



## The nocturnal zonation of decapods in the subtidal zone within the reef seascape—abiotic factors defining habitats

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The relationship between populations of marine organisms and physicochemical gradients directly influence distributions of species within associated seascapes. This study examines the impact that exposure to sunlight and substrate type has on the distribution of decapods in a tropical coastal reef environment. The study was performed at night when the species are at their most active using a visual census methodology to observe the natural nocturnal behaviour. The research revealed the existence of three distinct habitats housing specific decapod assemblages within tropical hard substrate environments; the External-Reef habitat which accommodates colonial benthic host decapods; the Crevicular-Reef habitat which accommodates the reef-stygofauna; and the Interface habitat between the reef and soft substrate which is inhabited by transient decapod species. The findings extend the previous zonation patterns for decapods to the subtidal zone using physical parameters as the rationale defining allocation. The study collated and reviewed documented taxonomic and ecological evidence which supports this division of decapods into similar reef seascapes worldwide. It further proposes that this format of subtidal zonation may be applicable on a global scale to species which inhabit a comparable ecological niche within tropical zones.

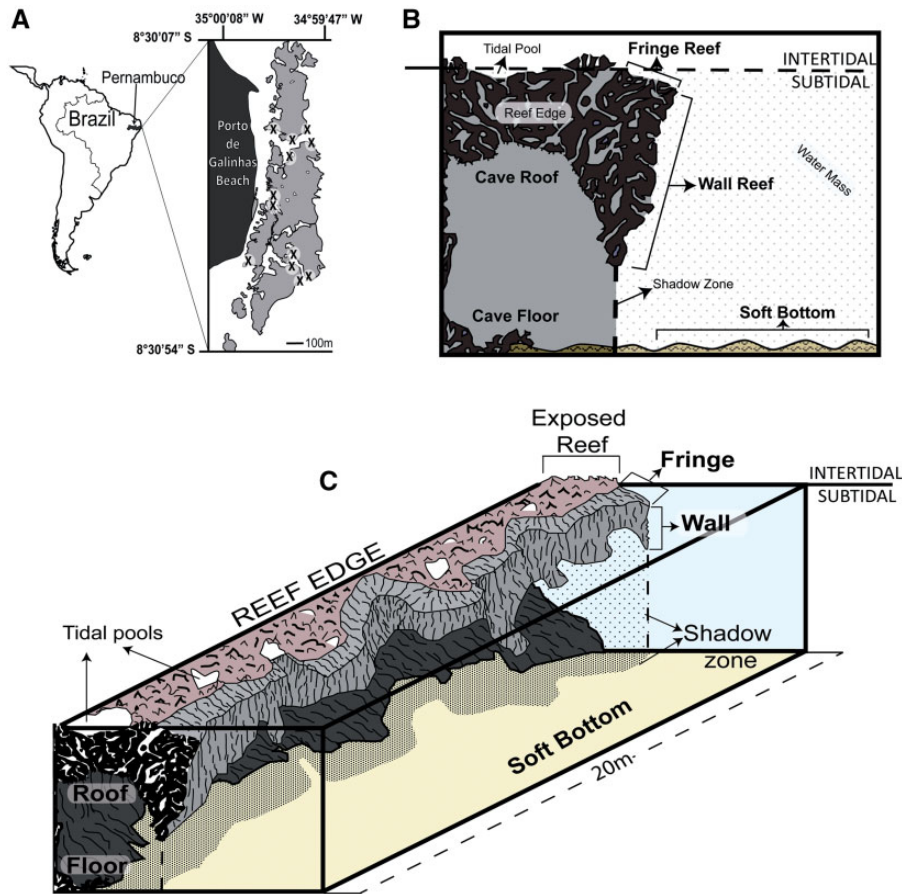
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### Introduction

Decapod species are integral taxa within marine ecosystems and account for some of the richest species diversity in the benthos (Abele, 1974; Williams, 1984; Coelho *et al.*, 2006, 2007, 2008; Ng *et al.*, 2008; Dubinsky and Stambler, 2011). They occupy essential roles in different trophic chains within marine seascapes. In some niches, they are top predators, while in others, they represent major prey items for fish and other animals (Randall and Bishop, 1967; Boudreau and Worm, 2012). They contribute a high proportion of crucial herbivorous species within reef systems (Coen, 1988; Wilber and Wilber, 1989; Rhyne *et al.*, 2005). In addition, due to their ecological importance as omnivorous and detritivore

species, they are recognized as the cleaning crew of the marine environment, an essential component in the maintenance of coral and fish health (Gleibs *et al.*, 1995; Stewart *et al.*, 2006; McCammon *et al.*, 2010; Stier *et al.*, 2010). The distribution of decapod species is generally restricted to a specific ecosystem, substrate, shore zone or depth, with several decapods also closely related to other benthic species (Abele and Patton, 1976; Williams, 1984; Melo, 1996, 1999; Wirtz *et al.*, 2009).

The presence or absence of benthic species in a particular habitual niche can be influenced by several factors such as inter- and intra-population densities, predation pressure and the environmental physicochemical gradient of the region. Variability of



**Figure 1.** (A) Highlights the position of fixed sample sites on the reef area at Porto de Galinhas beach, state of Pernambuco, northeastern Brazil. (B) Schematic profile for benthic area on the reef edge of the coastal reefs, with the division of five sample habitats - Fringe, Wall, Cave Roof, Cave Floor and Soft Bottom. (C) Schematic profile in three dimension illustrating the sample area at a fixed sample site.

environmental conditions in a particular region or benthic parameter can determine the degree of species diversity and richness; e.g. temperature, within a variety of ecosystems; salinity, influencing distinctive mangrove and coral reef communities; tidal cycles, associated with specific assemblages within each tidal level on a shore zone; substrate type, restricting taxa to a hard or soft substratum; and light incidence, influencing the density of photosynthesizer's in areas where the sunlight penetrates (Abele, 1974; Abele and Patton, 1976; Hart *et al.*, 1985; Alongi, 1990; Bellwood, 2002; Micael *et al.*, 2006; Coelho *et al.*, 2006; Almeida and Coelho, 2008; Huang *et al.*, 2011; Giraldes *et al.*, 2012a, 2015a; Levinton *et al.*, 2015).

