Journal of Tropical Biodiversity and Biotechnology
Volume 06, Issue 03 (2021): jtbb66435
DOI: 10.22146/jtbb.66435

Research Article

Shallow-water Sponges from a High-sedimentation Estuarine Bay (Brunei, Northwest Borneo, Southeast Asia)

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Submitted: 08 June 2021; **Accepted:** 29 July 2021; **Published online:** 29 September 2021

ABSTRACT

Tropical estuaries are important habitats for invertebrates including sponges, a group of marine organisms that fulfill significant ecological roles and provide ecosystem services. Here, we describe the sponge fauna from Pulau Bedukang, a small island in a turbid, variable salinity, acidified and eutrophic estuarine bay (Brunei Darussalam, northwest Borneo). We present records for 14 morphological species (OTUs). Six of these species belong to the Haplosclerida, an order of shallow-water sponges that usually tolerate more variable and extreme physical conditions. Our baseline data contribute to the regional biogeography of sponges and present a reference source for ecological studies on marine animals inhabiting variable estuarine environments. This is the first known record of sponges from the northwest Bornean region of the South China Sea that are not associated with a coral ecosystem; other studies have concerned Singapore, peninsular Malaysia, Thailand, Cambodia, Vietnam, southern China, and Taiwan.

Keywords: Brunei Darussalam, diversity, Extreme Aquatic Environment, Porifera

INTRODUCTION

Sponges are categorized as benthic filter-feeding metazoans that possess a range of size, shape, and color features. According to the World Porifera Database (WPD), more than 24 thousand species have been recorded and approximately more than nine thousand have been accepted as valid species worldwide (van Soest et al. 2018). Furthermore, sponges are a significant component of biodiversity in the Indo-Malayan region, with more than 1,500 described species (van Soest et al. 2012). The region's undisturbed natural substrata such as coral rubbles, rocks, and abandoned shells, provide for settlement and growth of a diverse fauna that dominates in a vast array of aquatic niches. Given the widespread diversity, distribution, and abundance, it is unsurprising that sponges are of ecological and biopharmaceutical importance. Ecologically, sponges impact the substratum through bioerosion and reef stabilization, but also potentially alleviate marine biofouling by filtering the water. Their sensitivity to environmental stress makes them suitable bioindicator species (Bell 2008). They are also of interest for medical and biochemical research, due to the remarkable range of bioactive compounds they possess (Belarbi et al. 2003; Proksch et al. 2002). Also, in line with the growing preference for natural products in the cosmetic industry, sponges have consolidated their market position as defoliating 'bath sponges'.

Situated on Southeast Asia's Borneo Island with Indonesia and Malaysia, Brunei borders the South China Sea, having extensive sandy beaches and pristine estuarine mangrove and mudflat ecosystems. Fragmented into a Sundaland element just outside the westernmost boundary of a global biodiversity hotspot, the Western Coral Triangle province, Brunei harbors a vast species richness (Silvestre 1992; Spalding et al. 2007; Mustapha et al. 2021) in relation to the spatially-limited habitat. Despite this high degree of biogeographical significance, our knowledge of the sponge fauna along the northwest Bornean coastline is underexplored compared to that of other marine invertebrates, like Cnidarians (Chua et al. 1987; Hoeksema & Lane 2014), and other regions of the South China Sea (Manconi et al. 2013; Lim et al. 2016; Mustapha et al. 2021). The only recent study on sponges near Brunei is that of Yong et al. (2018), but this focused on the biotechnology of coral-associated taxa, rather than specifically investigating sponge diversity. Since much of the sponge fauna remains unknown, the numerous functional roles they play in the environment are underappreciated. The limited surveys and inventories, both spatially and taxonomically, of these invertebrates hamper scientific endeavors and research initiates to evaluate and use their components. Furthermore, their poor representation undermines conservation efforts. Hence, alpha taxonomic work in the region remains a prerequisite for any scientific program involving sponges, because alpha-taxonomy facilitates the preliminary mapping of biodiversity and provides universal species names (Mayo et al. 2008).

The inner Brunei Bay of the Brunei Estuarine System (BES) was selected for this study following observations of well-developed sponge communities at Pulau Bedukang (PB; Marshall et al. 2016). These communities become established on rocky outcrops and mangroves roots and trunks, in the otherwise heavily-sedimented bay (Hossain et al. 2014). Although devoid of wave action, the water is variable in salinity, pH, and suspended-sediment loads (Proum et al. 2018), representing extreme circumstances for typical marine invertebrate animals. For example, the salinity at PB may vary between 19.6 and 31.2 psu and the pH between 7.7 and 8.3 units (Hossain et al. 2019). The rate of sedimentation at the outer bay can exceed 70 mg.cm^{-1}.day^{-1} (Lane & Lim 2013). The BES serves as an extensive nursery ground for fishes, though benthic animals are specifically adapted towards the variability in environmental conditions (Proum et al. 2017). In recent years, there has been a focus on understanding how the estuarine conditions and the extraordinary acidification of the BES affect communities and organisms (Marshall et al. 2021; Bolhuis et al. 2014; Marshall et al. 2016; Hossain et al. 2019). The aim of the present study was to improve understanding of local and regional sponge diversity, and of the sponge taxa associated with highly turbid tropical Asian estuaries.

