



# Macro- and microhabitat use patterns of holothurians in Buena Vista, Nggela, Solomon Islands: rock climber and bottom crawler species

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**ABSTRACT:** Densities and habitat use patterns of holothurians, including nocturnal species, were assessed in Buena Vista, Nggela, Solomon Islands, for community-based resource management. Nighttime snorkeling surveys were conducted along transects (maximum 1.6 km) with 3 to 5 searchers in nearshore, channel, and outer reef macrohabitats. Only the population in the seagrass macrohabitat was separately assessed in 30 m line transects during the daytime. Microhabitats were clearly separated between species living on 3-dimensional structures (e.g. surfaces of knolls and reef slopes; rock climber group) and those on flat bottoms (bottom crawler group), although they coexisted at macrohabitat scales. Potential shelters adjacent to each individual differed between the 2 groups. Among bottom crawler species, *Bohadschia koellikeri*, which was recently taxonomically divided from *B. vitiensis*, occupied macrohabitats intermediately ranging between those of *B. argus* in the channel and outer reef macrohabitats and those of *B. vitiensis* and *B. marmorata* in the nearshore and seagrass macrohabitats. The high-density population was observed in the seagrass macrohabitat, mainly composed of *Holothuria scabra*, *B. marmorata*, and *H. fuscogilva*, although most individuals of these species were smaller than the national legal size limits. Moreover, the body lengths of *H. atra* and *H. fuscogilva* increased from the seagrass macrohabitat to the outer reef macrohabitat, implying their migration during growth and the roles of seagrass areas as nurseries. These results revealed diversity of macro- and microhabitat use patterns among species and their growth stages and highlight the importance of considering these factors for conserving diverse species by areal-based protection measures.

**KEY WORDS:** Habitats · Holothuroidea · Bêche-de-mer · Distributions · Community-based resource management

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## 1. INTRODUCTION

Tropical holothurians in shallow waters belonging to the order Holothuriida and Synallactida (Purcell et al. 2012) are consumed as luxury seafood (bêche-de-mer and trepang), mainly in China (Purcell 2014, Purcell et al. 2018). With the recent economic devel-

opment and increase in demand in China, these resources have been overexploited worldwide, and conservation is required (Toral-Granda et al. 2008, Anderson et al. 2011, Purcell et al. 2013, Conand et al. 2014). Because these resources are relatively sedentary, spatially heterogeneous, and targeted by small-scale fisheries, local-scale management in

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addition to national-scale regulations is vital (Purcell et al. 2010). Community-based resource management (CBRM) is generally utilized in small-scale fisheries worldwide (Hviding & Baines 1994, Aswani 2000, Johannes 2002, Cohen et al. 2015, Aswani et al. 2017); however, local case studies regarding CBRM approaches to holothurian resources are limited.

For CBRM to impose protective measures such as marine protected areas (MPAs) or restocking by releasing hatchery-produced juveniles, it is essential to understand species-specific habitat use patterns in the field. Presently, although qualitative knowledge regarding holothurian habitats has been available for most commercial species (e.g. Purcell et al. 2012), quantitative data are still limited because most stock assessment studies have only described macrohabitats (hereafter defined as geographical ranges related to reef-scale topographical features, such as reef flats, lagoons, and outer reefs) (e.g. Pakoa et al. 2014b). However, studies considering microhabitats (hereafter defined as substrate types or structures on which each individual is present, such as sand flats and knolls) have often examined only a single species (Wiedemeyer 1994, Mercier et al. 2000a,b, Džeroski & Drumm 2003, Shiell & Knott 2008, Slater et al. 2010, Palomar-Abesamis et al. 2017, 2018). Therefore, previous studies that simultaneously evaluated macro- and microhabitat use patterns across multiple species are rare (Kerr et al. 1993, Bellchambers et al. 2011, Eriksson et al. 2012a).

Previously, differences in habitat use by holothurian species have been described in terms of the macro- and microhabitat (Kerr et al. 1993, Eriksson et al. 2012a). Based on these parameters, Eriksson et al. (2012a) classified the habitat use patterns of 6 species and pointed out their association with different substrate types. Eriksson et al. (2012a) also quantitatively evaluated the effect of topographic relief on the habitat use of sea cucumbers, which was, however, less important than substrate types in their study. On the other hand, some species are distributed across a wide range of macro- and microhabitats (e.g. substrate type) showing complex overlaps of habitat ranges among species (Kerr et al. 1993, Eriksson et al. 2012a), which implies that variable factors other than substrate type also affect the habitat use of sea cucumbers depending on environments. In particular, it is possible that holothurian distributions at microhabitat scales are greatly affected by topographic relief, when considering a spatially broad area across multiple macrohabitats with variable topography. In addition, the availability of potential shelters in the environment could also

affect their macrohabitat selection because microhabitat use by some holothurians is related to their sheltering behavior (Palomar-Abesamis et al. 2018).

Holothurians are the second-largest fishery next to tuna in Solomon Islands (Kinch et al. 2006, Pakoa et al. 2014a) and are an important income source for the local people, particularly in coastal areas with limited land for agriculture (e.g. Ontong Java atoll) (Christensen 2011, Christensen & Gough 2012). Therefore, resource sustainability is essential to satisfy a rapidly increasing human population at 2% yr<sup>-1</sup> (<https://www.statistics.gov.sb/>). Holothurian resources, however, have been overexploited since the early 1990s, resulting in fishery closure over the country since 2005, with occasional openings (Carleton et al. 2013, Pakoa & Bertram 2013, Purcell et al. 2014).

The Ministry of Fisheries and Marine Resources (MFMR) of the Solomon Islands Government introduced CBRM (Schwarz et al. 2020) by providing a legal basis for customary marine tenures and permitting local communities to set their own bêche-de-mer management plans (Solomon Islands Government 2014). However, data on the densities and habitat use patterns of holothurians with adequate spatial resolution to be used for CBRM are limited, although national-scale surveys have been held regularly in this country (Ramohia 2006, Pinca et al. 2009, Pakoa et al. 2014a). In particular, scarce data are available on nocturnal species (Pinca et al. 2009), which can be missed during daytime surveys (Shepherd et al. 2003, Hearn & Pinillos 2006, Buckius et al. 2010).

The present study investigated the densities, body length compositions compared to legal size limits (Solomon Islands Government 2014), and macro- and microhabitat use patterns of holothurians at the fishing site of the Nagotano Island community, one of the pilot communities for the CBRM holothurian program by the Solomon Islands Government. The present study aims to collect sufficient data on holothurian distributions around an MPA in the Danisavo Harbor in support of extension of the MPA under consideration by the community.

