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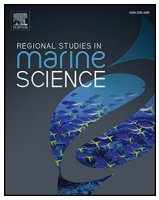

Structuring patterns of the epilithic algal matrix cryptofauna in a tropical oceanic reef

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ABSTRACT

Reef systems are one of the most biodiverse and complex marine ecosystems. Invertebrate cryptic epifaunal communities (i.e, cryptofauna) associated with the epilithic algal matrix make up a large part of the reef biodiversity and play a critical role in their food webs. Yet, few studies have investigated the composition and abundance of the cryptofauna associated with EAM and the major drivers influencing patterns of community structure. Algae biomass, rates of predation, depth, and trapped particles (detritus and sediment) are among the main drivers of cryptofauna composition changes. In the South Western Atlantic, the epilithic algal matrix composes up to 70% of the benthic cover both in tropical (biogenic) and subtropical (non-biogenic) reefs, but information about the associated cryptofauna is limited. We sampled the epilithic algal matrix (EAM) of two sites in an equatorial Brazilian oceanic island, at three depth strata. In total, 106 operational taxonomic units (OTUs) belonging to 14 taxa were recorded (Foraminifera, Gastropoda, Bivalvia, Polyplacophora, Amphipoda, Tanaidacea, Cumacea, Ostracoda, Decapoda, Polychaeta, Cnidaria, Sipuncula, Echinodermata and Chironomidae). Gastropods were the most diverse group (48 OTUs) and second most abundant (n = 1585). Total invertebrate abundance and composition, as well as abundance of each taxa, were influenced by EAM characteristics (algae biomass and coarse particulates) and depth. Foraminifera abundance increased as algae biomass increased, due to the presence of Large Benthic Foraminifera (LBF) which may associate with algae for sunlight protection. Mollusks were mainly represented by the detritivorous *Barleeia rubrooperculata*. Richness of taxa in EAM observed here was similar to values observed in frondose macroalgae elsewhere despite the low taxonomic resolution applied, indicating its potential as a cryptofauna biodiversity reservoir.

1. Introduction

Reef systems are present in only a small portion of the ocean (Buddemeier, Kleypas, and Aronson, 2004). Nonetheless, they represent one of the most diverse ecosystems, harboring a third of all marine life on the planet (Moberg and Folke, 1999). A significant portion of this diversity is comprised of small invertebrate species (ranging from 0.06 to 40 cm) (Enochs et al., 2011; Wolfe et al., 2020; Ruppert et al., 2004; Peyrot-Clausade, 1980; Takada et al., 2012; Enochs and Manzello, 2012). Despite their abundance, these small invertebrates have often been overlooked by scientists in comparison to larger and more charismatic organisms such as corals and vertebrates (e.g., sharks, fish, mammals, and turtles) (Ruppert et al., 2004; Stella et al., 2010; Netchy et al., 2015; Wolfe et al., 2020; Zeller, 1988).

These minute invertebrates can live in association with sessile invertebrates or algae. They are referred to as cryptofauna when inhabiting the interstices of invertebrates (e.g. corals, bryozoans, sponges) in marine ecosystems, or as phytofauna when exclusively dwelling on macrophytes in marine or freshwater environments (Lalonde and Downing, 1992; Kramer et al., 2012; Head et al., 2018; Vicente et al., 2022; Morgado and Tanaka, 2001; Canterle et al., 2020; Macdonald et al., 2006). Cryptofauna encompasses organisms from both meio- and macrofauna (Enochs et al., 2011; Klumpp et al., 1988; Kramer et al., 2013; Head et al., 2018). The importance of these invertebrates extends

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beyond their diversity, as they potentially account for more biomass than any other non-cryptic fauna in reef systems (Stella et al., 2010; Enochs et al., 2011). They also play significant functional roles as grazers of epilithic algae and epiphytes (Altman-Kurosaki et al., 2018; Klumpp et al., 1988), capturing and recycling nutrients (Kramer et al., 2013; Wolfe et al., 2020), particularly in the carbon cycle (Moran et al., 2014; Dawson et al., 2014), and as food sources for fishes (Klumpp et al., 1988; Kramer et al., 2013; Jones, Ferrell, and Sale, 1991) and invertebrates (Kohn and Nybakken, 1975; Reaka, 1987). However, the factors driving the abundance and distribution patterns of these cryptic assemblages remain poorly studied (Stella et al., 2010; Head et al., 2018).

The majority of studies focusing on cryptofauna have been limited to communities associated with frondose macroalgae or corals, leaving a significant gap in our understanding of the cryptofauna inhabiting short-thallus algae. These short-thallus algae, also known as turfs, can form dense mats of algae only a few centimeters in height (Connell, Foster, and Airoldi, 2014). These mono or multi-species algal mats are referred to as epilithic turf, epilithic algal communities (EAC), or epilithic algal matrices (EAM), with EAM encompassing not just the algae but also the microbial, detritus, and sediment components trapped within the complex three-dimensional structure formed by these algae (Connell, Foster, and Airoldi, 2014; Wilson and Bellwood, 1997). This intricate EAM also hosts numerous small-bodied invertebrates that find shelter from predators and environmental stressors (e.g., wave action, temperature, and desiccation) (Kramer et al., 2012; Klumpp, McKinnon, and Mundy, 1988), while accumulating abundant food resources such as detritus, cyanobacteria, and epiphytes.

Only a handful of studies, mostly concentrated in the Pacific Ocean, have investigated the factors influencing the structure and dynamics of EAM-associated cryptofauna, including depth (Bussell et al., 2007; Berthelsen et al., 2015), predation (Stier and Leray, 2013), and sediment (Kramer et al., 2014). While the reef substratum along the Brazilian coast and oceanic islands is dominated by EAM (Aued et al., 2018), knowledge about EAM-associated cryptofauna is scarce (Ferreira et al., 1998). Invertivorous fish represent a substantial portion of fish biomass in Brazilian reefs (Morais et al., 2017), making an understanding of cryptofauna community patterns crucial for elucidating the importance of these invertebrates as trophic resources for fish (Kramer et al., 2013; Mendes et al., 2018).