In order to understand the factors that drive decapod zonation in the subtidal zones, this study investigated the influence of exposure to sunlight and substrate type over their distribution in a tropical coastal reef seascape. It was carried out at night when the decapods were most active and nocturnal behaviour could be observed.

## Material and methods

### Study site

The study area was located on a biogenic tropical reef bench at Porto de Galinhas beach, on the southern coast of Pernambuco state, northeastern Brazil (8°30'07"–8°30'54" S and 35°00'08"–34°59'47" W)

(Figure 1a). The coral reef formations within this ecosystem consisted of patchy coral growth, forming elongated reef banks with characteristic seascape features. The banks continued to the shoreline, making up part of the lower intertidal. The reef formations grew on sandstone ridges which lay parallel to the shore, forming densely aggregated sub-surface structures with interconnected cave systems, rarely exceeding depths in excess of 10 m (Dominguez *et al.*, 1990; Leão *et al.*, 2003). The area of studied reef belongs to a large coral ecosystem within one of the most extensive coral formations in the entire southwestern Atlantic Ocean and is considered to be one of the most species rich areas in the region (Leão *et al.*, 2003, 2016); it is a tropical reef system which presents one of the highest diversities of decapods specific to the coral reef environment (Melo, 1996, 1999, Coelho *et al.*, 2002, 2006, 2007, 2008). This biogenic tropical reef at Porto de Galinhas represents the perfect model for decapods associated with this unique tropical coastal system (Coelho *et al.*, 2002; Giraldes *et al.*, 2015a).

Sample sites were located along the main subtidal benthic domain of the reef edge and were studied during the low tide. The reef edges were schematically divided based on abiotic factors. The first division was based on substrate type, and included hard substrate (reef) and a soft bottom habitat, which surround the reef structures (Figure 1b). The second division was in relation to sunlight incidence and the reef was divided according to the external reef habitat exposed to sunlight and the cavernous reef habitat sheltered from sunlight. The external reef habitat was

further divided into Fringe and Wall in relation to the angle of inclination relative to sunlight incidence. The cavernous reef habitat was divided into Cave Roof and Cave Floor (Figure 1b).

The reef edges at the sites were further divided into five subtidal habitats (Figure 1b): (i) Fringe—hard substrate with intense sunlight incidence; (ii) Wall—vertical hard substrate with lesser sunlight incidence but exposed to the tidal currents; (iii) Cave Roof—the true cave, a dark habitat with a hard substrate; (iv) Cave Floor—dark habitat limited by the shadow zone, which sometimes invades the soft substrate; (v) Soft Bottom—the soft substrate which surrounds the reefs, with occasional small reef fragments such as dead corals.

### Data sampling

Scuba diving surveys were undertaken monthly from June 2004 to May 2005 on low spring tides on a full moon at night. All dives occurred after sunset during nocturnal hours at lowest chart datum water level, forecasted as per national tide tables. Surveys started 90 min before low water and ended 90 min after. All dives took place during a full moon cycle when tides were lowest allowing for a total of approximately two dives per night with three to four transects. Ecological data regarding decapod distribution was collected using Underwater Visual Census (UVC) surveys with a fixed Strip Transect Technique specifically adapted for decapods. This methodology required a 20 m transect to be fixed to the reef edge (schematic sample area in Figure 1c). Surveys were carried out at night using the light of the full moon to locate survey sites. In an attempt to avoid disturbing specimens prior to sampling, low light intensity dive lights were only turned on once the diver was in position and ready to begin the survey. When scanning the substrate for decapods, the light beam was moved using the “U search” technique. Twelve monthly transects (UVC repetitions) were conducted at all 12 sample sites, totalling 144 transects for this study.

During the nocturnal visual censuses, 30 target decapods were observed (Table 1). These same species were previously, photographed, collected, identified in laboratory and reported in Giraldes *et al.* (2015a) and therefore acknowledged as the main decapod species which could be visually identified underwater (subtidal zone) at the survey site. A local taxonomist from Giraldes *et al.* (2015a) specializing in decapods identified species *in situ* underwater. The related site and position of each species was recorded by the diver on underwater diving slates. Specimen locations were allocated to zones based on the schematic habitat format previously described.

### Analysis

The following ecological indexes were used to determine the main habitat for each species and understand the proportion of species associated with a specific habitat. Abundance—average number of individuals in each habitat for transect ( $A = n/T$ ) where  $n$  is the number of individuals observed in each habitat and  $T$  is the number of transect per habitat. Frequency of occurrence (%)—Percentage of occurrence of a certain species in relation to total number, calculated by  $Fa = (Pa \times 100)/P$ , where  $Fa$ , frequency of occurrence for a species;  $Pa$ , number of transects where the species was present; and  $P$ , total number of samples (transects) performed. Based on the frequency values, species were considered to be Rare ( $Fa < 10\%$ ), Occasional ( $10\% \leq Fa < 25\%$ ), Common ( $25\% \leq Fa < 50\%$ ), Very Common ( $50\% \leq Fa \leq 75\%$ ) or

Constant ( $Fa > 75\%$ ). Dominance was considered to be the relationship between the number of individuals of a given species and the number of individuals of all species found at each sampling habitat was calculated by the formula;  $Da = (Na \times 100)/Nt$ , where  $Da$ , Dominance of the species;  $Na$ , Number of individuals of the species; and  $Nt$ , Number of individuals of all species. Based on the dominance values, species were considered, Dominant ( $Da > 50\%$ ), Very Representative ( $10\% \leq Da < 50\%$ ) Representative ( $1\% \leq Da < 10\%$ ) and Inexpressive ( $Da < 1\%$ ).

