

# Natural and Artificial Rocky Shores of Brunei, Including a Preliminary Checklist of Invertebrate Species

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## Abstract

This review summarises current knowledge of Brunei Darussalam's rocky shore ecosystems. Although wave-washed rocky shores comprise a small fraction of the local coastal habitats, which are dominated by sandy beaches, mangroves, and mudflats, they support distinct and diverse faunal communities. We describe the formation, physical environment and biotic zonation of both natural and artificial rocky shores and compare the factors driving habitat heterogeneity for each shore. We also outline the known species diversity and the human impact on these shores. Two hundred and ten (210) invertebrate species are reported to occur on these shores, with intertidal gastropods (61 species) and subtidal cnidarians (45 species) being the best represented. Other typically diverse taxa, including sponges, crustaceans (decapods and amphipods) and polychaetes, however, remain poorly documented. The natural shores are continuously being disturbed and degraded by human activity, threatening local species extinction and reducing resilience and population recovery potential. This pressure is somewhat offset by the recent establishment of artificial rocky shores, which enhance the subtidal habitat and present novel intertidal habitat with respect to wave action exposure, especially the sheltering of rocky shores in modified embayment systems. Ecologically, artificial structures should facilitate greater colonization and recolonization potential by enhancing habitat and local larval supply. However, these structures present a small subset of the habitat types found on natural shores. Importantly, the artificial shores lack low-sloped or horizontal surfaces that trap waterbodies (tidal pools) during emersion and microhabitat/substratum complexity, both of which drive habitat heterogeneity and species diversity. We therefore call for further coastal research as a priority, to support effective conservation management of the remaining natural shores and to improve understanding of the ecological functions of artificial shores. Because of their limited extent, these ecosystems have been overlooked in the past, and this undermines Brunei's responsibility for biodiversity conservation and its commitments within its national jurisdiction under international treaties.

*Index Terms:* rocky shores, Southeast Asia, Borneo, Brunei Darussalam, physical environment, biotic zonation, species diversity, human impacts

## 1. Introduction

Brunei Darussalam's location on the northwestern coast of Borneo close to or possibly within the zone global maximum marine biodiversity<sup>1,2</sup> suggests a distinct and diverse

marine fauna, which remains relatively underexplored. This distinctiveness reflects the combined influence of the Sulu Sea part of the megadiverse Coral Triangle to the east and the various shelf and deep-water zones of the South

China Sea (SCS) itself. Within the SCS, Brunei lies on the eastern edge of the Sunda Shelf, implying broad connectivity across the sea and with its northern regions; the Hainan current system in some seasons culminates in an anticlockwise circulation around the shelf.<sup>3</sup> Several analyses group Brunei with Sabah (Malaysia) and Palawan (Philippines) within a distinct biogeographical unit, the Palawan North Borneo ecoregion.<sup>4-6</sup> Despite these features and Brunei's commitments under international biodiversity and sustainability conventions, research on its marine biodiversity has fallen behind that of other SCS countries, particularly Singapore and China (including Hong Kong). This gap is largely historical: government environmental management has focused mainly on the fishes and coral reefs,<sup>7,8</sup> and a broader marine research culture has been slow to develop.

Despite its small size, Brunei contains a diverse set of largely pristine marine biomes. For practical purposes, these can be grouped into four main areas: (1) the Brunei Shelf (BS), from the coast to the continental-shelf edge (~70 km offshore; ~200 m depth); (2) the South China Sea (SCS) coastline, comprising shallow (<10 m) and intertidal habitats; (3) inner Brunei Bay (BB); and (4) the Sungai Brunei estuarine system (BR) (see *Appendix Figure 1*). These areas broadly align with biomes in the IUCN Global Ecosystem Typology 2.0,<sup>9</sup> a marine shelf biome (M1), a shoreline biome (MT1; mainly SCS), and a semi-confined transitional waters biome (FM1; BB and BR). Together, they encompass >10 benthic ecosystem functional groups (EFGs; see IUCN report), defined by abiotic drivers and processes, including ambient environmental features and disturbance regimes that influence resource availability. Along the SCS, the shore ecosystem is dominated by a narrow linear sandy beach, punctuated by small mangrove-fringed estuarine inlets or lagoons at Belait, Seria, Tutong and Meragang (see *Figure 1*). Natural hard substrates are largely limited to two Tertiary sandstone ridges at Pantai Tungku (Empire) and Tanjong Batu, which extend seaward subtidally to Pulau

Punyit (nearshore) and Pelong Rocks (offshore), respectively. Artificial hard substrates classified as the anthropogenic shoreline biome (MT3; along the SCS) occur mainly as breakwaters with rock-armoured revetments along the Brunei/Muara coastline, built to curb coastal erosion, form small harbors, and maintain channels to the sea.

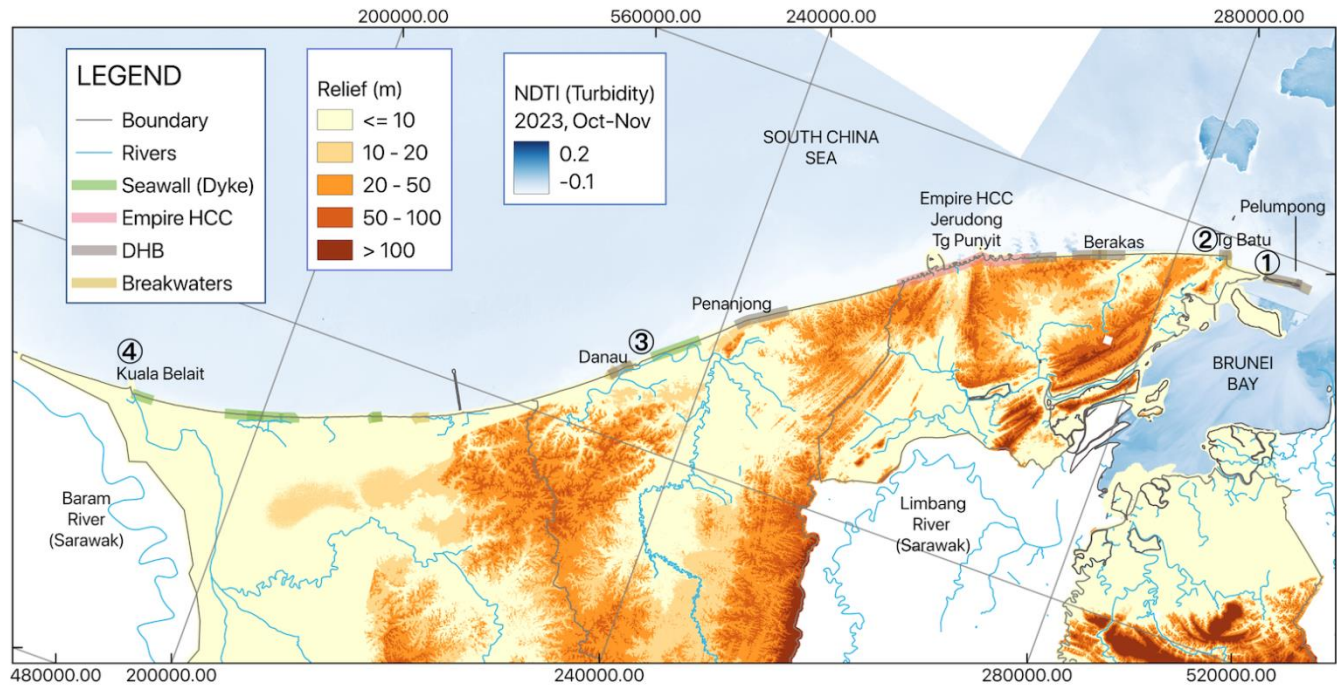
Rocky shores are key marine ecosystems that support biodiversity and underpin many functions across coastal biomes. In Brunei they occupy only a small area, but previous studies indicate that they support a high benthic invertebrate diversity. This review provides a baseline overview of Brunei's rocky benthic ecosystems to facilitate research and inform conservation management. We describe the physical setting of these shores, contrast natural and artificial habitats, assess the species diversity and summarise current and emerging threats. The review draws on published studies,<sup>10-15</sup> as well as extensive observations and unpublished records of UBD marine researchers (co-authors) whose combined field experience in Brunei spans decades. Although not fully comprehensive, this synthesis intends to serve as a reference point for future research on and conservation of the local rocky-shore ecology and diversity, and towards a holistic understanding of Brunei's marine biomes.