In this study, we investigate the potential key drivers affecting the community structure of EAM-associated cryptofauna in tropical reefs on an oceanic island. We analyze patterns of cryptofauna abundance and distribution at different depths, hypothesizing that algae composition and biomass are the primary factors influencing the cryptofauna associated with short-thallus algae in the EAM, similar to findings for the phytofauna of frondose macroalgae (Lalonde and Downing, 1992; Becerra-Muñoz and Schramm, 2006; Barbosa et al., 2019).

2. Material and methods

2.1. Study site

Fernando de Noronha Island (03°50′ S; 32°25′ W) is the largest Brazilian oceanic island (16.4 km^2) and is located 350 km offshore. It is characterized by tropical rocky reefs mostly covered by EAM and macroalgae (Sargassum spp., Dictyota spp., Dictyopteris spp., Amphiroa sp., and Jania sp.), with low coral cover (0–5%) in shallow habitats (Krajewski and Floeter, 2011; Almeida and de Almeida, 2015; Aued et al., 2018; Zamoner et al., 2021). The northeastern portion of the island is dominated by EAM and macroalgae (~50%), with foliose, filamentous, and crustose coralline algae being the dominant algal morphotypes (Zamoner et al., 2021). This part of the island is sheltered from the prevailing SE winds, experiencing low wave exposure year-round, except during the high swell season between November and March. The southwestern portion is also dominated by turfs and macroalgae (~45%), composed of the same algal morphotypes. However, a higher cover of crustose coralline algae and corals can be found, with greater abundance at depths between 10 and 12 m (Zamoner et al., 2021).

2.2. Sampling procedures

We sampled two sites in November 2019: Cagarras in the northwestern region and Ponta da Sapata in the southwestern region of the island (Fig. 1). At each site, EAM was sampled at three different depths (5, 10, and 15 m), with seven samples collected per depth (quadrats of 100 cm^2) using an air-lift device. Samples were placed in fabric bags inside larger containers with 4% formaldehyde immediately after sampling, then transferred to Falcon tubes containing 70% alcohol and stored.

The air-lift consists of a stainless steel blade attached to a PVC pipe with a hose connected to the SCUBA cylinder and a collection bag at the pipe's end. The scraped EAM is lifted by the air flux and retained in the filter bag with a mesh size of 0.5 mm, capable of trapping organisms from the macrofauna. This method has a 10% loss of coarse particles (mainly fine sediments) and causes little to no fragmentation of the material, making it efficient in sampling all EAM components.

2.3. Laboratory procedures

In the laboratory, the collected material was analyzed using a stereomicroscope and then separated into categories: cryptofauna, algae, sediment, and detritus. Detritus and sediment were combined and referred to as 'coarse particulates' since a 0.5 mm mesh size cannot capture fine sediments and most detritus (< 0.125 mm). Wet biomass measurements were taken for each of the four categories from all samples.

The cryptofauna comprises organisms with a broad size range, spanning from smaller meiofaunal organisms (between 0.04 and 0.5 mm) to larger macrofaunal organisms (> 0.5 mm). For this study, only the macrofaunal component was considered due to the use of a 0.5 mm mesh-size filter bag. The cryptofauna was carefully sorted, identified to the lowest possible taxonomic level, and then counted. Organisms were classified into operational taxonomic units (OTUs), which are defined here as morphologically similar taxa grouped within the same taxonomic level of a broader taxon. For instance, distinguishable taxonomic entities from the same Order but not identified at the Family level were included. Taxa with low abundance, generally accounting for less than 2% of the total abundance, were grouped under the overarching category called 'others'.

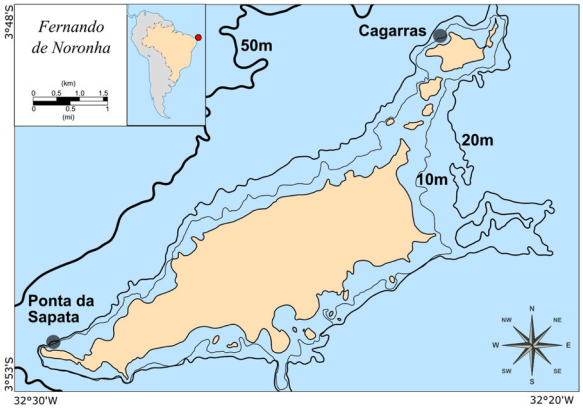

Fig. 1. Map showing the location of Fernando de Noronha Archipelago at 250 km from Brazil's northeastern coast and the two sampling sites Cagarras and Ponta da Sapata.

2.4. Data analysis

We used linear models (LMs) to test if the four EAM categories (crypto biomass, algae biomass, crypto abundance, and coarse particulates weight) and the four cryptofauna groups (Crustacea, Mollusca, Polychaeta, and Foraminifera) varied between sites and depth. The models included the wet weight of each EAM category or abundance (for cryptofauna) as the dependent variable, and site and depth strata as independent variables. We also included the interaction of fixed effects (site and depth strata) in all models, and algae biomass and particulate material in the models where cryptofauna was the dependent variable. The significance of each independent variable was obtained by the F-value using the function "anova". Prior to analysis, we tested all independent variables for colinearity using the VIF (VIF < 4, Zuur et al., 2009), and we did not find any colinearity between them. If the interaction factors were significant, we used the "emmeans" function from the emmeans package (Lenth, 2023) to identify differences between levels of fixed factors by applying pairwise comparisons. Lastly, the model's fits were analyzed by visual inspection of residuals and fitted values, Q-Q plots of residuals, and residual distribution. Only the cryptofauna biomass was log-transformed to achieve distribution normality prior to running the model.

