July 2011 (dry and rainy seasons, respectively) under the MARSEAL project – Environmental Characterization of Sergipe and Alagoas Basin, coordinated by Petrobras/Cenpes, in the Sergipe-

Alagoas Basin, northeastern Brazil. Eight transects (A to H) were established over the area studied (10°36' to 11°21'S and 36°32' to 37°05'W) each covering three stations in the 10, 25 and 50 m isobaths, so counting twenty-four stations sampled (Fig. 1). Each sampling event involved bottom trawls performed using fishing trawlers with net sizes and mesh openings: 50 mm in the sleeve, 40 mm in the body and 26 mm in the drawer (Carneiro and Arguelho 2018). The trawlings were diurnal and lasted approximately 30 min at a speed of 2 to 2.5 knots, carried out in the opposite direction to the prevailing sea current. The coordinates shown (Table 1) represent the midpoint between the start and end coordinates of the drag.

Laboratory procedures, identification and analysis

Collected leafy macroalgae and associated fauna were immediately stored in a cold container. All material was sent to the Coastal Ecosystems Laboratory at the Federal University of Sergipe (LABEC/UFS) for washing on a 500 µm sieve and fixed with formaldehyde. Bivalves were separated from other taxa and identified mainly based on Rios (2009), Tunnell Jr. et al. (2010) and Redfern (2013). Juvenile mollusks and individuals with damaged shells were considered only to make up the total abundance of the community. Specimens were preserved in 70% ethanol and deposited into the scientific zoological collection of the Federal University of Sergipe (CZUFS), Sergipe, Brazil.

We estimated Bivalvia richness and abundance at each station where macroalgae were found. The frequency of occurrence (FO) of each taxon was determined by dividing the total number of stations at which the taxon was found by the total number of stations with bivalves and multiplying by 100. Frequency was classified based on Dajoz (1983): species present in more than 50% of the samples were considered constant; those found in 25 to 50% were considered common; and those found in less than 25% of the samples were classified as rare. Taxa identified to the genus level were considered for the determination of richness when only one species in the genus was found.

The structure of the bivalve community was defined using the following ecological descriptors: abundance (N)—number of individuals present in samples; richness (S)—number of taxa in each sample (Nibbaken 1982); diversity (H')—calculated by the Shannon-Wiener index, expressed as $H' = -\sum (p_i * \ln p_i)$, according to Pielou (1975); equitativity (J)—determined by the Pielou (1969) index using the formula $J = J' / \ln S$, in which H' is diversity expressed by the Shannon-

Wiener index and S is the number of species, with values ranging from 0 to 1. Results close to 1 represent an even distribution of the number of individuals among the species. The relative frequency (Fr) was calculated using the following formula: $Fr = n/N*(100)$, in which n is the abundance of each species divided by N (total abundance) multiplied by 100.

Generalized linear models (GLM) were developed to determine spatial (depth) and seasonal (dry and rainy seasons) variations. To do so, all descriptors (N, S, H' and J) were logarithmized by $\log(x+1)$ to correct asymmetry in the data due to very large differences between samples, which is a common pattern in biological and count data. Subsequently, the occurrence of *overdispersion* (residual deviance >> residual *d.f.*) or *underdispersion* (residual deviance << residual *d.f.*) was determined using the *arm* package (Gelman and Su 2018). As a result, quasi-Poisson distribution was considered for abundance, richness and evenness due to *overdispersion* and nonparametric error distribution, and Gaussian distribution was considered for diversity due to *underdispersion* and parametric error distribution (Crawley 2013). The ecological descriptors (N, S, H' and J) were used as a response factor and continuous variables, whereas the dry and rainy seasons and isobaths were treated as explanatory variables, fixed factors and categorical variables. The adequacy of the models was determined using the *RT4Bio* package (Reis-Jr et al. 2015) in the R software (R Core Team 2017) to determine the adequacy of the error of the response variable regarding the chosen statistical family (quasi-Poisson and Gaussian). A contrast analysis was performed to determine binary (peer to peer) temporal and spatial differences.

Species richness was compared among the three depths (10, 25 and 50 m) using the number of individuals as the sampling effort. From this, a cut line was defined to standardize the sample size of the three communities (Gotelli and Colwell 2001; Colwell et al. 2012). This analysis was performed using the *Past* software (Hammer et al. 2001).

RESULTS

A total of 1384 living individuals (276 and 1108 in the dry and rainy season, respectively) were captured in the 24 sampling stations associated with macroalgae. These individuals belong to 20 families, 28 genera and at least 40 bivalve species (Table 2). Most of the bivalves studied were represented by adult individuals. A few taxa belonging to the families Arcidae, Chamidae, Corbulidae, Gastrochaenidae, Limidae, Lyonsiidae, Mytilidae, Ostreidae, Pectinidae,