## 2. Rocky Shores of Brunei

Brunei's coastline extends ~130 km, from Sungai Tujoh (4°635'12.17"N 114 °60 4'33.16"E) to the tip of the Pelumpong spit/island (5°60 2'31.10"N 115°60 8'13.39"E) in Brunei Bay. Natural rocky shores are found only at (i) Tanjong (Tg) Batu and Pelong Rocks, located 3.6 km offshore, and (ii) Tg Punyit and Pulau ('island') Punyit, 750 m offshore (hereafter the Empire or Punyit; see *Figure 1*). The scarcity of rocky shores relates to geology, particularly, the deposition of Tertiary sedimentary rocks in a sequence of deltas that prograded north-westerly into SCS; the western third of the coastline is part of the active Baram Delta.<sup>16</sup> Differential erosion of folded, faulted, tilted and uplifted sandstone-shale strata produced the characteristic ridge and valley

terrain, which occurs as headlands and valleys/bays at the coast (see *Figure 1*). The coastline from Penanjong to Tg Batu is eroding

due to regional tectonics and Holocene Sea Level Rise, and this has been further accelerated due to coastal development and sand mining.



**Figure 1.** Relief, artificial coastal structures and turbidity map of Brunei. The map shows sections of coasts protected by seawalls (green lines), detached headland breakwaters (DHB, grey lines), revetments (yellow lines) and reconstructed coast at Jerudong (pink) digitised by authors. Circular labels 1-4 are training breakwaters at the (1) Pelumpong access channel, (2) Api Api Wetland, (3) Tutong River, and (4) Belait River. The relief pattern is generated using 2009 Lidar image from the Surveyor General licensed to UBD. Off the coast, the Normalised Difference Turbidity Index (NDTI) pattern is generated from two Landsat images (2023, 27 Oct & 21 Nov, available from USGS Earth Explorer). It shows that turbidity is markedly lower (white patches) in the vicinity of coastal sections protected by rock-armoured revetments (grey, pink & yellow lines). Map grid reference: WGS84/UTM 50N.

Artificial rocky shoreline construction has been implemented in response to coastal development, sand mining and the vulnerability of narrow beaches of the SCS facing coast to storm waves. Following severe coastal recession due to beach sand mining in the 1950's and 1990's, a seawall was first constructed in 1959 and was later remediated by much more extensive reconstruction of the Jerudong-Tungku coast in 1997.<sup>17,18</sup> Coastal protection structures changed with advancement in engineering. Large rock blocks, which are more effective in dissipating wave energy, replaced concrete walls. These were deployed in the form of offshore Detached Breakwaters (DB), rock-armoured revetments to protect vulnerable shores, and training breakwaters to maintain navigation channels. The Jerudong-Tungku reconstruction furthermore

involved the creation of artificial headlands, protected by rock armour and use of DB (see *Figure 2*). During this reconstruction, a part of the original natural headland at Tg Punyit was removed.

A Detached Headland Breakwater (DHB) is designed to work with the environmental dynamics to stabilise the coast. Orientation and pacing distance are based on optimal wave-energy dissipation. DHBs induce sedimentation in their wave shadow, resulting in the formation of a land connection with the shore resembling a headland or tombolo. The reduced wave energy in between gives rise to 'bay beaches' (see *Figure 2*).<sup>19,20</sup> A total of 77 DHBs currently protects ~16 km of the Brunei coastline, including the Pelumpong spit (built in 1983,

1990), Berakas (1996), Penanjong camp and Tungku (1977), Danau (2006) and west of Tanjong Batu (2015). Rock-armoured revetments cover ~3 km, excluding Jerudong-Tungku coast, while training breakwater-jetties total ~5 km. These artificial structures (excluding training

breakwaters) now account for ~35% of the coastline, constituting 11% seawalls, 12% DHB, 2% revetments, and 10% reconstructed coast. The boulder blocks of the artificial rocky shores facilitate colonization by marine biota.



**Figure 2.** (A) Satellite image of the Tungku coastline (South China Sea) showing artificial rocky structures in two semi-enclosed embayments. W, X, artificial headlands with rock armoured revetments; Y, sheltered part behind curved breakwater; Z, detached breakwater (DB). (B) An adjoining coastline to that above. (C) L-head breakwater and (D) detached headland breakwater (DHB). The names Tungku North and Tungku South are not official. Blue arrow indicates ‘outfall’. Upward arrows indicate high sublittoral species diversity in deeper-water. Sheltered areas subject to sand deposition are indicated. Downward arrows indicate low species diversity, due to shallow water and sand influence on rocky structure. Red circle indicates reference point 4°54’46.7”N, 114°52’46.7”E.

### 3. Climate and Physical Environment

Rocky shores are physically stressful habitats, with conditions becoming increasingly extreme higher on the shore as emersion time increases. Local conditions also vary with regional and seasonal weather. In Brunei, the climate is dominated by the southwest (SW) and northeast (NE) monsoons, driven by the latitudinal shift of the Intertropical Convergence Zone (ITCZ)

between boreal summer and winter. ITCZ further influences the South China Sea (SCS) upper layer circulation, contributing to the weather, as well as regional species connectivity.<sup>5,21</sup> These current systems are extremely complex and vary in strength and direction across seasons and with El Niño conditions.<sup>21</sup> Although strong biotic connections are implied mostly with the regions south of Brunei, velocity models suggest that a

powerful southeast current off Vietnam (deriving from Hainan in the north) during winter months turns eastwards along the edge of the Sunda shelf and projects towards Borneo.<sup>21</sup> During the NE monsoon, the SCS receives substantial wave energy (12-18 kW/m/a slightly north of the coastline),<sup>22</sup> while nearshore wave power is typically 1-2 kW/m/a; wavefronts largely approach the coastline perpendicularly to its NE orientation. Wave heights are generally 0.3-0.6 m from March to August, increasing to 0.6-1.8 m during tropical cyclone and typhoon activity in the northern SCS between December and February. Wave periods are usually 4-6 s but can reach 9-10 s during winter storms. Winds are generally light; only 0.1% reach moderate gale strength (Champion 7 autoweather station, 29 km north of Punyit).