Shannon-Wiener diversity index was calculated using the function "diversity" from the *vegan* package (Oksanen et al., 2020), and the function "specnumber" from the same package for richness. Afterward, we performed linear models applying the same previously indicated variables and syntax, using those indexes as explained variables in models.

Assemblage structure of the most abundant taxa and total fauna were compared between sites through permutational multivariate analysis of variance (PERMANOVA), based on Bray–Curtis dissimilarity of abundance values. Permutational tests were performed using the "adonis" function from the package *vegan* in the R software (R Core Team, 2020; Oksanen et al., 2020).

To test whether the sampling effort was sufficient, we applied multivariate pseudo-standard error (MultSE) to our data, a metric in which a random number of samples are drawn from a community and MultSE is calculated, with the goal of setting the minimum sample size to a value at which MultSE is acceptable and affordable (Montes et al., 2021). MultSE stated a minimum of five samples per depth must be taken to account for community diversity, confirming that the seven samples per depth were sufficient.

Detailed statistical results were added to the Appendix section, also including images of the EAM-associated cryptofauna found here.

3. Results

3.1. Cryptofauna composition

Overall, we counted a total of 4577 individuals from 14 taxa at the two sampled sites, classified into five primary taxonomic groups: Foraminifera, Mollusca (Gastropoda, Bivalvia, and Polyplacophora), Crustacea (Amphipoda, Tanaidacea, Cumacea, Ostracoda, and Decapoda), Polychaeta, and Others (Cnidaria, Sipuncula, Echinodermata, and Chironomidae). The most abundant groups were Foraminifera ($n = 2444$ individuals) and Mollusca ($n = 1585$), with the latter primarily dominated by gastropods. Community composition was similar between the sites (PERMANOVA, $p = 0.09$; $R2 = 0.05$); however, more crustaceans were observed in Ponta da Sapata and "Others" in Cagarras (Table 1). The composition differed based on algae biomass (PERMANOVA, $p = 0.02$; $R2 = 0.08$), showing a positive correlation between the richness of crustaceans, foraminiferans, gastropods, and algae biomass.

Taxa identification resulted in 111 OTUs, with Gastropoda and Foraminifera being the most diverse taxa, comprising 48 and 22 OTUs, respectively (Table S1). Cryptofauna richness (Cagarras = 92 OTUs, Ponta da Sapata = 81, LM, $p < 0.05$) and diversity (Shannon-Wiener Index) differed between sites but were similar between depths considering OTUs. Neither richness nor diversity were correlated with either algae biomass (LM, $p > 0.05$) or coarse particulates (LM, $p > 0.05$). More details on the composition of the OTU groups can be found in the Supplementary Material.

3.2. EAM components

Algae biomass was similar between sites, although higher values occur in Cagarras (mean ± SE: Sapata = 2.06 g ± 1.6 g; Cagarras = 2.35 g ± 0.98). Also, there were no differences between depths, although lower values occur in the shallow depth (Sapata = 1.59 g ± 1.76 g; Cagarras = 1.8 g ± 0.8 g), and higher values in the intermediate-deep stratum of both sites (Sapata = 2.3 g ± 1.53 g; Cagarras = 2.7 g ± 0.9 g; Fig. 2).

Coarse particulates were similar between sites (LM, $p = 0.4$), and depths (LM, $p = 0.14$). Yet, the lowest values occur in the deep depth of Ponta da Sapata (0.46 g ± 0.45 g) and the shallow depth of Cagarras (0.45 g ± 0.28 g). A marginal significant correlation occurred between coarse particulates and algae biomass, with increasing amounts of coarse particulates as algae biomass increases (LM, $p = 0.06$).

Total cryptofauna abundance was similar between sites (LM, $p = 0.5$). Abundance was also similar between depths, with the exception of the shallow depth of Cagarras which presented the lowest

Table 1
Abundance of recorded taxa (mean ± standard error) according to site and depth strata (5, 10, and 15 m) in rocky reefs of Fernando de Noronha island, Brazil.

	Ponta da Sapata			Cagarras			
Taxa	5	10	15	5	10	15	Total
Crustacea	12.14 ± 12.09	4.86 ± 2.73	6.29 ± 3.40	1.83 ± 1.47	4.86 ± 2.79	3.00 ± 1.00	229
Amphipoda	6.86 ± 6.36	2.57 ± 2.57	4.14 ± 2.91	0.83 ± 0.98	2.71 ± 1.80	1.00 ± 1.15	126
Tanaidacea	5.14 ± 6.64	0.86 ± 1.21	0.43 ± 0.79	0.17 ± 0.41	0.43 ± 0.53	0.29 ± 0.49	51
Cumacea	0.00 ± 0.00	0.29 ± 0.76	0.57 ± 0.79	0.17 ± 0.41	0.29 ± 0.49	0.14 ± 0.38	10
Decapoda	0.14 ± 0.38	1.00 ± 1.15	0.29 ± 0.76	0.33 ± 0.52	0.14 ± 0.38	0.14 ± 0.38	14
Ostracoda	0.00 ± 0.00	0.14 ± 0.38	0.86 ± 0.90	0.33 ± 0.82	1.29 ± 0.95	1.43 ± 0.79	28
Mollusca	43.57 ± 21.73	43.00 ± 22.46	50.86 ± 25.11	13.50 ± 12.86	55.71 ± 19.35	28.57 ± 5.86	1633
Gastropoda	42.29 ± 20.93	42.43 ± 22.32	48.71 ± 24.68	13.17 ± 13.11	54.14 ± 18.68	27.57 ± 5.44	1585
Bivalvia	0.00 ± 0.00	0.29 ± 0.49	1.71 ± 3.30	0.17 ± 0.45	1.00 ± 1.15	0.14 ± 0.38	23
Polyplacophora	1.29 ± 1.98	0.29 ± 0.76	0.43 ± 0.53	0.17 ± 0.41	0.57 ± 0.79	0.86 ± 1.21	25
Echinodermata	0.14 ± 0.38	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.43 ± 1.13	0.14 ± 0.38	5
Polychaeta	8.00 ± 3.42	4.14 ± 2.48	4.14 ± 2.79	2.50 ± 2.51	5.86 ± 2.54	5.29 ± 3.86	207
Sipuncula	0.43 ± 0.79	0.14 ± 0.38	0.00 ± 0.00	2.17 ± 2.32	0.57 ± 0.79	0.43 ± 0.53	24
Foraminifera	43.86 ± 14.94	75.14 ± 24.22	47.71 ± 20.56	28.83 ± 12.01	74.0 ± 12.97	83.71 ± 24.2	2444
Chironomidae	0.43 ± 0.79	0.00 ± 0.00	0.00 ± 0.00	0.17 ± 0.41	2.29 ± 1.80	1.71 ± 1.38	32
Cnidaria	0.14 ± 0.38	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.14 ± 0.38	0.14 ± 0.38	3
Total	761	891	763	294	1007	861	4577