Multivariate analysis was employed to understand the similarities and dissimilarities between decapod species assemblage and schematic habitat niche. The abundance data of the most prevalent species was used with the less frequent species excluded (<10 individuals); a Bray-Curtis similarity matrix transformed ( $\log-1$ ) to perform cluster analysis, which was ordinated with non-Metric Multidimensional Scaling (nMDS). A dendrogram grouping of the main species according to habitat was then carried out. Using the same data, a bifactorial analysis of similarity evaluating the differences among the habitats, where  $R$ -values  $> 0.5$  and a significance  $< 5\%$  were considered statistically significant. The Similarity Percentages (SIMPER) analysis was then used to identify the main components at each habitat, aiming to compare the main habitat for each species with the results at ecological indexes. After observing the grouping of species per habitat, ecological indexes of abundance and diversity (Shannon-Wiener) were used to compare the external, crevicular, and soft bottom habitats. To evaluate the differences between the populations at each habitat, a “Student T test” with 95% CI and a significance level of 5% ( $p < 0.05$ ) was employed. All multivariate ecological calculations were carried out using Primer v6 software (Clarke and Gorley, 2006); Box-plots, ecological and statistical analysis were performed using the PAST statistical software package. Ecological index was based on Odum and Barrett (2007) (Figure 2).

### Results

Decapod species were absent in 9% of total transects in the Fringe; 14.6% in Wall; 2.7% in the Cave Roof; 27.1% in the Cave Floor; and in 34% of the Soft Bottom. With a richness average of 2.15 species per transect in the Fringe; 1.8 in the Wall; 2.5 in Cave Roof; 1.3 in the Cave Floor; and 1.2 in the Soft Bottom. The abundance per habitat was 1472 specimens in the Fringe with average of 10.2 specimens per transect; 882 in the Wall with average of 6.1 specimens; 3034 in the Cave Roof with average of 21.1 specimens; 548 in the Cave Floor with average of 4.1 specimens; and a total of 314 in the Soft Bottom with average of 2.2. The frequency, abundance and dominance of each species in relation to the sampled habitats are presented in Table 1. Each species displayed one or two main habitat preferences, which were identified by higher abundance or frequency, highlighting the preferred, and secondary habitat for each species. The proportion of each Infraorder according to habitat is presented in Figure 3, where brachyuran crabs dominate the Fringe and Wall and Caridean and Achelata dominate the Cave Roof and Cave Floor habitats, thus demonstrating the similarity within infraorder by a coalescing presence at the Fringe + Wall and Cave Roof + Cave Floor.

The SIMPER analysis (Table 2) identified the most representative species in relation to habitat and confirmed for the majority of species, the ecological index of dominance and frequency as presented in Table 1. Two species *Cinetorhynchus rigens* and *Panulirus echinatus* were among the most representative throughout all habitats; *Mithraculus forceps* was the only species recorded

**Table 1.** Target decapods with ecological index data according to the sampled habitats (Fringe Reef, Wall Reef, Cave Roof, Cave Floor, and Soft Bottom).

Species		Fringe	Wall	Cave Roof	Cave Floor	Soft Bottom
<b>Infraorder STENOPODIDEA</b>						
<i>S. hispidus</i> (Olivier, 1811)	A	<0,1	0,1	0,1	<0,1	<b>0,2</b>
	F	Ra	Ra	Ra	Ra	<b>Ra</b>
	D	Ine	Rep	Rep	Rep	<b>Rep</b>
<b>Infraorder CARIDEA</b>						
<i>C. rigens</i> (Gordon, 1936)	A	1,4	2,1	<b>14,5</b>	2,7	0,9
	F	VC	VC	<b>CT</b>	VC	CO
	D	VRe	VRe	<b>Dom</b>	Dom	VRe
<i>Brachycarpus biunguiculatus</i> (Lucas, 1846)	A	<b>0,1</b>	<0.1	*	*	<0.1
	F	<b>Ra</b>	Ra	*	*	Ra
	D	<b>Ine</b>	Ine	*	*	Rep
<i>Brachycarpus holthuisi</i> (Fausto Filho, 1966)	A	*	*	<b>&lt;0.1</b>	<0.1	*
	F	*	*	<b>Ra</b>	Ra	*
	D	*	*	<b>Ine</b>	Ine	*
<i>J. antiguensis</i> (Chace, 1972)	A	<0.1	<0.1	<b>0,4</b>	0,4	<0.1
	F	Ra	Ra	<b>CO</b>	OC	Ra
	D	Ine	Ine	<b>Rep</b>	Rep	Rep
<b>Infraorder ASTACIDEA</b>						
<i>Enoplometopus antillensis</i> (Lütken, 1865)	A	*	*	*	<b>&lt;0.1</b>	<0.1
	F	*	*	*	<b>Ra</b>	Ra
	D	*	*	*	<b>Rep</b>	Ine
<b>Infraorder ACHELATA</b>						
<i>P. gundlachi</i> (von Martens, 1878 )	A	<0.1	<0.1	<b>0,1</b>	<0.1	*
	F	Ra	Ra	<b>OC</b>	Ra	*
	D	Ine	Ine	<b>Rep</b>	Ine	*
<i>Panulirus meripurpuratus</i> (Giraldes and Smyth, 2016)	A	<0.1	*	<0.1	<b>0,1</b>	<0.1
	F	Ra	*	Ra	<b>Ra</b>	Ra
	D	Ine	*	Ine	<b>Rep</b>	Rep
<i>P. echinatus</i> (Smith, 1869)	A	0,5	0,6	<b>5,6</b>	0,7	0,6
	F	CO	CO	<b>CT</b>	CO	CO
	D	Rep	Rep	<b>VRe</b>	VRe	VRe
<i>Panulirus laevicauda</i> (Latreille, 1817)	A	*	*	<0.1	*	<b>&lt;0.1</b>
	F	*	*	Ra	*	<b>Ra</b>
	D	*	*	Ine	*	<b>Rep</b>
<i>P. antarcticus</i> (Lund, 1793)	A	<b>0,1</b>	<0.1	<b>0,1</b>	*	<0.1
	F	<b>Ra</b>	Ra	<b>Ra</b>	*	Ra
	D	<b>Ine</b>	Ine	<b>Ine</b>	*	Ine
<b>Infraorder ANOMURA</b>						
<i>C. tibicen</i> (Herbst, 1791)	A	<0.1	<b>0,1</b>	<0.1	<0.1	<0.1
	F	Ra	<b>Ra</b>	Ra	Ra	Ra
	D	Ine	<b>Rep</b>	Ine	Ine	Rep
<i>Cancellus ornatus</i> (Benedict, 1901)	A	*	*	*	<0.1	<b>&lt;0.1</b>
	F	*	*	*	Ra	<b>Ra</b>
	D	*	*	*	Ine	<b>Rep</b>
<i>Dardanus venosus</i> (H. Milne Edwards, 1848)	A	*	*	*	*	<b>&lt;0.1</b>
	F	*	*	*	*	<b>Ra</b>
	D	*	*	*	*	<b>Ine</b>
<i>Paguristes erythroptus</i> (Holthuis, 1959)	A	*	*	<0.1	*	<b>&lt;0.1</b>
	F	*	*	Ra	*	<b>Ra</b>
	D	*	*	Ine	*	<b>Rep</b>
<i>P. provenzanoi</i> (Forest and de Saint Laurent, 1968)	A	<b>0,2</b>	0,1	*	*	<0.1
	F	<b>Ra</b>	Ra	*	*	Ra
	D	<b>Rep</b>	Rep	*	*	Rep
<b>Infraorder BRACHYURA</b>						
<i>Dromia erythropus</i> (Edwards, 1771)	A	*	<b>&lt;0.1</b>	*	*	*
	F	*	<b>Ra</b>	*	*	*
	D	*	*	*	*	*
<i>Calappa ocellata</i> (Holthuis, 1958)	A	*	*	*	*	<b>&lt;0.1</b>
	F	*	*	*	*	<b>Ra</b>
	D	*	*	*	*	<b>Rep</b>
<i>C. corallinus</i> (Herbst, 1783)	A	*	<b>&lt;0.1</b>	*	*	*