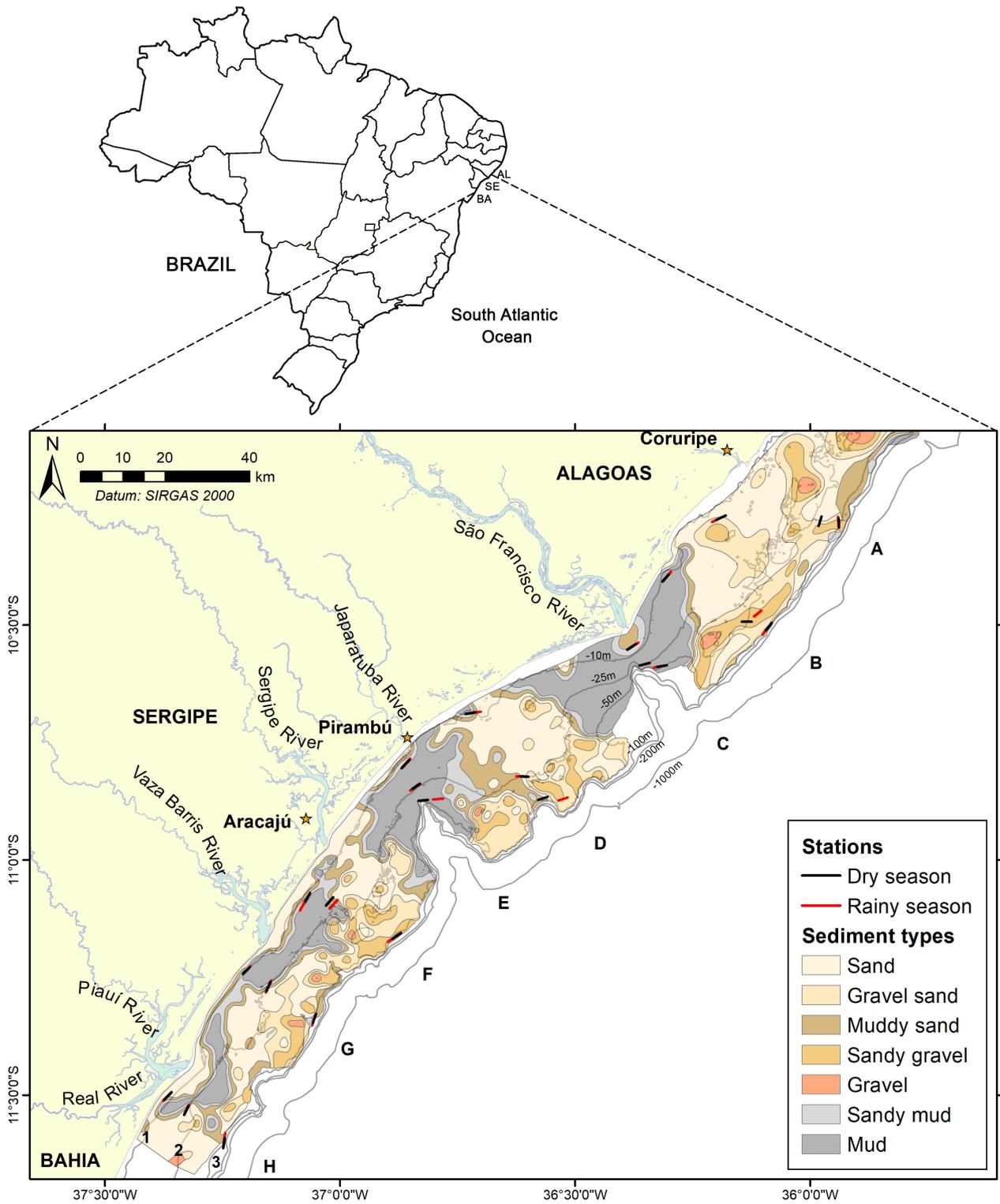


Fig. 1. Map of study area showing sampling stations and transects on the continental shelf between the southern portion of the state of Alagoas (AL) and the northern portion of the state of Bahia (BA), including the state of Sergipe (SE), during oceanographic campaigns conducted in February and July 2011 (Carneiro and Arguelho 2018).

Philobryidae, Spondylidae, Ungulinidae and Veneridae were not identified to the species level due to the poor state of preservation of the shells or the fact that the specimens were juveniles. We found no species of bivalves that were considered invasive.

The families with the largest number of species were Arcidae (S = 7), Corbulidae (S = 6) and Mytilidae (S = 5) (Fig. 2). These three groups accounted for 42% of all species collected. In contrast, Chamidae, Crassatellidae, Gastrochaenidae, Limidae, Lyonsiidae, Myidae, Noetiidae, Nuculanidae, Ostreidae, Propeamussiidae, Semelidae, Spondylidae and Ungulinidae were the least represented families in the samples, accounting for approximately 23.8% of all species collected.

All bivalves studied here are suspension feeders, except Semelidae, which is a marine bivalve family of deposit and suspension feeders. All the taxa identified to the species level are widely distributed in the Western Atlantic between the coast of North America (states of Massachusetts, North Carolina, Georgia and Florida, USA) to South America (Brazil, Uruguay and Argentina). Among the bivalves in the area studied, very limited information is available on members of the

family Lyonsiidae along the Brazilian coast. *Lyonsia* sp. may be a new and endemic species for the coast of Brazil. On the other hand, *Sphenia fragilis* and *Crenella decussata* are distributed in the eastern Pacific and Arctic circumboreal regions.

Arcidae was the most abundant group (N = 905; Fr = 67.68%) (Table 2; Fig. 2). *Arca zebra* was the most abundant bivalve and arcid, with 549 individuals, followed in abundance by *Anadara* sp. 1, with 311 individuals (Table 2; Fig. 3). These species together accounted for 64% of the total abundance of individuals found. Pteriidae was the second most abundant family (N = 123; Fr = 9.19) (Table 2; Fig. 2). *Pinctada imbricata* was the third most abundant bivalve and the most abundant pteriid, with a total of 117 individuals collected at 45.83% of the stations (Table 2; Fig. 3). Mytilidae was the third most abundant group (N = 97; Fr = 7%) (Table 2; Fig. 2). These three families together accounted for 84.14% of the total abundance of the individuals found.

Chamidae, Crassatellidae, Gastrochaenidae, Limidae, Lyonsiidae, Noetiidae, Nuculanidae, Ostreidae, Propeamussiidae, Semelidae, Spondylidae and Ungulinidae comprised about 33% of the bivalve

Table 1. Geographic coordinates (SIRGAS 2000) show midpoints between the start and end of the trawlings. Oceanographic campaigns were carried out in February and July 2011

Station	Coordinates		Depth
	x	y	
A1	807103.72	8862859.78	10 m
A2	830916.53	8862189.55	25 m
A3	835234.61	8860839.75	50 m
B1	795260.13	8849649.61	10 m
B2	815935.95	8840373.82	25 m
B3	818232.21	8836817.84	50 m
C1	787288.88	8833271.62	10 m
C2	789893.64	8828868.86	25 m
C3	792974.52	8828232.73	50 m
D1	749725.19	8817701.98	10 m
D2	760609.30	8802660.27	25 m
D3	770510.18	8797283.35	50 m
E1	733813.90	8805712.77	10 m
E2	735635.38	8800020.33	25 m
E3	740730.52	8797459.45	50 m
F1	709695.25	8772501.83	10 m
F2	716955.40	8772951.71	25 m
F3	730893.14	8764884.31	50 m
G1	697031.20	8757925.49	10 m
G2	701339.44	8752870.67	25 m
G3	711976.07	8745238.54	50 m
H1	677573.24	8727459.93	10 m
H2	682342.64	8724538.79	25 m
H3	691110.92	8716999.39	50 m

Table 2. Checklist of bivalves associated with macroalgae on the continental shelf between the southern portion of the state of Alagoas and the northern portion of the state of Bahia, including the state of Sergipe, collected during the dry and rainy seasons. The number after each sampling station indicates an isobath: 1 = 10 m, 2 = 25 m and 3 = 50 m. The voucher indicates the collection into which the specimens were deposited in Brazil. Ab = abundance. Juveniles and individuals without intact shells were not considered