Because the study area contains variable environments from seagrass to outer reef macrohabitats in relatively narrow spatial ranges, variable topography was expected to be a potential factor in determining the composition of holothurians. Particularly, we hypothesized that the dimensions of microhabitats (namely, flat or bumpy topography) are important to separate microhabitat use patterns among holothurian species, which also relates to available

nearby shelters and macrohabitat use patterns. To test this hypothesis, we classified the whole areas into several macrohabitats having different depths and topographic complexity. Then, macro- and micro-habitat use patterns and potential nearby shelters were compared among holothurian species. As the holothurians were sparsely distributed in the outer reef environments, we conducted long-transect surveys with multiple searchers to collect sufficient data. We also examined nocturnal species by nighttime surveys to cover a wider range of holothurian species.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The study site ( $8^{\circ}53'30''\text{S}$ ,  $159^{\circ}59'00''\text{E}$ ) was located in the coastal areas of western Buena Vista Island and around Danisavo Island, which is located in the western part of the Nggela (Florida) Islands in the Central Province (Fig. 1). This area corresponds to the fishing site of the Nagotano community. The environments of the study site were classified into the following macrohabitats based on topographical

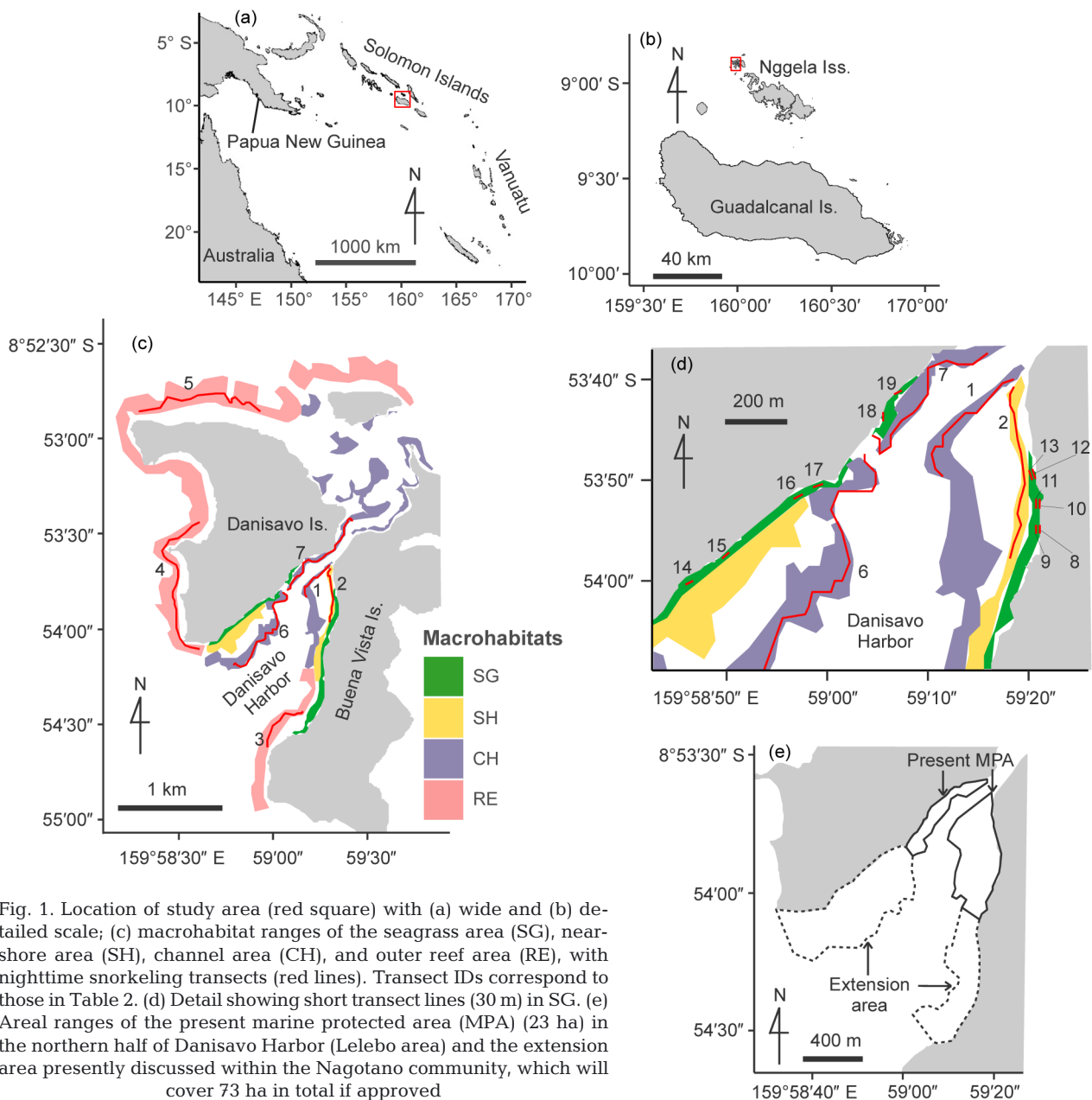


Fig. 1. Location of study area (red square) with (a) wide and (b) detailed scale; (c) macrohabitat ranges of the seagrass area (SG), near-shore area (SH), channel area (CH), and outer reef area (RE), with nighttime snorkeling transects (red lines). Transect IDs correspond to those in Table 2. (d) Detail showing short transect lines (30 m) in SG. (e) Areal ranges of the present marine protected area (MPA) (23 ha) in the northern half of Danisavo Harbor (Lelebo area) and the extension area presently discussed within the Nagotano community, which will cover 73 ha in total if approved

features (Table 1, Fig. 1): seagrass areas (SG), near-shore areas (SH), outer reef areas near the channel in Danisavo Harbor (CH), and outer reef areas open to the ocean (RE). The macrohabitat spatial ranges were manually determined using satellite imagery (Google Maps, <https://www.google.com/maps/>, accessed 27 February 2021) based on preliminary field observations (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m687p079\\_supp.pdf](http://www.int-res.com/articles/suppl/m687p079_supp.pdf)).

## 2.2. Field surveys

Holothurians were surveyed on transects by snorkeling in SH, CH, and RE during August and October 2019 and January 2020 and by wading in SG in January 2020. The number of transects was 1, 3, 3, and 12 in SH, CH, RE, and SG, respectively (Fig. 1, Table 2). Only 1 transect was surveyed on each day in SH, CH, and RE, while all transects were surveyed on a single day in SG.

In SH, CH, and RE, holothurians including nocturnal species were surveyed during nighttime by 3 to 5 searching snorkelers (Table 2). The searching

snorkelers swam parallel to the shore or reef, maintaining distance from each other and searching for holothurian species. The widths of the observations were 4 m per searching snorkeler. When a holothurian was found, the searching diver signaled the recording snorkeler using an underwater torch. Then, the recording snorkeler measured the body length and recorded it with the species name, time of observation, microhabitat, and shelter-like structures if present in the vicinity of the individual. Continuous tracks were recorded using a GPS (eTrex 10, Garmin), from which the lengths of the observed transects (0.43–1.6 km) were calculated with QGIS (QGIS Development Team 2020) (Table 2). Locations of all individual sea cucumbers were also recorded using GPS. Regardless of the number of searching snorkelers, each transect shown in Fig. 1 and Table 2 was treated as a single transect; the transect width varied as 4 m × the number of searching snorkelers working side by side, each covering a width of 4 m.