Continued

Table 1. Continued.

Species		Fringe	Wall	Cave Roof	Cave Floor	Soft Bottom
	<b>F</b>	*	<b>Ra</b>	*	*	*
	<b>D</b>	*	<b>Ine</b>	*	*	*
<i>Menippe nodifrons</i> (Stimpson, 1859)	<b>A</b>	<0.1	<0.1	<0.1	<b>&lt;0.1</b>	<0.1
	<b>F</b>	Ra	Ra	Ra	<b>Ra</b>	Ra
	<b>D</b>	Ine	Ine	Ine	<b>Rep</b>	Rep
<i>S. seticornis</i> (Herbst, 1788)	<b>A</b>	<0.1	<b>0,2</b>	<0.1	*	0,1
	<b>F</b>	Ra	<b>Ra</b>	Ra	*	Ra
	<b>D</b>	Ine	<b>Rep</b>	Ine	*	Rep
<i>M. bicornutus</i> (Latreille, 1825)	<b>A</b>	<b>0,5</b>	0,1	*	<0.1	<0.1
	<b>F</b>	<b>Oc</b>	Ra	*	Ra	Ra
	<b>D</b>	<b>Rep</b>	Rep	*	Ine	Ine
<i>M. forceps</i> (A. Milne-Edwards, 1875)	<b>A</b>	<b>6,9</b>	2,4	<0.1	*	0,2
	<b>F</b>	<b>CO</b>	CO	Ra	*	Ra
	<b>D</b>	<b>Dom</b>	VRe	Ine	*	Rep
<i>M. braziliensis</i> (Rathbun, 1892)	<b>A</b>	<b>0,2</b>	0,1	<0.1	*	<0.1
	<b>F</b>	<b>Oc</b>	Ra	Ra	*	Ra
	<b>D</b>	<b>Rep</b>	Rep	Ine	*	Rep
<i>Mithrax hemphilli</i> (Rathbun, 1892)	<b>A</b>	<0.1	<b>0,1</b>	<0.1	*	<0.1
	<b>F</b>	Ra	<b>Ra</b>	Ra	*	Ra
	<b>D</b>	Ine	<b>Rep</b>	Ine	*	Ine
<i>D. hispidus</i> (Herbst, 1790)	<b>A</b>	0,1	<b>0,1</b>	<0.1	*	<0.1
	<b>F</b>	Ra	<b>Ra</b>	Ra	*	Ra
	<b>D</b>	Rep	<b>Rep</b>	Ine	*	Ine
<i>Callinectes marginatus</i> (A. Milne-Edwards, 1861)	<b>A</b>	*	*	*	<0.1	<b>0,1</b>
	<b>F</b>	*	*	*	Ra	<b>Ra</b>
	<b>D</b>	*	*	*	Ine	<b>Rep</b>
<i>Charybdis hellerii</i> (A. Milne-Edwards, 1867)	<b>A</b>	<0.1	*	*	*	<b>0,1</b>
	<b>F</b>	Ra	*	*	*	<b>Ra</b>
	<b>D</b>	Ine	*	*	*	<b>Ine</b>
<i>D. acanthophora</i> (Desbonne, in Desbonne and Schramm, 1867)	<b>A</b>	<0.1	<b>0,1</b>	*	*	*
	<b>F</b>	Ra	<b>Ra</b>	*	*	*
	<b>D</b>	Ine	<b>Rep</b>	*	*	*
<i>Platypodiella spectabilis</i> (Herbst, 1794)	<b>A</b>	<b>&lt;0.1</b>	*	*	*	*
	<b>F</b>	<b>Ra</b>	*	*	*	*
	<b>D</b>	<b>Ine</b>	*	*	*	*

Abundance [A] (average); Frequency [F] being, Constant (CT), Very Common, (VC), Common (Co), Occasional (Oc) and Rare (Ra); and Dominance [D] Dominant (Dom), Very Representative (VRe), Representative (Rep) and Inexpressive (Ine). \*Indicates the absence of the species. Data in bold shows the sites where species were most abundant or frequent.