TAXA	STATION AND ISOBATHS																											Ab	VOUCHER
	A1	A2	A3	B1	B2	B3	C1	C2	C3	D1	D2	D3	E1	E2	E3	F1	F2	F3	G1	G2	G3	H1	H2	H3					
BIVALVIA																													
Arcidae																													
<i>Arca zebra</i> Swainson, 1833			13		01	12				04	369						147			01		01	01	549	CZUFS BIV-00035				
<i>Anadara</i> aff. <i>notabilis</i> (Röding, 1798)									02	04						01				01				08	CZUFS BIV-00044				
<i>Anadara</i> sp. 1												01						36	07			255	12	311					
<i>Anadara</i> sp. 2				01	02							01											02	06					
<i>Barbatia domingensis</i> (Lamarck, 1819)											21						08							29	CZUFS BIV-00046				
<i>Barbatia</i> aff. <i>candida</i> (Helbling, 1779)	01																							01	CZUFS BIV-00047				
<i>Fugleria tenera</i> (C. B. Adams, 1845)										01														01	CZUFS BIV-00048				
Chamidae																													
Corbulidae																													
<i>Corbula operculata</i> Philippi, 1848			03								03					41	01			02				50	CZUFS BIV-00028				
<i>Corbula</i> sp.											01													01					
<i>Caryocorbula contracta</i> (Say, 1822)																	01							01	CZUFS BIV-00029				
<i>Caryocorbula</i> aff. <i>contracta</i> (Say, 1822)											01													01	CZUFS BIV-00030				
<i>Caryocorbula swiftiana</i> (C. B. Adams, 1852)										01							01							02	CZUFS BIV-00032				
<i>Caryocorbula chittiyana</i> (C. B. Adams, 1852)								01									05							06	CZUFS BIV-00033				
Crassatellidae																													
<i>Crassinella lunulata</i> (Conrad, 1834)				01							01					01	02			01				06	CZUFS BIV-00099				
Gastrochaenidae																													
<i>Lamychaena hians</i> (Gmelin, 1791)			01			01																01		02	CZUFS BIV-00105				
Limidae																													
<i>Lyonsia</i> sp.					02						03													05					
Myidae																													
<i>Sphenia fragilis</i> (H. Adams & A. Adams, 1854)	01																		01			13	04	19	CZUFS BIV-00100				
Mytilidae																													
<i>Amygdalum sagittatum</i> (Rehder, 1935)															15									15					
<i>Musculus lateralis</i> (Say, 1822)			01		02						06					05	03				02	05		24	CZUFS BIV-00048				
<i>Botula fusca</i> (Gmelin, 1791)																	01							01	CZUFS BIV-00056				
<i>Dacrydium vitreum</i> (Möller, 1842)						06					29						08							43	CZUFS BIV-00057				
<i>Crenella decussata</i> (Montagu, 1808)			03								07						01			01				12	CZUFS BIV-00062				
Noetiidae																													
<i>Arcopsis adamsi</i> (Dall, 1886)	03		01								01						01							06	CZUFS BIV-00109				
Nuculanidae																													
<i>Nuculana concentrica</i> (Say, 1824)											01				01									02	CZUFS BIV-00092				
Ostreidae																													
<i>Crassostrea</i> sp.		01																01				14		15					
Pectinidae																													
<i>Leptopecten bavayi</i> (Dautzenberg, 1900)	01																02				02			05	CZUFS BIV-00072				
<i>Spathochlamys benedicti</i> (Verrill & Bush [in Verrill], 1897)			02		02					01	01						05							11	CZUFS BIV-00069				
<i>Lindapecten</i> sp.																	02							02					
Philobryidae																													
<i>Cratis antillensis</i> (Dall, 1881)					06						49													55	CZUFS BIV-00083				
<i>Cratis</i> sp.											01						05							06					
Propeamussiidae																													
<i>Parvamussium pourtalesianum</i> (Dall, 1886)											01													01	CZUFS BIV-00093				
Pteriidae																													
<i>Pinctada imbricata</i> Röding, 1798	39		02		05	01				03	01						48	01	01			06	10	117	CZUFS BIV-00080				
<i>Pteria colymbus</i> (Röding, 1798)	02									04														06	CZUFS BIV-00081				
Semelidae																													
<i>Cumingia lamellosa</i> G. B. Sowerby I, 1833											01													01	CZUFS BIV-00090				
Spondyliidae																													
Ungulinidae																													
Veneridae																													
<i>Gouldia cerina</i> (C. B. Adams, 1845)			01			01				01	01										02			05	CZUFS BIV-00089				
<i>Cyclinella</i> sp.										01														01					
Abundance	48	00	28	02	07	33	00	01	00	00	18	504	02	00	16	00	58	240	39	08	08	295	34	01	1342				
Richness	07	00	10	01	03	09	00	01	00	00	09	23	02	00	01	00	08	15	04	02	06	10	06	01					

richness found (although some of the taxa were not identified on the species level) and approximately 3.81% of the individuals associated with macroalgae.

The bivalves associated with macroalgae were widely distributed across the three areas of the continental shelf studied (southern Alagoas, Sergipe and northern Bahia). However, only Arcidae (FO = 66.6%) was considered to occur constantly in more than 50% of the samples. The families Pteriidae (FO = 45.83%), Mytilidae (FO = 33.3%), Pectinidae (33.3%) and Corbulidae (FO = 29.1%) were considered common (FO ≥ 25% ≤ 50%), while most families (S = 14) were considered rare (FO ≤ 25%) (Fig. 2). No species was considered constant, but *Pinctada imbricata* (FO = 45.8%), *Arca zebra* (FO = 37.5%) and *Musculus lateralis* (FO = 29.1%) were common. Most species (S = 33) occurred in less than 25% of the samples and were therefore considered rare.

Regarding the variation in ecological descriptors, abundance varied significantly ($p = 0.01$) between seasons, with higher abundance during the rainy season (N = 1108 individuals). In contrast, no significant seasonal differences were found regarding richness ($p = 0.1$), diversity ($p = 0.6$) or equitativity ($p = 0.6$).

