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Sponge species composition, abundance, and cover in marine lakes and coastal mangroves in Berau, Indonesia

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Abstract

This is the first study to show that mangroves in the Indo-Pacific harbor a diverse array of sponge species. Our aim was to quantify variation in the species composition, abundance and cover of sponges in two marine lakes (Kakaban lake and Haji Buang lake) and adjacent coastal mangroves in the Berau region, East Kalimantan, Indonesia. We recorded a total of 115 sponge species, 33 of which were restricted to Kakaban lake, 18 to Haji Buang lake and 30 to coastal mangroves. Only 13 species were shared among all three locations. Assemblages of the two marine lakes at 10 km distance were more similar to each other than to the coastal mangrove systems at just 200-500 m distance. Our results show that marine lakes may represent a distinct habitat from coastal mangroves with significantly higher sponge cover and abundance as well as a markedly different species composition. In both lake and outer coastal mangrove habitats there was a pronounced gradient in composition away from the shore with the primary difference between hard (root or rock) and soft substrates (mud or sand). Each substrate type harbored different sets of species in both lake and outer mangrove habitats. Time was not a significant predictor of variation in sponge species composition, abundance and cover between semi-permanent transects sampled in 2008 and 2009. The isolated habitat of marine lakes with many new species to science warrants further study and conservation.

Keywords: mangrove roots • species assemblage • Principal Coordinates Analysis • Borneo • East Kalimantan • Kakaban • anchialine systems

Introduction

Mangrove forests grow pantropically on protected coasts and can host diverse colorful assemblages of epibionts (Farnsworth & Ellison 1996, Diaz et al. 2004). The vast majority of mangrove-epibiont studies have been conducted in the Caribbean where sponges together with algae, cnidarians and ascidians are the most dominant taxa covering mangrove roots (e.g. Ellison et al. 1996, Farnsworth & Ellison 1996, Diaz 2005). There is a facultative mutualism between sponges and the mangroves: mangroves provide the only hard substrate for sponges in the mangrove systems, and passively leak carbon from their roots that is assimilated by sponges, while sponges directly protect roots from isopod attack and enhance cable root growth by inducing adventitious rootlet formation (Ellison et al. 1996). Sponge communities in Caribbean mangrove systems are spatially heterogeneous, whereby a species can dominate one site, and be absent from another (Farnsworth & Ellison 1996, Diaz et al. 2004, Hunting et al. 2008, Guerra-Castro et al. 2011). Sponge communities in mangroves are, furthermore, distinct from those in reefs and contain species that appear to be specifically adapted to survive extremes in salinity, temperature and sedimentation (Wulff, Rützler 1995, Wulff 2000, Engel & Pawlik 2005, Wulff 2005b, Pawlik et al. 2007, Nagelkerken et al. 2008). Biotic factors such as predation and competition for space with other marine invertebrates likely limit their distribution in coral reefs (Nagelkerken et al. 2008, Pawlik 1997, Dunlap & Pawlik 1997, Aerts & van Soest 1997, de Voogd et al. 2004). Competition for space in the mangroves is, however, also intense as there is limited hard substrate which most sponges require to survive, favoring species with high growth rates and the production of possible allelochemicals to ward off spatial competitors (Engel & Pawlik, 2005; Wulff 2006, Nagelkerken et al. 2008). The composition of these epibiont communities can either be seasonally dynamic (Florida, Jamaica) or be stable over longer time periods (Belize, Venezuela) (Sutherland 1980, Bingham & Young 1995, Farnsworth & Ellison 1996, Wulff 2004, Pawlik et al. 2007).

Indonesia contains the most diverse mangrove ecosystems in the world covering an area of almost 50000 km² (Spalding et al. 1997, Alongi 2002), but to date there have been no comprehensive studies of mangrove epibionts. A recent review of the habitat function of mangroves for terrestrial and marine fauna suggested that the mangrove systems in the Indo-Pacific may not house the high diversity of sponges found in the Caribbean (Nagelkerken et al. 2008). Indeed, East African mangroves have a low diversity of sponges with just three species (Barnes 1999). Furthermore, two surveys of the faunal diversity in mangroves in the Indian Ocean and Malaysia did not record any sponge species associated with mangrove roots (Rützler 1964, Sasekumar & Chong 1998). There is, however, a relative paucity of information on sponges and mangroves in the Indo-Pacific, e.g. only three published papers in the Indo-Pacific referred to sponges and mangroves compared to over 40 for the Caribbean. In Indonesia, mangroves do not only occur along coasts, but also within marine lakes (Becking et al. 2011, *CHAPTER 1*). Marine lakes are anchialine systems, which are small bodies of landlocked seawater isolated to varying degrees from the surrounding marine environment (Holthuis 1973, Hamner & Hamner 1998, Colin 2009, Becking et al. 2011, *CHAPTER 1*). The marine character of these systems is maintained by subterranean tunnels, fissures, or small dissolution channels in the surrounding rock, connecting the lakes to the adjacent sea, and as such display a wide variety in the degree of connection to the sea and environmental regimes within the lakes (Hamner & Hamner 1998, Cerrano et al. 2006, Azzini et al. 2007, Becking et al. 2011, *CHAPTER 1*). The total number of marine lakes worldwide is estimated at only ~ 200 with clusters of ten or more lakes occurring in areas with a karstic limestone landscape such as Croatia, Bermuda, Vietnam, Palau, and Indonesia (Dawson et al. 2009). Preliminary surveys of macro-biota in marine lakes in Indonesia, Vietnam and Palau have shown that sponges, algae, ascidians

and mollusks are the most dominant taxa in terms of abundance and diversity (Hoeksema 2004, Cerrano et al. 2006, Colin 2009, Becking et al. 2011, *CHAPTER 1*). This enclosed environment has set the stage for small, isolated, rapidly evolving populations, and possibly endemic (sub)species (Holthuis 1973, Maciolek 1983, Tomascik & Mah 1994, Franssen & Tomascik 1996, Massin & Tomascik 1996, Dawson & Hamner 2005). The present study is the first comprehensive assessment of sponges in marine lakes and mangroves in Indonesia. Our aim is to quantify spatial and temporal variation in the abundance and species composition of sponges in marine lakes and coastal mangroves in the Berau region, East Kalimantan, Indonesia. We relate variation in composition to the habitat (marine lake or coastal mangrove), substrate and sampling event. Our aims are to 1) assess if sponge composition in the marine lakes is distinct from that in the outer coastal mangroves, 2) identify species that are unique to each major habitat, 3) relate variation in sponge abundance, cover and species composition to substrate type and cover of other spatial competitors, and 4) determine if these sponge communities are stable over longer time periods (> 6 months).

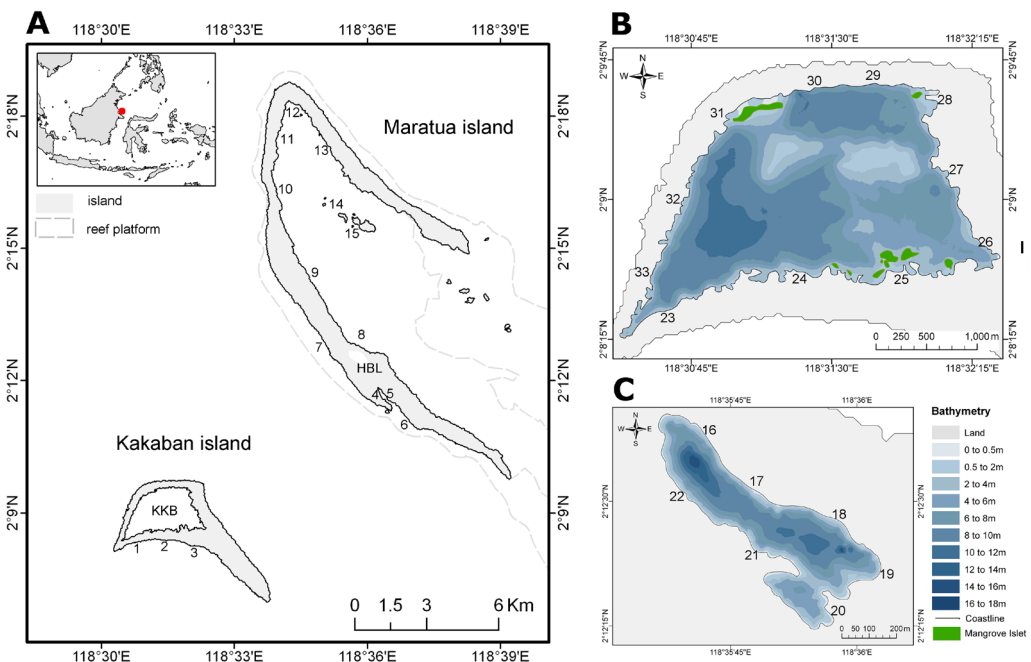


Figure 1 A Map of Kakaban and Maratua islands in Berau region, East Kalimantan Province, Indonesia, **B** bathymetry map of Kakaban lake, **C** bathymetry map of Haji Buang lake (note that scale differs between B and C). Sample site locations indicated with numbers 1-33. Sites 1, 2, 3, 6, 7, 10, 11, 12, and 14 in coastal mangroves contained no sponge epibionts.

Material & Methods

Study area

The comparison of sponge fauna was between mangroves within the marine lakes, and mangroves along the coast (and other substrata that co-occur in both habitats). We surveyed marine lakes and coastal mangroves of the islands Kakaban and Maratua in the Berau region, East Kalimantan Province (Fig. 1). These islands fall within the Berau Marine Protected Area and provide a setting to survey sponge assemblages at varying scales (metres to kilometres) in marine lakes and coastal mangroves (Tomascik et al. 1997, Becking et al. 2011, CHAPTER 1). The annual rainfall in Berau is approximately 2000 mm with no particular rainy season, though there is less rainfall June-September (average 110-125 mm per month) compared to the rest of the year (average 150-200 mm per month) and an increase of strong winds from the North between December-March (Tomascik et al. 1997, Mantel 2001, Renema 2006).