MATERIALS AND METHODS

Study area

Pulau Bedukang (PB; 4.9784° N 115.0622° E) is a 20-ha island in the Inner Brunei Bay (Figure 1) and is fringed with *Avicennia* sp. and *Sonneratia* sp. dominated mangroves. Extensive mudflats project from the southwest boundary of the island towards a rocky outcrop, informally named as Oyster rocks. This outcrop comprises a substratum of mixed mud and coral and rock rubble that is exposed during spring low tides (Figure 1). The mudflat

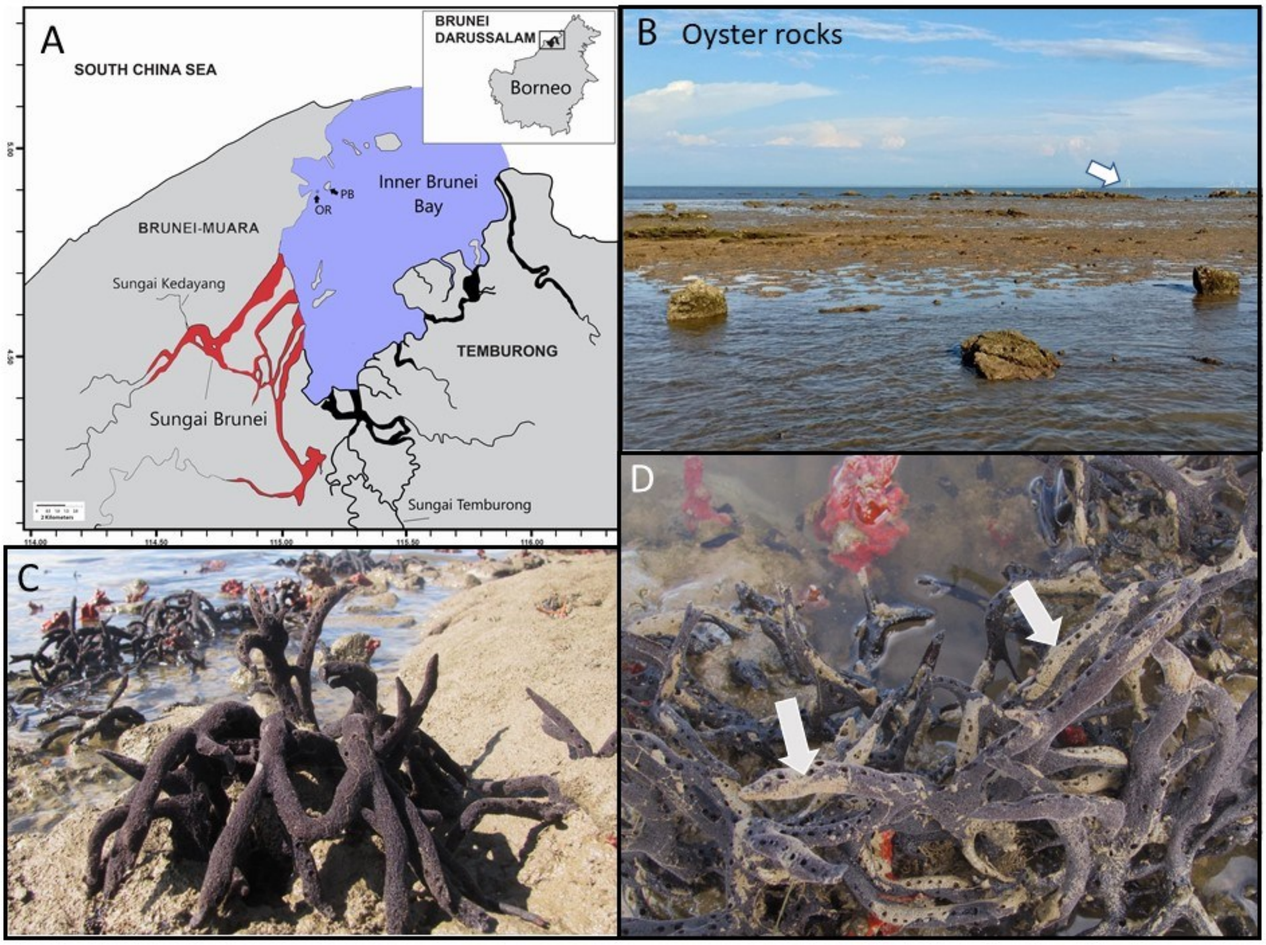

Figure 1. A. Map of the Inner Brunei Bay, showing locations of study sites at Pulau Bedukang (PB) and Oyster rocks (OR); **B.** Oyster rocks during spring low tide (0.2 m CD) revealing the mixed coral gravel, mud, and boulder substratum. Brunei Temburong Bridge construction on the south of PB (block arrow); **C & D.** Massive form of *Haliclona* sp. 1 exposed in air during low tide at Oyster rocks. *Haliclona* sp. 1 and *Niphates* sp. during low tide, arrows indicate sediment deposited on the sponge surfaces. Colour coding of the waterbodies in (A) refers to different salinity and pH regimes (Hossain et al. 2019). Fig C was taken from Marshall et al. 2016.

between the mangroves and Oyster rocks supports prominent communities of juvenile horseshoe crabs, edible mangrove crabs, penaeid shrimps, and gastropod and bivalve mollusks. Generally, the intertidal soft benthic system of Brunei Bay experiences a tropical climate with temperatures averaging around 27°C and an annual rainfall of 2880 mm per year (1966 – 2006). Its semi-diurnal tide ranges to 2.5 m Chart Datum (Marshall et al. 2016).

Sampling

Sponge specimens were sampled between February and June 2018, the dry season, during low tide from Oyster rocks and mangroves at Pulau Bedukang. Sponges in the mangroves were collected from pneumatophores and trunks. More importantly, we avoided collecting cryptic and sciophilous specimens. An area of ~ 100 m^2 was surveyed at each site, and duplicate specimens were collected, with the aim of representing the conspicuous sponge species in the area. Sampling was undertaken on two separate days.