The variation in bivalve fauna among isobaths was significant for richness ($p = 0.03$), with an increase in species richness directly correlated with the increase in

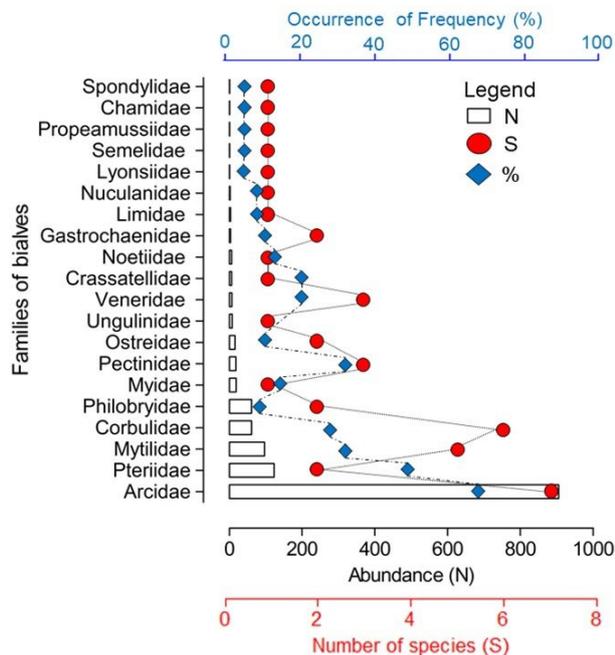


Fig. 2. Abundance (N), number of species (S) and frequency of occurrence (%) per bivalve family associated with macroalgae on the continental shelf between the southern portion of the state of Alagoas and the northern portion of the state of Bahia, including the state of Sergipe, in the dry and rainy seasons.

depth to the 50 m isobath (greatest depth sampled). No significant differences among isobaths were found for abundance ($p = 0.2$), diversity ($p = 0.1$) or equitativity ($p = 0.4$).

Among the predominant taxa, *Anadara* sp. 1 (Fr = 73%), *Corbula operculata* (Fr = 33%) and *Arca zebra* (Fr = 67%) were well represented at depths of 10, 25 and 50 m, respectively. *Pinctada imbricata* was well distributed at all depths, whereas a considerable number of the taxa were not representative in each bathymetric zone (Fig. 4). When standardizing the sampling effort using the number of individuals, the rarefaction curves indicate no variation in the number of species among the isobaths (Fig. 5), differing from the pattern found in the analysis weighted by the number of samples used in the GLM.

DISCUSSION

The present study provides important insights regarding the composition of bivalves associated with macroalgae in shallow areas of the continental shelf between the southern portion of the state of Alagoas and the northern portion of the state of Bahia, with a greater sampling effort on the continental shelf off the state of Sergipe. The richness of bivalve taxa found in this study was higher than those found in a number of previous studies. Rocha and Martins (1998) found nine families and 24 species associated with calcareous algae

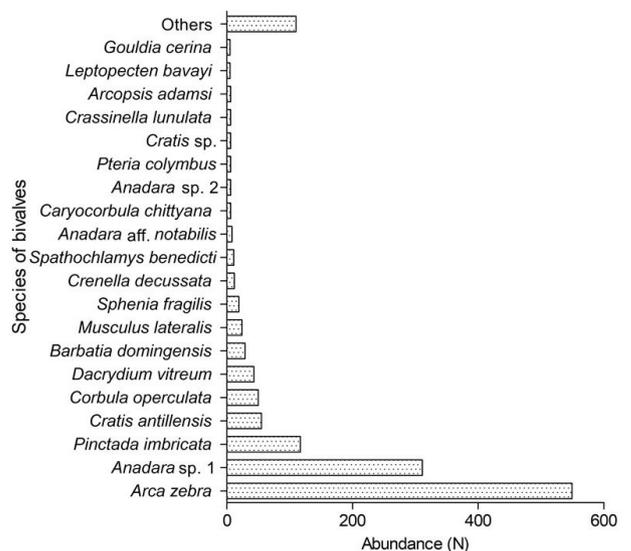


Fig. 3. Total abundance of bivalve species associated with macroalgae on the continental shelf between the southern portion of the state of Alagoas and the northern portion of the state of Bahia, including the state of Sergipe, in the dry and rainy seasons.

on the continental shelf off the state of Ceará. Jacobucci et al. (2006) recognized seven families and six species associated with *Sargassum* spp. off Queimada Pequena Island, on the southern coast of the state of São Paulo. Lacerda et al. (2009) identified seven families and 10 species associated with three different species of algae off Caiobá Beach in the state of Paraná. Cunha et al. (2013) found four families and only three species associated with brown algae of the genus *Dictyota* spp. in the Sebastião Gomes Reef and Abrolhos Archipelago of the state of Bahia. In contrast, Soares-Gomes and Pires-Vanin (2003) found greater bivalve richness (31 families and 59 species) compared to the present investigation and previous studies that collected specimens using a dredger and beam trawler. Soares-Gomes and Fernandes (2005) also found high bivalve richness (27 families and 44 species) on the continental shelf off Cabo Frio in the state of Rio de Janeiro, which is similar to the richness found in the present study. However, there were substantial differences regarding species composition between the study conducted by Soares-Gomes and Fernandes (2005) and the present investigation. It is noteworthy that all these studies were conducted in habitats with distinct algal species and/or substrate types, sample sizes and sampling efforts and employed different collection methods. The lack

of standardization with regards to sampling explains the differences in richness and abundance among invertebrates associated with macroalgae (Nascimento and Rosso 2007).

In the bivalve fauna of the areas studied, there was a predominance of the families Arcidae, Corbulidae and Mytilidae. The latter two have stood out in some studies due to the richness found on macroalgae along the Brazilian coast and other ecoregions of the Western Atlantic (Jacobucci et al. 2006; Lacerda et al. 2009; Miloslavich and Huck 2009; Rodríguez and Campos 2013). A high abundance of taxa of the family Mytilidae has also been reported in studies on mollusk assemblages associated with the phytal environment off Caiobá Beach in the state of Paraná (Lacerda et al. 2009) and with seagrasses off Guayaacán Beach in Venezuela (Miloslavich and Huck 2009). That families had low richness and abundance (e.g., Chamidae, Crassatellidae, Gastrochaenidae, Lyonsiidae and Spondylidae) in this study and other surveys of phytal bivalves (Rocha and Martins 1998; Jacobucci et al. 2006; Lacerda et al. 2009; Miloslavich and Huck 2009; Cunha et al. 2013; Rodríguez and Campos 2013) may be related to the unusual association between the individuals and macroalgae (*i.e.*, lyonsiids are mostly known as infaunal bivalves and unusual in