A general description of the lakes of Kakaban and Maratua islands is provided by Tomascik & Mah (1994), Tomascik et al (1997) and Becking et al. (2011). Kakaban island is a trapezoidal shaped island with a protected southern coast that is fringed by mangroves dominated by *Avicennia marina* with aerial roots exposed to air at low tide. In the centre of Kakaban island is a large, approximately 4 km², marine lake with the southern, western and eastern coasts fringed by mangroves dominated by *Bruguiera gymnorrhiza* with roots submerged in the water (Fig 2D); the northern coast is a predominantly rocky shore. The dominant algae in this lake are species of the genus *Halimeda*. Bathymetric surveys revealed that Kakaban lake averages 8 m depth, with a 12 meter deep depression at the western portion of the lake (Figure 1B). The tidal amplitude in Kakaban lake (19 cm) is dampened to 11% of adjacent sea amplitude (200 cm) and the tidal phase has a delay of 3 h 30 min compared that to the surrounding sea, indicating that there is little connection between the lake and the sea (Becking et al. 2011, CHAPTER 1).

Maratua is a horse-shoe shaped island that partly encloses a large lagoon of approximately 29.5 x 6.5 km with a depth of 0.5-5 m at low tide. Parts of the lagoon are rimmed by patches of *Avicennia marina*, *Sonneratia alba*, and *Rhizophora mucronata* mangroves with aerial- or proproots exposed to air at low tide (Fig. 2B). The mangrove transitions to a sandy reef flat away from the coast. On Maratua island there are at least nine anchialine systems, of which Haji Buang lake is the largest marine lake (Fig 2A). Haji Buang lake is an elongated lake of 0.14 km² surface area located on the western arm of Maratua. Haji Buang lake averages 10 m depth, with two deep depressions at the northern (19 m) and southern (15 m) end of the lake (Figure 1C). The largest part of the lake's coastline is formed by limestone rock with only a small patch of the southern coast fringed by mangroves (predominantly *B. gymnorrhiza*) with a seagrass field (*Enhalus* sp.) in front. The dominant algae in this lake are species of the genus *Caulerpa*. The tidal amplitude in the lake (90 cm) is dampened to 48% of the adjacent sea amplitude (200 cm) and the tidal phase had a delay of 2 h 30 min (Becking et al. 2011, CHAPTER 1), indicating that the connection to the sea is limited, but higher than in Kakaban lake. Coastal mangrove were patchy along the coasts of Maratua and Kakaban islands. In addition to this, sponge abundance varied greatly within the mangroves; a number of locations along the coast of Maratua and Kakaban did not contain a single sponge. Transects were laid down randomly in the coastal mangroves, but in 9 sites out of 15 we recorded no sponges (Fig. 1).

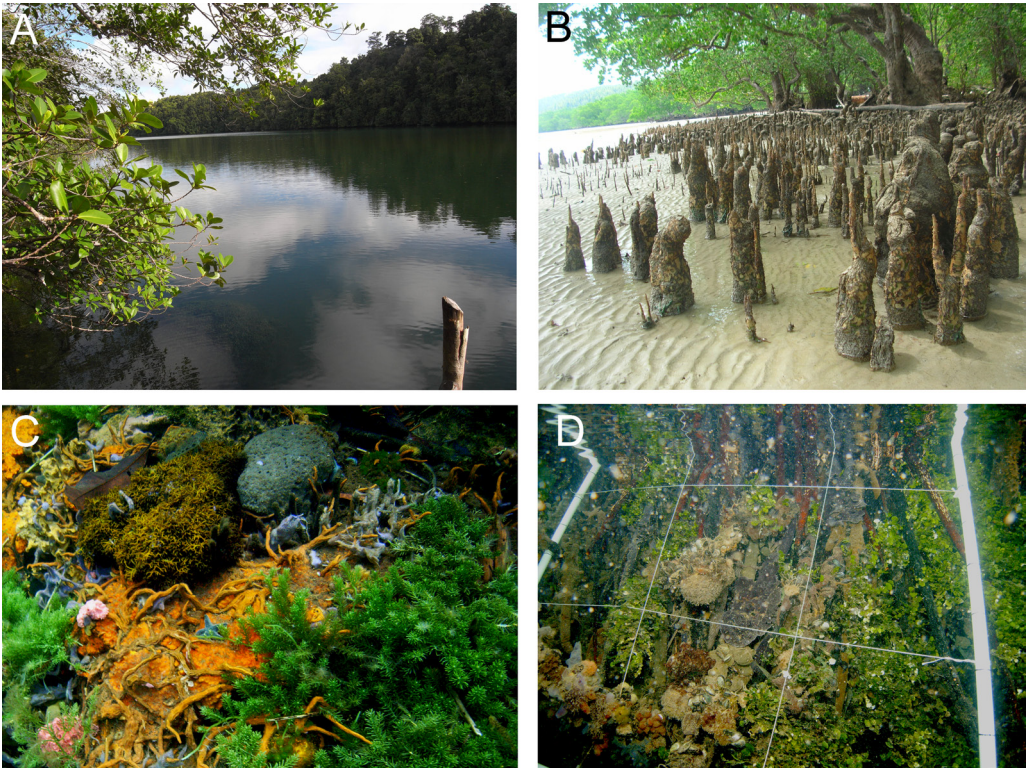


Figure 2 Images of the two habitats (marine lakes and outer coastal mangroves) in Berau, East Kalimantan, Indonesia. **A.** Haji Buang marine lake, **B.** coastal mangrove in Maratua bay with roots fully exposed to air and sun at low tide, **C.** Sponge and algae cover in Haji Buang Lake, **D.** ‘root-wall’ and quadrat in mangroves of Kakaban lake.

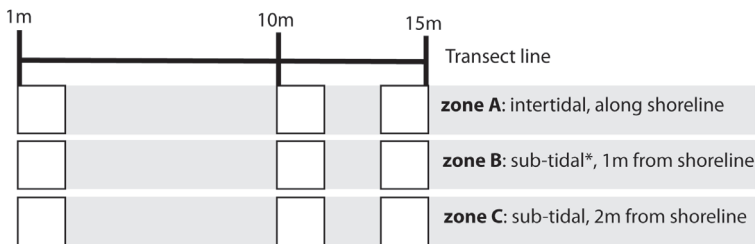


Figure 3 Sketch of experimental set-up. A 15 m transect line was placed along the shore, squares represent 1x1m quadrats that were placed along the transect and away from shore. Not to scale. *zone B was intertidal in coastal mangrove habitat.

Data collection

Transects

Study sites were randomly distributed within Kakaban lake, Haji Buang lake, and Maratua Bay (Fig. 1 & 2), within each site three transects were surveyed (Fig. 3). Some sites were eventually omitted from analysis because they contained no sponges. Likewise some transects were omitted because they contained less than 5 sponge individuals. We recorded data in semi-permanent transects in two periods: between 30 August – 20 September 2008 and 10 - 31 May 2009. The location of the transect was marked with biodegradable red tape and the coordinates were located with a handheld GPS (Garmin GPS60) with 5m variation. The roots of the mangroves in the lakes were so intertwined/meshed, that they created a ‘wall-like’ structure (Fig. 2D), which did not allow us to use the more common method of quantifying mangrove epibiont species richness and diversity by haphazardly selecting roots along a transect to be surveyed (e.g. Ellison & Farnsworth 1992, Farnsworth & Ellison 1996, Hunting et al. 2008). An alternative method was thus devised to quantify epibiont species abundance and composition on these ‘root-walls’ that enabled a consistent comparison with the variety of substrates that occur in the lakes and the coastal mangroves (e.g. rock-wall, sand, reef flat): a 15m transect was placed along the shore and three 1 m² quadrats were surveyed at the 1m, 10m and 15m mark, this was repeated three times away from the shore in order to determine if there was a zonation in species composition with distance from shore (Fig. 3). Zone A: quadrat on the shore within the tidal zone; zone B: 1m offshore, following the contour of the bottom or directly in front of the mangrove roots; Zone C: 2m offshore, following the contour of the bottom. The quadrats in Zone A were fully exposed to air at low tides in the coastal mangrove systems, were mostly (75-90%) exposed to air in Haji Buang lake, and were only partially (5-10%) exposed to air in Kakaban lake. The maximum depth of the quadrat was recorded, as well as the general substrate within the quadrat (root, rock, root & rock, sand, mud). The percentage cover within the quadrat was measured visually with the aid of 33x33 cm subdivisions of the quadrat. The following categories of cover were recorded: algae, ascidians, coral, mud, mussels, rock, root, sand, seagrass and sponges. These classes of higher taxonomic groups of associated organisms were selected based on preliminary data that showed that these groups were abundant in marine lakes (Hoeksema 2004, Cerrano et al. 2006, Colin 2009, Becking et al. 2011, CHAPTER 1) and potentially may affect the species composition, abundance and cover of sponges. Subsequently, sponge species and their abundance (number of individuals per species) were recorded within the 1 m² quadrats. Only sponge individuals larger than 1 cm² were included in the present study. We also recorded what species were exposed to air at low tide.