Identification

Morphological features were first recorded in live specimens, including color, form, and size. Specimens were then preserved in 99% ethanol and transported to the laboratory at University Brunei Darussalam (UBD). Identification followed (Hooper & van Soest 2002) and the Thesaurus of

Sponge Morphology (Boury-Esnault & Rützler 1997). The examination required two kinds of histological preparation. The first was spicule preparation, to determine the kinds of spicules in the skeleton. Bleach digestion was used for this preparation. Small fragments of 'tissue', including from both the surface and deeper parts of the sponge were placed in sample bottles, into which a small quantity of active bleach (sodium hypochlorite) was added. After a short time, the organic components had dissolved leaving only the skeletons. This was followed by three washes of distilled water and a final wash of 99% ethanol. Spicule suspensions were allowed to settle for about 10 to 15 mins between each wash to avoid accidental decanting of smaller spicules. Clean spicule suspensions were then pipetted onto a glass slide and topped with a cover slide. Spicule type and size data are given as minimum–mean–maximum for 25 spicules unless stated otherwise. The second preparation involved cutting a thick section through the sponge tissue to determine the structure of the skeleton, the structure of the water-canal system, and other aspects of histology. Thick tangential and perpendicular hand-cut sections of 1.0 – 1.5 mm were procured from a preserved fragment to examine their skeletal arrangement. Sections were placed onto a glass slide and left to dry, while stacked with weight. After the sections were completely dried, they were mounted on glass slides with a cover slip using DPX mountant (06522 Sigma-Aldrich) to adhere both the spicules and the skeleton to the slides. Finally, both slides were observed using an Olympus SZX10 microscope and camera (DP-75) and digitized using cellSens software (OLYMPUS).

RESULTS AND DISCUSSION

Results

The specimens collected from the mangroves at PB and Oyster rocks consisted of 14 OTUs, constituting seven genera (Table 1). Species richness at both sites was represented predominantly by the *Hippospongia* and *Haliclona* (three species each), from the orders Dictyoceratida and Haplosclerida, respectively.

Species (OTU) descriptions based on morphological characters are given below. *Hippospongia* (three OTUs). *Hippospongia* sp. 1 (Figure 2A) has a

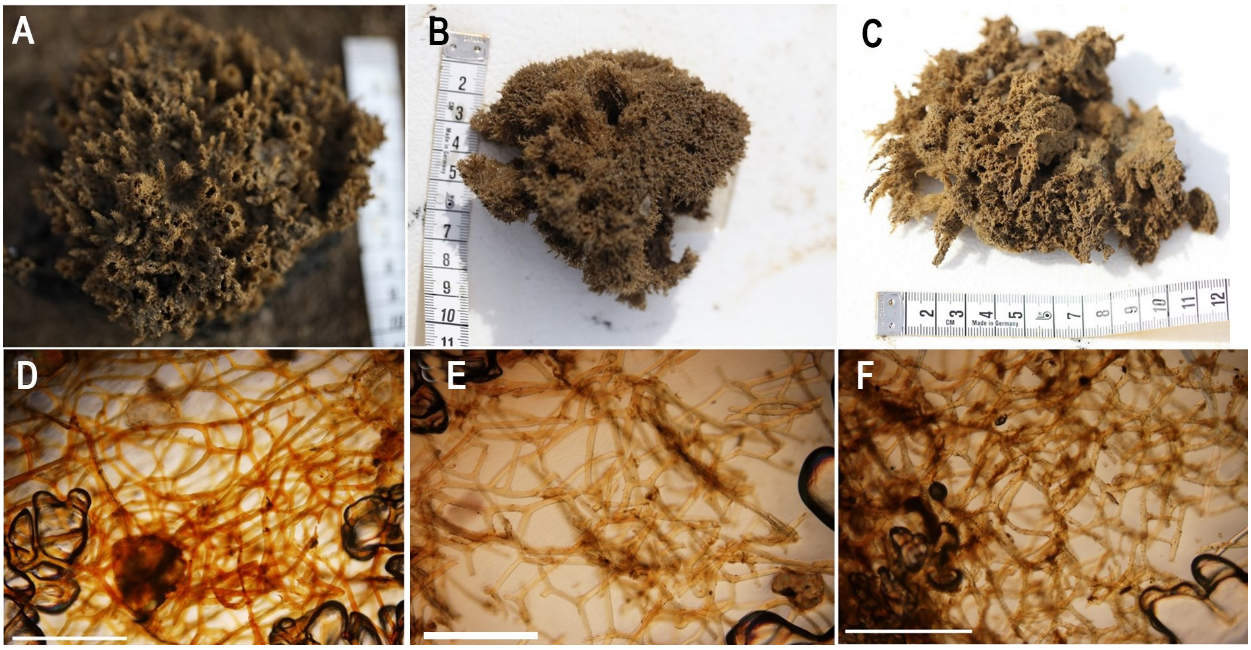

Figure 2. A. Specimen *Hippospongia* sp. 1; B. *Hippospongia* sp. 2; C. *Hippospongia* sp. 3. D. Spongin fiber reticulation for *Hippospongia* sp. 1; E. *Hippospongia* sp. 2; F. *Hippospongia* sp. 3. Scale Bar D - E, 1= 500 μm.

Table 1. Identified sponge specimens based on macroscopic and microscopic examinations. Haploscleriids sponges were the dominant OTUs, followed by sponges from the Dictyoceratiid order.

Class	Subclass	Order	Family	Genus	Species
Demospongiae (Sollas 1885)	Keratosa (Grant 1861)	Dictyoceratida, (Minchin 1900)	Spongiidae (Gray 1867)	Hippospongia (Schulze 1879)	*Hippospongia sp. 1*
					Hippospongia sp. 2
					Hippospongia sp. 3
	Heterosclero morpha (Lévi 1953)	Axinellida (Lévi 1953)	Axinellidae (Carter 1875)	Axinella (Schmidt 1862)	*Axinella sp. 1*
					Axinella sp. 2
		Clionaida, (Morrow & Cárdenas 2015)	Family Clionidae (Orbigny 1851)	Spheciospongia (Marshall 1892)	*Spheciospongia sp. 1*
					Spheciospongia sp. 2
		Haplosclerida (Topsent 1928)	Chalinidae (Gray 1867)	Halicona (Grant 1836)	*Haliclona sp. 1*
					Haliclona sp. 2
					Haliclona sp. 3
				Chalinula (Schmidt 1868)	*Chalinula sp. 1*
					Chalinula sp. 2
			Niphatidae (van Soest 1980)	Niphates (Duchassaing &Michelotti 1864)	*Niphates sp*
		Poecilosclerida (Topsent 1928)	Tedaniidae (Ridley & Dendy 1886)	Tedania (Gray 1867)	*Tedania sp*