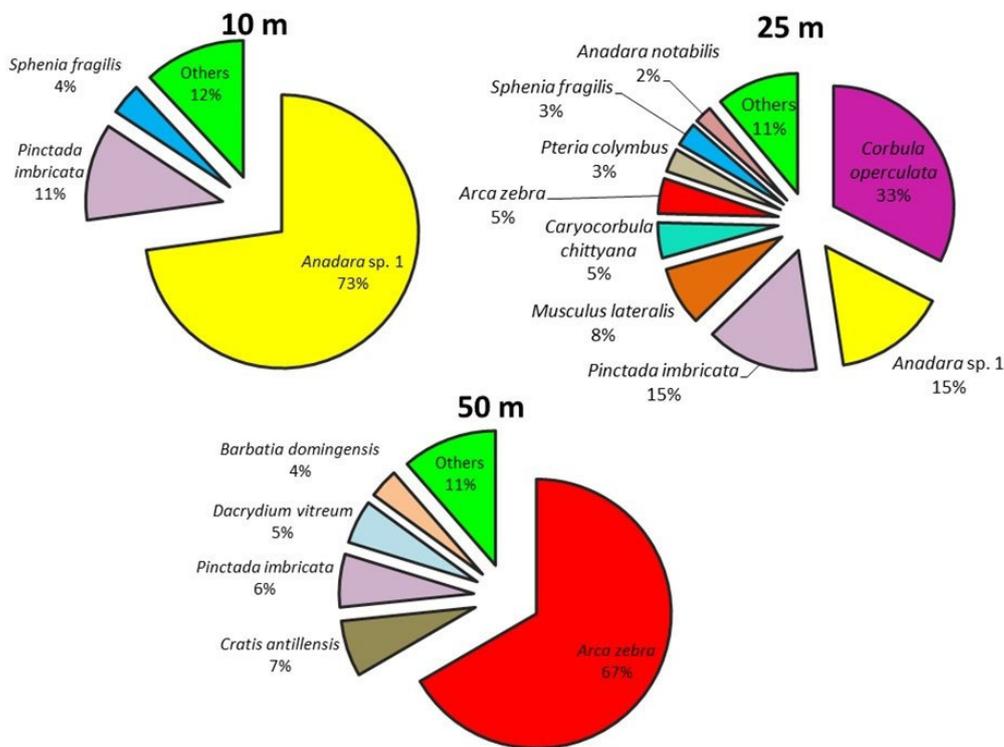


Fig. 4. Percentage abundance of bivalve species associated with macroalgae on the continental shelf between the southern portion of the state of Alagoas and the northern portion of the state of Bahia, including the state of Sergipe, at 10 m, 25 m and 50 m isobaths in the dry and rainy seasons.

algal holdfasts, spondylids are more diverse on hard substrate (Mikkelsen and Bieler 2008), and limids are frequent in small rocky crevices and uncommon on algae/algae-covered rocks (Redfern 2013)), aspects inherent to the structural complexity of macroalgae (Chemello and Milazzo 2002), hydrodynamic features as well as physical and environmental constraints (*i.e.*, chamids are epifaunal bivalves, most are stenohaline and intolerant to water turbidity conditions), predation rate (*i.e.*, crassatellids are preyed on by vertebrates and other invertebrates and likely have a higher predation rate compared to other bivalves), sampling difficulty due to a restricted habitat (*i.e.*, gastrochaenids are endolithic bivalves that construct calcareous tubes in hard substrate (Mikkelsen and Bieler 2008)), the lack of different sampling methods, etc.

Most bivalves sampled in this study typically occur in shallow coastal habitats, while a few taxa have also been recorded in deeper areas of the continental shelf, including the upper continental slope. In the present survey, the greatest richness and abundance of arcids, corbulids and mytilids was found at depths of 50 m. The taxa identified are usually collected on the inner continental shelf (Rios 2009; Tunnell Jr. et al. 2010; Redfern 2013), with some rarely found on the

outer continental shelf and slope (Rios 2009; Tunnell Jr. et al. 2010).

The bivalves co-occurring with the macroalgae in the area studied were mainly members of the genera *Arca*, *Anadara* and *Barbatia* (Arcidae); *Corbula* and *Caryocorbula* (Corbulidae); and *Musculus*, *Dacrydium* and *Crenella* (Mytilidae). The association with arcids, corbulids, mytilids and other groups is recurrent in ecological studies (Soares-Gomes and Pires-Vanin 2003; Soares-Gomes and Fernandes 2005; Lacerda et al. 2009; Miloslavich and Huck 2009; Rodríguez and Campos 2013). Among the bivalves found in the present investigation, very limited information was found on members of the genus *Lyonsia* and in association with macroalgae along the Brazilian coast. Species in this genus usually live in shallow areas of the continental shelf with sandy bottoms (Mikkelsen and Bieler 2008; Tunnell Jr. et al. 2010). We did not identify any invasive bivalves in this survey.

The study area has well-defined dry and rainy seasons (greater rainfall in winter) and is strongly influenced by the variation in rainfall throughout the year. The bivalve fauna was ~ 4-fold more abundant during the rainy season (N = 1108) compared to the dry season (N = 276). Studying the structure and dynamics of the benthic megafauna off the coast of Sergipe, Guimarães (2010) found temporal variability in the mollusk fauna, with higher abundance during the rainy season. However, Cocentino et al. (2018) found no significant difference in the occurrence of the macroalgae that housed the Bivalvia used in this present study between the dry and rainy periods.

The richness of bivalves associated with macroalgae differed significantly among the bathymetric zones (10, 25 and 50 m), with the greatest richness found for the 50 m isobath. This is the same pattern obtained by Cocentino et al. (2018) for both richness and biomass of the macroalgae. This is in agreement with data reported by Soares-Gomes and Pires-Vanin (2003), who also found a significant difference in bivalve fauna among the isobaths studied on the continental shelf off Ubatuba in the state of São Paulo and reported higher bivalve diversity values in the bathymetric range of 50 m. Soares-Gomes and Fernandes (2005) also found a very well-structured bivalve taxocenosis along the depth gradient studied on the continental shelf off Cabo Frio in the state of Rio de Janeiro.