Sponge species were visually identified in the field. Of all species two or more vouchers were collected for closer examination of skeletal structure for taxonomic identification. Sponges were identified based on spicule characters and skeletal structure by L.E. Becking and N. J. de Voogd, preserved in 70% ethanol and deposited in the Porifera collection of the Naturalis Biodiversity Center (catalogued as RMNH POR). Ideally, the specimens were identified to species level, however many of the surveyed sponges belonged to novel or little known species and rare genera, so these were preliminary assigned to morphospecies awaiting formal description. Some sponges consisted of a species complex and could not be separated visually in the field; these were grouped together such as *Placospongia* spp (consisted of *P. carinata*, *P. melobesoides* and *P. mixta* (CHAPTER 5) and *Cinachyrella* spp (consisted of *C. porosa*, *C. australiensis*, *C. paterifera* (Santodomingo & Becking *in prep*).

The salinity, temperature and pH was measured twice in each location at each transect in both sampling

periods with a handheld multimeter YSI63-50. Where possible, measurements were made at the surface, 1m and 2m depth.

Data analysis

Abbreviations used for locations: KKB - Kakaban lake, HBL - Haji Buang lake, BAY - coastal mangrove habitat on Maratua island.

Sponge composition

Data matrices of species abundance per transect were $\log_{10}(x + 1)$ transformed and distance matrices constructed using the Bray-Curtis index with the *vegdist* function in the *vegan* package in R (Oksanen et al. 2009). The Bray-Curtis index is one of the most frequently applied (dis)similarity indices used in ecology (Legendre & Gallagher 2001, Cleary 2003, Cleary et al. 2005, de Voogd et al. 2006). Matrices were constructed for 1. all transects and 2. all transects within each location (KKB, HBL and BAY) separately. Transects with five or fewer individuals (24 out of 153 transects) were removed prior to analysis. Of the 15 transects dropped, 12 were in Kakaban and 3 in Maratua; 14 of the transects were, furthermore, on a mud substrate and one on a rock substrate. After removal, 60, 33 and 36 transects from KKB, HBL and BAY (respectively) remained for the analyses. Variation in sponge species composition among location class groups (KKB-mud, KKB-root, KKB-rock, HBL-mud, HBL-root, HBL-rock, BAY-reef, BAY-root, BAY-sand) and sample year was assessed with Principal Coordinates Analysis (PCO) using the *cmdscale* function in R with the Bray-Curtis distance matrix as input. Variation among location and year was tested for significance using the *adonis* function in *vegan*. In the *adonis* analysis, the Bray-Curtis distance matrix of species composition was the response variable with location and sample year as independent variables. We also included the interaction term between location and year. The number of permutations was set at 999; all other arguments used the default values set in the function. For the analyses within each habitat, we followed the above analytical approach but used the *adonis* analysis to test for significant variation in substrate (mud, rock and root for KKB and HBL; reef, rock and root for BAY) and sample year. We also included the interaction term between substrate and year. The *adonis* function is an analysis of variance with distance matrices using permutations that partitions distance matrices among sources of variation; in this case location class and sampling year. In addition to the above, we also tested for associations between species composition and sample depth and measured substrate class variables, namely the percentage cover of **mussels, algae, soft substrate (mud and sand), rock, mangrove roots, seagrass, ascidians, corals and sponges**. These were fit onto PCO ordinations of each habitat with the *envfit* function in *vegan*. Using the *envfit* function, we also tested for significant relationships between these variables and PCO ordinations of sponge composition using 999 permutations; all other arguments in the function were left as default. The contribution of sponge species to the ordinations was assessed using weighted averages scores for the first two axes of each ordination with the *wascor* function in the *vegan* package. Detailed descriptions of the functions used here can be found in R (e.g., *?cmdscale*) and online in the reference manuals (e.g. <http://cran.r-project.org/web/packages/vegan/index.html>; checked 2011 04 08).

In addition to environment and time, spatial processes may also play an important role structuring assemblages. We tested for an effect of space on species composition using principal coordinates of neighbor matrices (PCNM), a novel method for quantifying spatial trends across a range of scales. PCNM is based on eigenvalue decomposition of a truncated matrix of geographic distances among sampling sites (Borcard & Legendre 2002, Dray et al. 2006). Significant PCNM eigenvectors were selected using the PCNM function

with 999 permutations in the PCNM package in R. Additional arguments for the PCNM function included Hellinger transformed matrices of species abundance and distance matrices (longitude, latitude); analyses were run for each location (KKB, HBL and BAY) separately. The forward selection test used was based on a novel forward selection procedure that corrects for the inflated Type I error and overestimation of explained variance associated with classical forward selection (Blanchet et al. 2008). The PCNM package is freely available at the website of Pierre Legendre (<http://www.bio.umontreal.ca/legendre/indexEn.html>, last checked: 20-09-2011)

Sponge abundance and cover

After testing for normality with the *shapiro.test* function in R (all tests deviated significantly ($P < 0.001$) from a normal distribution), we tested for significant differences in sponge abundance and cover at the transect level among substrate type (mud, rock and root for KKB and HBL and reef, rock and root for BAY) and sampling year within locations (KKB, HBL and BAY) with 'distribution free' *Adonis* tests using the *adonis* function in *vegan* (Oksanen et al. 2009). In the *adonis* analysis, the Euclidean distance matrix of sponge abundance or sponge cover was the response variable with substrate type and sample year (2008 or 2009) as independent variables. We also included the interaction term between substrate type and depth. The number of permutations was set at 999; all other arguments used the default values set in the function.

Table 1 Recorded species in marine lakes and mangroves in East Kalimantan, Indonesia. Majority of marine lake species are undescribed, therefore many species are denoted with 'sp.' or 'aff.'. Given are the species codes that are used in the methods and results section, whether a species was recorded exposed to air (exp.), the occurrence on substrate type (root, rock, sand, mud, reef), and the occurrence in the three locations of this study Kakaban lake (KKB), Haji Buang lake (HBL), and the costal mangroves of Maratua island (BAY). See appendix 1 for images of marine lakes species.

code	species	exp	substrate	KKB	HBL	BAY
ASTROPHORIDA						
Ancorinidae						
St-sp	<i>Stelletta</i> sp. "icing"	no	root/rock	•	•	
Chondrillidae						
Ch-ch	<i>Chondrilla</i> aff. <i>chucala</i>	yes	rock	•	•	
Ch-bl	<i>Chondrilla australiensis</i>	yes	root/rock	•	•	•
Geodiidae						
Ge-bl	<i>Geodia</i> sp. "black"	yes	root/rock	•		
Ge-ch	<i>Geodia</i> sp. "chimney"	yes	rock		•	
Ge-ye	<i>Geodia</i> sp. "yellow"	yes	root/rock	•		
CLATHRINIDA						
Clathrinidae						
Cl-wh	<i>Clathrina</i> sp. "white"	no	root/rock	•	•	
Cl-ye	<i>Clathrina</i> sp. "yellow"	no	rock	•		
DENDROCERATIDA						
Darwinellidae						
Da-sp	<i>Darwinella</i> aff. <i>gardineri</i>	yes	root/rock	•	•	
De-bl	<i>Dendrilla</i> sp. "black"	no	root	•	•	
De-pa	<i>Dendrilla</i> sp. "pale"	no	root	•		
De-pu	<i>Dendrilla</i> sp. "purple"	no	root	•		
Dictyodendrillidae						
Ac-bu	<i>Acanthodendrillasp.</i> "burgandy"	no	root	•		
Ch-go	<i>Chelonaplysillasp.</i> "gold"	no	root	•		
Sa-gr	<i>Spongionella</i> sp. "green"	no	root	•	•	
Sa-pu	<i>Spongionellasp.</i> "purple"	no	root	•	•	
DICTYOCERATIDA						
Dysideidae						
Dy-bl	<i>Dysidea</i> sp. "blue"	yes	root/rock	•	•	
Dy-ta	<i>Dysideasp.</i> "tan"	no	root/rock	•		
Dy-wh	<i>Dysideasp.</i> "white"	no	root/rock	•	•	
La-bl	<i>Lamellodysidea</i>	yes	root/rock	•		
La-he	<i>Lamellodysidea herbacea</i>	yes	rock/sand			•
Irciniidae						
Ir-sp	<i>Ircinia ramosa</i>	yes	rock/sand			•
Spongiidae						
Sp-br	<i>Spongia</i> sp. "black"	no	rock	•		

code	species	exp	substrate	KKB	HBL	BAY
Sp-sh	<i>Spongia</i> sp. "shiny"	no	rock		•	
Sp-fs	<i>Spongia</i> sp. "fistules"	yes	rock	•		
Sp-do	<i>Spongia ceylonensis</i>	yes	sand/reef			•
Thorectidae						
Ca-bl	<i>Cacospongia</i> sp. "shiny"	yes	root/rock	•		
Se-ho	<i>Cacospongia</i> sp. "honeycomb"	no	rock		•	
Se-sp	<i>Semitaspongia</i> sp. "black"	no	root	•		
Sm-sp	<i>Smenospongia</i> sp. "beige"	yes	root/rock		•	
HADROMERIDA						
Clionidae						
Sp-pe	<i>Cliona peleia</i>	yes	rock	•	•	•
Cl-or	<i>Cliona</i> sp. orange"	no	rock	•	•	
Sc-va	<i>Sphaciospongia vagabunda</i>	yes	sand/reef			•
Placospongiidae						
Pl-cx	<i>Placospongia</i> spp.	yes	root/rock/mud/reef	•	•	•
Spirastrellidae						
Si-de	<i>Spirastrella</i> aff. <i>decumbens</i>	yes	root/rock	•	•	•
Si-gr	<i>Spirastrella</i> aff. <i>solida</i>	yes	root	•		
Si-or	<i>Spirastrella</i> sp. "orange"	yes	root/rock	•		
Si-tu	<i>Spirastrella</i> sp. "tubes"	yes	rock		•	
Suberitidae						
Ps-sp	<i>Pseudosuberites andrewsi</i>	yes	rock		•	
Su-di	<i>Suberites diversicolor</i>	yes	root/rock	•	•	•
Tethyidae						
He-sp	<i>Laxotethya</i> sp. "spaghetti"	no	rock/mud	•		
Te-as	<i>Tethytimea</i> aff. <i>tylota</i>	yes	root/rock	•	•	
Te-bu	<i>Tethya</i> aff. <i>bulae</i>	yes	root/rock	•		
Te-co	<i>Tethya</i> aff. <i>coccinae</i>	yes	root/rock	•	•	•
Te-se	<i>Tethya</i> aff. <i>sechellensis</i>	yes	root/rock	•		•
Ti-ye	<i>Timea</i> sp. "yellow"	no	root	•	•	
HALICHONDRIDA						
Dictyonellidae						
St-ca	<i>Stylissa carteri</i>	yes	root/rock/sand	•	•	•
St-ma	<i>Stylissa massa</i>	yes	root/rock/sand			•
Halichondriidae						
Am-gc	<i>Amorphinopsis</i> sp.	yes	root			•
Ax-pi	<i>Axinyssa mertoni</i>	yes	root/rock/mud	•	•	•