The holothurians in SG were surveyed on line transects 30 m long and 2 m wide. The lines were set parallel to the shoreline, within which any type of holothurian was recorded as described above. Usu-

Table 1. Approximate water depths and environmental characteristics in each macrohabitat type

Macrohabitat	Water depth (m)	Environment
Seagrass areas in inner reefs (SG)	0–1	Slightly subtidal seagrass meadows, mainly composed of <i>Enhalus acoroides</i>
Nearshore sandy areas in inner reefs (SH)	2	Massive corals and knolls on muddy sand flats; slightly muddy water and slow currents
Outer reef areas along the channel (CH)	2–3	Crests are narrow or absent; narrow and steeply inclined reef slopes; sandy–rocky seabeds with massive corals and knolls; clear water and strong tidal currents
Outer reef areas open to ocean (RE)	0–3	Wave-affected, widely developed crests and reef slopes; sandy–rocky seabeds with massive corals and knolls; clear water and medium currents

Table 2. IDs, date, time, number of searching divers, width, length, and macrohabitat type of each transect. Transect widths for Nos. 1 to 7 were 4 m (per diver) × parallel divers. Macrohabitats as defined in Table 1. (–) not applicable

ID	Date	Start (h:min)	End (h:min)	Duration (h:min)	Divers	Transect width (m)	Transect length (m)	Macrohabitat
1	7 Aug 2019	21:57	22:58	01:00	3	12	430	CH
2	8 Aug 2019	19:47	20:51	01:03	3	12	537	SH
3	25 Oct 2019	20:39	21:37	00:58	3	12	590	RE
4	27 Oct 2019	20:39	22:55	02:16	4	16	1641	RE
5	27 Oct 2019	21:14	23:16	02:01	4	16	1415	RE
6	22 Jan 2020	20:47	22:58	02:11	5	20	1222	CH
7	24 Jan 2020	21:22	00:45	03:23	5	20	1137	CH
8–19	24 Jan 2020	07:49	15:52	–	–	2	30 (× 12 transects)	SG

ally, sand-burrowing species appear on the sand during the night. However, during our surveys, the tide was too low during the night to expect their appearance. Therefore, we surveyed during the daytime, with 3 to 5 people carefully searching for sand-burrowing individuals by eye and hand. Locations of individual sea cucumbers within the transects were also recorded.

Species of sea cucumbers were visually identified underwater and also using photographs, referring to pictorial identification manuals (Féral & Cherbonnier 1986, Purcell et al. 2012) and taxonomic articles (Kim et al. 2013).

### 2.3. Evaluation of densities and habitat use patterns

The densities of holothurians were separately evaluated for each type of macrohabitat, assuming that holothurian densities were homogeneous within each macrohabitat. Using count data (Table S2) and observation areas in each transect, densities were calculated using a generalized linear model based on Poisson distribution with a logarithmic link function. Because the transect was not replicated (single) in SH, equally trisected subsections of the original transect were alternatively treated as site replicates.

Variability in the species composition of holothurians was tested (1) among macrohabitats and (2) among sites (transects) within each macrohabitat by permutational multivariate analysis of variance (PERMANOVA) using the 'adonis' function in the 'vegan' package (Oksanen et al. 2017). To test (2), each transect was divided into 3 subsections having equal length. These subsections were treated as replicates in each site. Data in SH were not analyzed for (2), because the surveyed transect was single.

As the microhabitat and shelter data were evaluated for each individual holothurian (not for each site), these data were expressed as compositions for each species. The microhabitat use patterns of each species were clustered with Ward's method based on Bray-Curtis dissimilarity ('hclust') using R 4.0.5 (R Core Team 2020). Then, the clusters were classified into 2 groups based on their preference for topographic relief: the bottom crawler group, preferring 2-dimensional microhabitats, and the rock climber group, that preferred 3-dimensional microhabitats. Then, the difference in microhabitat use patterns between the 2 groups was tested by PERMANOVA. Similarly, interspecies variability in nearby shelters was also tested by PERMANOVA between the 2 groups. In addition, principal coordinate analysis

(PCO) was performed to visualize the interspecies variability in compositions of microhabitats and nearby shelters.

### 2.4. Body lengths and conservation effects by size limits

To compare body length compositions among macrohabitats for species which were distributed across several macrohabitats (but  $\geq 3$  individuals in each macrohabitat), the normality of the variation of data was tested using Levene's method ('levene.test') in the 'lawstat' package (Gastwith et al. 2013). Analysis of variance ('aov') and the Tukey-Kramer test ('TukeyHSD') were then conducted for multiple comparisons in R.

The body length of each individual was compared with national legal size limits (Solomon Islands Government 2014). Then, an exploitable ratio was calculated for each species using the data from all individuals.

## 3. RESULTS

### 3.1. Densities and body lengths relative to size limits

In total, 24 species of sea cucumbers were observed throughout the study area. Holothurian density in the seagrass macrohabitat (SG) was generally higher than that in the other macrohabitats, where the population was mainly composed of *Holothuria (Metriatyla) scabra*, *Bohadschia marmorata*, *Synapta maculata* (non-commercial), *H. (Microthele) fuscogilva*, and *B. vitiensis* (Fig. 2). Other observed species of sea cucumbers were *H. (Halodeima) atra*, *H. (Mertensiothuria) leucospilota*, *Actinopyga echinites*, *H. (Microthele) whitmaei*, and *Opheodesoma* sp. (non-commercial).

The sea cucumber population in the near-shore macrohabitat (SH) was dominated by *H. (Acanthotrapeza) coluber* (Fig. 2). The composition of other species of sea cucumbers was similar to that in SG, i.e. *H. atra*, *B. vitiensis*, *H. fuscogilva*, *A. miliaris*, and *B. koellikeri*.

The highest number of species (15 species) of sea cucumbers was observed in the channel macrohabitat (CH) among all macrohabitats (Fig. 2). The dominant species were *Stichopus horrens*, *Pearsonothuria graeffei*, *H. atra*, *B. argus*, and *B. vitiensis*. Other species of sea cucumbers were *H. (Theleothuria) tur-*