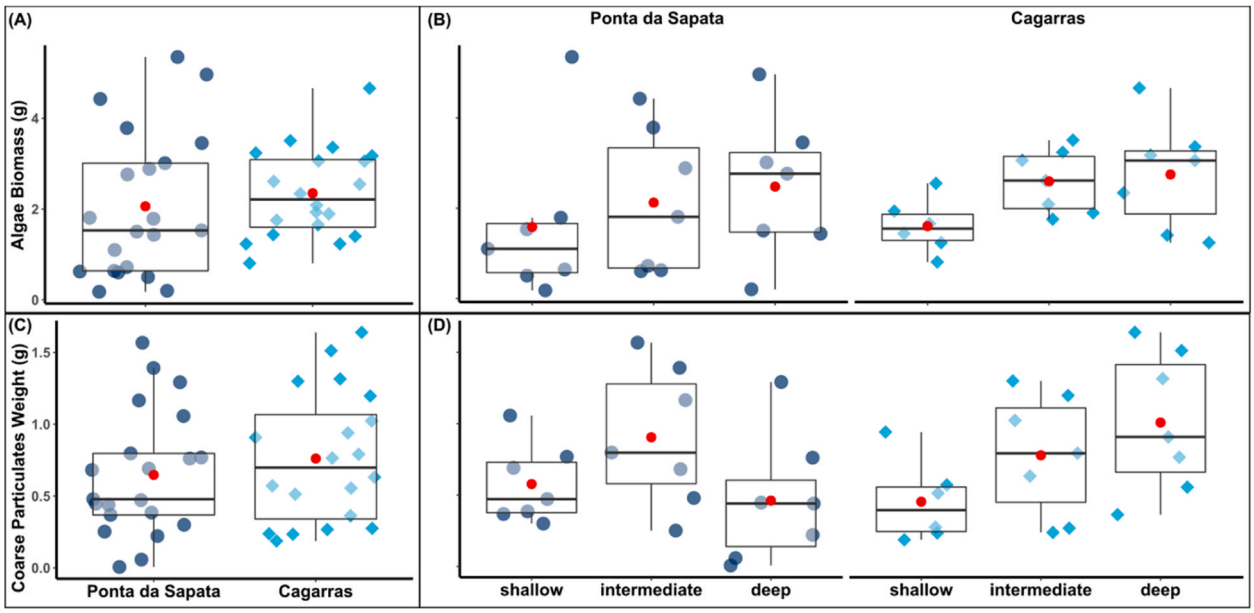

Fig. 2. Comparisons of epilithic algal matrix characteristics between sites (A and C) and depths (B and D) in rocky reefs of Fernando de Noronha island, Brazil. First row represents graphs for algae biomass and the second row for trapped coarse particulates. Circles and diamonds represent each replicate, red circles represent the mean value, and significant p-values are shown in the graphs. p-values correspond to Linear Models (LM) results. Depth categories stand for shallow (5 m); intermediate (10 m); deep (15 m).

abundance levels (Fig. 3). Total cryptofauna abundance was positively correlated with coarse particulates (LM, $p = 0.003$), but only marginally correlated with algae biomass (Fig. 4).

Total cryptofauna biomass was similar between sites (LM, $p = 0.2$). Fauna biomass did not differ between depths (LM, $p = 0.3$). Despite not differing significantly between depths, in Ponta da Sapata cryptofauna biomass decreased with depth, exhibiting higher values in the shallow (mean $\pm$ SE $= 0.96 \pm 0.72$ g) and declining in the intermediate-deep depths (0.17 g ± 0.27 g and 0.32 g ± 0.31 g, respectively). Conversely, in Cagarras, biomass followed the opposite trend, increasing with depth. The lowest biomass values were recorded in the shallow stratum of Cagarras (0.12 g ± 0.13 g), while it increased with depth (intermediate $= 0.26$ g ± 0.3 and deep $= 0.29$ g ± 0.45 g) (Fig. 5). Cryptofauna biomass did not show any significant relationship with algae biomass or coarse particulates.

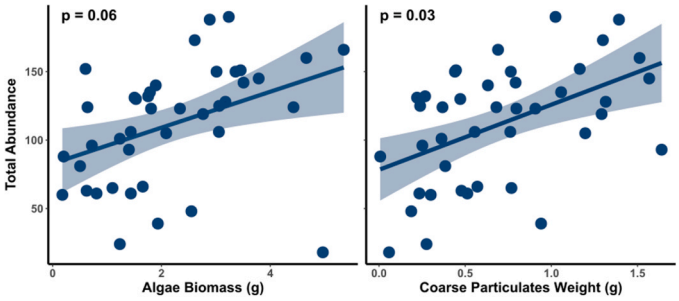

Fig. 4. Total cryptofauna abundance and epilithic algal matrix characteristics (algae biomass and coarse particulates) correlations in rocky reefs of Fernando de Noronha island, Brazil. Significant p-values are shown in bold text in the graphs, corresponding to LM results.