code	species	exp	substrate	KKB	HBL	BAY
Ax-or	<i>Axinyssa</i> sp. "orange"	no	rock	•		
Ha-tg	<i>Halichondriasp.</i> "green"	yes	sand/reef			•
Ha-cr	<i>Halichondria</i> sp. "crown"	no	mud	•		
Ha-or	<i>Halichondria</i> sp. "orange"	no	root			•
Sp-ye	<i>Hymeniacion</i> sp. "yellow"	yes	root/rock	•	•	
Heteroxyidae						
Hi-mi	<i>Higginsia mixta</i>	yes	root/rock	•	•	•
Hi-en	<i>Higginsia</i> sp. "encrust"	yes	root/rock	•	•	
My-gr	<i>Myrmekioderma granulata</i>	yes	root/rock	•	•	
HAPLOSCLERIDA						
Callyspongiidae						
Ha-pp	<i>Callyspongia diffusa</i>	no	root/rock/reef			•
Chalinidae						
Ch-co	<i>Chalinula confusa</i>	yes	sand/reef			•
Cl-bu	<i>Cladocroce burapha</i>	yes	reef/rock			•
Ha-pi	<i>Haliclona</i> aff. <i>baeri</i>	yes	root/rock	•	•	•
Ha-am	<i>Haliclona amboinensis</i>	yes	sand/reef			•
Ha-bc	<i>Haliclona</i> sp. "blue crumble"	yes	root			•
Ha-sl	<i>Haliclona</i> sp. "blue slimy"	yes	reef			•
Ha-bk	<i>Haliclona</i> sp. "blue soft branch"	no	root/rock	•		
Ha-bs	<i>Haliclona</i> sp. "blue sticky"	yes	root	•		•
Ha-wk	<i>Haliclona</i> sp. "blue-white cloud"	yes	root/rock	•		
Ha-bm	<i>Haliclonasp.</i> "blue branch"	yes	root/rock		•	
Ha-xs	<i>Haliclona</i> sp. "bordeaux soft"	yes	root			•
Ha-bo	<i>Haliclona</i> sp. "bordeaux"	yes	root	•		
Ha-bb	<i>Haliclona</i> sp. "brown branch"	no	mud	•		
Ha-pa	<i>Haliclona</i> sp. "pale beige"	yes	rock		•	
Ha-pc	<i>Haliclona</i> sp. "pink cloud"	no	root	•		
Ha-pr	<i>Haliclona</i> sp. "purple branch"	no	root/rock		•	
Ha-pb	<i>Haliclona</i> sp. "purple soft branch"	yes	rock		•	
Ha-pt	<i>Haliclona</i> sp. "purple tough"	yes	root			•
Ha-wo	<i>Haliclona</i> sp. "purple-white"	yes	rock		•	
Ha-py	<i>Haliclona</i> sp. "purple-yellow"	no	root/rock	•		
Ha-sp	<i>Haliclona</i> sp. "soft spikes"	no	root/rock	•	•	
Ha-k2	<i>Haliclona</i> sp. "spicky"	no	rock	•		
Ha-vb	<i>Haliclona</i> sp. "violet branch"	no	root/rock	•		
Ha-vc	<i>Haliclona</i> sp. "violet cloud"	no	root/rock	•	•	
Ha-vs	<i>Haliclona</i> sp. "violet soft"	yes	root/rock		•	
Ha-vt	<i>Haliclona</i> sp. "violet tube"	yes	root	•		
Ha-vv	<i>Haliclona</i> sp. "violet vase"	yes	root		•	
Ha-wm	<i>Haliclona</i> sp. "white cloud"	no	root/rock		•	
Ha-we	<i>Haliclona</i> sp. "white extentions"	yes	root/rock	•		

code	species	exp	substrate	KKB	HBL	BAY
Ha-rh	<i>Haliclona</i> sp. "yellow branch"	yes	root/rock	•	•	
Ha-ym	<i>Haliclona</i> sp. "yellow cloud"	yes	root/rock		•	
Ha-yk	<i>Haliclona</i> sp. "yellow"	yes	root/rock	•		
Ha-lo	<i>Haliclona</i> sp. "white"	no	root/sand			•
Niphatidae						
Am-br	<i>Amphimedon queenslandica</i>	yes	root/rock/sand			•
Am-pa	<i>Amphimedon paravidis</i>	no	reef			•
Am-gr	<i>Amphimedon</i> sp. "blue-green"	yes	root			•
Petrosiidae						
Ha-ca	<i>Neopetrosia</i> aff. <i>carbonaria</i>	yes	reef/rock			•
Ne-ex	<i>Neopetrosia exigua</i>	yes	reef/rock			•
Ha-bt	<i>Neopetrosia</i> sp. <i>blue</i>	yes	root			•
Phloeodictyidae						
Ak-mu	<i>Aka mucosa</i>	yes	sand			•
Oc-wh	<i>Oceanapias</i> sp. "white"	yes	sand			•
POECILOSCLERIDA						
Acarinidae						
Ac-sp	<i>Acarinus</i> sp.	no	root/rock		•	
Coelosphaeridae						
Bi-fo	<i>Biemna fortis</i>	yes	root/mud/sand	•	•	•
Li-sp	<i>Lissodendoryx</i> aff. <i>similis</i>	yes	root/rock		•	
Iotrochotidae						
Io-ba	<i>Iotrochota baculifera</i>	yes	reef			•
Isodictyidae						
Co-si	<i>Coelocarteria singaporensis</i>	yes	sand			•
Microcionidae						
An-th	<i>Antho ridleyi</i>	no	root/rock	•		
Cl-re	<i>Clathria reinwardti</i>	yes	rock/reef/sand			•
Raspailiidae						
Ah-sp	<i>Acanthostylatella cornuta</i>	yes	rock		•	
Ec-sl	<i>Echinodictyum conulosum</i>	yes	rock/reef/sand			•
Ra-bl	<i>Raspailia</i> aff. <i>bifurcata</i>	yes	rock/sand		•	•
Ra-ye	<i>Raspailia</i> aff. <i>clathrata</i>	no	mud	•		
Tedaniidae						
Te-re	<i>Tedania diraphis</i>	yes	root/rock			•
SPIROPHORIDA						
Tetillidae						
Ci-au	<i>Cinachyrella</i> spp.	yes	root/rock/mud/sand/reef	•	•	•
Pa-cx	<i>Paratetilla bacca</i>	yes	root/rock/mud/sand/reef	•	•	•
VERONGIDA						
Ianthellidae						
He-in	<i>Hexadella</i> aff. <i>indica</i>	no	root/rock	•		

Results

Abbreviations used for locations: KKB - Kakaban lake, HBL - Haji Buang lake, BAY - coastal mangrove habitat on Maratua island. Abbreviations used for species are indicated in Table 1. The salinity, temperature and pH did not differ between sampling periods or between transects within a location. The range of environmental variables per location is indicated in Table 2. A total of nine sites in the coastal mangrove system did not contain epibionts: Sites 1-3 (on Kakaban island) 6, 7, 10, 11, 12, and 14 (on Maratua island) (Figure 1A). These were not included in the analyses.

Table 2 Dominant mangrove genera and range in salinity, temperature and pH in Kakaban lake (KKB), Haji Buang lake (HBL) and the coastal mangroves of Maratua island (BAY). Measurements were taken in September 2008 and May 2009.

Lake	Salinity (ppt)	Temp. (°C)	pH	Mangroves
KKB	23-24	29-32	7.0-7.8	<i>Bruguiera</i>
HBL	26-28	29-30	7.3-7.8	<i>Bruguiera</i>
BAY	33-34	28-32	7.8-8.3	<i>Avicennia, Rhizophora, Sonneratia</i>

Sponge composition

10167 sponge individuals were recorded, belonging to 115 species, 10 orders, 32 families and 52 genera (Table 1). A total of 67 species were recorded in KKB, 53 species in HBL, and 47 in BAY. A total of 33 species were restricted to KKB, 18 to HBL and 30 to BAY. The two lakes (KKB & HBL) shared 18 species; only 13 species were recorded across all three locations. The lake habitat (KKB & HBL combined) harbored 85 species, 16 of which were shared with the coastal mangrove habitat (Table 1).