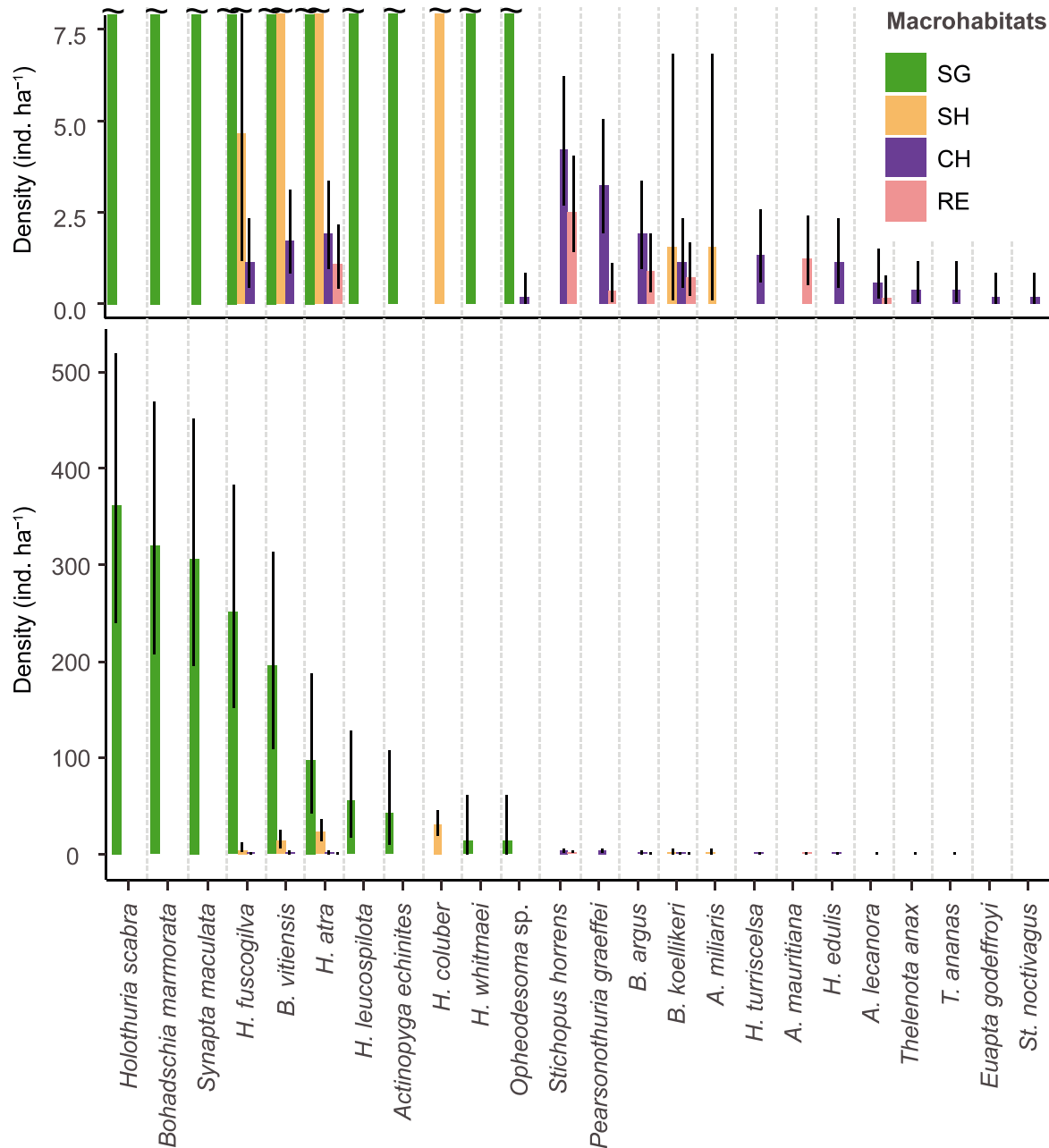


Fig. 2. Averaged densities of holothurians for each species in macrohabitats of the seagrass area (SG), nearshore area (SH), channel area (CH), and outer reef area (RE), with error bars showing 95% CIs. Zoomed bars are shown in the upper figure for low-density data. Species are ordered by their maximum densities

*riscelsa* (non-commercial), *H. fuscogilva*, *B. koellikeri*, *H. (Halodeima) edulis*, *A. lecanora*, *Thelenota anax*, *T. ananas*, *Ophedoesoma* sp., *Euapta godeffroyi* (non-commercial), and *St. noctivagus* (non-commercial).

Seven species of sea cucumbers were observed in the outer reef macrohabitat (RE) and were all common in the sea cucumber population in CH, except for *A. mauritiana*, which was only found in RE

(Fig. 2). Densities were generally lower than those in CH; dominant species of sea cucumbers were *St. horrens*, *A. mauritiana*, and *H. atra*. The other species of sea cucumbers were *B. argus*, *B. koellikeri*, *P. graeffei*, and *A. lecanora*.

PERMANOVA results showed that there was significant variation in the species composition of holothurians among the macrohabitats ( $p < 0.05$ , Table S3). On the other hand, the variability in spe-

cies composition among transects within the same macrohabitats was not significant for CH and RE ( $p > 0.05$ ), while it was significant for SG ( $p < 0.05$ ) (Table S4). The high variability in species composition among sites in SG can be also seen in the cluster analysis (Fig. S1).

Regardless of the high density, sea cucumber individuals in SG were mostly small (Table S5), and the exploitable ratios of individuals of legal size limits were generally low for species mainly living in SG, such as *H. scabra*, *B. marmorata*, and *H. fuscogilva* (Table 3). Compared to these species, the ratios of individuals over the size limits were higher for *St. horrens* and *H. coluber*, comprising a significant exploitable resource in this area (Table 3).

The body lengths of *H. atra* and *H. fuscogilva* were significantly increased from the seagrass area (SG) through the intermediate area (SH) to the deeper reef slope area (CH and RE) (Fig. 3d,e, Turkey-Kramer test,  $p < 0.05$ ), indicating macrohabitat utilization of SG by these small individuals. Both *B. argus* and *B. koellikeri* showed larger body sizes in

CH than in RE (Fig. 3a,b,  $p < 0.05$ ). The body lengths of *B. vitiensis* and *St. horrens* were not different among macrohabitats (Fig. 3c, f,  $p > 0.05$ ).

### 3.2. Habitats and shelter-like structures

The microhabitat use patterns of the holothurian species were clustered into 3 groups (Clusters I–III) at a height of 1.6 (Fig. 4). Cluster III was composed of species mainly living in seagrass bed microhabitats, such as *B. marmorata* and *H. scabra*. Cluster I was mainly composed of *H. atra*, *B. vitiensis*, *B. koellikeri*, *H. coluber*, and *B. argus*, whose microhabitats were mainly sand flats, sometimes with rubble and limestone flats. Cluster II consisted of rocky species, such as *A. mauritiana*, *P. graeffei*, and *St. horrens*. Their microhabitats were the surface of the hard substrate with undulating, 3-dimensional structures (diagonal shaded bars in Fig. 4). Even though Cluster I and II species often coexisted at the macrohabitat level and commonly used rocky

Table 3. Body length (mean  $\pm$  SD) for each species of sea cucumber calculated using data across all macrohabitats ( $n$  = no. of individuals). Ratios of exploitable individuals compared to the legal size limits in Solomon Islands are also shown. The same size limit is used for *Bohadschia koellikeri* and *B. vitiensis* because these species were classified as a single species when the law (Solomon Islands Government [2014]) was written. *B. marmorata* is described as chalkfish *B. similis* in the original text of the law. No size limits are imposed for non-commercial species. Body length data shown separately for each macrohabitat are presented in Table S5. Some recently described species have no common name. (–) not applicable