massive encrusting to microbenthic form, attached directly to the substratum. Brown when alive and olive green to rust when preserved. Numerous oscules, large with an almost consistent diameter at the apex of turrets. Consistency is firm and compressible. It is also elastic and not easily torn even after preservation. Skeleton has a fiber that protrudes from ostia circumference, producing a porous reticulated surface (Figure 2D). *Hippospongia* sp. 2 (Figure 2B) has a massive, thickly encrusting cushion on hard substrata with microbenthic shape. Color is brown when alive and turns to drab brown when preserved. Oscules are discrete with a slight fistula border, random. Ostia are dispersed over the entire surface. Consistency is soft, spongy, compressible, and difficult to tear. Skeleton fibers protrude from ostia circumference, producing porous reticulated surface (Figure 2E). *Hippospongia* sp 3 (Figure 2C) possesses an encrusting form with irregular folding shape, insinuating over the substratum. It is brown when alive and drab when preserved. Oscules are not visible. Texture is spongy and compressible. Skeleton also possesses fibers protruding from the ostium circumference, producing a porous reticulated surface (Figure 2F).

Haliclona (three OTUs). *Haliclona* sp.1 possesses a branching form which is apically Y-ended. It is grayish-black when alive and turns brown in ethanol. Oscules are recessed along the inside of finger-like projections, whereas ostia are not visible. Consistency is brittle and easily crumbled (Figure 3A). *Haliclona* sp. 2 possesses massive form, ended with a rosette structure at its apex. Oscules are inconspicuous with turquoise color when alive, turning whitish in ethanol. Has brittle and crumbly consistency (Figure 3B). *Haliclona* sp. 3 possesses massive to encrusting forms with a light to dark color when alive that changes to drab when preserved. Oscules are conspicuous, discrete, and often with a raised membranous lip; scattered over

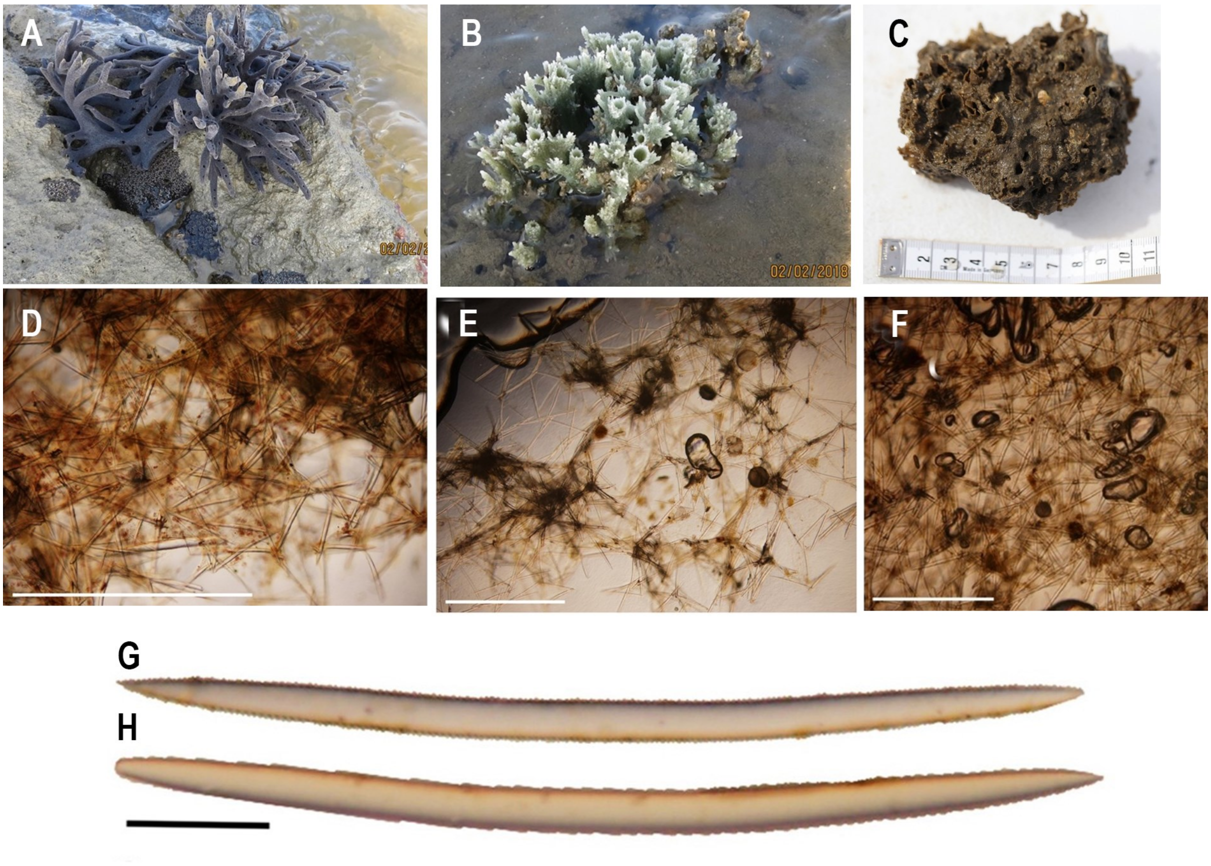

Figure 3. A. Specimen *Haliclona* sp. 1; B. *Haliclona* sp. 2; C. *Haliclona* sp. 3. D. Isodictyal reticulation *Haliclona* sp. 1; E. *Haliclona* sp. 2; F. *Haliclona* sp. 3; G. Oxeas; H. Style spicules. Scale Bar: D - F, 1=500 µm; G & H, 1=50 µm.

the surface. Flushed ostia are dispersed over lateral/external surfaces. The texture is unsubstantial, brittle, and easily crumbled. Surface uneven with dominant ridges of oscula 'lips'. All *Haliclona* spp. possess a skeleton with isodictyal reticulation (Figure 3D, E, F). Oxeas and style spicules are shown in Figure 3G, H & Table 2.