Sponge species composition differed significantly among locations (*adonis* $F_{2,123} = 34.74$, $P < 0.001$, $R^2 = 0.359$) but not between years (*adonis* $F_{1,123} = 0.40$, $P = 0.96$). There was no significant interaction between location and year (*adonis* $F_{2,123} = 0.20$, $P = 1.000$). Each location formed a distinct cluster (Fig. 4A), but the two lakes were clearly more similar to one other than to the mangroves (Fig. 4B). The lake transects on a mud substrate resembled the coastal transects more closely than the other transects (Fig. 4A). There was also some temporal variation in species composition as indicated by the vectors, particularly in lake habitats, although this differed among transects (Fig. 4A).

In all three locations, there was a significant difference in species composition among substrate types (*adonis*; KKB: $F_{2,54} = 8.58$, $P < 0.001$, $R^2 = 0.236$; HBL: $F_{2,27} = 15.31$, $P < 0.001$, $R^2 = 0.514$; BAY: $F_{2,30} = 13.96$, $P < 0.001$, $R^2 = 0.481$), but no significant difference between years (*adonis*; KKB: $F_{1,54} = 0.62$, $P = 0.776$; HBL: $F_{1,27} = 0.63$, $P = 0.690$; BAY: $F_{1,30} = 0.05$, $P = 0.999$). There was also no significant interaction (*adonis*; KKB: $F_{2,54} = 0.49$, $P = 0.955$; HBL: $F_{2,27} = 0.63$, $P = 0.791$; BAY: $F_{2,30} = 0.03$, $P = 1.000$). There was also no significant effect of spatial processes on species composition based on results of the PCNM analyses (all $P > 0.10$).

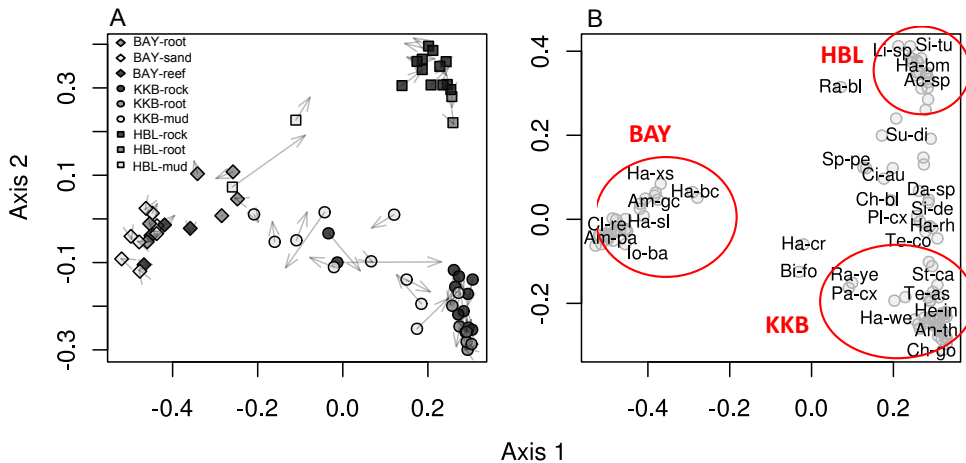


Figure 4 Ordination scores of transects (**A**) and Weighted Averages scores of sponge species (**B**) along the first and second Principal Coordinates Analysis (PCO) axes representing variation in sponge community composition among locations (KKB, HBL and BAY) and substrate types (mud, rock, root, reef and sand). Arrows in **A** represent temporal variation in composition from transects sampled in 2008 (symbols) to the same transects sampled in 2009 (arrow heads). In **B** Species are indicated by dots; selected species are indicated by codes following Table 1. The principal axis of variation represents variation from transects in marine lake habitats (KKB and HBL) to transects in coastal mangroves. The secondary axis of variation (axis 2) is primarily related to variation between lake habitats. Note that mud transects from both lakes tend to exhibit the greatest similarity in composition with mangrove transects. Weighted Averages scores of sponge species was estimated using the *wascors* function of the *vegan* library in R and based on the first two PCO ordination axes.

In KKB, the main gradient in composition was related to variation between transects on a mud substrate at greater depth and transects on a hard substrate with high mussel and ascidian cover (Fig. 5A and B). Species associated with a mud substrate include *Raspaillia* aff. *clathrata*, *Halichondria* sp. “crown”, and *Higginsia mixta*. Species mainly associated with rock and root substrates include *Placospongia* spp., *Cinachyrella* spp., *Cliona peleia*, *Tethytimea* aff. *tylota*. Variation in HBL was primarily related to differences between transects on mud versus hard (root and rock) substrates and secondarily between rock substrate with higher ascidian cover and root substrate with higher mussel cover (Fig. 5C and D). *Biemna fortis* was the most prevalent species on a mud substrate. Species strongly associated with a rock substrate included *Semitaspongia* sp., *Cliona peleia* and *Antho ridleyi*, *Tethytimea* aff. *tylota*. Species strongly associated with a root substrate included *Spongionella* sp. “green”, and *Haliclona* spp.. In BAY, the main gradient in composition was related to variation from transects on a root substrate in shallow water to transects in deeper water on a sand or reef substrate (Fig. 5E and F). Species mainly associated with a root substrate included *Tethya* aff. *coccinae*, *Haliclona* spp. and *Amorphinopsis* sp.. There was a secondary gradient related to transects with higher coral cover versus transects with higher sand and rock cover. Species more strongly associated with higher coral cover included *Placospongia* spp., *Iotrochota baculifera* and *Amphimedon paraviridis*, whereas species more strongly associated with higher sand and rock cover included *Axinyssa mertoni*, *Biemna fortis*, *Cliona peleia*, *Cinachyrella* spp..

Sponge abundance and cover

Sponge abundance differed significantly among substrate types in the marine lake habitat but not in the coastal mangrove habitat (adonis; KKB abundance: $F_{2,54} = 28.70$, $P < 0.001$, $R^2 = 0.502$; HBL abundance $F_{2,26} = 21.64$, $P < 0.001$, $R^2 = 0.590$; BAY abundance: $F_{2,30} = 2.33$, $P = 0.129$, $R^2 = 0.134$). Sponge cover also differed

significantly among substrate types in the marine lake habitat but again not in the coastal mangrove habitat (adonis; KKB cover: $F_{2,54} = 43.89$, $P < 0.001$, $R^2 = 0.617$; HBL cover $F_{2,26} = 10.28$, $P < 0.001$, $R^2 = 0.429$; BAY cover: $F_{2,30} = 1.65$, $P = 0.214$, $R^2 = 0.098$). Sponge abundance and cover was highest on root and rock substrates in the marine lake habitat and was lowest on mud substrate (Fig. 6). There was no significant difference in abundance between years in any habitat (adonis; KKB abundance: $F_{1,54} = 1.18$, $P = 0.252$, $R^2 = 0.010$; HBL abundance $F_{1,26} = 2.48$, $P = 0.132$, $R^2 = 0.034$; BAY abundance: $F_{1,30} = 0.00$, $P = 1.000$, $R^2 = 0.000$; BAY cover: $F_{1,30} = 0.18$, $P = 0.660$, $R^2 = 0.010$). There were also no significant interactions (adonis; KKB abundance: $F_{2,54} = 0.84$, $P = 0.419$, $R^2 = 0.015$; HBL abundance $F_{2,26} = 0.30$, $P = 0.738$, $R^2 = 0.008$; BAY abundance: $F_{2,30} = 0.04$, $P = 0.960$, $R^2 = 0.002$). There was also no significant difference in cover between years in any habitat (adonis; KKB cover: $F_{1,54} = 0.46$, $P = 0.511$, $R^2 = 0.003$; HBL cover $F_{1,26} = 0.36$, $P = 0.557$, $R^2 = 0.008$; BAY cover: $F_{2,30} = 0.18$, $P = 0.845$, $R^2 = 0.010$).