Tidal regimes alternate between diurnal (one high tide per day) and semi-diurnal (two high tides per day) cycles on a fortnightly schedule, consistent with lunar periodicity (see **Figure 3**). Spring tides span ~2.6 m, whereas neap tides have a smaller range of ~0.6 m (0.9–1.5 m) (see **Figure 3**). Daytime spring low tides (<0.5 m) occur in the morning (before 10.00 am) or late afternoon/evening (after 3.00 pm), so that low-shore species typically escape peak midday air temperatures (they are immersed at these times). Air temperature exposure of intertidal organisms increases with shore height but also depends on local topography (aspect, slope, and shading).<sup>23</sup> Upper-shore snails (gastropods) that are only infrequently inundated can experience and are adapted to withstand prolonged exposures to high temperatures, often exceeding 50°C at midday<sup>24-26</sup> (see **Figure 3**). Seasonally, mean daily air temperatures in the shade vary by 3.5°C (between ~27 and 30.5°C).

Coastal water temperatures are typically 28-29°C (9/Mar/2026, 10 a.m., COAST Toolkit), but habitat water temperatures can vary more widely (25-31°C).<sup>27</sup> Seawater pH is generally >8 and salinity ranges from 21.8 to 32.9 psu. Conditions in tidal rock pools are, however, more variable, particularly at low tide when they receive acidified groundwater discharge. The Empire

boulder beach low tide pool water pH can vary between 5.9 and 8.6 and salinity between 0.2 and 32.2 psu.<sup>13,28-30</sup> Turbidity data are limited, but suspended-sediment plumes, primarily arising from the Brunei Bay (northeast) and the Baram Delta (southwest), can traverse the coast for months during the wet season.<sup>31</sup>

#### 4. Rocky Shore Zonation and Species

Rocky shores show clear zonation of species and communities along a vertical tidal gradient. These patterns reflect differences among species in tolerance of air exposure, including thermal stress and water loss. In tropical systems, intertidal zonation is often described as three broad bands: (i) a high-shore littorinid snail assemblage, (ii) a mid-shore oyster–barnacle assemblage, and (iii) a low-shore algal-turf zone (see **Figure 4**). The local high shore is dominated by three littorinid snail species (*Echinolittorina malaccana*, *E. vidua* and *Littoraria articulata*) that graze on microbial and algal biofilms. The gastropod *Planaxis sulcatus* and occasional carnivorous gastropods that prey on littorinids also extend into this zone. The mid-shore is characterised by the sessile, typically embayment oyster, *Saccostrea scyphophilla*, often forming dense reefs (see **Figure 4**; until recently this species was referred to as *S. mordax*).<sup>14,32</sup> The habitat-forming *Saccostrea echinata* colonises the sheltered mid-shores of artificial structures and hosts numerous cryptic invertebrates, such as polychaetes, sipunculans, small (often boring) bivalves, and gastropods.<sup>14</sup> Other key mid-shore species are the barnacle *Chthamalus malayensis* and motile gastropods such as *Planaxis sulcatus*, *Cellana* sp., *Monodonta labio*, murid whelks and *Siphonaria* spp. The mid-shore forms a subzone below the *S. scyphophilla* belt, supporting the volcano barnacle (*Tetraclita kuroshioensis*), the chiton *Squamopleura miles* (in small rocky depressions), and the stalked barnacle *Capitulum mitella* in rock crevices (see **Figure 4**). The dense algal turf covering the low shore rocks comprises ~30 algal species that differ in air-exposure tolerance, producing a micro-zonation; generally, green and brown algae occur higher on the shore than red and coralline algae<sup>10</sup> (see **Figure 4** and **Appendix Table 1**). Algal turf

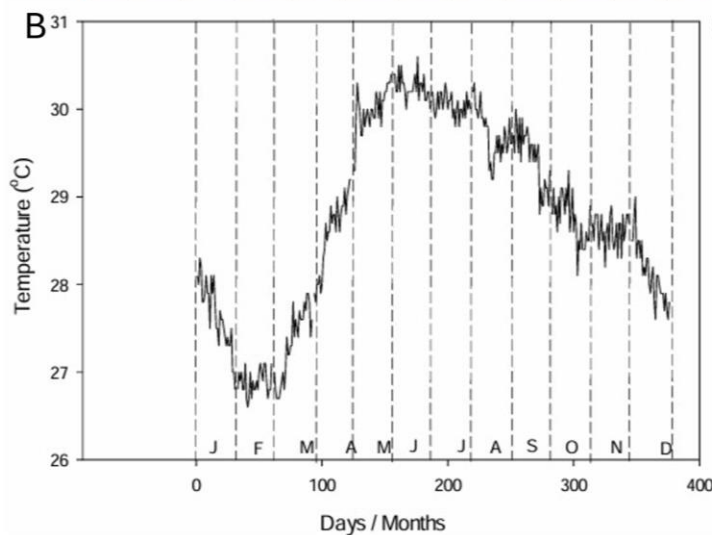
provides habitat for diverse small invertebrates, including polychaetes, amphipods, tanaidaceans, and ostracods, and meiofauna such as copepods, marine mites, and chironomid fly larvae.<sup>15</sup> Larger

motile vetigastropods, *Turbo articulatus*, *Lunella cinerea* and *Trochus radiata*, and decapod crabs are also common in this zone<sup>15</sup> (see **Figure 4**).