Species	Common name	Body length (cm)	n	Size limit (cm)	Exploitable ratio (%)
<i>Actinopyga echinites</i>	Deep-water redfish	13.0 $\pm$ 1.7	3	20	0.0
<i>A. lecanora</i>	Stonefish	14.8 $\pm$ 2.5	4	20	0.0
<i>A. mauritiana</i>	Surf redfish	17.4 $\pm$ 7.0	7	25	28.6
<i>A. miliaris</i>	Hairy blackfish	13.0	1	20	0.0
<i>Bohadschia argus</i>	Leopardfish, tigerfish	29.8 $\pm$ 8.7	14	30	50.0
<i>B. koellikeri</i>		21.0 $\pm$ 3.4	10	25	10.0
<i>B. marmorata</i>	Chalkfish	13.3 $\pm$ 2.8	23	20	8.7
<i>B. vitiensis</i>	Brown sandfish	20.2 $\pm$ 6.3	30	25	13.3
<i>Euapta godeffroyi</i>		50.0	1	–	–
<i>Holothuria atra</i>	Lollyfish	20.9 $\pm$ 6.6	33	30	9.1
<i>H. coluber</i>	Snakefish	60.5 $\pm$ 24.2	20	30	90.0
<i>H. edulis</i>	Pinkfish	29.4 $\pm$ 11.7	5	20	80.0
<i>H. fuscogilva</i>	White teatfish	16.6 $\pm$ 6.7	28	35	14.3
<i>H. leucospilota</i>	White threadfish	14.0 $\pm$ 3.5	4	20	0.0
<i>H. scabra</i>	Sandfish	14.5 $\pm$ 2.2	26	25	0.0
<i>H. turrisfelsa</i>		28.5 $\pm$ 3.6	6	–	–
<i>H. whitmaei</i>	Black teatfish	12.0	1	30	0.0
<i>Opheodesoma</i> sp.		67.0	1	–	–
<i>Pearsonothuria graeffei</i>	Flowerfish	27.7 $\pm$ 4.9	18	30	38.9
<i>Stichopus horrens</i>	Dragonfish, peanutfish	23.4 $\pm$ 5.9	36	15	94.4
<i>St. noctivagus</i>		24.0	1	–	–
<i>Synapta maculata</i>		63.0 $\pm$ 47.6	22	–	–
<i>Thelenota ananas</i>	Prickly redfish	42.0	1	35	100.0
<i>T.anax</i>	Amberfish	55.0	1	40	100.0

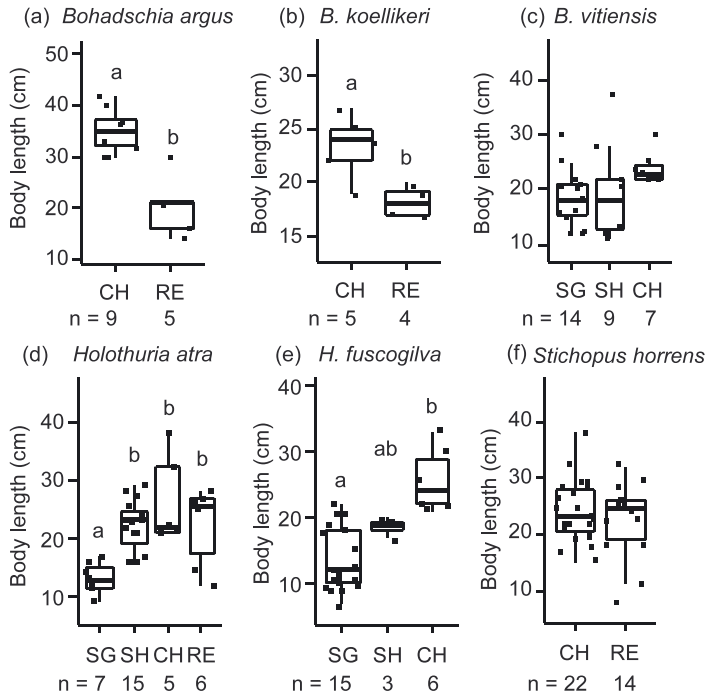


Fig. 3. Comparison of body length compositions among macrohabitats of (a) *Bohadschia argus*, (b) *B. koellikeri*, (c) *B. vitiensis*, (d) *Holothuria atra*, (e) *H. fuscogilva*, and (f) *Stichopus horrens* shown by boxplots, where lower, median, and upper hinges indicate 25, 50, and 75% quartiles, respectively. Upper and lower whiskers show the largest and smallest values no greater than 1.5 times the interquartile range, respectively. Jitters show all individual data. Lowercase letters on the plots express significant differences among the macrohabitats tested by multiple comparison (Tukey-Kramer test,  $p < 0.05$ ). Only species which were found in several macrohabitats at  $>3$  individuals were shown. Macrohabitats are the seagrass area (SG), nearshore area (SH), channel area (CH), and outer reef area (RE). The number of individuals (n) is shown under the x-axis labels of each macrohabitat. Body length data for all species are shown in Table S5

substrates as their microhabitat, Cluster I species mainly lived on flat, 2-dimensional microhabitats similar to Cluster III species. Therefore, the habitats of Cluster II species (hereafter rock climbers) were clearly separated from those of Cluster I and III species (hereafter bottom crawlers) at microhabitat levels with respect to topography. The differences in microhabitat use patterns between the rock climbers and bottom crawlers were significant by PERMANOVA ( $p < 0.05$ , Table 4a).

Habitat use patterns also varied within each group, which is partly explained by differences in macrohabitats. Among the bottom crawlers, *H. scabra*, *B. marmorata*, and *Sy. maculata* were only found in SG. In contrast, *H. atra*, *H. fuscogilva*, *B. vitiensis*, and *B. koellikeri* widely ranged across 3 to 4 types of macrohabitats. Comparing *B. vitiensis* and *B. koellikeri*, the former mainly occurred in the inner reefs (SG and SH), whereas the latter preferred more outer reef environments (CH and RE). Among the rock climbers, *St. horrens*, *P. graeffei*, and *A. lecanora* were found in CH and RE. In contrast, *A. mauritiana* was specific to wave-affected outer reefs open to the ocean (RE).

Compositions of shelter-like structures were largely different between rock climbers and bottom crawlers (Fig. 5), which was significant by PERMANOVA ( $p < 0.05$ , Table 4b). For rock climbers, holes and crevices on rocks were major potential shelters. However, potential shelters for bottom crawlers varied among species (Fig. 5) but roughly corresponded to their microhabitat use patterns (Fig. 4). The major shelter-like struc-