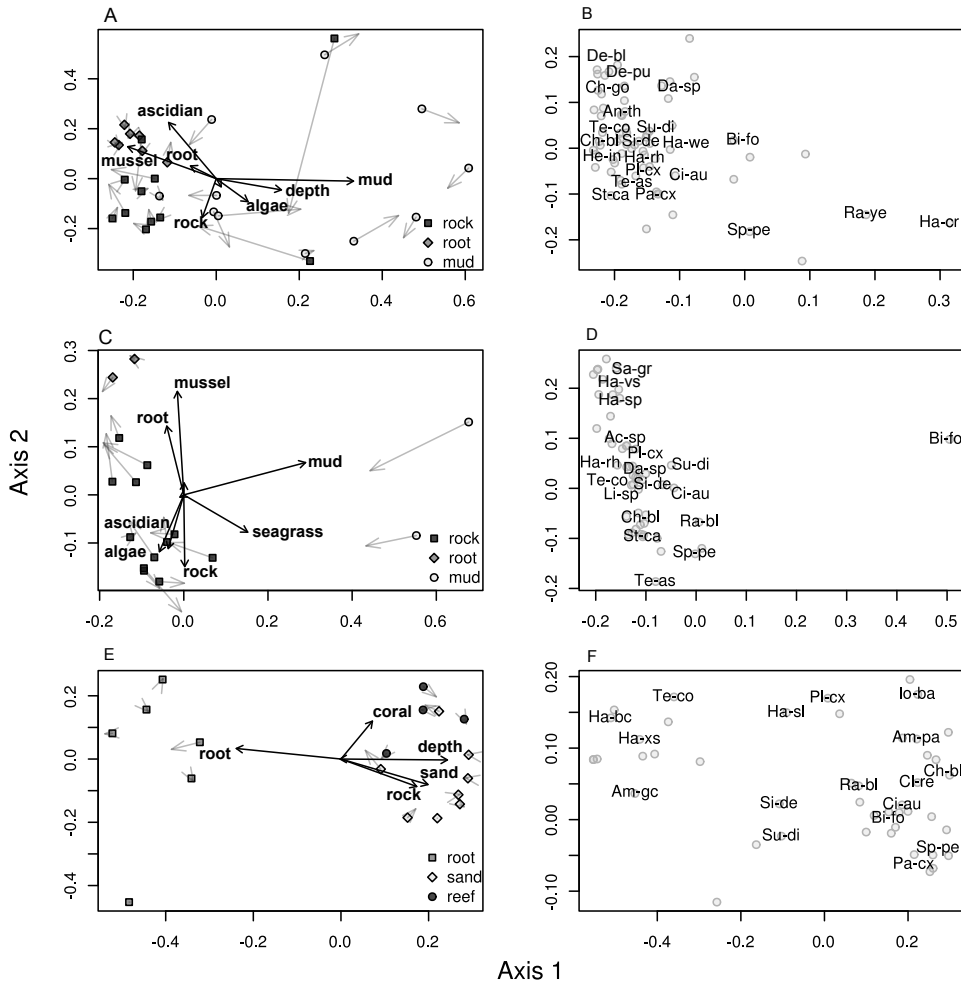


Figure 5 Ordination scores of transects and Weighted Averages scores of sponge species along the first and second Principal Coordinates Analysis (PCO) axes for Kakaban lake (A, B) Haji Bung lake (C, D) and coastal mangroves (E, F). Transects on different substrate types (mud, rock, root, reef and sand) are indicated by symbols. Codes in B, D and F represent sponge species following Table 1. Grey arrows represent temporal variation in composition from transects sampled in 2008 (symbols) to the same transects sampled in 2009 (arrow heads of grey arrows). Black arrows are vectors of environmental variables (cover of ascidians, mussels, mud, seagrass, bare rock, bare root, and coral in transect, depth of transect) representing maximal correlations with the ordination configuration obtained using the *envfit* function in the *vegan* library in R. The principal axis of variation (axis 1) represents variation among solid and soft substrate.

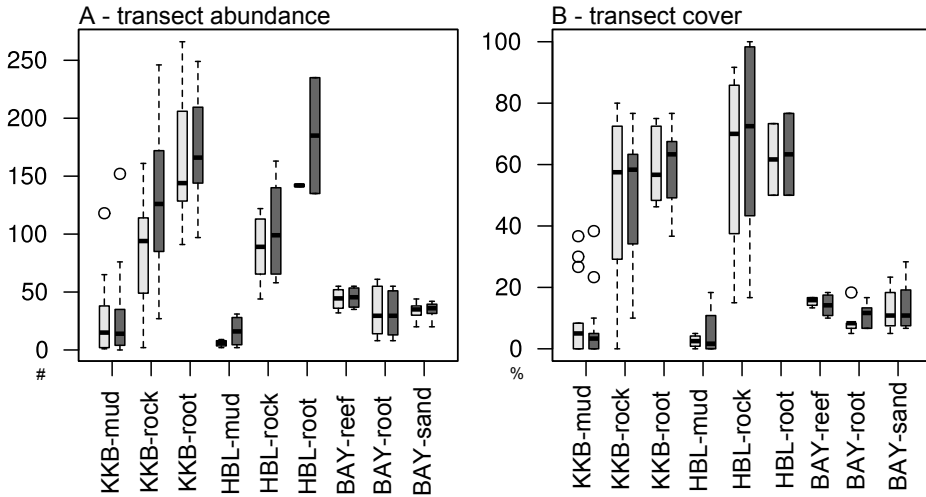


Figure 6 Box-and-whisker plots of **A** the abundance and **B** the cover of sponges across locations (KKB, HBL and BAY) and substrate types (mud, rock, root, reef and sand). Light grey represents data from 2008, dark grey from 2009. The thick black line intersecting each box-plot represents the median values. The boxplot hinges are versions of the first and third quartiles. Open circles represent outliers and the upper and lower whiskers represent the most extreme data point given that it is no more than 1.5 times the interquartile range from the box (graph created using the default values for the *boxplot* function in R)

Discussion

Differences between habitats

The marine lakes are true sponge gardens containing distinct assemblages of sponge species. The lakes displayed a markedly higher abundance and cover of sponges compared to the outer coastal mangrove habitat surrounding the islands containing the marine lakes (Figs. 2 & 5). Transects in the lakes could harbor great densities of sponges more than 200 individuals in an area of only 3 m², occupying at times up to 100% of available substrate. These abundances are comparable to the amounts recorded in areas 10 times as large (30 m²) in the adjacent reefs in Berau (de Voogd et al. 2009). The marine lake habitat provides a continuously sheltered and submerged environment with large sponges, while in contrast the coastal mangrove habitat is more exposed to waves and air at low tide, harboring smaller and fewer sponges (Figs. 2 & 5). Sponges were patchily distributed in the coastal mangrove system where some locations along the coast of Maratua and Kakaban did not contain a single sponge. This patchiness has frequently been noted in Caribbean mangroves and has been attributed in part to biotic factors, but mostly to abiotic environmental factors (e.g. Ellison & Farnsworth 1992, Farnsworth & Ellison 1996, Diaz et al. 2004, Wulff 2005a, Hunting et al. 2008, Guerra-Castro et al. 2011). Exposure to currents was, for example, the most reliable predictor of percentage cover and diversity of species in Belize mangroves (Farnsworth & Ellison 1996). Roots on protected coasts are typically dominated by massive sponges, ascidians, sea anemones, and fleshy algae, while the high energy windward coasts are generally dominated by hydroids and filamentous algae with no sponges (Farnsworth & Ellison 1996).

The three locations of this study (Kakaban lake, Haji Buang lake and the coastal mangroves of Maratua island) each had distinct assemblages (Fig. 4). The two marine lakes at 10 km distance, were, however, more similar to each other than to the coastal mangrove systems at just 200-500 m distance. The marine lakes harbored only a subset of the adjacent sea flora and fauna. The difference in species composition between different lakes and mangroves can for a large part be attributed to both the nature of the barrier between the lake and sea (the putative source of the species pool) as well as the various environmental characteristics within the lake systems (Becking et al. 2011, *CHAPTER 1*). Depending on the degree of connection to the sea, the lakes can more or less resemble a coastal lagoon in geomorphology and species assemblage. Kakaban lake and Haji Buang lake are highly isolated lakes following the classification of Becking et al. (2011). The substantially different environmental variables (salinity, pH, degree of exposure to waves and air) as well as the different species of mangroves between both habitats are possibly forces that structure sponge composition (Table 2, Fig. 5); salinity is lower in the lakes than in the adjacent coastal mangroves and coral reefs, which can be a limiting factor for sponges. Likewise the coastal mangrove habitat has a higher chance of extended periods of exposure to air, which only few sponge species can tolerate (Rützler 1995). In the Caribbean, mangroves and coral reefs have been shown to differ substantially in composition (Ellison & Farnsworth 1992, Farnsworth & Ellison 1996, Wulff 2000, Diaz et al. 2004, Hunting et al. 2008, Guerra-Castro et al. 2011). Species within the typical mangrove sponge community are specifically adapted to survive extremes in abiotic factors such as salinity, temperature and sedimentation, either through tolerance or through rapid recovery after storms (Rützler 1995, Engel & Pawlik 2005, Wulff 2005b, Pawlik et al. 2007, Nagelkerken et al. 2008). Pawlik et al. (2007) observed that reef species declined in health and died within 60 days of being transplanted to mangrove sites. This result was attributed to the inability of reef species to tolerate the abiotic conditions of high temperature, rainfall events and sedimentation in mangroves.

The lake and coastal mangrove habitats share only a few species and most of these shared species (e.g. *Cinachyrella* spp., *Paratetilla bacca*, *Biemna fortis*, *Suberites diversicolor*) are also known to occur in perturbed areas or extreme environments in Indonesia, Singapore, and Australia (e.g. Hooper et al. 2002, McDonald et al. 2002, Cleary & de Voogd 2007, de Voogd & Cleary 2007, Becking & Lim 2009, de Voogd & Cleary 2009, *CHAPTER 4*). Though the lakes are minimally perturbed by human influence, they do share some characteristics with perturbed bay environments such as high turbidity and low salinity. All sponge species in the coastal mangrove habitat are common, widely distributed and have been recorded in tropical sheltered bays, sandy reef flats or coral reefs across the Indonesia (e.g. Becking et al. 2006, de Voogd & Cleary 2008, de Voogd et al. 2009, de Voogd & Cleary 2009, *CHAPTER 3*). In contrast, a large portion of the species in the lakes is not known from any published records of the reefs; many are undescribed species new to science. Both Kakaban and Haji Buang lake housed species that were only recorded in one lake and possibly represent local endemics. In Kakaban lake, half the species recorded were restricted to this lake. Many rare and novel genera and species among a variety of taxa have been described from this highly isolated lake, such as a crab (*Orcovita saltatrix*), two holothurians (*Holothuria cavans* and *Synaptula spinifera*), and an ascidian (*Styela complexa*) (Ng & Tomascik 1994, Tomascik & Mah 1994, Massin & Tomascik 1996). It is nevertheless possible that these 'endemic' lake-dwelling species with large growth forms may occur elsewhere in cryptic locations such as crusts in reefs or marine caves and may thus have been overlooked during reef surveys (Pawlik 1998). We did, however, thoroughly scrutinize the coastal coral reefs, mangroves and sandy reef flats in search of these lake species.