3.2.1. *Foraminifera Assemblage*

Foraminiferans were mainly represented by Order Miliolida 1, a Large Benthic Foraminifera (LBF), which accounted for 43% and 35% of foraminiferans in Ponta da Sapata and Cagarras, respectively. Foraminifera assemblages differed between sites (PERMANOVA, $p = 0.005$, $R2 = 0.007$), with a larger contribution of Order Miliolida 1 and low-abundance OTUs in Ponta da Sapata, and a higher contribution of Order Rotaliida 1, Order Miliolida 2, Order Rotaliida 3, and Foraminifera 10 in Cagarras.

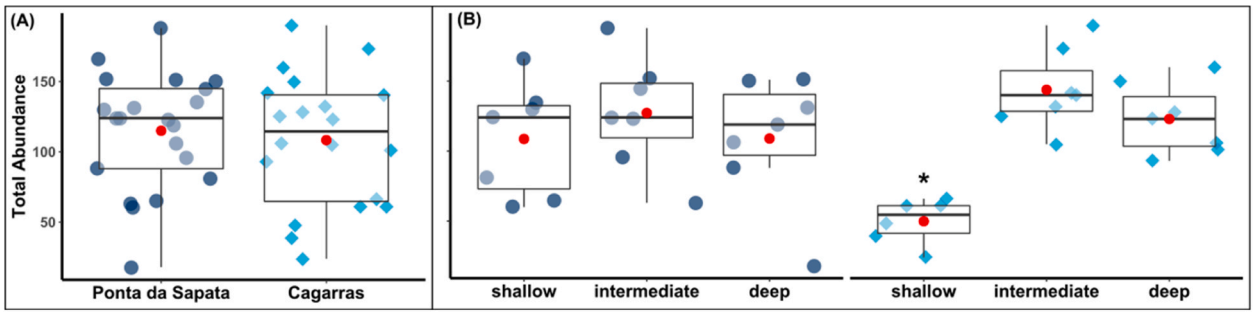

Fig. 3. Comparison of total epilithic algal matrix cryptofauna abundance between sites (A), and site and depths (B) in rocky reefs of Fernando de Noronha island, Brazil. Blue circles and diamonds = sample values, red circles = mean value, black bar = median, box = 1st/3rd quartiles, and whiskers = 1.5 * interquartile range. Statistical differences are shown with an asterisk in the graphs, corresponding to LM results. Depth categories stand for shallow (5 m); intermediate (10 m); deep (15 m).

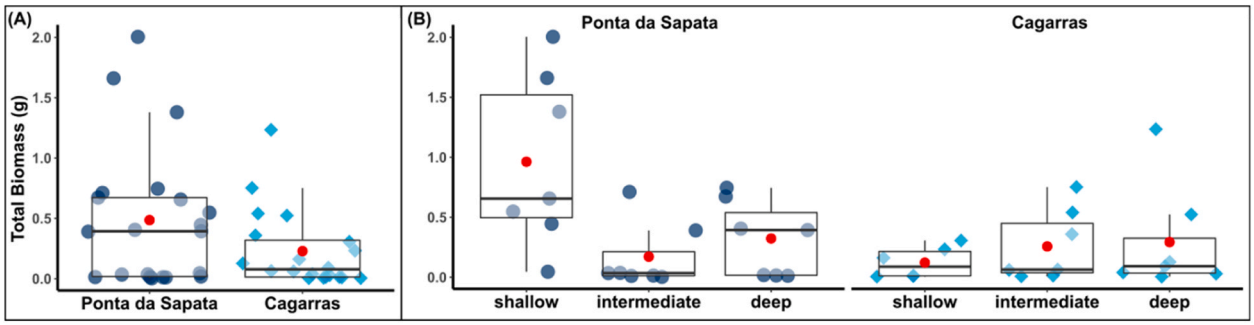

Fig. 5. Comparison of total epilithic algal matrix cryptofauna biomass between sites (A), and site and depths (B) in rocky reefs of Fernando de Noronha island, Brazil. Circles represent sample values, red circles represent the mean value and significant p-values are shown in the graphs. p-values correspond to LM results. Depth categories stand for shallow (5 m); intermediate (10 m); deep (15 m).

The abundance of Foraminifera differed between depths, with the lowest values in the shallow depth in both sites (Ponta da Sapata: 43,8 ± 14.9; Cagarras: 28.8 ± 12), and highest in the intermediate depth of Ponta da Sapata (75,1 ± 24,2) and deep of Cagarras (83,7 ± 24,2). Foraminifera abundance was positively related to both algae biomass (LM, p = 0.008; Fig. 6) and coarse particulates (LM, p = 0.008; Fig. 6).