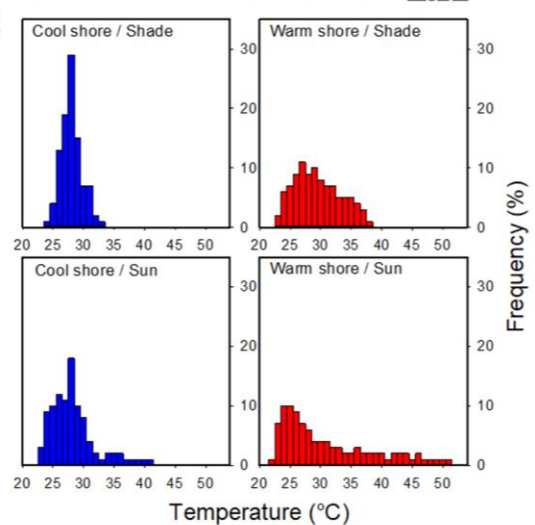
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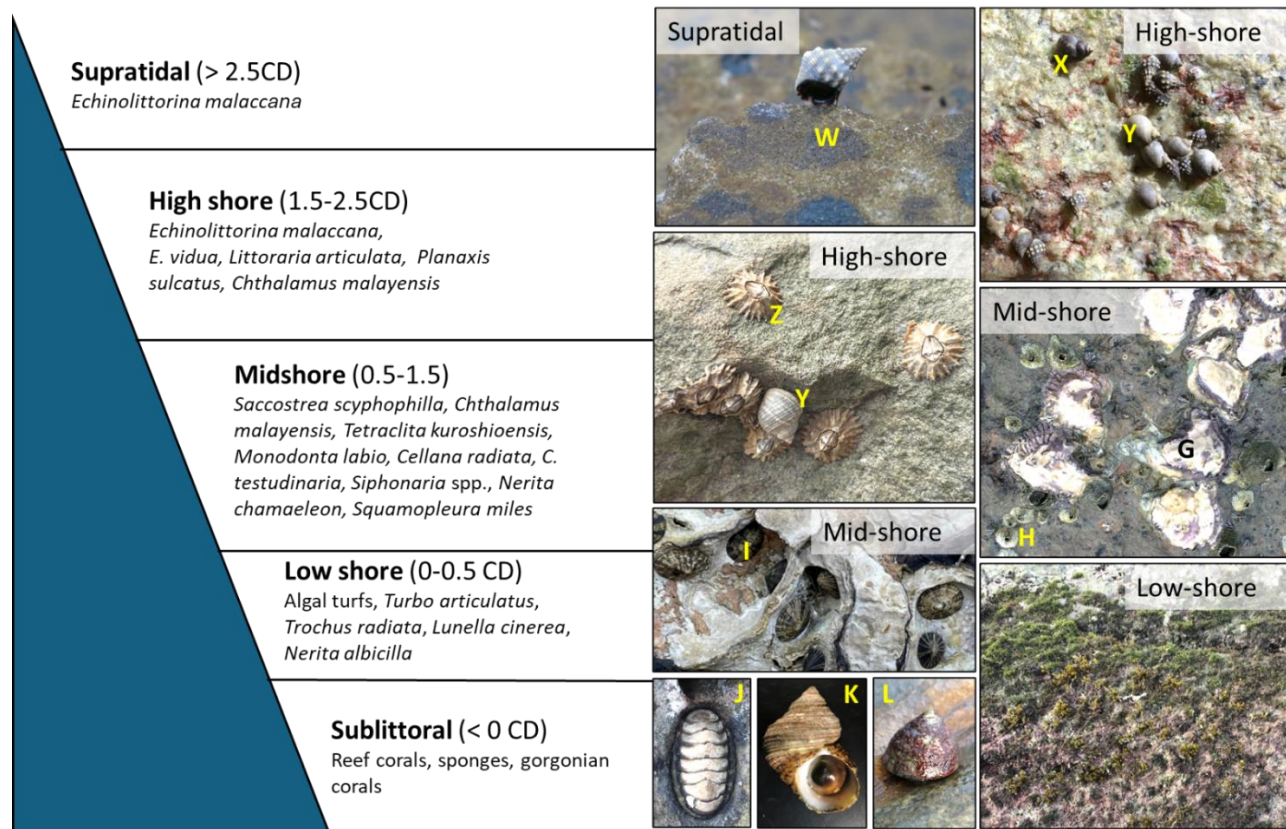
C



**Figure 3.** Physical conditions. (A) Modelled tidal rhythms (intermonsoon, 8 and 27 April 2026) showing semi-diurnal and diurnal, and neap and spring tide conditions. CD, Chart Datum, -0.2 to 2.4. (B) Mean daily surface water temperature showing seasonal effect. (C) Habitat temperature during emersion in the high rocky shore for different artificial faces directly exposed to the sun or in the shade; temperatures sometimes exceed 50°C (Brahim et al. 2019).<sup>23</sup>

The supratidal zone experiences prolonged air exposure (sometimes for months), being intermittently wetted by wave splash during the high seas usually associated with typhoon activity in the northern South China Sea. The only marine metazoan extending into this zone is the littorinid *Echinolittorina malaccana*, which is extremely thermotolerant and physiologically adapted for extended survival in air<sup>24,33-35</sup> (see **Figure 4**). Contiguous extension of the natural rocky substrata from the intertidal to the subtidal (sublittoral) zone is relatively limited in depth along the Jerudong ridge (the Empire), though it is more pronounced at the small islets of Pulau Punyit and the offshore Pulau Pelong Pelongan

(Pelong Rocks).<sup>10</sup> These substrata typically facilitate the establishment of hard coral colonies, gorgonian corals, sponges and other attached and motile invertebrates. **Appendix Figure 2** shows coral species occurring at the interface of the low shore and subtidal zone at the Empire. Coral communities, however, become more diverse in the deeper water adjacent to the natural rocky shore at the Empire and around many of the artificial shore structures. Subtidal organisms do not endure much air exposure, but are locally affected by coastal sediment plumes, salinity reduction due to runoff, wave energy and scouring by suspended sandy sediments during storms.<sup>7</sup>



**Figure 4.** Rocky shore zonation. Vertical zonation with images of some prominent large molluscs and barnacles defining the zones (to low shore). W, *Echinolittorina malaccana*, notably, exhibiting shell standing behaviour to limit heat transfer from the rock surface, X, *Littoraria articulata*, Y, *E. vidua*, Z, *Chthalamus malayensis*, G, *Saccostrea scyphophilla*, H, *Tetraclita kuroshioensis*, I, *Cellana radiata*, J, *Squamopleura miles*, K, *Turbo articulatus*, L, *Trochus radiata*.

### 5. The Natural Shore (Empire): Drivers of habitat heterogeneity

The drivers of habitat heterogeneity that influence species diversity differ between the natural and the artificial rocky shores (see **Table 1**). The primary drivers operate at different spatial scales on these different shores, with a shoreline scale apparently being more important to the artificial shores and a habitat level scale important to the natural shore (see **Table 1**). The uniform orientation of the Empire shoreline (at near 90° to the Brunei coastline), means that exposure to wave action (moderately exposed) and cooling winds is similar across most of the shore (sectors A-D; see **Figure 5**), though conditions become more variable towards Pulau Punyit (including sector E; see **Figure 5**). As previously mentioned, the depth associated with this shoreline (sectors A-D) is limited by the bordering shallow sandy banks and the gradual slope of the shore. The steepest and deepest part

occurs along northeastern face of Pulau Punyit (see **Figure 5**). Habitat heterogeneity of the Empire shore is predominantly driven by differential fragmentation of the original sandstone layers, producing shorefaces with varying slopes, as well as horizontal shores, and rocky blocks differing in size and shape (often flattened and platelike) (see **Table 1** and **Figure 5**). The most intense fragmentation has led to formation of a small, stable boulder-shore alcove, comprising angular blocks usually less than 20 cm in diameter (see **Figure 5B**). The area between the Empire's artificial breakwater point and Pulau Punyit comprises a low shore horizontal platform of flattened, variably sized blocks that are over-washed with muddy to shale sediments and are covered with *Padina*, *Sargassum* and coralline algal species (see **Figure 5E**). Details of the intertidal ecology and substratum at Pulau Punyit are published elsewhere<sup>10</sup>.

**Table 1.** The major shoreline and habitat drivers of habitat heterogeneity of the natural and artificial shores, from Brahim *et al.* 2019<sup>23</sup> and Lee *et al.* 2024.<sup>14</sup> High/Low indicates relative differences in effect.