To summarize, the lake assemblages contained three groups of species: 1) species that are widely distributed (e.g. *Cinachyrella* spp and *Placospongia* spp.), 2) species that are shared by both lakes and that have been observed in other Indo-Pacific lakes (e.g. *Darwinella* aff. *gardineri* and *Tethytimea* aff. *tylota*), and 3) species that have (thus far) only been observed in a single lake (e.g. several species of the genus *Haliclona*). The only representative study on sponge fauna in marine lakes in the Indo-Pacific so far was conducted in Ha Long Bay in Vietnam (Cerrano et al. 2006, Azzini et al. 2007). The Indonesian and Vietnamese marine lakes share few species, though similar patterns in assemblage structures are seen in both. A qualitative survey of species presence and absence on the rocky shore within lakes and adjacent coastal habitats in Vietnam revealed that the more isolated lakes harbored unique species where 23 species (of a total of 63 species) were only present in the lakes, 18 of which were uniques (i.e., species that were only observed in a single lake). In the lakes of Vietnam, there is a wide variation in the degree of connection to the sea. The well connected lakes harbored coral and sponge assemblages that did not differ from those in the adjacent bays, while the more isolated lakes had much less compositional overlap (Azzini et al. 2007). The mangrove fringed ponds of the Pelican Cays in Belize, though not anchialine, show some similarities to Indo-Pacific marine lakes. Comparison of the sponge fauna in these ponds with more common open mangrove systems indicated that the ponds contained a distinct species assemblage with a high number of rare and undescribed taxa (Rützler et al. 2000).

Differences between substrates and cover

In all habitats there was a clear zonation away from the shoreline. In the marine lakes, the hard substrates such as rock and root along the coast harbored multitudes of sponges, while the abundance, cover and number of species declined markedly with just 1-2 m distance from the shore in the soft flocculent mud substrate (Fig. 6). Mud and sediments can clog the oscula and pores of sponges, which can adversely affect their pumping (Gerrodette & Flechsig 1979). Certain species have adapted their morphology to circumvent the negative effects, for example by means of psammobiontic growthforms (e.g. *Biemna fortis*) or a hairy-bristly surface which can capture fine sediments (*Paratetilla bacca*, *Cinachyrella* spp, and *Raspaillia* spp.). In our study root, mussel, ascidian and algae cover was strongly related to variation in sponge composition in both Kakaban lake and Haji Buang lake. Roots almost always had a high cover of mussels, while the cover of mussels on a rock substrate was much lower (or absent as was the case in in Haji Buang lake). The relationship between mussel cover and sponge composition may therefore be simply correlative and not due to spatial competition or other inter-taxon interactions. Algae occurred on roots in Kakaban lake, but increased dramatically to almost 100% cover with depth in the more muddy substrates. In Haji Buang lake the subtidal quadrats could be 100% covered by algae that formed a blanket over an equally high sponge cover underneath. Remarkably this covering did not seem to adversely affect the sponges. More detailed research, however, is needed to understand how the various benthic taxa within marine lakes interact.

Within both habitats (marine lakes and coastal mangroves) sponge species composition differed markedly between mangrove roots and other substrates with certain species only occurring on mangrove roots. In Haji Buang lake there were only two transects in the mangrove roots (due to limited mangrove cover in this lake), yet these assemblages contained species that were not present in the remainder of the lake. Differential response of sponge larvae to concentration of tannins in mangrove roots may play a role in structuring the assemblages associated with mangroves (Hunting et al. 2008, Hunting et al. 2010). The ability to resist tidal exposure may, furthermore, be a strong selective trait for species survival in mangrove systems. The most speciose order associated with roots in the lakes and coastal mangroves is composed of the Haplosclerida,

particularly the family Chalinidae and within that the genus *Haliclona*. The majority of *Haliclona* spp. were recorded as exposed to air during low tide. In Caribbean mangroves, the Chalinidae is generally the most speciose family (e.g. De Weerd 2000, Diaz et al. 2004, Wulff 2004, Guerra-Castro et al. 2011). Many Caribbean *Haliclona* spp. can tolerate strong water movement, sudden oscillations in temperature and salinity, as well as exposure to air (de Weerd et al. 1991, De Weerd 2000). Certain *Haliclona* spp. are able to resist desiccation, including 4 hrs of exposure to sun, by being able to retain more water during exposure to sun than deeper water species (Rützler 1995).

Temporal variation

Sponge species composition, abundance and cover in marine lakes and coastal mangroves in Indonesia did not vary significantly between sampling dates. There is little evidence of a strong and consistent change in composition across plots based on the ordinations. Individual transects do exhibit, sometimes pronounced, differences in composition between sampling events, yet here are marked differences in the degree (and direction) of compositional change among plots as indicated in Figs 3 & 4. Our lack of directional change differs somewhat from results obtained in Vietnamese marine lakes where degeneration of species and subsequent variation in local assemblages was observed after half a year due to heightened temperature and extreme rainfall during the monsoon season (Cerrano et al. 2006, Azzini et al. 2007). Our contrasting results with Vietnam may be due to the fact that seasonal differences are much less pronounced in the Berau region than in Vietnam. That being said, longer term monitoring is necessary in order to gain a fuller understanding of sponge community dynamics in marine lake environments.

Sponges in Indo-Pacific mangroves

This is the first study to illustrate that mangroves in the Indo-Pacific can harbor a diverse array of sponge species. The number of sponge species associated with mangroves recorded for the Caribbean (scale of 1000's of kms) is just under 150 based on papers from the 1960s up until now (e.g., Rützler 1969, Diaz et al. 2004, Guerra-Castro et al. 2011). In only a single study at a much smaller scale (10 km), we have recorded a total of 115 sponge species in the marine lakes and coastal mangroves of Berau, of which 74 species were attached to mangrove roots. A large portion of the Indonesian coastline is fringed by a great diversity of mangrove species (Spalding et al. 1997, Alongi 2002) that have yet to be explored for epibionts. In recent years, over 45 marine lakes new to science have been discovered in Raja Ampat, Indonesia (Becking et al. 2011, Becking pers. obs., CHAPTER 1). As such, a vast amount of diversity remains to be unveiled in Indonesia, and likely beyond in the wider Indo-Pacific. The unique habitat and species composition of marine lakes warrants further study and conservation.

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Appendix 1. *In situ* images of sponges from Kakaban lake and Haji Buang lake in Berau, East Kalimantan, Indonesia

CALCAREA Bowerbank, 1864
Clathrinida Hartman, 1958
Clathrinidae Minchin, 1900



Clathrina sp. "white"



Clathrina sp. "yellow"

DEMOSPONGIAE Sollas, 1885
Astrophorida Sollas, 1887
Ancorinidae Schmidt, 1870



Stelletta sp. "icing"

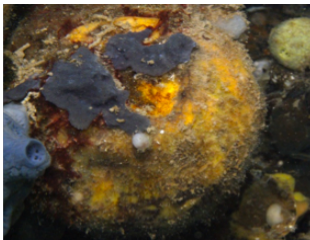


Stelletta sp. "icing"

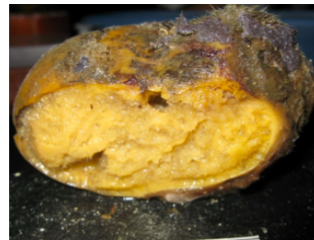
Geodiidae Gray, 1867



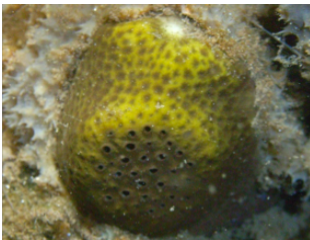
Geodia sp. "black"



Geodia sp. "yellow"

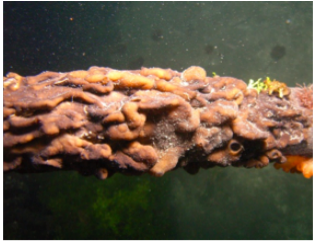


Geodia sp. "yellow"



Geodia sp. "chimney"

Chondrosida Boury-Esnault & Lopès, 1985
Chondrillidae Gray, 1872



Chondrilla aff. *australiensis*

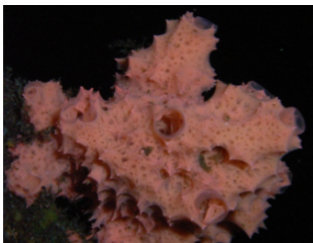


Chondrilla aff. *australiensis*



Chondrosia aff. *chucalla*

Dendroceratida Minchin, 1900
Darwinellidae Merejkowsky, 1879



Darwinella aff. *gardineri*



Chelonaplysilla sp. "gold"



Chelonaplysilla sp. "black"



Dendrilla sp. "black"



Dendrilla sp. "black"



Dendrilla sp. "purple"

Dictyodendrillidae Bergquist, 1980

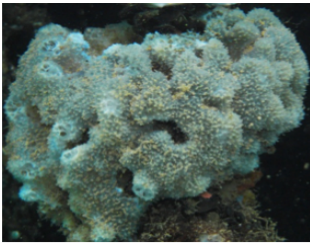


Spongionella sp. "purple"

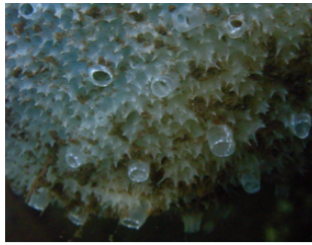


Spongionella sp. "green"

Dictyoceratida Minchin, 1900
Dysideidae Gray, 1867



Dysidea sp. "blue"



Dysidea sp. "blue"



Dysidea sp. "beige"



Dysidea sp. "white"

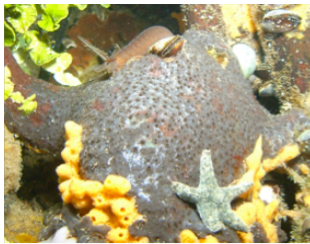


Dysidea sp. "white"



Lamellodysidea "blue"

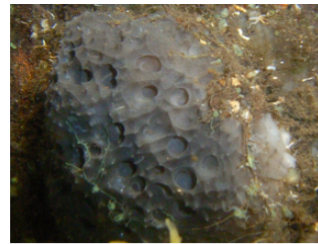
Thorectidae Bergquist, 1978



Cacospongia sp. "shiny"



Cacospongia sp. "shiny"



Cacospongia sp. "honeycomb"



Semitaspongia sp.