Chalinula (two OTUs). *Chalinula* sp. 1 possesses a microbenthic shape and enlarged basal portion. Oscula possess 'chimney-like' lips protruding through the benthic substratum. Color is brown when alive and drab when preserved. Oscula are conspicuous, but discrete with raised membranous lips. Ostia are not visible. The surface is uneven and unornamented, predominanted with oscula lips, unsubstantial, brittle and easily crumbled (Figure 4A). Isodictyal skeletal reticulation (Figure 4C). Spicules are styles and oxeas (Figure 4F, G, Table 3).

Chalinula sp.2 (Figure 4B) is cushion-shaped, with brown coloration when alive and drab when preserved. Oscules are inconspicuous and the sponge has a brittle and easily crumbled consistency. Skeleton is isotropic (Figure 4D) with secondary lines longer than one long spicule; spicules consist of strongyles, styles, and oxeas (Figure 4E, 4F, 4G, Table 3).

Niphates (one OTU) has a stipitate form, a spheroidal body with a basal stalk approximately the size of the body diameter. Surface uneven and with tubercules. Stalk attaches directly to crevices of rock substratum. Color is bright orange when alive, but beige in alcohol. Oscules are not visible but minute ostia are observed on lateral surface. The texture is firm but is friable and non-elastic in consistency, due to the lack of spongin (Figure 5A). Skeleton is plumoreticulate (Figure 5B), showing a radiate megasclere tract mainly consisting of styles and oxeas spicules (Figure 5C, D & Table 4).

Table 2. Spicule type and size of *Haliclona* spp. specimens based on minimum–**mean**–maximum for 25 spicules.

Specimen	Oxeas	Styles
Haliclona sp. 1	142.1–**159.2**–180.3 µm × 5.7–**7.7**–9.8 µm	130.3–**147.5**–180.3 µm × 6.9–**8.1**–9.6 µm
Haliclona sp. 2	167.9–**198.8**–221.6 µm × 5.1–**8.9**–10.7 µm	–
Haliclona sp. 3	297.9–**345.7**–374.7 µm × 11.8–**14.4**–16.2 µm	315.4–**334.2**–355.1 µm × 14.23–**15.7**–16.4 µm
Haliclona (Haliclona) oculata (Linnaeus 1759) type species of *Haliclona* subgenus *Haliclona* (van Soest et al. 2018)	80–250 µm × 5–10 µm up to 370 × 15 µm	–

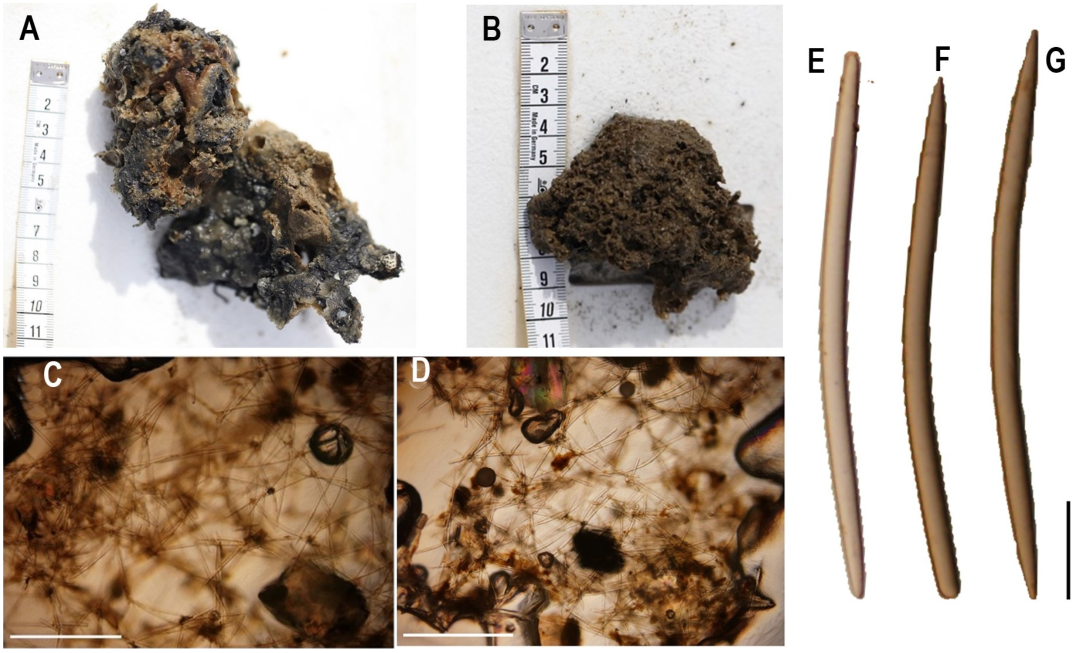

Figure 4. A. Specimen *Chalinula* sp. 1; B *Chalinula* sp. 2; C. Isotropic reticulation in *Chalinula* sp. 1; D. *Chalinula* sp. 2. E. Strongyles; F. Styles; G. Oxeas spicules. Scale Bar: C - D, 1=500 µm; E-G, 1=50 µm.

Table 3. Spicule type and size of *Chalinula* spp. specimens based on minimum–**mean**–maximum for 25 spicules.