	NATURAL		ARTIFICIAL
<b>SHORELINE (100 m)</b>			
<b>A1. Orientation: aspect - north, east, west and south facing</b>	Linear, NW aspect at Empire; aspect variable at Pulau Punyit but spatially limited; thermal regime similar across the shore, sheltered from cooling NE winds [1].	Low	Variable aspects facing all directions; some cooler habitats due to NE winds and warmer habitats in sheltered alcove of breakwaters [1]. <b>High</b>
<b>A2. Orientation: direction to wave front</b>	NW aspect oblique to prevailing wave fronts; exposure to moderate wave energy.	Low	Variably angled shore faces relative to wave fronts; high, moderate and sheltered (leeward faces) wave exposure; latter encourages colonization of embayment species [2]. <b>High</b>
<b>A3. Orientation and position: subtidal depth</b>	Limited associated subtidal depth, except the NW face of Pulau Punyit.	Low	Variable subtidal depths, with deeper areas facilitating reef coral formation. <b>High</b>
<b>A4. Shore slope (gradient)</b>	Variable slopes including extended low gradient and horizontal surfaces, facilitating intertidal pool formation [Figure 6].	High	Steep slope gradient constrained by construction; drainage rapid and no intertidal pools. <b>Low</b>
<b>HABITAT (&lt;10 m)</b>			
<b>B1. Rock blocks</b>	Variable sizes and heterogeneously packed creating many angled surfaces; horizontal surfaces trap waterbodies and form tidal pools when emersed; excessive block fragmentation forms boulder shore [Figures 5 and 6].	High	Relatively uniform size and packing of blocks; water drains rapidly during tidal emersion; no horizontal slopes in intertidal zone and no pools formed. <b>Low</b>
<b>B2. Microrefugia (within block)</b>	Block structuring, fragmentation and weathering creates more complex refugia – fine cracks and crevices that accumulate sediment.	High	Less complex refugia formed by block structure. <b>Low</b>
<b>B3. Substratum</b>	Substratum often weathered and cracked, and forming honey-comb weathering patterns.	High	Rocky substratum is relatively smooth. <b>Low</b>

At a finer, within-shore scale (<10 m), the horizontal surfaces, together with block fragmentation, create small mid-shore and low-shore pools during tidal emersion enhancing habitat heterogeneity and species diversity (see **Table 1** and **Figure 5**). These pools support zoanths (*Palythoa cf. mutuki*), sea urchins (*Stomopneustes variolaris*), sea cucumbers (*Holothuria leucospilota*), and vetigastropods, *Turbo articulatus* and *Trochus radiata* (see **Appendix 3**). Three predominant vertically separated species of hermit crab, *Clibanarius rutilus*, *C. ransonii*, and *C. merguensis*, are also conspicuous, with the latter sometimes forming large aggregations (piles) in the lower boulder-shore pools (see **Appendix Figures 3** and **4**). Notably, the acidified groundwater drainage during low tide into the upper boulder-shore pools causes significant shell dissolution and

likely influences the communities there (see above and **Appendix Figure 3A**). Fine-scale habitat heterogeneity is further enhanced by the varying size and packing of the rocky blocks, and the creation of irregularities, between block cracks and crevices (see **Appendix Figure 4**). Microtopographical weathering of the natural rock substrate, including honeycombing and the formation of crevices and fine pits, provides refugia in the mid to high shore during tidal emersion for small snails, limpets and chitons (see **Appendix Figure 4**).

**6. Artificial Shores: Drivers of habitat heterogeneity**

Artificial shore habitat heterogeneity primarily relates to shoreline-scale drivers (see **Table 1**). Artificial structures create shorefaces with multiple orientations/aspects (N, S, E, W), such

that some faces are substantially warmer because they are sheltered from cooling winds, lie within protected engineered alcoves, and receive direct solar radiation at different times of the day<sup>23</sup> (see **Table 1**). However, thermal differences mainly affect the relatively depauperate upper-shore communities, which are already well adapted to extreme temperature exposure. A more important driver of functional habitat heterogeneity and species diversity relates to how shoreface orientation affects the near-substratum hydrodynamics. Relative to incoming wave fronts, the artificial shorefaces can be classified as highly exposed (direct or 90° to the wave front), moderately exposed (oblique or between 90° and 0°) or sheltered (facing landward or 0° to

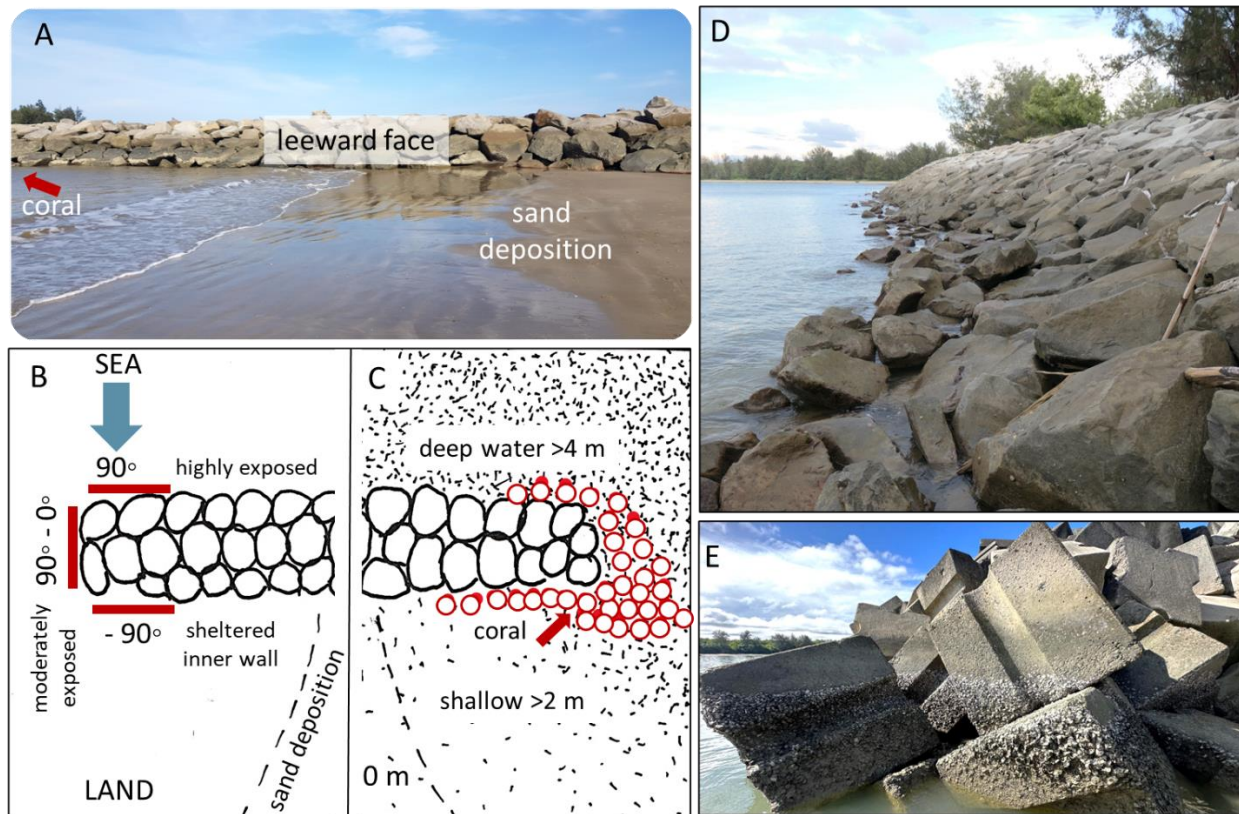
-90°), in contrast to only moderately-exposed shores found at Empire (45°; see **Table 1** and **Figure 6**). Artificial shores thus support greater diversity in terms of (i) species tolerant of high wave exposure and (ii) species that prefer embayment-like, low-wave energy conditions. In particular, the algal turf zone, including coralline algae, may support a diverse assemblage of sessile (attached) animal species resilient to high-energy hydrodynamics. Consistent with this prediction for low-wave-energy habitats, a previous study reported colonization of the leeward artificial shorefaces by *Saccostrea echinata*, a habitat-forming estuarine oyster, and its associated robust epifaunal community (around 90 species).<sup>14</sup>