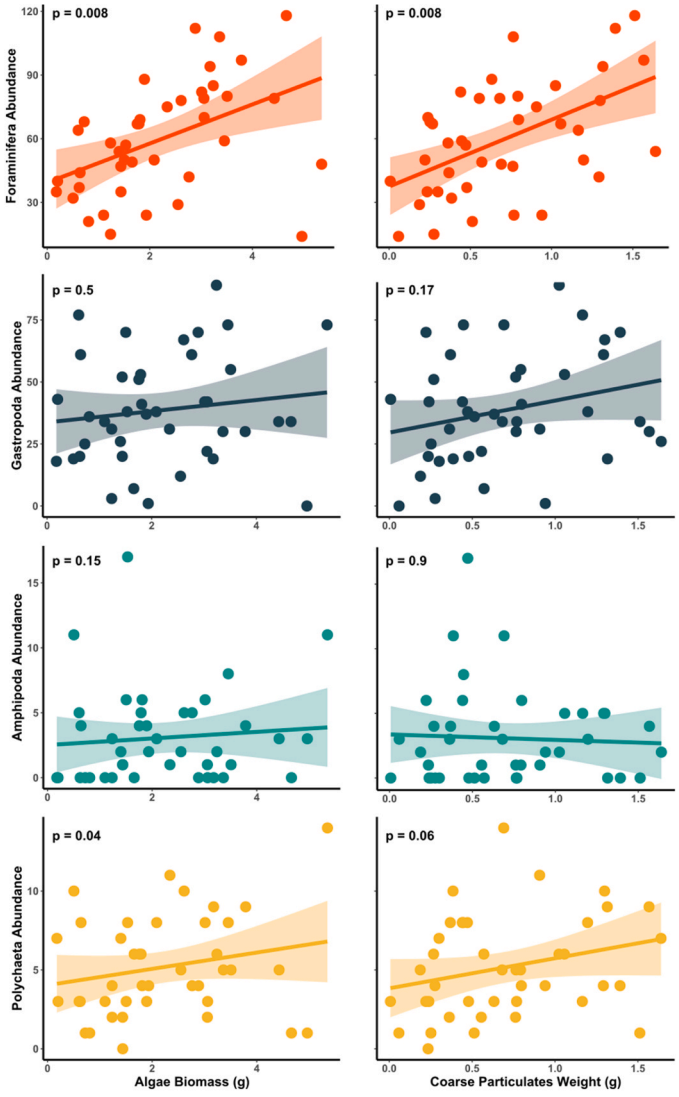

Fig. 6. Cryptofaunal most abundant taxa abundance and epilithic algal matrix characteristics (algae biomass and coarse particulates) correlations in rocky reefs of Fernando de Noronha island, Brazil. Statistical p-values are shown in bold text in the graphs, corresponding to LM results.

3.2.2. *Gastropoda Assemblage*

The molluscan assemblage was predominantly composed of gastropods (97% of all mollusks) but also included Bivalvia and Polyplacophora (*Acanthochitona* sp., *Ischnochiton* sp., Polyplacophora 1, and Polyplacophora 2) with four OTUs each. Gastropod assemblages were dominated by the detritivorous micromollusk *Barleeia rubrooperculata* on both sites, recorded for the first time on Fernando de Noronha Island. Despite this, the assemblages differed between sites (PERMANOVA, p = 0.04, R2 = 0.08), with less dominance of *Barleeia rubrooperculata* in Cagarras (Cagarras n = 651; Sapata n = 934), where we detected a higher contribution of low-abundance OTUs.

Gastropod abundance differed between sites with higher abundance levels in Ponta da Sapata (44.5 ± 21.2), and depths. In Cagarras gastropod abundance was comparatively lower in the shallow and deep depths (shallow: 13,2 ± 13,1; deep: 27,6 ± 5,4), while in Ponta da Sapata abundance values did not vary as much (shallow: 42,3 ± 20,9; intermediate: 42,4 ± 22,3; deep: 48,7 ± 24,7). No correlations occurred between gastropods' abundance and EAM components (biomass and coarse particulates).

3.2.3. *Amphipoda Assemblage*

The crustacean community comprised five taxa (Amphipoda, Tanaidacea, Decapoda, Cumacea, and Ostracoda). Amphipoda was the most abundant taxa, representing 47% (Ponta da Sapata, n = 95) and 58% (Cagarras, n = 31) of all crustaceans. Amphipoda assemblages differed between sites (PERMANOVA, p = 0.007, R2 = 0.11). In Ponta da Sapata, Family Maeridae 2 was the most abundant (n = 51), whereas Amphipoda 4 (n = 11) and Family Maeridae 2 (n = 7) were the most abundant in Cagarras.

Amphipod abundance differed between sites, with higher values in Ponta da Sapata (4,52 ± 4,3), but not between depths (LM, p = 0.47). The higher values seen in Ponta da Sapata are driven by the shallow depth (6,9 ± 6,4) which presented the highest values of all depths across both sites. No correlations occurred between amphipod's abundance and EAM components (biomass and coarse particulates).

3.2.4. *Polychaeta Assemblage*

Polychaeta was the fourth most abundant group and was composed of 8 OTUs, of which morphotype 5 (Polychaeta sp. 1) was the most abundant one. Poliquets' abundance was overall similar between sites and depths, although the shallow depth of Ponta da Sapata was statistically different (LM, p = 0.02). Poliquets showed positive correlations to both algae biomass and coarse particulates (Fig. 6).

4. Discussion

Our study is the first to analyze the community structure and main

drivers influencing patterns of composition and abundance of the cryptofauna in the epilithic algal matrix (EAM) of the Southwestern Atlantic reefs. We found that the abundance and composition of the cryptofauna inhabiting the EAM were, as expected, shaped by the algae characteristics. These short-thali algae, mainly composed of filamentous and articulated calcareous algae, are as influential as the erect macroalgae over associated phytal invertebrate communities (Lalonde and Downing, 1992; Becerra-Muñoz and Schramm, 2006; Berthelsen et al., 2015; Kramer et al., 2012). The significant impact of the algal habitat on the associated invertebrate communities is unsurprising, given the well-established correlation between habitat structure and assemblage characteristics, as previously highlighted in studies (Hacker and Steneck, 1990; Chemello and Milazzo, 2002; Fraser et al., 2020a; Fraser et al., 2020b). Total abundance and cryptofauna composition were influenced by EAM characteristics, but cryptofauna biomass, richness, and diversity were not. Multiple studies dealing with the phytal fauna on frondose macroalgae have shown a positive relationship between algae structure and epifaunal assemblages in different habitats and biogeographical Provinces (Lalonde and Downing, 1992; Becerra-Muñoz and Schramm, 2006; Tararam, 1977). These studies clearly showed that algae characteristics (biomass, shape, branching, size) influenced the abundance, biomass, diversity, and composition of the associated fauna (Lalonde and Downing, 1992; Barbosa et al., 2019; Leite et al., 2021).