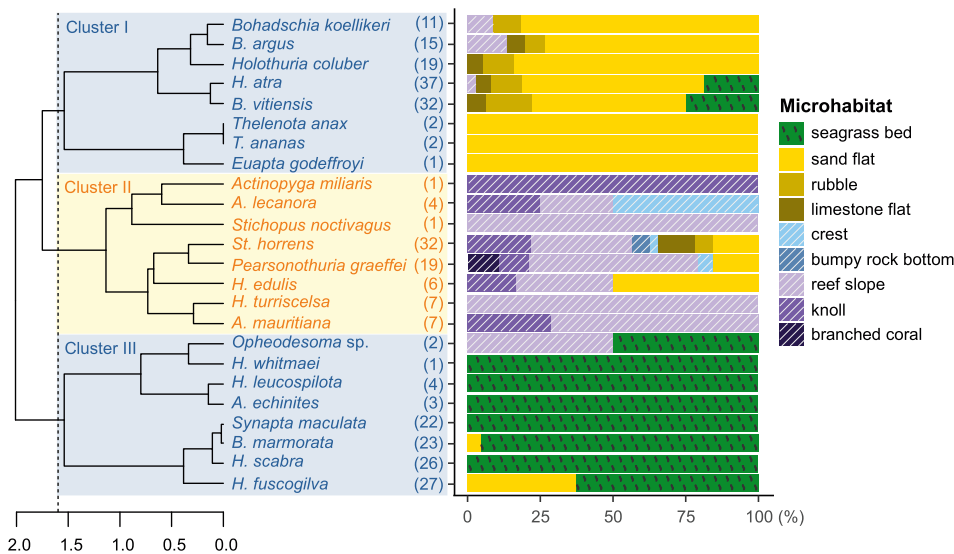


Fig. 4. Composition of microhabitat types for each species (cumulative bars) and Ward's clustering using Bray-Curtis dissimilarity (dendrogram). The number of individuals is shown in brackets after the species names. Species are clustered into 3 groups at a height of 1.6 (vertical dashed line). Ratios of use of 3-dimensional microhabitats (diagonal shading) were low ( $\leq 50\%$ ) and high ( $\geq 50\%$ ) for species in Clusters I and III (bottom crawler type, blue) and those in Cluster II (rock climber type, orange), respectively



Table 4. Result of permutational multivariate analysis of variance based on Bray-Curtis dissimilarities to compare patterns of (a) microhabitat use and (b) nearby shelters between the rock climber and bottom crawler species groups. Species composition of the rock climber and bottom crawler groups is shown in Fig. 4, based on preference of 3- and 2-dimensional microhabitats, respectively. df: degrees of freedom; SS: sum of squares; MS: mean square; **bold**:  $p < 0.05$ ; no. of permutations: 999

	df	SS	MS	Pseudo-F	R <sup>2</sup>	p
<b>(a) Microhabitat</b>						
Group	1	1.78	1.78	5.80	0.209	<b>0.001</b>
Residuals	22	6.75	0.30		0.791	
Total	23	8.52			1	
<b>(b) Shelter</b>						
Group	1	1.07	1.07	3.43	0.135	<b>0.01</b>
Residuals	22	6.86	0.31		0.865	
Total	23	7.93			1	

tures were the canopies of *Enhalus acoroides* for species mainly inhabiting the seagrass microhabitat. The sides of (and among) knolls or rocks, sides of (and among) rubble, and cavities under rocks or massive corals were major shelter-like structures for *B. argus*, *B. koellikeri*, and *H. atra*. All *H. coluber* individuals anchored the posterior body into a cavity under rocks or massive corals. Even though these bottom crawlers utilized 3-dimensional rocky and coral structures as shelters, they never climbed up

the structures away from the seabed. In PCO plots of both microhabitats (Fig. 6a) and shelters (Fig. 6b), rock climber species and bottom crawler species showed patterns that were relatively distinct from each other.

#### 4. DISCUSSION

##### 4.1. Classification of habitat use patterns

Our results demonstrated that the microhabitat use patterns of holothurians in tropical shallow areas were largely classified into bottom crawler and rock climber types, which preferentially utilized 2- and 3-dimensional microhabitats, respectively. There was little overlap of microhabitats between the 2 groups, although they coexisted in the same macrohabitats, such as the channel (CH) and outer reef (RE), where 3-dimensional structures and flat bottoms were mixed. This inference about the importance of topographical relief (flat or undulating) for separating holothurian habitats is slightly different from previous studies. Eriksson et al. (2012a) argued that the type of bottom substrate is a major

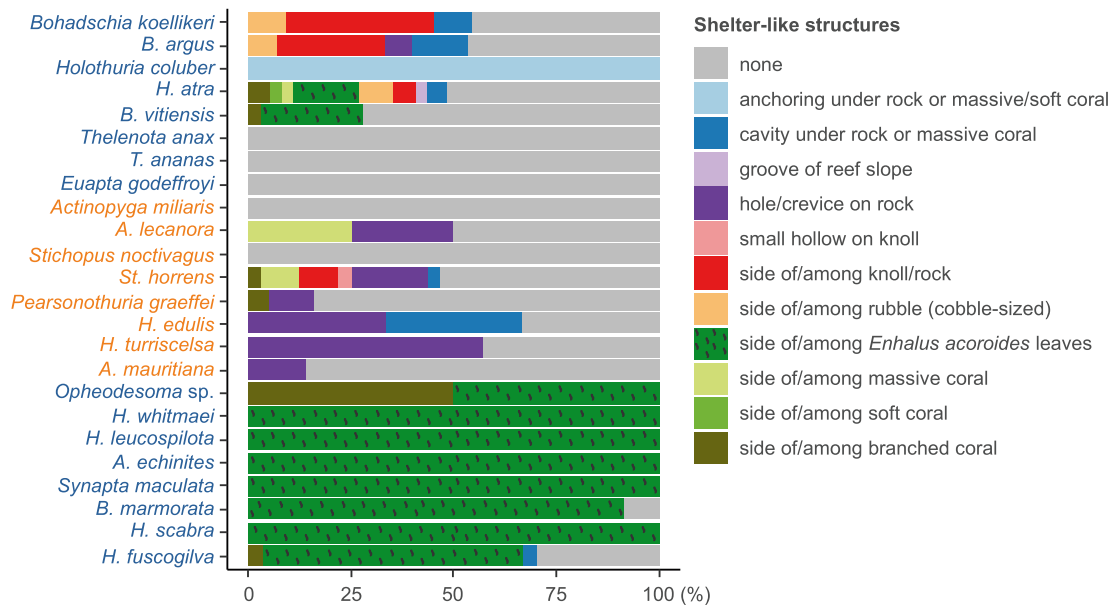


Fig. 5. Patterns of shelter-like structures closely adjacent to the observed individuals for each species. None indicates that there was no shelter-like structure nearby where the sea cucumber can hide, i.e. flat surface without shading structures. Note that sandy flat can be a shelter for some sand-burrowing species of sea cucumbers, but it was not evaluated as a shelter here. The number of individuals used for this analysis was the same as that shown in Fig. 4. Colors of species names correspond to bottom crawlers (blue) and rock climbers (orange), which are defined in Fig. 4 based on preference of 2- and 3-dimensional microhabitats, respectively