**Figure 5.** Satellite images of different sections of the Empire shoreline extending to Punyit. (A) Shore influenced by shallow water and sandy beach in close proximity; flattened block structure in foreground. (B) Stable boulder shore alcove of relatively small rocky blocks, devoid of thick macroalgal growth and supporting abundant gastropods. (C) Large flattened blocks with macroalgae on upper surfaces (dominated by *Padina* sp., *Sargassum* sp., and finely-branched coralline algae), (E) extensive horizontal area similar to C. Tan and green areas in the satellite images indicate coral and low rocky shore communities, respectively.

A third shoreline-scale factor that uniquely affects habitat conditions on Brunei's artificial rocky shores is variable water depth, contrasting with the generally limited contiguous subtidal extent of the natural rocky shores. The greatest depths associated with the artificial shores usually occur along the more exposed rock faces that preclude sediment accumulation, whereas leeward (landward) faces receive substantial sediment deposition (see **Figure 6**). On detached breakwaters (e.g., Tungku), sand build up occurs centrally reducing rocky shore depth to above

zero Chart Datum and eliminating the lowshore zone (see **Figure 6**). Construction of some detached breakwaters (DBs) at around 6 m depth creates moderately exposed contiguous artificial shore faces of deeper water that support diverse coral communities<sup>7</sup> (see **Figure 2Z**, **Figure 6** and **Appendix Table 2**). Notably, 43 species of scleractinian reef corals are able to colonise (even if only temporarily) the spring tide low water mark or the near-shore sublittoral of these shores<sup>11</sup> (see **Appendix Table 2**).



**Figure 6.** Artificial shores. (A) Detached breakwater (DB) at Tungku (North, Figure 2Z), showing the leeward face and sand deposition towards the beach. Subtidal reef coral communities have developed in the deeper water along the moderately exposed edge. (B,C) Diagrammatic surface view of a detached breakwater showing expected wave front exposure and approximate seawater depths (m) associated with this structure. (D) Shore along artificial headland at Tungku North (Figure 2). (E) Outer seaward face of artificial headland at Tungku North incorporating manufactured blocks with flat steep sloped surfaces; the oyster belt zone is shown in foreground. Photographs A and E are courtesy of Huan Chiao Lee.

Because shore slope of the artificial shores is dictated by construction criteria, this is relatively steep and intertidal surface drainage during emersion is rapid (see **Table 1** and **Figure 6**). Both shore slope and rocky block features and packing prevent tidal pool formation on artificial rocky shores. Furthermore, the relatively smooth,

unweathered sandstone blocks of artificial shores provide less substratum complexity than natural shores. In summary, artificial and natural shores present different forms of habitat complexity operating at different spatial scales. Artificial shores often support greater habitat in deeper subtidal zones, and their habitat complexity and

species diversity are apparently enhanced by contrasting wave-energy conditions across their multi-orientated faces. In contrast, habitat heterogeneity on natural shores is driven largely by the packing and fragmentation of broad flatter blocks and horizontal surfaces that form intertidal pools, along with more complex substratum features (see *Table 1*).

## 7. Species Diversity

We compiled a list of benthic rocky-shore species from published studies and coauthors' field observations over a period spanning three decades. In some cases, animals were collected and are held in private and/or museum collections, but otherwise for conservation purposes animals were sometimes photographed *in situ*. Taxonomic experts were frequently sought to confirm species identifications, at least to genus level. The list covers macrofauna (> 500 µm) and excludes meiofauna (180 to 150 µm), such as crustaceans (e.g., harpacticoid copepods and ostracods), hexapods (e.g., dipteran chironomid larvae and collembolans), and marine mites (Acari). New species and records of halacarid and pontarachnid mites have been described from these rocky shores.<sup>36,37</sup> The tanaidaceans (Crustacea) are well studied for the region, and although littoral species are only described for the soft benthic estuarine system, two algal turf rocky shore species were recently collected.<sup>15,38</sup> With respect to marine protozoans, epibiotic ciliates are reported from Brunei's rocky shores<sup>39</sup>. Compilation of the intertidal faunal species records relied heavily on seven faunistic and ecological studies, ecological studies at Pulau Punyit,<sup>10,12</sup> a crustacean study,<sup>40</sup> gastropod studies at the Empire and on Neritidae,<sup>41</sup> a study of epifauna associated with oyster reefs on sheltered rocky shores,<sup>14</sup> a recent study of algal-turf fauna at the Empire,<sup>15</sup> and a study of subtidal reef corals associated with an artificial breakwater.<sup>11</sup> Notably, the typically species-rich amphipods, isopods, and polychaetes are greatly underrepresented as identification to even genus-level is difficult from whole specimens and photographs.<sup>15</sup> The current list nonetheless provides a baseline for Brunei's

rocky-shore species to facilitate future research and management.