The GLMs revealed greater species richness in the 50 m isobath. This may be related to the greater water transparency and the occurrence of thicker, poorly selected sediments capable of creating a more heterogeneous environment in the middle area of the continental shelf (Guimarães 2010; Lemos Júnior 2011),

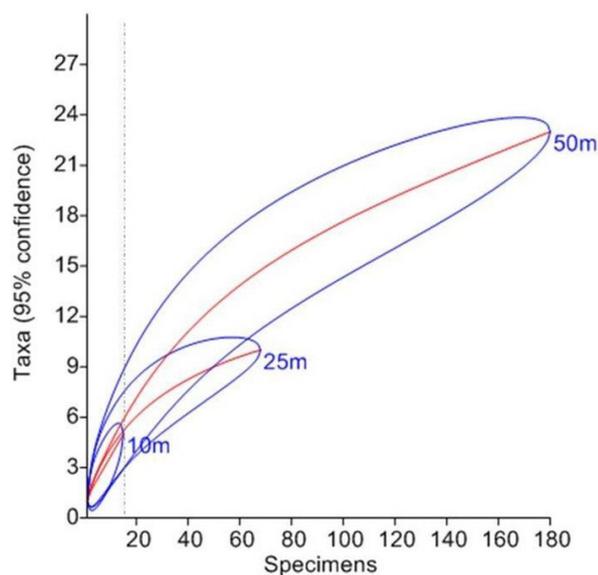


Fig. 5. Rarefaction curves representing number of bivalve species associated with macroalgae on the continental shelf between the southern portion of the state of Alagoas and the northern portion of the state of Bahia, including the state of Sergipe, at the 10 m, 25 m and 50 m isobaths in the dry and rainy seasons. Red solid lines are rarefaction curves and blue polygons are 95% confidence intervals calculated from variance. Vertical dashed line represents the comparison among species among communities, standardizing the number of individuals at 17, which was the lowest abundance recorded among the three depths.

which enables more algae to develop (Pereira et al. 2014; Cocentino et al. 2018) and consequently provides more available habitats for colonization.

Soares-Gomes and Pires-Vanin (2003) also estimated greater bivalve richness for the 50 m isobath on the inner continental shelf off Ubatuba, Brazil using rarefaction analysis. The authors attributed this greater richness mainly to the physical factors of the habitat, such as changes in sediment characteristics and hydrological events, which cause bioturbation and make such environments unstable, contributing to increased richness and diversity. In addition to these factors, the heterogeneity of the bottom also contributes to greater shellfish diversity, as evidenced by Absalão (1991) on the continental shelf off of southern Brazil. In the state of Sergipe, the continental shelf has greater environmental heterogeneity beginning with the 25-m isobath, which translates to greater resource availability (Souza 2018) as well as greater richness, abundance and diversity of biological groups (Lemos Júnior et al. 2014; Pereira et al. 2014; Santos et al. 2017; Alcântara and Siqueira 2018; Cocentino et al. 2018; Guimarães et al. 2018; Vieira and Lemos Júnior 2018; Mendonça et al. 2019a b). Among the groups studied in the region, only the meiofauna does not follow the bathymetric pattern, but instead follows the bottom type pattern (Pinto et al. 2018).

CONCLUSIONS

The present study expands on the knowledge about the richness and composition of bivalves associated with the phytal environment over an extensive area of the continental shelf off northeastern Brazil. It can be concluded that bivalve richness has a direct relationship with depth, as there were fewer species in the shallower areas sampled and richer and consequently greater harboring capacity in the deepest zone of the continental shelf of the studied area. Unlike S , H' or J , abundance varied significantly between seasons, with higher number of bivalves collected in the rainy season. The study recorded a taxon in the family Lyonsiidae and genus *Lyonsia* that may be a new and endemic species for the coast of Brazil.

Acknowledgments: The authors are grateful to PETROBRAS S.A. (Brazilian Petroleum Co.) for making the collection and studying the material, the team of the Coastal Ecosystems Laboratory of the Federal University of Sergipe for processing the material and making the data available for study, Dr. Ivan C. Lemos Júnior (UFS) for helping us obtain the literature, CNPq (Proc. n° 870361/1997-0) and FAPESP

(Proc. n° 19/20108-7) for the PhD scholarship granted to JWSS, and the anonymous reviewers for their contributions to revising the manuscript.

Authors' contributions: CRPG conceived the research ideas and designed the study. LRS, SFBL, JWSS and CRPG performed data analysis. All authors wrote and approved the final manuscript.

Competing interests: The authors declare that they have no competing interest.

Availability of data and materials: All the data are provided within the manuscript.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

- Absalão RS. 1991. Environmental discrimination among soft-bottom mollusc associations off Lagoa dos Patos, South Brazil. *Estuar Coast Shelf Sci* 32:71–85.
- Alcântara AV, Siqueira KLF. 2018. Ictiofauna demersal da plataforma continental de Sergipe e sul de Alagoas. *In: Carneiro MER and Arguelho MLPM (eds) Plataforma Continental de Sergipe e sul de Alagoas: Geoquímica e Comunidade bêntica*. UFS, São Cristóvão, pp. 379–419.
- Araújo TCM, Lima RCA, Seoane JCS, Manso VAV. 2006. Alagoas. *In: Muehe D (ed) Erosão e Prograduação do Litoral Brasileiro*. MMA, Brasília, pp. 197–212.
- Balasuriya A. 2018. Coastal Area Management: Biodiversity and Ecological Sustainability in Sri Lankan Perspective. *Biodiversity and Climate Change Adaptation in Tropical Islands* 2018:701–724. doi:10.1016/B978-0-12-813064-3.00025-9.
- Barros KVS, Rocha-Barreira CA. 2010. Caracterização da dinâmica espaço-temporal da macrofauna bentônica em um banco de *Halodule wrightii* Ascherson (Cymodoceaceae) por meio de estratificação. *Rev Nord Zool* 4:73–81.
- Brawley SH. 1992. Mesoherbivores. *In: John DM, Hawkins SJ, Price JH. (eds) Plant–Animal Inter-actions in the Marine Benthos*. Clarendon Press, Oxford, pp. 235–263.
- Carneiro MER, Arguelho MLPM. 2018. Plataforma Continental de Sergipe e sul de Alagoas: Geoquímica e Comunidade bêntica. UFS, São Cristóvão.
- Chavanich S, Harris LG. 2002. The influence of macroalgae on seasonal abundance and feeding preference of a subtidal snail, *Lacuna vineta* (Montagu) (Littorinidae) in the Gulf of Maine. *J Molluscan Stud* 68:73–78. doi:10.1093/mollus/68.1.73.
- Chemello R, Milazzo M. 2002. Effect of algal architecture on associated fauna: Some evidences from phytal molluscs. *Mar Biol* 140:981–990. doi:10.1007/s00227-002-0777-x.
- Cocentino ALM, Vieira IB, Reis TNV, Paes ET. 2018. Fitobentos da plataforma continental de Sergipe e sul de Alagoas. *In: Carneiro MER, Arguelho MLPM (eds) Plataforma Continental de Sergipe e sul de Alagoas: Geoquímica e Comunidade bêntica*. UFS, São Cristóvão.