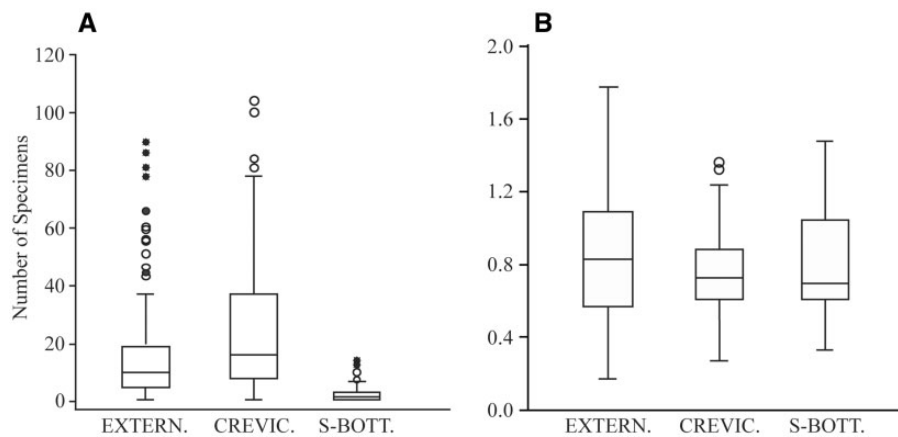
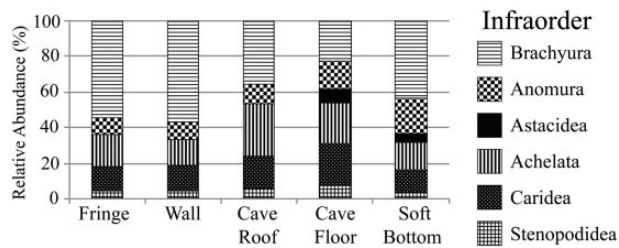


Figure 2. Box plot charts with ecological indexes comparing the external, crevicular and soft bottom habitats: (A) abundance of decapods, (B) diversity of Shannon-Wiener.





**Figure 3.** Proportion of Decapods Infraorder found in the studied reef, according to each sample habitat—Fringe, Wall, Cave Roof, Cave Floor, and Soft Bottom.

in higher densities than *C. rigens* and *P. echinatus* and this was only within the Fringe and part of the Wall habitat. In the external habitats (Fringe and Wall), *M. forceps* and *Mithrax brasiliensis* were among the most representative species; while *Microphrys bicornutus*, *Damithrax hispidus*, and *Pagurus provenzanoi* were present only in the Fringe. *Calcinus tibicen*, *Stenorhynchus seticornis*, and *Stenopus hispidus* were represented only in the Wall habitat. In the cave habitat, *Janicea antiguensis*, *C. rigens*, and *P. echinatus* was among the most abundant in Cave Roof and Cave Floor, while *Palinurellus gundlachi* and *Parribacis antarcticus* were recorded only on the Cave Roof. *S. hispidus* and *S. seticornis* were among the most abundant species on the soft bottom habitat. However, the SIMPER analysis excluded several representative and inexpressive species which were only present in one or two habitats. The habitual niche associated with these species and their ecological indexes are displayed in Table 1. The low abundance of some inexpressive species is representative of their natural proportion (biocenosis) within the studied reef environment.

The nMDS (Figure 4 upper) displays two visibly dominant habitats: one group representing the Fringe and Wall, “the external habitat”; and the other group representing the Cave Floor and Cave Roof from the “crevicular habitat”—terminology from Hart et al. (1985). The grouping of soft bottom samples is orientated closer to the external group, while the remaining samples were closer to the crevicular group. The cluster analysis (Figure 4 lower) presents the main species in three separate groups: A, B, and C. A comparison of the species in the cluster is made with the information in Table 1, a relationship can be seen with species in group A and external habitats (Fringe and Wall). The species in group B occur mainly in the crevicular habitat (Cave Roof and Floor), but also appear in other habitats. The most divergent group C consists of species that were recorded only inside the cave habitat and were never observed foraging in the external habitats (Fringe and Wall). The same data was subjected to different multivariate analysis and as a result, the groups of habitats presented in the nMDS are reflected in the groups within the cluster (Figure 4 upper and lower). The assemblages of species grouped in the cluster (Figure 4 lower) are divided into the external (Fringe and Wall) and crevicular (Cave Roof and Cave Floor) habitats. The pattern observed in Figure 4 was confirmed using an ANOSIM (Table 3) with the main separations identified as being between the External (Fringe and Wall) and Crevicular (Cave Roof and Cave Floor) habitats. No differences were portrayed between the external habitats (Fringe vs. Wall) or between crevicular habitats (Cave Roof vs. Cave Floor). The soft bottom presented similar species composition with almost all habitats differing only within the Fringe.

**Table 2.** SIMPER results presenting the most representative species according to habitats (Fringe, Wall, Cave Roof, Cave Floor, and Soft Bottom).

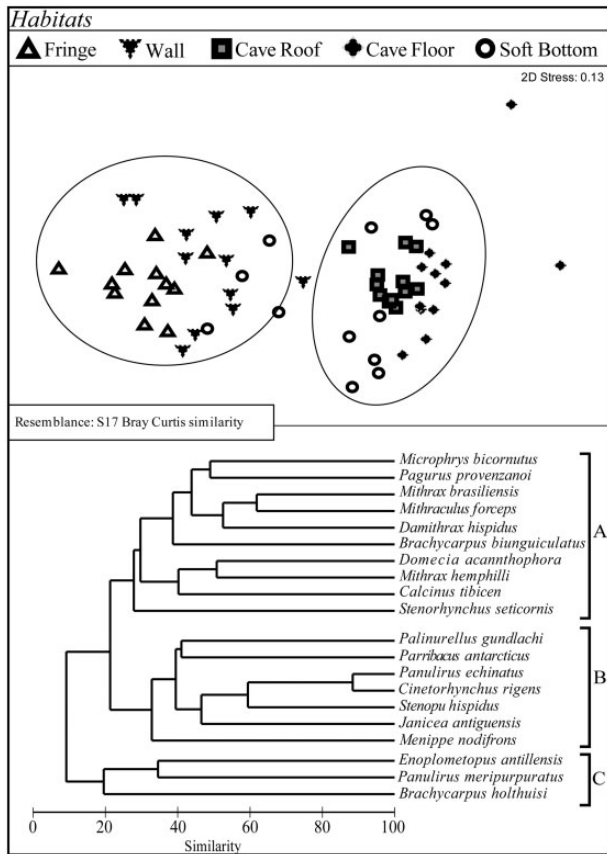
Species	Sim/SD	Contribution %
<b>Fringe</b> —average similarity: 70.68		
<i>M. forceps</i>	10.17	36.11
<i>C. rigens</i>	6.17	22.49
<i>P. echinatus</i>	1.86	11.41
<i>M. bicornutus</i>	1.66	10.02
<i>D. hispidus</i>	2.02	5.32
<i>Mithrax brasiliensis</i>	0.79	4.22
<i>P. provenzanoi</i>	0.64	3.03
<b>Wall</b> —average similarity: 63.94		
<i>C. rigens</i>	3.9	29.94
<i>M. forceps</i>	3.33	29.84
<i>P. echinatus</i>	2.43	16.71
<i>S. seticornis</i>	0.99	4.66
<i>M. brasiliensis</i>	1.03	4.34
<i>S. hispidus</i>	0.84	3.49
<i>C. tibicen</i>	0.67	3.4
<b>Cave Roof</b> —average similarity: 75.86		
<i>C. rigens</i>	12.95	42.47
<i>P. echinatus</i>	15.37	35.11
<i>J. antiguensis</i>	0.97	7.02
<i>P. gundlachi</i>	1.34	5.15
<i>P. antarcticus</i>	1.41	3.91
<b>Cave Floor</b> —average similarity: 65.60		
<i>C. rigens</i>	6.78	56.99
<i>P. echinatus</i>	1.34	24.33
<i>J. antiguensis</i>	1.27	11.86
<b>Soft Bottom</b> —average similarity: 56.44		
<i>C. rigens</i>	5.23	45.92
<i>P. echinatus</i>	3.21	35.35
<i>S. hispidus</i>	0.75	7.9
<i>S. seticornis</i>	0.5	3.63