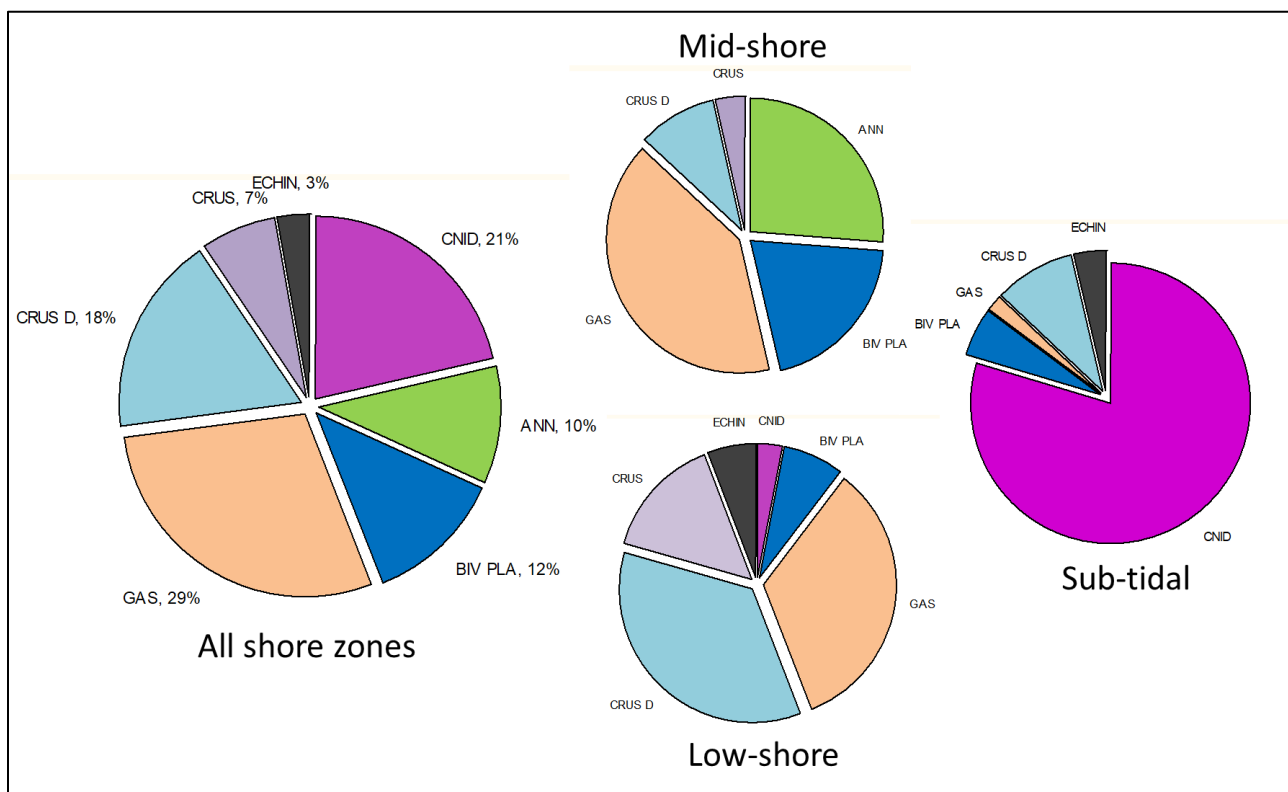
We report the occurrence of 210 species on Brunei's rocky shores, distributed across the Cnidaria (45), Annelida (21), Mollusca (85), Crustacea (50), and Echinodermata (6) (see *Figure 7* and *Appendix Table 2*). By major group, the molluscan Gastropoda (snails, limpets, etc.) is the most-species-rich taxon, with 61 species (29%). Cnidaria (corals, etc.) accounts for 45 species (21%), Annelida (polychaete worms, tubeworms, and sipunculan worms) for 21 species (10%), molluscan Bivalvia (mussels and oysters) and Polyplacophora (chitons) for 25 species (12%), decapod Crustacea (true crabs, anomurans/hermit crabs, and shrimps) for 31 species (18%), other crustaceans (amphipods, isopods) for 20 species (7%), and Echinodermata (sea urchins, sea stars, etc.) for 6 species (3%) (see *Figure 7* and *Appendix Table 2*). Although some generalist and more motile species traverse multiple shore zones, most occur in a single vertical zone. The mid-shore species are dominated by gastropods, bivalves, and annelids; however, this breakdown is influenced by a single study on oyster reef (*Saccostrea echinata*) fauna of sheltered artificial breakwaters that recorded ~90 species.<sup>14</sup> Crustaceans (amphipods) and gastropods are prominent in low-shore algal turfs, but many remain unresolved at the species level.<sup>15</sup> Coral species (Cnidaria) dominate the subtidal hard benthos.<sup>11</sup> *Appendix Figure 5* shows some interesting and less common invertebrates collected from the shores. The apparent greater species richness in the artificial shore systems relates to these being more intensively studied.<sup>11,14</sup> Natural habitats need more comprehensive sampling, including fine rock crevices (especially shaded crevices and overhangs) and the rocky area between the Empire headland and Pulau Punyit (see *Figure 5E*).

## 8. Human Impact on Rocky Shore Habitats

Anthropogenic stress responses of rocky shore animals should be framed within the background of strong natural physical stresses experienced. At the Empire, temperature, desiccation and

sedimentation appear to be major natural factors undermining communities and diversity. Although high-shore animals tolerate extreme heat exposure, the frequently observed bleaching of low-shore coralline algae is likely driven by thermal stress (see *Appendix Figure 6*). These algae play a key role in structuring the low-shore community, as their epiphytic symbionts are preferred food for amphipods.<sup>15</sup> During the monsoon seasons, highly turbid coastal waters promote deposition of fine sediment on the horizontal rock surfaces of the mid and low shore, including extensively on the Empire boulder shore (see *Figure 8B*). Persistent muddy deposits smother algal turf and limit animal grazing opportunities (gastropods; see *Figure 8*).

This kind of sedimentation relating to seasonal water turbidity, could however become more destructive under changing regional and global climate that drives more frequent storms and local river flooding events. Other natural stressors at the Empire are sand scour of low-shore turf algae (because of proximity to the sandy beach) and the acidification of tidal-pool water (see *Appendix Figure 3*). While several studies show that combined reductions in pH, carbonate and salinity severely corrode tidal-pool gastropod shells and reduce organismal size, population-level effects are unexplored, though the overall community structure is likely to be impacted.<sup>13,28,29</sup>



**Figure 7.** Proportional species representation for taxonomic groups. Pie charts for all habitats combined, the mid-shore, lower shore and subtidal zones. CNID, Cnidaria; ANN, Annelida; BIV PLA, Bivalvia and Polyplacophora; GAS, Gastropoda; CRUS D, decapod Crustacea; CRUS, other Crustacea; ECHIN, Echinodermata.

The Empire (and Pulau Punyit) is effectively the only remaining natural rocky shore in Brunei, following the recent development at Tunjong Batu. No rocky-shore ecological data are available from before construction of the Empire (hotel and country club) in the mid-1990s;

however, reduction of the original shore is unlikely to have been ecologically neutral. The small but ecologically important mid-to-low shore static boulder shore system has been impacted by ongoing landscaping works since 2014, to remove the fringing natural forest for the

construction of recreational facilities (as of writing this paper; see **Figure 8**). Loss of the protective forest has triggered landslides during periods of heavy seas, leaving thick, muddy deposits covering much of this shore for extended periods. Together with the ongoing natural settlement of suspended sediment, these events have altered the boulder-shore community

and the sandy strip above it. Several formerly recorded species, including the sea cucumber *Holothuria leucospilota*, cryptic seastar *Cryptasterina* sp., and upper sand-rock interface neritid, *Nerita polita*, appear to have been lost from the boulder shore system (see **Appendix Figure 5**).



**Figure 8.** Empire boulder shore. (A) Rocks devoid of sediment cover before the removal of the fringing forest (background; photo towards land; pre-2015). (B) Lower (mid-shore) rocks covered with a fine layer of marine-derived sediment, relating to seasonal high turbidity loads (foreground; same photograph direction and time as in A). (C) Rocks covered with mud after landslide following removal of forest shown in A and B; forest patch in top left corner has subsequently also been removed (photograph, seaward direction).