Specimen	Strongyles	Styles	Oxeas
Chalinula sp. 1	–	328.9–**342.3**–365.7 µm × 12.9–**14.4**–16.5 µm	330.2–**358.5**–385.3 µm × 9.6–**13.4**–5.7 µm
Chalinula sp. 2	252.5–**269.3**–298.5 µm × 12.1–**12.9**–13.7 µm	225.3–268**.5**–292.7 µm × 8.8 –**12.8**–15.4 µm	215.5–**271.7**–300.1 µm × 4.5–**10.4**–14 µm
Chalinula renieroides (Schmidt 1868) type species of genus *Chalinula* (van Soest et al. 2018)	–	–	81–93.9–105 µm × 3.6–5.1–6.6 µm

Table 4. Spicule type and size of *Niphates* sp. specimens based on minimum–**mean**–maximum for 25 spicules.

Specimen	Styles	Oxeas
Niphates sp.	131.5–**176.7**–261.8 µm × 4.6–**6.1**–7.5 µm	247.1–**426.8**–617.9 µm × 6.6–**12.9**–18.9 µm
Niphates erecta (Duchassaing & Michelotti 1864) type species of genus *Niphates* (van Soest et al. 2018)	–	99–**139**–154 µm × 2–**5**–6 µm

Figure 5. A. Specimen of *Niphates* sp.; B. Plumoreticulate reticulation of skeleton; C Styles; D. Oxeas spicules. Scale Bar: B, 1=500 µm; C - D, 1=50 µm.

Figure 6. A. Specimen *Axinella* sp. 1; B *Axinella* sp. 2. C. Plumose reticulation of skeleton *Axinella* sp. 1; D *Axinella* sp. 1. E. Long styles; F. Long oxeas and common oxeas spicules. Scale Bar: C - D, 1=500 µm; E - G, 1=50 µm.

Axinella (two OTUs). *Axinella* sp.1 possesses a palmate body form, with several flattened digitate branches, 4 cm high by 2 cm wide, fused together at a common base with a short peduncle. Attaches directly to the substratum with its enlarged basal holdfast (Figure 6A). Its brown color in live specimens turns to olive green in alcohol. Oscules are small, less than 2 mm in diameter, with a slightly raised membranous lip, flushed, and positioned at the base of digitate fusion. The texture is hispid, brittle, easily crumbled and furry/brush. Skeleton, plumose in form (Figure 6C) and consisting of long styles; long oxeas and common oxeas spicules (Figure 6E, F, G & Table 5). *Axinella* sp.2 possesses a bushy microbenthic shape with

Table 5. Spicule type and size of *Axinella* spp. specimens based on minimum–**mean**–maximum for 25 spicules.

Specimen	Long styles	Long oxeas	Common oxeas
Axinella sp. 1	752.6–**992.8**–1113.4 µm × 12.2–**14.4**–23.2 µm	742.9–**949.9**–1008.7 µm × 12.9–**16.4**–19.5 µm	–
Axinella sp. 2	835.1–**900.4**–1001.4 µm × 16.1–**18.2**–20.3 µm	700.3–**823.9**–908.9 µm × 15.9 –**17.3**–19.1 µm	115.2–1**71.2**–200.5 µm × 12.1–**13.2**–14.6 µm
Axinella polypoides (Schmidt 1862) type species of genus *Axinella* (van Soest et. al 2018)	210–500 µm × 8–12 µm	–	270–420 µm × 5–12 µm

Table 6. Spicule type and size of *Spheciospongia* spp. specimens based on minimum–**mean**–maximum for 25 spicules.

Specimen	Long tylotes	Short tylotes
Spheciospongia sp. 1	546.1–**695.9**–764.9 µm × 37.8–**38.7**–39.3 µm	204.9–**259.9**–270.7 µm × 11.9–**12.4**–13.5 µm
Spheciospongia sp. 2	665.1–**788.4**–800.4 µm × 36.1–**38.2**–38.3 µm	200.3–**226.9**–238.9 µm × 10.9–**11.3**–12.1 µm
Spheciospongia vesparium (Lamarck 1815) type species of genus *Spheciospongia* (van Soest et. al 2018)	–	280–410 µm × 6–9 µm

Table 7. Spicule type and size of *Tedania* sp. specimens based on minimum–**mean**–maximum for 25 spicules.

Specimen	Styles	Tornotes	Onychaete
Tedania sp. 1	212.1–**255.9**–244.9 µm × 14.8 –1**8.7**–19.9 µm	204.9–**229.9**–240.7 µm × 11.1 –**12.1**–13.3 µm	404.9–**459.9**–470.7 µm × 3.9–**4.4**–5.5 µm
Tedania anhelans (Vio in Olivi 1792) type species of genus Tedania subgenus Tedania (van Soest et. al 2018)	173–280.9 µm × 5–12 µm	140–302 µm × 2–7 µm	40–220 µm × 0.5–2 µm and 240–270 µm × 7–12 µm

arborescent to flattened digitate branching. Branching shows complex reticulation to thickly branching in more than one place. The body attaches directly to the substratum. It has a brown color when alive and pale brown when preserved. Oscules are not visible. Has a fibrous and hispid consistency, showing spicule projections on the surface. Skeleton also possesses a plumose form (Figure 6D) that consists of long styles; long oxeas and common oxeas spicules (Figure 6E, F, G & Table 5).

Spheciospongia (two OTUs). *Spheciospongia* sp. 1 (Figure 7A) possesses branching forms, which basally form a massive or bulb that is usually buried under the substratum. Oscules are conspicuous. Brown to black live specimens turn pale brown in ethanol. *Spheciospongia* sp. 2 possesses a massive form without oscules. Brown to black live specimens turn pale brown in ethanol (Figure 7B). Both *Spheciospongia* specimens possess a brittle and crumbly consistency. Likewise, their skeleton is irregular in form (Figure 7C, D) with spicules consisting of two classes of tylotes (long and short; Figure 7E, F & Table 6).