Analysis of the external, crevicular and soft bottom habitats revealed the crevicular possessing the highest density of decapods (Figure 4a). The crevicular was significantly higher than the external ( $p = 0.0055/F = 1.595$ ). The soft bottom habitat had a significantly lower abundance than the external habitat ( $p = 0.0001/F = 43.26$ ) and crevicular ( $p = 0.0001/F = 69.02$ ), but with different variance and consequent higher  $F$  value. The diversity of species between habitats was similar (Figure 4b), though the external habitat displayed a significantly higher diversity when compared with the crevicular habitat ( $p = 0.0049/F = 1.92$ ). This analysis confirms that the numbers of species found in the crevicular habitat are higher, but only few species have adapted to live in this habitat exclusively. In the high diversity external habitat, several crevicular species were observed foraging (see also Table 1). Similar behaviour was documented in the predator exposed soft bottom area, which presented a low species abundance and a diversity index similar to the external habitat. The data in Table 1 indicates that several species from the external and crevicular habitats also occur on the soft bottom.

## Discussion

### Light incidence defining habitats on hard substrate within the subtidal zone

The schematically divided Fringe and Wall habitats described in this study possess specific assemblages of decapod species which were characteristic for the overall “external habitat” classification.



**Figure 4.** (Upper) nMDS using decapod assemblages to compare the five sampled habitat - Fringe, Wall, Cave Roof, Cave Floor and Soft Bottom. (Lower) Dendrogram of similarities grouping the most significant species in (a–c) groups.

**Table 3.** ANOSIM results comparing the similarities among the habitats

habitat vs. habitat	R-statistic	Significance level %
Fringe vs. Wall	0.411	0.1
<b>Fringe vs. Cave Roof</b>	<b>1</b>	<b>0.1</b>
<b>Fringe vs. Cave Floor</b>	<b>0.977</b>	<b>0.1</b>
<b>Fringe vs. Soft Bottom</b>	<b>0.751</b>	<b>0.1</b>
<b>Wall vs. Cave Roof</b>	<b>0.89</b>	<b>0.1</b>
<b>Wall vs. Cave Floor</b>	<b>0.872</b>	<b>0.1</b>
Wall vs. Soft Bottom	0.442	0.1
Cave Roof vs. Cave Floor	0.239	0.1
Cave Roof vs. Soft Bottom	0.349	0.1
Cave Floor vs. Soft Bottom	0.3	0.1

Global R: 0.63. Significance level of sample statistic: 0.1%. Results in bold represents the significant difference.

The diversity and abundance of benthic species present on this hard-substrate habitat are influenced directly and indirectly by constant exposure to sunlight during daylight hours. These high light incidence areas are typified by the abundance of photosynthetic species such as colonial algae and corals (Leão *et al.*, 2003, 2016; Barradas *et al.*, 2010). Several decapods are closely associated with colonial species and in some cases co-evolve, with a specific decapod acting as the host. In the Caribbean Sea,

*Ancylomenes pedersoni* (Chace, 1958) has a strong association with the anemone *Bartholomea annulata* (Le Sueur, 1817) or *Periclimenes rathbunae* (Schmitt, 1924) with *Lebrunia danae* (Duchassaing and Michelotti, 1860) (Briones-Fourzán *et al.*, 2012). Examples of this coexistence between host decapod and colonial are found globally, some with different hosts throughout their life cycle and some with exclusive hosts (Abele and Patton, 1976; Bruce, 1978; Wirtz *et al.*, 2009; Blanco *et al.*, 2011). Some species visibly display a coevolutionary pattern similar to that reported for insect and plant relationship (van Tussenbroek *et al.*, 2016).

In this study, the majority of decapods from the external habitual niche were observed in association with colonial benthic species and have been recorded in further studies associated to hosts. Examples include herbivorous Mithracinae species captured among algae and corals (Coen, 1988; Wilber and Wilber, 1989; Melo, 1996; Rhyne *et al.*, 2005; Blanco *et al.*, 2011; Giraldes *et al.*, 2015a); *S. seticornis* among sponges, corals, octocorals, gorgonians, anemones, sea lilies and urchins (Hayes *et al.*, 1998; Wirtz *et al.*, 2009); *Domécia acanthophora* in corals such as *Myllepora* and *Acrophora* (Patton, 1967); *Dromia erythropros* and other dromioideas holding sponges and near sponges in reefs (Melo, 1996); species of the genus *Platypodiella* associated with the zooanthus *Palythoa* (Hartog and Türkay, 1991; Gleibs *et al.*, 1995; Araujo and Freitas, 2003); *Carpilius corallinus* and other species of this genus associated with coral reef areas (Melo, 1996; Wetzer *et al.*, 2003); species of the genus *Calcinus* associated with corals (Malay and Paulay, 2010). Species within this habitat are generally small decapods with low displacement capacity with a specific adaptive anti-predator strategy related to the hosts. They presented a crypsis mimicry of colour, shape, and behaviour and found refuge between the structures of colonial species (B. W. Giraldes, pers. obs.). These observations demonstrate how decapods from the hard substrate external habitats have developed behavioural strategies and adaptations in conjunction with colonial species which allow them to inhabit this illuminated and exposed subtidal zone.