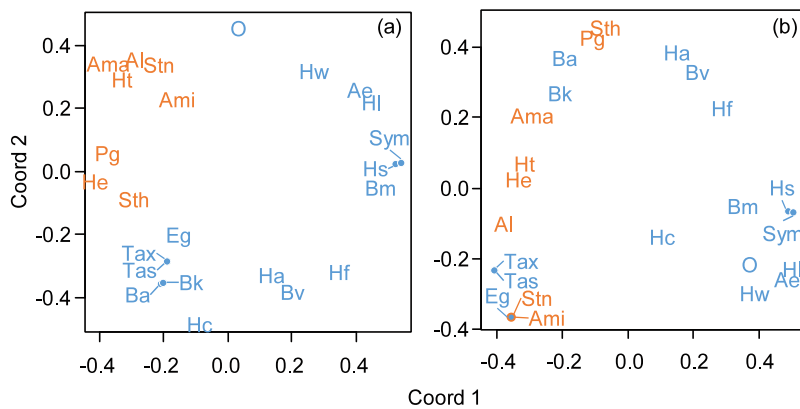


Fig. 6. Principal coordinate analysis plots for (a) microhabitat and (b) shelter use patterns of each holothurian species, based on Bray-Curtis dissimilarity. Ae: *Actinopyga echinites*; Al: *A. lecanora*; Ama: *A. mauritiana*; Ami: *A. miliaris*; Ba: *Bohadschia argus*; Bk: *B. koellikeri*; Bm: *B. marmorata*; Bv: *B. vitiensis*; Eg: *Euapta godeffroyi*; Ha: *Holothuria atra*; Hc: *H. coluber*; He: *H. edulis*; Hf: *H. fuscogilva*; Hl: *H. leucospilota*; Hs: *H. scabra*; Ht: *H. turiscelsa*; Hw: *H. whitmaei*; O: *Opheodesoma* sp.; Pg: *Pearsonothuria graefei*; Sth: *Stichopus horrens*; Stn: *St. noctivagus*; Sym: *Synapta maculata*; Tas: *Thelenota ananas*; Tax: *T. anax*. Blue and orange letters indicate bottom crawler and rock climber species of sea cucumbers, which are classified based on their microhabitat use patterns and correspond to Clusters I and III and to Cluster II in Fig. 4, respectively

factor, whereas relief is a relatively minor factor in separating habitats among holothurian species. This difference was because all the species examined in the habitat analysis by Eriksson et al. (2012a), i.e. *Bohadschia atra*, *Holothuria atra*, *H. (Microthele) fuscopunctata*, *H. (Microthele) nobilis*, *Stichopus chloronotus*, and *Thelenota ananas*, are usually found in relatively flat environments (Purcell et al. 2012), except for *St. chloronotus*, which also utilizes 3-dimensional microhabitats (Eriksson et al. 2012b). Therefore, relief is probably a more important factor in determining holothurian habitats than has been recognized previously, especially when considering diverse species, including those living in bumpy areas of the outer reefs.

Several factors are assumed as to why habitat use patterns were specific to either 2- or 3-dimensional microhabitats. The most relevant factor was preference for specific shapes and properties of the substrate, as has been shown for *Actinopyga echinites*, which prefers plate-like substrates of limestone or corals (Wiedemeyer 1994). This species is also found on other kinds of flat microhabitats such as reef flats, sandy beds, and seagrass beds (Massin & Doumen 1986, Kohler et al. 2009); seagrass beds are utilized mainly by small individuals as observed in the present study (Kohler et al. 2009). Such preferences for specific structures are closely related to their sheltering

behaviors. For example, among bottom crawlers, the sheltering sand-burrowing behavior by *H. scabra*, *B. marmorata*, *B. vitiensis*, and *B. koellikeri* (Yamanouchi 1956, Mercier et al. 1999, Kim et al. 2013) and anchoring behavior by *H. coluber* (the present study) and adult *H. leucospilota* (Bonham & Held 1963) are highly specialized to certain substrates for shelters. The sheltering of all rock climbers depends on the holes and shade on the surface of large structures (Graham & Battaglione 2004, the present study). Because adult holothurians generally have limited motility (Mercier et al. 2000a) and their behavioral ranges are restricted around shelters (Graham & Battaglione 2004) through diel migration between shelters and outside, these species-specific preferences for structures might have generated the 2 distinct patterns of microhabitat use.

Another relevant factor is the selectivity of substrate type for feeding. The types of feeding substrate by holothurians, such as benthic sediment or rock surface, are species specific and closely correspond to their macro- and microhabitat use patterns (Roberts & Bryce 1982). Some holothurians migrate and selectively feed on sediment patches rich in organic or microalgal contents, as reported for *St. chloronotus*, *H. atra*, *H. nobilis* (original description), *St. variegatus* (original description) (Uthicke & Karez 1999), *Australostichopus mollis* (Slater et al. 2011), and *H. sanctori* (Navarro et al. 2013), which determines their distributions at the microhabitat level. Sediment patch selectivity can further affect broader macrohabitat-scale distributions, as in the case of *A. mollis* (Slater et al. 2010), but such an effect is not always apparent for tropical holothurians (Tanita & Yamada 2019). In addition, holothurians are also selective for the physical properties of the substrate, such as grain size (Altamirano et al. 2017); in fact, distributions of *H. scabra*, *H. atra*, and *H. edulis* are related to these sediment characteristics (Mercier et al. 2000a, Disanayake & Stefansson 2012). Considering these kinds of strong selectivity to substrate properties by holothurians, the largely different environments between 2- and 3-dimensional microhabitats (e.g. only the former contains sandy bottoms) could be a barrier for holothurian distributions in terms of feeding environments. Investigation of differences in food sources (e.g. by stable isotopes) between rock

climber and bottom crawler species may provide further insight into this matter.

Regarding the 2 types of habitat utilization (i.e. rock climbers and bottom crawlers), species within the genera *Bohadschia* (also see Kim et al. 2013) and *Thelenota* are commonly bottom crawlers. However, both types of species are included within the genera *Actinopyga*, *Holothuria*, and *Stichopus*; although all species of *Stichopus* in this study were rock climbers, *St. herrmanni* inhabits flat sandy bottoms (Eriksson et al. 2013, Wolfe & Byrne 2017a). Presently, it is unclear whether some morphological characteristics are associated with the difference between the 2 groups. Although dense tube feet and strong suckers are present in some rock climber species, such as *A. mauritiana*, which is distributed in the upper reef slopes, these morphological characteristics are not consistent among other rock climber species and are also found in some bottom crawlers (e.g. *T. ananas*).

#### 4.2. Variability of habitat use patterns among *Bohadschia* species

Habitat use patterns of 4 bottom crawler species of the genus *Bohadschia* were distinguished from each other by the composition of their macrohabitats. As reported previously (Purcell et al. 2012, 2016), *B. argus* only appeared in the coral reef area of the channel and outer reef macrohabitats (CH and RE) with sand, rubble, and limestone flats and was not found in the shallow and muddy nearshore and seagrass macrohabitats (SH and SG), which was distinct from the other 3 *Bohadschia* species. *B. vitiensis*, *B. koellikeri*, and *B. marmorata* are sand-burrowing species (Kim et al. 2013) and commonly inhabited sand flats in the present study. Among them, *B. marmorata* showed a smaller body size than the other 2 species, and their distributions were limited to shallow seagrass beds (SG), which is consistent with previous studies (Clouse 1997, Purcell et al. 2012, Kim et al. 2013). *B. koellikeri* has recently been separated from *B. vitiensis* after taxonomical revision (Kim et al. 2013), and knowledge on ecological differences between the 2 species is lacking. In the present study, however, differences were observed in macrohabitats between *B. vitiensis* and *B. koellikeri*; distribution of *B. vitiensis* was limited to the harbor (SG, SH, and CH), and densities were higher than those of *B. koellikeri*, whereas *B. koellikeri* was also distributed outside the harbor (RE) but not found in SG. In outer reef areas, *B. koellikeri* was found on microhabitats of flat bottoms in grooves between the

spurs of reef slopes, or between knolls or rubble, similar to *B. argus*. Therefore, the macrohabitat use patterns of *B. koellikeri* covered intermediate ranges between those of *B. vitiensis* (relatively inshore) and *B. argus* (relatively offshore). This variability of habitats among species implies necessity of species-based management of these resources. These characteristics of the macrohabitat patterns, however, might be a specific trend in Buena Vista and, thus, should be further confirmed by broader-scale surveys.