Tedania (one OTU) sponges possess branching forms with massive ramose, having irregular branches with flattened fistula-like projections. Live

Figure 7. A. Specimen *Spechiospongia* sp. 1; B *Spechiospongia* sp. 2. C. Irregular reticulation of skeleton *Spechiospongia* sp. 1; D *Spechiospongia* sp. 2. E. Long; F. Short tylotes spicules. Scale Bar: C - D, 1=500 μm; E-F, 1=50 μm.

specimens are orange turning beige in alcohol. Consistency is soft, easily torn and compressible. Oscula inconspicuous despite ostia observed in furrows of the corrugated surface of branched elevations (Figure 8A). Skeleton is predominantly plumose (Figure 8B), composed of tracts of style spicules (Figure 8C). Other spicule forms include tornotes (Figure 8D) and onychaetes (Figure 8E; Table 7).

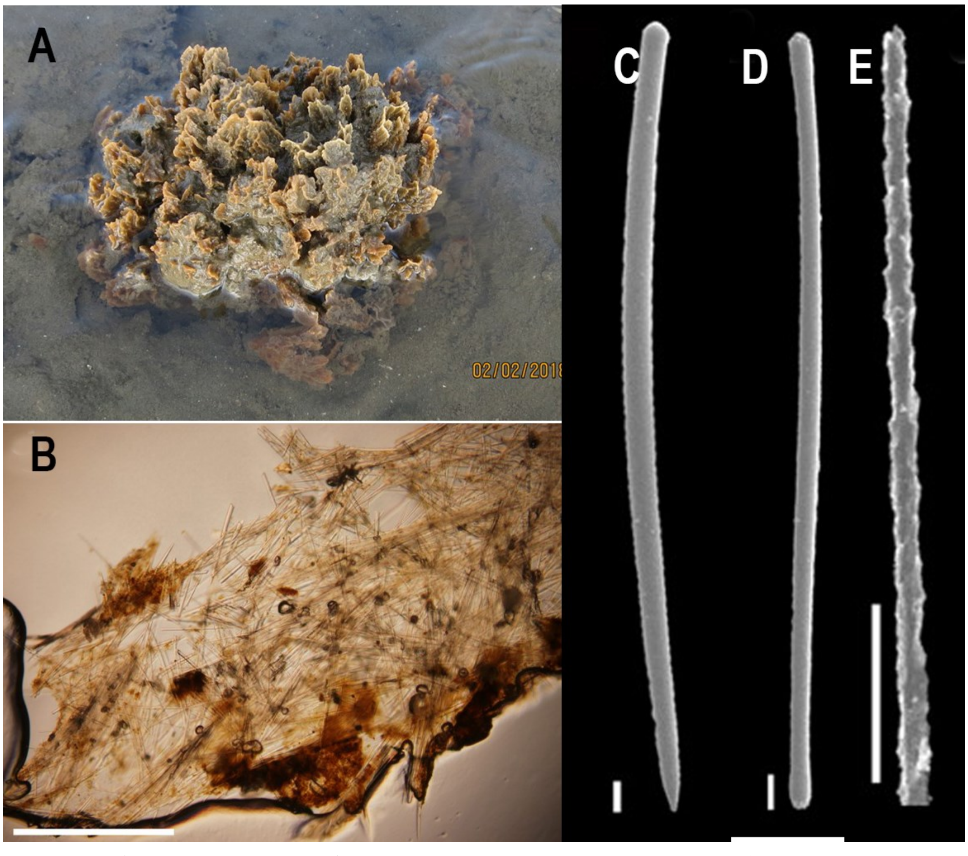

Figure 8. A. Specimen of *Tedania* sp.; B. Plumose reticulation of skeleton, C. Style; D. Tornote; E Onychaete spicules. Scale Bar: B1, 1=500 μm; C - E, 1=20 μm.

Discussion

Studies of sponge taxonomy for northwest Borneo are scarce to non-existent. This first known record for Brunei shows that the shallow-water estuarine conditions near Pulau Bedukang (including Oyster rocks) support at least 14 species. Studies from several other Southeast Asian regions, including coral ecosystems, show distinctly higher diversities, e.g., 33 species from Cebu, Philippines (Longakit et al. 2005), 118 species from Jakarta Bay, Indonesia (de Voogd & Cleary 2008), 126 species from the Eastern Gulf of Thailand (Kritsanapuntu et al. 2001), 197 from Singapore (Lim et al. 2012) and 299 species from Vietnam (Quang 2013). The low number of species reported at PB can be attributed to the highly turbid conditions in the estuary and the very small sampling area (100s of square meters), but possibly also the short sampling duration and the exclusion of cryptic and sciophilous specimens. Nonetheless, the dominance of Haplosclerida at PB is comparable to that of Singapore with 30% (Lim et al. 2012) and the Philippines with 28% (Longakit et al. 2005). This suggests that the species number for Brunei should increase significantly with more sampling effort that including samples from local coral reefs. When considering overlapping species, the PB sponges had a close affinity with Singapore, where inshore marine environments are turbid. Compared to Singapore, there is a similarly high number of *Haliclona* species, with *Haliclona* sp. 2 reported from an area known as the *Haliclona* "chimney" (Lim et al. 2012). *Haliclona* is considered to be a robust, generalist genus that shows unselective larval settlement and a preponderance for harsh environmental conditions, e.g., *Haliclona tenuiramosa* occurs in heavy metal polluted waters and *Haliclona tubifera* in thermally-stressful environments (Rao et al. 2009; Guzman & Conaco 2016). Our findings suggest that *Hippospongia* and *Axinella* also contain species suited to extreme habitats (variable turbidity and salinity).