In contrast to the prevalence of colonial species found in the illuminated external zone, the crevicular habitats have few such associations and an obvious absence of photosynthetic organisms. The crevicular habitat consisted of a dark zone within the interconnected cave systems among the natural overhanging features of the reef structure. This dark habitat was lined by shadow zones formed by variations of natural light intensity created by breaks within the reef structure. These shadow zones have very few colonial benthic organisms covering the substrate, with a decreasing density gradient of colonial benthic species in relation to the intensity of penetrative sunlight. Micael *et al.* (2006) described a similar pattern in the subtidal marine tunnels of the Azores, Portugal. The decapods, which inhabit these shaded zones, do not possess associations or mimicry patterns with photosynthetic hosts such as algae and corals like the specimens from external habitats. The species observed in this study within the crevicular habitat can be considered as reef stygofauna (i.e. any fauna that live in groundwater systems, such as caves, fissures, and vugs). They presented specific adaptations to life in a dark, light-restricted environment such as: large sensory structures, red or orange coloration, strong large bodies, and/or fast displacement (see original taxonomic description for each species). Examples include species from the families Rhynchocinetidae and Barbouriidae with long antennae and antennules and in some cases with long and tactile pereopods, inhabiting cavities and caves

(Iliffe *et al.*, 1983; Manning and Hart, 1984; Okuno, 1997; Caillaux and Stotz, 2003; De Grave and Fransen, 2011; Giraldes *et al.*, 2012b); species of the genus *Palinurellus* with tactile bristles covering the body and inhabiting deep cavities in reefs (Holthuis, 1991; Melo, 1999; Chan, 2010); *Enoplometopus antillesis* with a tuft of bristles in the cheliped and inhabiting caves and cavities (Melo, 1999; Poupin, 2003); *P. meripurpuratus* and *P. echinatus* with long antennas and recorded as inhabiting cave and cavities in reefs (Giraldes *et al.*, 2015b; Giraldes and Smyth, 2016). These represent anti-predator characteristics for decapods which live in a dark habitat without the protection or shelter provided by colonial benthic organisms. Similar adaptations for life in crevicular habitats which have been documented during this study have been identified and described previously in relation to the stygofauna in deep marine caves (Iliffe and Bishop, 2007; Iliffe and Kornicker, 2009) and also for species which inhabit the deep ocean aphotic zones (Hart *et al.*, 1985; Johnsen, 2005). A clear evolutionary adaptation for decapods which inhabit dark environments such as the crevicular habitat (Hart *et al.* 1985). This study has identified that this present zonal allocation is in relation to caves and cavities within the subtidal zone, and therefore describes the existence of stygofauna in the reef environment.

#### Soft bottom reef boundary—the interface habitat sharing assemblages

The soft bottom environment is the most extensive benthic habitat in the marine ecosystem, with its own particular group of decapods (Alongi, 1990; Melo, 1996). To avoid predation in soft-bottom habitats, decapods must have efficient anti-predator strategies such as disruptive camouflage and the burrowing behaviour. Decapods from this soft bottom environment usually burrow themselves in the soft substrate as their primary predator avoidance strategy. As result of this behaviour, body shapes have evolved accordingly, with the eyes and a breathing area the only parts of the animal exposed. Bellwood (2002) suggested that this behaviour may be an ancestral condition, related to a decapod group which evolved in soft sediment habitats (see also Garstang, 1897). The large number of decapod species within Superfamilies like Calappoidea, Leucosioidea, found worldwide with morphological adaptations for burrowing in soft-substrate habitats (Melo, 1996; Ng *et al.*, 2008; De Grave *et al.*, 2009) demonstrates the phylogenetic efficiency of this burrowing behaviour for such decapods. These physical characteristics differentiate between species inhabiting hard and soft substrate, thus acting as visible taxonomic evolutionary developments which can be used to group assemblages of decapods to a specific substrate type. The morphology associated with a specific decapod species phylogeny appears to be driven by the properties of the habitual zone and the associated anti-predatory behavioural strategies. These parameters subsequently account for the proposed subtidal zonation of these habitual niches.

The majority of decapods documented during this study in the soft bottom were representative of the hard reef habitat, with only 16% of species considered characteristic to the soft substrate habitat, even with the great amount of existent species from this zone. In other words, soft substrate decapods were considered rare in this study, even within their associated habitat. Therefore, the high diversity assemblages recorded on the soft-bottom habitat were visiting the zone to forage or hunt. Barros *et al.* (2001) demonstrated that richness of benthic macrofauna increases in

soft-sediments close to rocky-reefs as this was certainly the scenario witnessed during this study. This increase in macrofauna is the instigator of the natural displacement of decapods from their hard substrate environments explaining the degree of interaction between species from different habitats. This transient behaviour within the decapod species and their associated habitats follows the ecological premises of a higher heterogeneity of habitats supporting a richer assemblage of species (Levin *et al.*, 2010). As demonstrated in this study, the interface between hard substrate and soft-bottom presents a richer faunal suite of decapods, in agreement with Barros *et al.* (2001) where it was shown that microtopography clearly influenced the structure of benthic macrofaunal assemblages.