- Colwell RK, Chao A, Gotelli NJ, Lin S, Mao CX, Chazdon RL, Longino JT. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation, and comparison of assemblages. *J Plant Ecol* **5**:3–21. doi:10.1093/jpe/rtr044.
- Crawley MJ. 2013. *The R Book*. 2^o edition. Wiley, London, UK.
- Cunha TJ, G uth AZ, Bromberg S, Sumida PYG. 2013. Macrofauna associated with the brown algae *Dictyota* spp. (Phaeophyceae, Dictyotaceae) in the Sebastião Gomes Reef and Abrolhos Archipelago, Bahia, Brazil. *Cont Shelf Res* **70**:140–149. doi:10.1016/j.csr.2013.09.001.
- Dajoz R. 1983. *Ecologia Geral*. Vozes, Petr polis.
- Dominguez JML, Ramos JMF, Rebouças RC, Nunes AS, Melo LCF. 2011. A Plataforma Continental do Munic pio de Salvador: geologia, uso m ltiplos e recursos minerais. Companhia Baiana de Pesquisa Mineral, Salvador.
- Flynn MN, Tararam AS, Wakabara Y. 1996. Effects of habitat complexity on the structure of macrobenthic association in a *Spartina alterniflora* marsh. *Rev Bras Oceanogr* **44**:09–21. doi:10.1590/S1413-77391996000100002.
- Fontes LCS, Santos JR, Santos LA, Mendonça JBS, Santos MS. 2017. Geomorfologia da plataforma continental de Sergipe-Alagoas. In: Fontes LCS, Kowsmann RO, Puga-Bernab u A (eds) *Geologia e Geomorfologia da Bacia de Sergipe-Alagoas*. UFS, S o Crist v o, pp. 24–61.
- Gelman A, Su Y. 2018. *arm: Data Analysis Using Regression and Multilevel/Hierarchical Models*. R package version 1.10-1.
- Gotelli NJ, Colwell RK. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* **4**:379–391. doi:10.1046/j.1461-0248.2001.00230.x.
- Guimar es CRP. 2010. *Estrutura e din mica dos sedimentos superficiais e da fauna b ntica na plataforma continental de Sergipe*. PhD dissertation, Federal University of Bahia.
- Guimar es CRP, Landim MF. 2017. Plataforma continental de Sergipe: caracteriza o, usos e progn sticos. In: Crestana S, Castellano EG, Rossi A (eds) *Bens e Recursos Ambientais e o Direito Ambiental*. Embrapa, Bras lia, pp. 811–826.
- Guimar es CRP, Carvalho MAO, Sousa GS, Paes ET. 2018. Comunidade macrob ntica da plataforma continental de Sergipe e sul de Alagoas. In: Carneiro MER, Arguelho MLPM (eds) *Plataforma Continental de Sergipe e sul de Alagoas: Geoqu mica e Comunidade b ntica*. UFS, S o Crist v o.
- Hammer O, Harper DAT, Ryan PD. 2001. Past – Paleontological Statistics software package for education and data analysis. *Palaeontologia Electronica* **41**:1–9.
- Jacobucci GB, Leite FPP. 2002. Distribui o vertical e flutua o sazonal da macrofauna associada a *Sargassum cymosum* C. Agardh, na Praia do L zaro, Ubatuba, S o Paulo, Brasil. *Rev Bras Zool* **19**:87–100. doi:10.1590/S0101-81752002000500004.
- Jacobucci GB, G uth AZ, Turra A, Magalh es CA, Denadai MR, Chaves AMR, Souza ECF. 2006. Assessment of *Sargassum* spp. Macrofauna at Queimada Pequena Island, Ecological Station of Tupiniquins, Southern coast of S o Paulo State, Brazil. *Biota Neotrop* **6**:1–8. doi:10.1590/S1676-06032006000200023.
- Johnson SC, Scheibling RE. 1987. Structure and dynamics of epifaunal assemblages on intertidal macroalgae *Ascophyllum nodosum* and *Fucus vesiculosus* in Nova Scotia, Canada. *Mar Ecol Prog Ser* **37**:209–227.
- Knoppers BA, Carneiro MER, Fontes LCS, Souza WFL, Medeiros PRP. 2018. Plataforma continental de Sergipe e Alagoas. In: Carneiro MER, Arguelho MLPM (eds) *Plataforma Continental de Sergipe e sul de Alagoas: Geoqu mica e Comunidade b ntica*. UFS, S o Crist v o.
- Lacerda MB, Dubiaski-Silva J, Masunari S. 2009. Malacofauna de tr s fitais da Praia de Caiob , Matinhos, Paran . *Act Biol Paran* **38**:59–74. doi:10.5380/abpr.v38i0.16413.
- Leite FPP, Tambourgi MRS, Cunha CM. 2009. Gastropods associated with the green seaweed *Caulerpa racemosa*, on two beaches of the Northern coast of the State of S o Paulo, Brazil. *Strombus* **16**:1–10.
- Leite FPP, Turra A. 2003. Temporal Variation in *Sargassum* Biomass, *Hypnea* Epiphytism and Associated Fauna. *Braz Arch Biol Techn* **46**:665–671. doi:10.1590/S1516-89132003000400021.
- Lemos J nior IC. 2011. *Distribui o e aspectos tafon micos de foraminiferos recentes na plataforma continental de Sergipe, Brasil*. PhD Dissertation, Federal University of Bahia.
- Lemos J nior IC, Machado AJ, Andrade EJ, Vieira FS, Guimar es CRP. 2014. Macroforaminiferos da plataforma continental de Sergipe, Brasil. *Sci Plena* **10**:1–11.
- Masunari S. 1983. The phytal of the alga *Amphiroa fragilissima* (Linnaeus) Lamaroux, 1816. *Stud Neotrop Fauna E* **18**:151–161. doi:10.1080/01650528309360628.
- Masunari S, Forneris L. 1981. O ecossistema fital - uma revis o. Academia Brasileira de Ci ncias, Rio de Janeiro.
- Mendonça LMC, Guimar es CRP, Lima SFB. 2019a. Mollusk bycatch in trawl fisheries targeting the Atlantic seabob shrimp *Xiphopenaeus kroyeri* on the coast of Sergipe, northeastern Brazil. *Pap Avulsos Zool* **59**:1–12. doi:10.11606/1807-0205/2019.59.33.
- Mendonça LMC, Guimar es CRP, Santos RC, Alves DFR, Barros-Alves SP, Silva SLR, Hirose GL. 2019b. Decapod Crustaceans from the continental shelf of Sergipe, northeastern Brazil. *Zootaxa* **4712**:301–344. doi:10.11646/zootaxa.4712.3.1.
- Mikkelsen PM, Bieler R. 2008. *Seashells of Southern Florida: Living Marine Mollusks of the Florida Keys and Adjacent Regions*. Princeton University Press, Princeton, USA.
- Miloslavich P, Huck E. 2009. Mollusk assemblages in seagrasses and macroalgal rocky shores in Venezuela: implementing the NaGISA Protocol. *Memoria de la Fundaci n La Salle de Ciencias Naturales* **171**:81–98.
- Nakaoka M, Toyohara T, Matsumasa M. 2001. Seasonal and between-substrate variation in mobile epifaunal community in a multispecific seagrass bed of Otsuch Bay, Japan. *Mar Ecol* **22**:379–395. doi:10.1046/j.1439-0485.2001.01726.x.
- Nascimento EFI, Rosso S. 2007. Fauna associada  s macroalgas marinhas bent nicas (Rhodophyta e Phaeophyta) da Regi o de S o Sebastião, S o Paulo. *Braz J Ecol* **1**:38–51.
- Nibbaken JW. 1982. *Marine Biology: an ecological approach*. Harper & Row, New York, USA.
- Oliveira Junior EA, Kowsmann RO, Schreiner S, Ferreira ETI. 2017. Geomorfologia do talude da bacia de Sergipe-Alagoas. In: Fontes LCS, Kowsmann RO, Puga-Bernab u A (eds) *Geologia e Geomorfologia da Bacia de Sergipe-Alagoas*. UFS, S o Crist v o, pp. 97–136.
- Pereira SMB, Torres J, Gestinari LMS. 2014. Composition and distribution of Deep Water Macroalgae Species from the Continental Shelf of Sergipe State, Brazil. *Phytotaxa* **190**:250–267. doi:10.11646/phytotaxa.190.1.15.
- Pielou EC. 1969. *An Introduction to Mathematical Ecology*. Willy-Interscience, New York, USA.
- Pielou EC. 1975. *Ecological Diversity*. John Wiley & Sons Inc., New York, USA.
- Pinto TK, Rocha EM, Ferreira RC, Silva MC, Guilherme BC. 2018. Meiofauna da plataforma continental de Sergipe e sul de Alagoas. In: Carneiro MER, Arguelho MLPM (eds) *Plataforma Continental de Sergipe e sul de Alagoas: Geoqu mica e Comunidade b ntica*. UFS, S o Crist v o.