Shallow-water estuarine ecosystems are typically variable and unpredictable (Barnes 1999; Steindler 2002; Lim et al. 2016; Marshall et al. 2016). The intertidal zone imposes conditions of periodic air exposure, variable temperatures, and greater irradiance (Steindler et al. 2002; Marshall et al. 2010). Despite these circumstances, the sponges recorded at PB were mostly intertidal and air exposed during low tides. Their abundance and ubiquitous nature in this heterogeneous habitat likely relate to plasticity in structural organization and morphology. Morphological remodeling could allow them to overcome the variable environmental conditions and ensure their survival. Species such as *Haliclona* sp. 3 apparently survive direct sun exposure by remaining buried in the mud. While sponges that occur encrusted on the surfaces of boulders usually become established in shaded 'refugia', reducing the threats of high temperature and desiccation (Barnes 1999). During air exposure when filter feeding is curtailed, alternative food sources are often needed. Some sponges adapted for periodic air exposure produce energy through photosynthesis by establishing associations with photosymbionts, including *Haliclona* sp. (Steindler et al. 2002).

Dredging activity poses an additional environmental risk to sponges, as sediments from the dredge or disposal site may smother the sponge surface, potentially affecting water filtration and light penetration (Pineda et al. 2017). With the dredging in the Brunei bay for the construction of a four-lane bridge in Pulau Muara Besar, together with the iconic bridge that transverses from Sungai Besar to Temburong, benthic organisms at PB were likely exposed during the sampling time to periodically high sediment loads (Marshall et al. 2016). Although sponge habitat-generalists may vary in body form to survive a variety of different environmental conditions, this capability is genetically predetermined (Swierts et al. 2013; Setiawan et al. 2016; Lopez-Legentil & Pawlik 2009). There are limited numbers of body forms within this genetic framework, and only certain morphologies will survive the ensuring environmental conditions. Hence, the shift from a relatively mature and stable to a more unstable, less diverse community dominated by encrusting species may indicate chronic environmental stress (Easson et al. 2015). This observation is consistent with studies showing that morphological variation in sponge communities decreases as perturbation increases. High sediment conditions can clog the aquifer systems of sponges, and adversely affect pumping and reduce feeding efficiency. Consequently, sponges under high sedimentation conditions should be energetically stressed and should attempt to expel unwanted material, which presents a drain on their energy reserves and should impact growth. Pineda et al. (2017) suggested that high sediment loading particularly affects the massive form of encrusting and wide cup morphologies. The prevalence of the massive *Haliclona* sp. 1 at Oyster rocks (Figure 1) is, however, not consistent with this observation. Compensatory mechanisms for life in turbid conditions include elevated mucus production, psammobiotic growth forms, and the protrusion of spicules. Spicule protrusion functions to capture fine sediments and is seen in *Paratetilla bacca*, *Cinachyrella* spp. and *Raspailia* spp. (Becking et al. 2013). We also observed surfaces with protruding spicules in *Axinella* sp. Although the literature suggests that sponges are influenced by suspended sediment in multiple ways, there is a need for further exploration of these different responses.

Difficulties in this study in determining the species level of the sponges relate to the use of only a classical morphological approach. Traditional sponge identification has been based almost completely on their skeletal structure and organization (Hooper & van Soest 2002; Wörheide & Erpenbeck 2007). This proves to be a major problem because sponges exhibit a great diversity of skeletal types which often poorly distinguish species (McCormack et al. 2002; Pöppe et al. 2010; Xavier et al. 2010; Setiawan et al. 2016; Swierts et al. 2013). Taxonomists have also relied on morphological features such as color, shape, and skeletal elements to identify sponges. This is acknowledged to be difficult due to the lack of fixed diagnostic morphological characters, and limited knowledge of phenotypic plasticity among species (Hill & Hill 2002; Guardiola et al. 2016; Bell & Barnes 2000). Such limitations have become apparent during this study when attempting species identifications. For instance, the taxonomy of the Order Haplosclerida (Porifera: Demospongiae), which is a dominant group in this study, is made particularly difficult by their reduced spicule diversity and simplified skeletal structures (Redmond et al. 2007; Redmond et al. 2011; McCormack et al. 2002). This order is typically characterized as having a skeleton that reticulates in an isodictyal arrangement (triangular mesh) with unornamented diactinal megascleres (oxeas). In the genus *Haliclona* however, although the subordinates were diagnosed as *Haliclona* sp. for possessing isodictyal reticulation, spicules in species 1 and 3 did not conform to the features of having only analogous oxea. Palumbi (1986) suggested that the increase in the size and number of spicules are ecophenotypic responses to changing environmental stress such as waves. For this reason, reliability and “a sound classification” of the order are far from being established (Borchiellini et al. 2004; Redmond et al. 2011).

CONCLUSION

This preliminary study of shallow water and intertidal sponges of Brunei Darussalam recorded at least 14 species (OTUs). These mainly constituted the Haplosclerida, an order of sponges known to tolerate adverse and high sedimentation conditions, as are found in the Brunei Estuarine System (BES). This first inventory of these underexplored benthic animals is considered useful to improve understanding of ecological and community responses to variable environmental conditions and general conservation issues. Despite the absence of definitive species determinations, our study suggests a significant diversity of sediment-tolerant sponges in the region. We advocate further investigation based on molecular taxonomy, as well as into the phenotypic plasticity of these sponges.

AUTHOR CONTRIBUTION

E.S. and D.J.M. designed and supervised the overall research project. D.R. collected, curated and captured the data for the sponges. All authors wrote and revised the manuscript. E.S. and D.J.M. read and approved the final paper.

ACKNOWLEDGMENTS

E.S. thanks the Directorate Global Engagement and Biology Department of Institut Teknologi Sepuluh November, Surabaya that enabled D.R. to conduct an internship and final year research at the institute. The research of D.J.M. was funded through a UBD grant UBD/RSCH/1.4/FIBF.(b)/2018/016. We appreciated the help of local Bruneians who assisted in the field. We also acknowledge two anonymous reviewers for their constructive suggestions.

CONFLICT OF INTEREST

The authors declared that there is not any conflict of interest regarding this research work.

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