The complexity generated by phytal habitats can minimize predation, decrease hydrodynamic impact, and function as a trap for larvae and eggs (Dean and Connell, 1987; Hacker and Steneck, 1990). In the Brazilian Province, the EAM represents 70% of the benthic cover (Aued et al., 2018), suggesting that the associated cryptofauna may be a critical trophic component. Despite that, only a few studies have assessed the cryptofauna in Brazilian reef systems (Ferreira et al., 1998; Cassamali, 2020). Comparisons between associated fauna of frondose macroalgae and EAM are also rare, which stresses the importance of reinforcing initiatives to understand cryptofauna dynamics. For instance, in the Baltic Sea, the biomass and richness of the cryptofauna differed between substrates but with similar biomass and abundance in turf and canopy algae (Kraufvelin and Salovius, 2004; Wikström and Kautsky, 2007). Figueiredo et al. (2020) found differences in assemblages associated with canopy and turf algae, with composition changes related to algae biomass and seasonality on the southwestern Brazilian coast (São Paulo state). Here, we showed a static pattern of the community not including temporal variations because of the high costs associated with multiple campaigns to this oceanic island. Though we restricted our generalizations to a snapshot, we managed to describe the local spatial variability of cryptofauna composition and added insights to the still hazy global panorama of EAM-associated fauna.

The significance of microhabitat in shaping the structure and composition of associated fauna, as previously noted (Stella et al., 2010; Chemello and Milazzo, 2002), is unsurprising. Microhabitat structure can even outweigh the influence of environmental factors on the composition of cryptofauna across broad-scale latitudinal gradients (Fraser et al., 2020a; Fraser et al., 2020b). However, we demonstrate here that although microhabitat plays a pivotal role in influencing its associated communities, other factors also influence the composition and abundance of fauna. Depth influenced the abundance and composition of the cryptofauna, as well as the abundance of the most prevalent taxa (Foraminifera and Gastropoda), without any correlation with microhabitat characteristics, such as algae biomass and the amount of coarse particulates, which remained consistent across the depth range. In a study by Wolfe et al. (2023) on coral rubble at Heron Island (Southern Great Barrier Reef), it was found that environmental parameters (depth and exposure) influenced microhabitat complexity, thus affecting the motile cryptofauna communities. At the microhabitat scale, complexity influenced the structure, diversity, and size spectra of motile cryptofauna. Even though our study did not reveal a clear association between environmental variables (site and depth) and EAM characteristics (algae biomass and amount of coarse particulates), these drivers could potentially be influencing other algal characteristics related to complexity (e.g. branching degree, composition) that in turn affect the cryptofauna. This suggests that further studies addressing additional algal characteristics, as well as other drivers (e.g. predation pressure, sedimentation), are necessary for a comprehensive understanding of the complexity of these cryptic communities.

Cryptofauna communities of Fernando de Noronha reefs were composed of a few abundant taxa and several low-abundance OTUs (e.g., singletons and doubletons), following a typical pattern reported for reef cryptic communities (Kramer et al., 2012; Head et al., 2018; Renema, 2006; Head et al., 2018), as well as for the phytal fauna in the Brazilian coast for multiple habitats (Tararam, 1977; Tanaka and Leite, 2003; Leite et al., 2021). The large proportion of low-abundance species may be an important characteristic of the system as rare species may support the most distinct trait combinations, perhaps having critical contributions to ecosystem functioning (Mouillot et al., 2013; Head et al., 2018; Bracken and Low, 2012). However, a clear understanding of the functions of cryptic communities is still obscure, as studies lack standardized information and continue to use broad traits that do not have a clear function associated with them (de Juan et al., 2022; Streit and Bellwood, 2022).

Species identification is the main obstacle for scientists working with multispecific and diverse invertebrate communities (Hochkirch et al., 2020), as in those found in EAM. Most cryptic invertebrates are difficult to identify at the species level (Klumpp and Polunin, 1989), and the use of OTUs that address organisms based on their phenotype may be a workable solution to this shortcoming. Similar to the results of Berthelsen et al. (2015) for temperate northeastern New Zealand, our results showed considerable changes in community properties when using different taxonomic resolutions (OTUs and phylum/subphylum, in this study). However, the use of low taxonomic resolution in cryptofauna studies may hinder the understanding of ecological drivers in these communities. The use of approaches that consider the "devil in the details" (e.g. taxonomy experts, genetic analyses) is needed to understand the importance of cryptic invertebrates to reef ecosystems (Longenecker, 2007), but there is a tradeoff between those approaches. As for several cryptobenthic invertebrates, there is a clear lack of specialists for many taxonomic groups, which can hinder more refined analysis and conservation efforts (Oliveira et al., 2020). EAM is an undervalued but highly important ecological component of consolidated marine environments (Tebbett et al., 2023a), thus simple methods would help to advance research in this field.