- Ray GC. 1991. Coastal-Zone Biodiversity Patterns. *BioScience* **41**:490–498. doi:10.2307/1311807.
- R Core Team. 2017. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed 10 Oct. 2019.
- Redfern C. 2013. Bahamian Seashells: 1161 species from Abaco, Bahamas. Bahamianseashells.com Inc., Florida, USA.
- Reis-Jr R, Oliveira ML, Borges GRA. 2015. RT4Bio: R Tools for Biologists (RT4Bio). R package version 1.0.
- Rios EC. 2009. Compendium of Brazilian sea shells. Evangraf, Rio Grande.
- Rocha CA, Martins IX. 1998. Estudo da malacofauna bêntica na plataforma continental do litoral oeste do estado do Ceará, Brasil. *Arq C Mar* **31**:65–72.
- Rodrigues CSL. 2001. Fauna de moluscos gastrópodes associados a *Ulva lactuca* L. (Chlorophyta) no Recife Ponta do Percevejo, Maceió, Alagoas, Brasil. PhD Dissertation, Federal University of Pernambuco, Brazil.
- Rodríguez JQ, Campos NH. 2013. Moluscos asociados a ensamblajes macroalgales en el litoral rocoso de Córdoba, Caribe Colombiano. *Boletín de Investig Mar y Costeras* **42**:101–120.
- Rosenfeld S, Aldea C, Ojeda J, Marambio J, Hüne M, Troncoso JS, Mansilla A. 2017. Molluscan assemblages associated with Gigartina beds in the Strait of Magellan and the South Shetland Islands (Antarctica): a comparison of composition and abundance. *Polar Research* **36**:1297915. doi:10.1080/17518369.2017.1297915.
- Ruttenberg BI, Granek EF. 2011. Bridging the marine–terrestrial disconnect to improve marine coastal zone science and management. *Mar Ecol Prog Ser* **434**:203–212. doi:10.3354/meps09132.
- Santos RC, Silva SLR, Costa RC, Davanzo TM, Hirose GL. 2017. Evaluation of the management plan for penaeid shrimps in the Continental Shelf of Sergipe, Brazil. *Bol Inst Pesca* **43**:308–321. doi:10.20950/1678-2305.2017v43n3p308.
- Soares-Gomes A, Fernandes FC. 2005. Spatial distribution of bivalve mollusc assemblages in the upwelling ecosystem of the continental shelf of Cabo Frio, Rio de Janeiro, Brazil. *Rev Bras Zool* **22**:73–80. doi:10.1590/S0101-81752005000100009.
- Soares-Gomes A, Pires-Vanin AMS. 2003. Padrões de riqueza e diversidade de moluscos bivalves na plataforma continental ao largo de Ubatuba, São Paulo, Brasil: uma comparação metodológica. *Revista Landa* **20**:717–725.
- Souza JWS. 2018. Capitellidae (Annelida) na plataforma continental de Sergipe, Nordeste do Brasil: estrutura da comunidade e do habitat. PhD Dissertation, Federal University of Sergipe.
- Tararan AS, Wakabara Y. 1981. The mobile fauna especially Gammaridea of *Sargassum cymosum*. *Mar Ecol Prog Ser* **5**:157–163.
- Taylor RB, Cole RG. 1994. Mobile epifauna on subtidal brown seaweeds in northeastern New Zealand. *Mar Ecol Prog Ser* **115**:271–282. doi:10.3354/meps115271.
- Tunnell Jr. JW, Andrews J, Barrera NC, Moretzsohn F. 2010. *Encyclopedia of Texas Seashells: Identification, Ecology, Distribution, and History*. Natural History. College Station, Texas A & M University Press, Texas, USA.
- Vieira FS, Lemos Júnior IC. 2018. Foraminíferos da plataforma continental de Sergipe e sul de Alagoas. In: Carneiro MER and Arguelho MLPM (eds) *Plataforma Continental de Sergipe e sul de Alagoas: Geoquímica e Comunidade bêntica*. UFS, São Cristóvão, pp. 224–249.
- Viejo RM. 1999. Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain. *Aquatic Botany* **64**:131–149. doi:10.1016/S0304-3770(99)00011-X.