#### 4.3. Seagrass meadows as a nursery

In the present study, the holothurian population in SG was mainly composed of small individuals, and the seagrass meadow was considered as a nursery for these species. Among the holothurian species, *H. atra* and *H. fuscogilva* showed increased body lengths from SG to SH and CH, which implied that these species migrated from seagrass beds (SG) through intermediate areas (SH) to adjacent deeper areas (CH) as they grew. The role of seagrass meadows as nurseries is well known in many species of holothurians (Shiell 2004). In particular, *H. scabra* utilizes seagrass leaves as a substrate for its settling larvae (Mercier et al. 2000b) and stays in seagrass meadows until migration to deeper areas during growth (Mercier et al. 2000a). A similar migration pattern has been reported for *H. fuscogilva* (Reichenbach 1999), which is consistent with our results. Migration to deeper sites through growth is to some extent a common pattern which can be seen for other holothurians such as *St. herrmanni* (Conand 1993, Wolfe & Byrne 2017b) and *Cucumaria frondosa* (Hamel & Mercier 1996), while such a pattern is not found for *A. mollis* (Slater et al. 2010) or for the same species (*St. herrmanni*) in other areas (Eriksson et al. 2013). For *H. atra*, asexual fission (Bonham & Held 1963) as well as migration might be responsible for the variability of body lengths among macrohabitats because this species adjusts its body size via fission for adaptation to the environment (Uthicke 2001, Lee et al. 2008), and large and small morphotypes are usually found in subtidal and intertidal areas, respectively (Chao et al. 1993).

The major potential shelter in SG was seagrass leaves. The effect of seagrass leaves as a shelter has been proven for echinoids (*Tripneustes gratilla*) (Eklöf et al. 2009) and is important for small individuals of holothurians in this area because they are vulnerable to similar predators (mainly triggerfish Balis-

tidae) (Dance et al. 2003, Eklöf et al. 2009). Thus, these shelters might have partly contributed to the high densities of small individuals in this area. In addition, recent studies on the isotopic ratios of carbon and nitrogen indicate the importance of organic matter produced by seagrass as a food source for holothurians (Lepoint et al. 2000, Costa et al. 2014, Palomar-Abesamis et al. 2017, Belbachir et al. 2019); therefore, high productivity in seagrass meadows is likely also responsible for the high densities.

#### 4.4. Density and habitat of *Stichopus horrens*

In the present study, we conducted nighttime long-transect surveys to examine low-density nocturnal populations in outer reefs and revealed that the nocturnal species *St. horrens* was dominant in CH and RE, the densities of which were 4.2 and 2.5 ind. ha<sup>-1</sup>, respectively. However, these densities were 4 orders of magnitude lower than the highest values reported in Fiji and the Galápagos Islands (Shepherd et al. 2003, Hearn & Pinillos 2006, Lalavanua et al. 2017). One reason for these low densities might be limited recruitment, as juveniles were very rare during our surveys. This was in contrast to previous reports of a high density of juveniles of this species (as high as 2.9 ind. 100 m<sup>-1</sup>) in inner reefs (Palomar-Abesamis et al. 2017). Significant differences in microhabitats have been suggested between the 2 environments: in inner reefs, previous studies consistently reported that the bottoms of rubble and sand, sometimes with seagrass cover, were microhabitats for this species (Harriott 1980, 1997, Kerr et al. 1993, Palomar-Abesamis et al. 2017), where these juveniles utilize numerous small interstices between rubble, suitable for their body sizes, and vegetation of seagrass and macroalgae (Palomar-Abesamis et al. 2017, 2018). Alternatively, in outer reefs, their microhabitats were limited to much larger rocky structures, such as crevices and hollows on knolls, crest, and reef slopes. These differences in microhabitats might be related to the different abundances of juveniles in the 2 environments. Although the present study did not evaluate compositions of microhabitats and shelters available within each macrohabitat, evaluation of these availabilities could reveal preferences of the sea cucumber to specific types of microhabitats or shelters (Slater et al. 2011, Dissanayake & Stefansson 2012).

There were, however, also potentials for underestimation by missing sea cucumbers during the surveys, especially for small juveniles, because of our methodology (night snorkeling with long transects)

and the environments with deep sites and complex topography with many blind spots. In addition, it is unclear how many individuals of the total population left their shelters during our surveys. Variable factors such as time, moon phase, tide, temperature, salinity, predators, and body sizes can affect the diel activity of sea cucumbers (Yamanouchi 1939, Mercier et al. 1999, 2000a, Wolkenhauer 2008, Purcell 2010). These factors may have affected our results, particularly in the SH and SG, where sampling was conducted on a single day. Therefore, the densities shown in the present study should be regarded as conservative values.

#### 4.5. Implications for conservation

The present study observed variation of habitats among holothurian species at both macro- and microhabitat levels in Buena Vista. Moreover, topographic relief and its role as shelter were revealed to be important factors to define holothurian microhabitats, in addition to type of bottom substrate. These findings have implications for understanding ecosystem services of the area as holothurian habitats, which is required in areal-based management (e.g. setting MPAs in CBRM).

In addition, it is beneficial to focus on the roles of each habitat in relation to growth stages of holothurians. Holothurian resources in SG were mostly composed of individuals smaller than the size limits; therefore, SG was considered a less valuable fishing site. Nevertheless, the high-density population of small individuals of holothurians in SG would be significantly important for the resource over the entire area, as it would supply spillover of adults to the outer areas (Purcell et al. 2010), as observed for *H. fuscogilva* and *H. atra*, if properly protected within their habitats.

Preferably, MPAs should protect a large enough population of holothurians to enable a resource recovery effect through successful reproduction. For this purpose, correct estimation of densities and abundance of holothurians is essential. Some precision issues, however, remain in our density estimation: (1) the large errors of density estimates in SG, which are attributable to intertransect variability in the species composition of holothurians within SG, and (2) a single transect (no replication) in SH, which fails to eliminate spatial confounding. Holothurian distributions are highly heterogeneous, affected by many environmental factors at various spatial scales, only some of which were investigated in the present study. In future research, consideration of the spatial

scales of these variabilities and sampling of a high enough number of replicates would help to more precisely estimate densities and abundance and to elucidate other causative factors of the spatial heterogeneity of holothurian distributions.

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