The most abundant group of the cryptofauna from Fernando de Noronha was the Foraminifera. Benthic foraminifera, especially Large Benthic Foraminifera (LBF), are cosmopolitan in marine environments and often associated with macrophytes (BouDagher-Fadel, 2008; Holbourn et al., 2013). These organisms are especially abundant in oceanic environments (oceanic islands, reefs, and atolls), living also in association with turf algae (Baker et al., 2009; Kramer et al., 2012; Dawson et al., 2014). The abundance of foraminifera was also positively correlated with algae biomass, coarse particulates, and depth, indicating that they may respond to habitat availability. LBFs have complex tests and may harbor microalgae as symbionts, which provide more energy than heterotrophic feeding (BouDagher-Fadel, 2008). These organisms use the fronds of macroalgae or stems and leaves of seagrass to regulate the amount of sunlight they receive to prevent harm and escape of the symbionts (BouDagher-Fadel, 2008; Renema et al., 2001). This adaptive advantage of symbiosis may facilitate the dominance of LBFs in the Fernando de Noronha EAM. In islands with low coral reef cover, biogenic activities (e.g., bioerosion, foraminifera's tests, shells, and calcareous algae) constitute an important source of sediment production (Dawson et al., 2012). Fernando de Noronha shelf is composed of bioclastic calcareous sediment ($CaCO3 \approx 88.3\%$), with large contributions from foraminifera's tests (Barcellos et al., 2018). Because of the abundance of foraminifera in the EAM, we can suggest that EAM may also represent an important role in Fernando de Noronha sedimentary

dynamics.

The most diverse and second most abundant group in the EAM was Mollusca, with dominance of gastropods. Mollusks are the most conspicuous organisms in phytal ecosystems, especially micro gastropods which live in the interstitial spaces created by the algae (Dame, 2016; Barbosa et al., 2019). The taxonomic richness of gastropods in Fernando de Noronha (48 OTUs) is comparable to those found for frondose macroalgae in both tropical (Barbosa et al., 2019; Queiroz and Dias, 2014) and subtropical (Leite et al., 2009; Zamprogno et al., 2013) Brazilian coast. This highlights the importance of cryptofauna in multiple phytal environments and the equivalent richness between short-thalli and frondose algae. Mollusks' abundance was not correlated to EAM components. Yet, a positive trend exists, even though non-signifficant, between gastropods and coarse particulates. This trend might happen due to the dominance of *Barleeia rubrooperculata*, a detritivorous species that may feed on the detritus-rich coarse particulates (Castellanos & Fernández, 1972). Furthermore, this was the first record of *B. rubrooperculata* on Fernando de Noronha island, previously recorded in Argentina, Uruguay, and along the Brazilian coast, but not in the oceanic islands (Amorim, 2018; Ponder and Worsfold, 1994; Benkendorfer and Soares-Gomes, 2009; Barroso et al., 2016).

The cryptofauna is composed of organisms from both meio- and macrofauna, ranging in size from 0.04 mm to a few centimeters. Around the globe, harpacticoid copepods are the major constituent of this fauna and are predominantly associated with an important nutritional role as prey for reef fishes (Sarmento and Santos, 2012; Kramer et al., 2012; Kramer et al., 2013; Fraser et al., 2021). The meiofaunal component of the cryptofauna was not considered in this study due to difficulties in sampling and identification of these small specimens. Yet, studies remark that the macrofaunal component of the cryptofauna does not come as unimportant (Ochoa-Rivera et al., 2000; Wolfe et al., 2020; Head et al., 2018), with macro-crustaceans, mollusks, and poliquets playing significant roles as a nutritional source for fishes and invertebrates (Kohn and Nybakken, 1975; Peyrot-Clausade, 1980), grazing on macroalgae (Klumpp et al., 1988; Altman-Kurosaki et al., 2018), and recycling nutrients (Wolfe et al., 2020; Campos-Vázquez et al., 2015).

Phytal ecosystems are the major contributors to reef primary production, with their small mobile invertebrates playing a crucial secondary production role in reef trophic webs (Gibbons and Griffiths, 1986; Taylor, 1998; Fraser et al., 2021). The EAM, being a dominant substrate in marine reef ecosystems (Tebbett et al., 2023b; Aued et al., 2018), supports key functions including high primary production, nitrogen fixation, and energy sourcing (McCook, 1999; Russ, 2003; Fong and Paul, 2011). The algae, detritus, and associated cryptofauna from EAM are a food resource for many reef fishes, sustaining many food webs in reefs (Kramer et al., 2013; Mendes et al., 2018; Wilson et al., 2003). Crustaceans, in particular, which were the third most abundant group in Fernando de Noronha, are an important trophic link, connecting the basis of the food chain and higher trophic levels (Kramer et al., 2013). Therefore, as most of the substrate coverage in Brazilian tropical and subtropical, coastal and oceanic reefs is dominated by EAM (Aued et al., 2018), while invertivorous fish represent the bulk of total fish biomass (Morais et al., 2017), understanding the dynamics and structure of the cryptofauna should be a priority.

In conclusion, we have demonstrated that the EAM-associated cryptofauna can exhibit diversity comparable to that of canopy algae, with large importance as a habitat and biodiversity reservoir of invertebrate communities. Specifically, foraminiferans were notably influenced by algae biomass, particularly the Large Benthic Foraminifera which dominated and are typically associated with macrophytes. Among mollusks, a single species, *Barleeia rubrooperculata*, a detritivorous micro mollusk, was dominant, first recorded in Fernando de Noronha during this study. Both depth and algal characteristics (algae biomass and amount of coarse particulates) influenced the abundance and composition of the cryptofauna, as well as the prevalence of the most abundant taxa (Foraminifera and Gastropoda). Further taxonomic refinement and the incorporation of additional drivers and algal characteristics are the next steps for EAM cryptofauna studies, along with approaches that provide a functional perspective on this fauna. The cryptofauna's crucial trophic role underscores the necessity for further investigation into abundance and biomass patterns, in order to develop comprehensive and more robust trophic model for reef systems.

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CRediT authorship contribution statement

CELF and GS conceived the ideas. G.S. performed laboratory procedures, data analysis, graphic designs, and writing. C.E.L.F. performed sampling and text review. C.A.M.M.C. text and analysis review.

Declaration of Competing Interest

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

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2023.103292.

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