#### Is subtidal zonation in reefs a global or a regional pattern?

After the first ontogeny, from the larval stage to benthic life, decapods need to “find” their associated habitual niche. They have evolved to take advantage of the particular nuances a habitat possesses within a specific zone. They are generally observed in this habitat throughout the remainder of their life cycle. This dependence for survival within a fixed habitual niche is observed globally and demonstrated in several taxa. For instance, species belonging to the ghost-crab genus *Ocypode* inhabit similar soft substrate environments in intertidal and supratidal zones throughout the world (Sakai and Türkay, 2013). Likewise species at genus *Panulirus* inhabit shallow tropical areas (George and Main, 1967), while the genus *Uca* inhabits intertidal soft substrates (Crane, 1975) and the family Rhynchocinetidae is characteristically found in shallow hard substrate environments of marine caves and crevices (Okuno, 1997; Caillaux and Stotz, 2003). The ecological equivalence between decapods of the same genus from different regions of the world allows the species to be observed and associated to similar habitat types. The similarities in body shape and behaviour evident in their phylogeny evolved to exploit the resources of that particular niche.

The division of soft or hard substrate types is described in most taxonomic descriptions in relation to habitat preference for subtidal decapods (Abele, 1974; Williams, 1984; Melo, 1996, 1999). A recognizable global pattern of zonation for subtidal decapods that inhabit a soft substrate environment has been documented, but the question of subtidal habitat divisions within hard substrate reef zones remains. Do external and crevicular habitats for specific decapod assemblages exist globally? Not all coastal reefs possess unique cave systems like the ones studied during this research (Dominguez *et al.*, 1990; Leão *et al.*, 2003), however any cavity or fissure in hard substrate can provide a dark shadow zone. The natural formation of a reef seascape (Boström *et al.*, 2011) addresses the suggested light and crevicular habitat to this specific ecosystem. For numerous decapods, hard substrate crevices provide the habitat equivalence of dark zone cave structures, thus accommodating the behavioural needs of a crevicular species. Therefore, if the zonation pattern proposed here is a global pattern, different marine areas in the world with hard substrate types having cavities, holes or fissures creating shadow zones should also possess genera or family similar to those found in this study. Their presence within such crevicular habitats should adhere to the theory of ecological equivalence, where similar morphological adaptations and behaviours are common within the phylogeny. The most abundant species of the



crevicular habitat in this study are members of the Family Rhynchocinetidae. Similarities in their morphology, behaviour and habitual niche can be seen in other regions worldwide, with species living in shallow hard substrate, where they occupy caves and crevices during the day and moving out at night; they also display similar colour patterns and long tactile structures to accommodate the challenges of life in a dark crevicular habitat (Okuno, 1997; Caillaux and Stotz, 2003). The same for the family Barbouriidae where all species within the genus *Barbouria*, *Janicea*, and *Parhippolyte* are considered stygobionts, displaying the same colour crypsis to accommodate for life in a dark environment (Iliffe *et al.*, 1983; Manning and Hart, 1984; De Grave and Franssen, 2011; Giraldes *et al.*, 2012b). Another example ecological equivalence is displayed within the genus *Palimurellus*, where the Indo-Pacific *Palimurellus wieneckii* (de Man, 1881) and Atlantic *P. gundlachi* have the same nocturnal behaviours, orange colouration and tactile structures needed for life in a dark hard substrate environment (Holthuis, 1991; Chan, 2010). The majority of species within the genus *Enoplometopus* have an orange colouration and tactile structures adapted to life in dark zones. Several species live within the deep sea environment and possess the same adaptations as those that live in the shallow subtidal (Poupin, 2003). Highlighting connectivity between the requirements for crevicular subtidal hard substrate habitats and the dark light reduced conditions of the aphotic deep sea habitat.

This world-wide pattern of ecological equivalence of decapods associated with a reef seascape is also observed within colonial benthic host species from the external zone habitats. Globally, the majority of decapods within the genera *Platypodiella* are colourful species, associated with the Zoanthid *Palythoa* sp. They present an aposematic pattern recognized as an indicator of being a poisonous species (Hartog and Türkay, 1991; Gleibs *et al.*, 1995), an evolutionary trait within this genera's phylogeny which can be directly related to their habitat/host and colour. The association between decapod and host has been well documented within taxonomic descriptions (Abele and Patton, 1976; Bruce, 1978; De Grave, 1999; Wirtz *et al.*, 2009) and co-evolutionary relations are obvious for some species within a common genus. Several categories can be associated with decapod relationships, they may be harmless, mutually beneficial, parasitic, or predatory. Wicksten and Hernandez (2000) highlight these associations and emphasize the difficulties in confirming if the relationship is truly symbiotic. It is therefore quite possible that phylogenetically linked co-evolutionary developments and habitual patterns between associated invertebrate species and decapod are as yet undescribed (Stewart *et al.*, 2006). This is demonstrated in the recently described co-evolutionary patterns of brachyuran crab larvae pollinating seagrass flowers (van Tussenbroek *et al.*, 2016). The symbiotic relationship may in fact begin at the early ontogenetic stages and may play a vital role in successful recruitment and persistence of the hosts.

Further studies from specific regions in different parts of the world will be required to more completely understand the dynamics governing the decapod association with subtidal habitual zones, and the host species relationship within the external habitats in each particular reef seascape. However, evidence exists within the taxonomic description of species and their phylogeny, to support the proposed association of decapods with a specific subtidal habitat and the global ecological equivalence between species of the same niche. This research suggests that abiotic

factors drive a recognizable global zonation pattern for decapods within subtidal reefs and supports the argument for describing decapod habitat patterns within the subtidal zone as an extension of those observed from intertidal zones.

## Overview

This study revealed the existence of three distinct habitats housing specific decapod assemblages within tropical hard substrate environments; the External-Reef habitat which accommodates colonial benthic host decapods; the Crevicular-Reef habitat which accommodates the reef-stygofauna; and the Interface habitat between the reef and soft substrate which is habituated by transient decapod species. The study is extending to the subtidal zone the previous zonation patterns recorded for decapods in the benthic environment using physical parameters as the rationale defining allocation.

The UVC methodology employed during this research and the proposed zonation pattern presents new opportunities for applied ecological studies with specific decapod assemblages. It has the potential to be used as a useful bio-monitoring tool to assess anthropogenic impact within specific zones. This application will become ever more pertinent as the pressure increases on economically valuable fishery resources such as lobster and crab within the reef environment. In addition, it allows the correlation of distinct decapod assemblages with further taxa like corals, algae, and reef-fish in ecosystem evaluation.

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