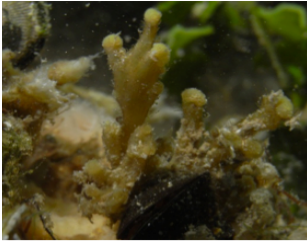


Semitaspongia sp.



Smenospongia sp.

Spongiidae Gray, 1867



Spongia sp. "fistules"



Spongia sp. "black"

Hadromerida Topsent, 1894
Clionidae d'Orbigny, 1851



Cliona aff. *peleia*



Cliona aff. *peleia*

Placospongiidae Gray, 1867



Placospongia *carinata*



Placospongia *mixta*



Placospongia *melobesioides*

Spirastrellidae Ridley & Dendy 1886



Spirastrella aff. *decumbens*



Spirastrella sp. "tubes"

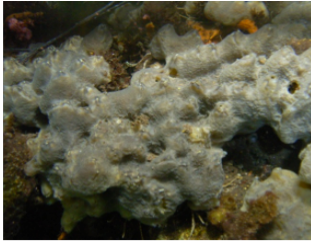


Spirastrella sp. "orange"



Spirastrella sp. "solida"

Suberitidae Schmidt, 1870



Pseudosuberites andrewsi



Suberites diversicolor



Suberites diversicolor

Tethyidae Gray 1848



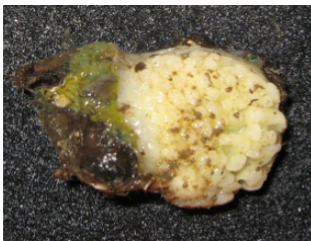
Laxotethya sp. "spaghetti"



Tethya aff. *bullae*



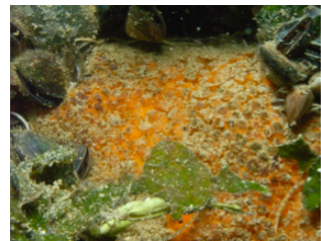
Tethya aff. *seychellensis*



Tethya aff. *coccinae*



Tethya aff. *coccinae*



Tethytimea aff. *tylota*



Tethytimea aff. *tylota*



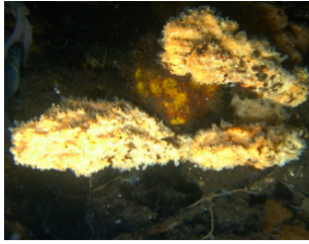
Timea sp. "yellow"

Halichondrida Gray, 1867

Dictyonellidae Van Soest, Diaz & Pomponi, 1990

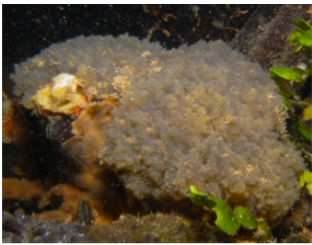


Stylissa carteri



Stylissa carteri

Halichondriidae Gray, 1867



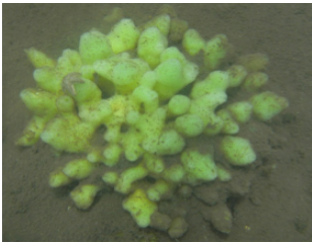
Axinyssa mertoni



Axinyssa mertoni



Axinyssa sp. "orange"



Halichondria sp. "crown"



Halichondria sp. "crown"



Hymeniacidon sp. "yellow"

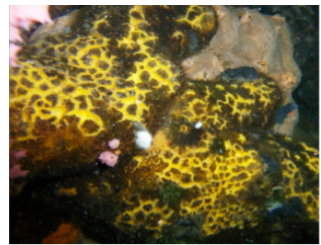
Heteroxyidae Dendy, 1905



Higginsia mixta



Higginsia sp. "encrust"



Myrmekioderma granulatum

Haplosclerida Topsent 1928
Chalinidae Gray 1867



Haliclona sp. "blue sticky"



Haliclona sp. "blue sticky"



Haliclona sp. "blue soft branch"



Haliclona sp. "blue branch"



Haliclona sp. "violet branch"



Haliclona sp. "purple branch"



Haliclona sp. "purple soft branch"



Haliclona sp. "brown branch"



Haliclona sp. "brown branch"



Haliclona sp. "yellow branch"



Haliclona sp. "yellow branch"



Haliclona sp. "yellow branch"



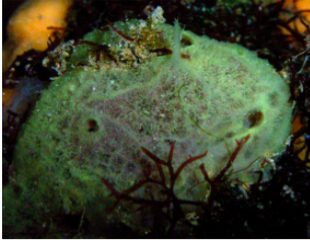
Haliclona sp. "translucent"



Haliclona sp. "violet tube"



Haliclona sp. "bordeaux"



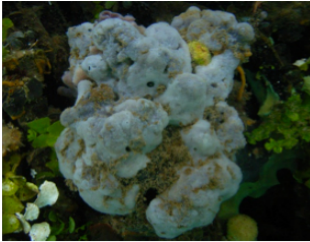
Haliclona sp. "purple-yellow"



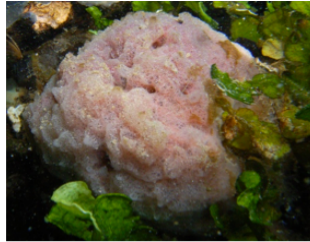
Haliclona sp. "white oscules"



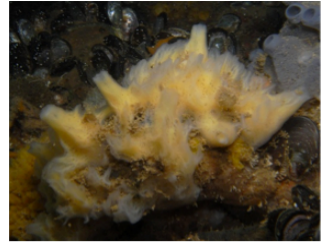
Haliclona aff. *baeri*



Haliclona sp. "violet cloud"



Haliclona sp. "pink cloud"



Haliclona sp. "yellow cloud"



Haliclona sp. "soft spikes"



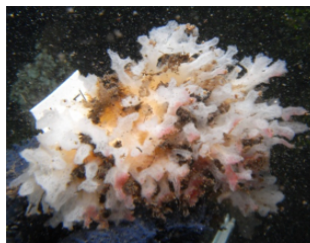
Haliclona sp. "blue-white cloud"



Haliclona sp. "purple vase"



Haliclona sp. "crunchy"



Haliclona sp. "crunchy"



Haliclona sp. "crunchy extensions"



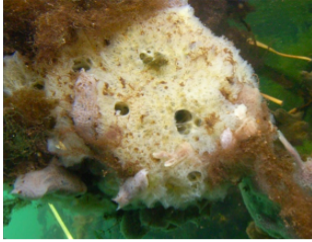
Haliclona sp. "white extension"



Haliclona sp. "white extension"



Haliclona sp. "white"



Haliclona sp. "yellow"

Poecilosclerida Topsent, 1928
Acarinidae Dendy, 1922

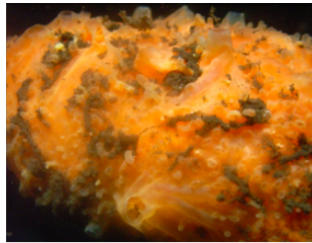


Haliclona sp. "beige"

Coelosphaeridae Dendy, 1922



Acarnus sp.



Acarnus sp.



Lissodendoryx aff. *similis*

Desmacellidae Ridley & Dendy, 1886



Biemna fortis



Biemna fortis



Biemna fortis

Microcionidae Carter 1875



Antho ridleyi



Antho ridleyi

Raspailiidae Nardo, 1833



Raspailia aff. *clathrata*



Raspailia aff. *clathrata*



Raspailia aff. *bifurcata*



Acanthostylotella *cornuta*



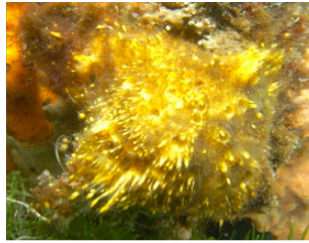
Acanthostylotella *cornuta*

Spirophorida Bergquist & Hogg 1969

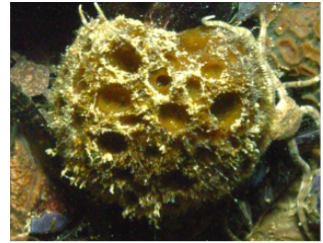
Tetillidae Sollas, 1886



Cinachyrella sp.



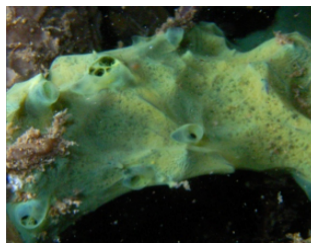
Cinachyrella sp.



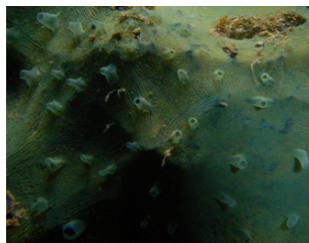
Paratetilla *bacca*

Verongida Bergquist, 1978

Ianthellidae Hyatt, 1875



Hexadella aff. *indica*



Hexadella aff. *indica*