Coastal development has extensively altered the natural rocky shore at Tanjong Batu. Development elsewhere has caused erosion of both the headland and the adjacent headland-valley coast, which extends from the sandy shore of Pelumpong spit (Maura; see *Appendix Figure 7*). In 2015, a rock-armoured revetment with a 5-m wide road/promenade was constructed to protect these coastal features from direct wave exposure (see *Appendix Figure 7*). These structures have resulted in the loss of an estimated 90% of the natural intertidal rocky shore there and its associated communities, though the construction provides a vast artificial shoreline for the establishment of marine rocky shore communities. The project involved stabilizing the sandy shore coastline directly to the west by means of two DHBs and a pair of training breakwaters to fix the mouth of Sungai Pemburungan, which naturally shifts by as much as 200 m between the NE and SW monsoons. The impact of this development on the Api-Api wetland, the only site in Brunei where *Avicennia marina* is the sole mangrove species and is adjacent to the SCS,<sup>42</sup> requires priority investigation.

### 9. Concluding Remarks

This study describes Brunei's natural and artificial rocky shores and provides the first comprehensive baseline inventory of their invertebrate fauna. Because species richness and composition are straightforward indicators of ecological condition, the study provides a foundation for assessing ecosystem health and integrity. Monitoring is especially important given ongoing, largely human-driven disturbances of these shores, from local to global scales. While we call for stronger protection of the remaining natural rocky shores, we highlight the substantial contribution of the artificial shores in diversity enhancement and resilience. These shores are relatively extensive, support novel hard-substratum communities, and provide habitat for many species also found on natural shores. Our study considered only a few examples of the much greater structural variation present in the artificial shores; for instance, unreported above is a low-profile scattered

shallow water boulder patch on the eastern shore of Tungku North, supporting a robust population of the rock urchin, *Stomopneustes variolaris*. The artificial structures provide habitat for prolific fish assemblages which remain unexplored. During the inter-monsoon clear water periods (May/June), anglers routinely catch large fish exceeding 500 cm length off the Tungku artificial headlands. Sea turtles are commonly seen sheltering in the deeper coral waters around Tungku's detached breakwaters. In addition, the altered soft substratum sediments associated with the Tungku artificial structures have attracted species more typically found in natural embayments or nearshore subtidal environments, including Olividae snails and *Astropecten* sea stars<sup>43</sup>; the iconic *Rapana venosa-Meretrix* clam interaction that becomes established in the modified Tungku sediments is currently under pressure from excessive shellfish overfishing. More-intensive research is clearly needed to determine the significance of the artificial shores in contributing to the ecology and biodiversity of Brunei's coastal biome, including both hard- and soft benthic ecosystems. This is especially important in the context of holistic marine environmental management and sustainability in the country.

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## References

- [1] B. W. Hoeksema and D. J. W. Lane, "The mushroom coral fauna (Scleractinia: Fungiidae) of Brunei Darussalam (South China Sea) and its relation to the Coral Triangle", *Raffles Bulletin of Zoology*, 62, 566-580, 2014.
- [2] D. J. W. Lane, and B. W. Hoeksema, "Mesophotic mushroom coral records at Brunei Darussalam support westward extension of the Coral Triangle to the South China Sea waters of Northwest Borneo", *Raffles Bulletin of Zoology*, 64, 204-212, 2016.
- [3] P.-T. Shaw and S.-Y. Chao, "Surface circulation in the South China Sea," *Deep Sea Research Part I: Oceanographic Research Papers*, 41, 1663-1683, 1994.
- [4] M. D. Spalding *et al.*, "Marine ecoregions of the world: A bioregionalization of coastal and shelf areas," *BioScience*, 57, 573-583, 2007.
- [5] M. de Bruyn *et al.*, "Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity," *Systematic Biology*, 63, 879-901, 2014.
- [6] M. J. Costello *et al.*, "Marine biogeographic realms and species endemism," *Nature Communications*, 8, 1057, 2017.
- [7] L. DeVantier and E. Turak, *Field Guide to the Reef Building Corals of Brunei Darussalam*, Fisheries Department, Ministry of Industry and Primary Resources, Government of Brunei Darussalam, pp. 256, 2011.
- [8] G. R. Allen, *Reef Fishes of Brunei Darussalam*, Department of Fisheries, Ministry of Industry and Primary Resources, Government of Brunei Darussalam, pp. 280, 2009.
- [9] D. A. Keith *et al.*, "IUCN global ecosystem typology 2.0: descriptive profiles for biomes and ecosystem functional groups," *IUCN*, 2020.
- [10] W. E. Booth *et al.*, "A survey of the flora and fauna of Pulau Punyit, Brunei Darussalam," *Sandakanian*, 9, 55-66, 1997.
- [11] D. J. W. Lane and G. P. C. Lim, "Reef corals in a high sedimentation environment on the mainland coast of Brunei, Northwest Borneo," *Galaxea, Journal of Coral Reef Studies*, 15, Supplement, 166-171, 2013.
- [12] D. J. Marshall *et al.*, "Gastropod diversity at Pulau Punyit and the nearby shoreline – a reflection of Brunei's vulnerable rocky intertidal communities," *Scientia Bruneiana*, 16 (2), 34-40, 2017.
- [13] N. Mustapha and D. J. Marshall, "Tracking coastal acidification from erosion of gastropod shells: spatial sensitivity and organism size effect," *Environmental Monitoring and Assessment*, 193, 2021.
- [14] H. C. Lee *et al.*, "Dramatic enhancement of macrozoobenthic species  $\beta$ -diversity in response to artificial breakwater construction along a tropical coastline," *Diversity*, 16, 742, 2024.
- [15] A. Johari *et al.*, "Benthic faunal ecology in the algal turf zone of a Bornean rocky shore: The influence of habitat-forming species," *Scientia Bruneiana*, 24, 128-143, 2025.

- [16] T. S. Sandal (ed), *The geology and hydrocarbon resources of Negara Brunei Darussalam*, Brunei Shell Petroleum, 1996.
- [17] G. Y. V. Yong, "Coastal Geomorphology in Brunei Darussalam". In K. U. Sirinanda and P. Michael (eds). *Geography at Universiti Brunei Darussalam: The First Decade*, Universiti Brunei Darussalam, 1996.
- [18] G. Y. V. Yong, "Brunei (Negara Brunei Darussalam)". In Eric C.F. Bird (ed.), *Encyclopedia of the World's Coastal Landforms*, Springer Science + Business Media B.V. (Dordrecht), 2010.
- [19] M. A. Chasten *et al.*, *Engineering design guidance for detached breakwaters as shoreline stabilization structures*, US Army Corp of Engineers, 1993.  
<https://apps.dtic.mil/sti/tr/pdf/ADA275241.pdf>
- [20] M. M. Latif and G. Y. V. Yong, "Coastal erosion in the unprotected and protected sections at Berakas: a comparative study", *Southeast Asia: A Multidisciplinary Journal*, 21, 45-62, 2021.
- [21] T. Zu *et al.*, "A revisit of the interannual variation of the South China Sea upper layer circulation in summer: correlation between the eastward jet and northward branch," *Climate Dynamics*, 54, 457-471, 2019.
- [22] Y. Tong *et al.*, "Long-term (1979–2024) variation trend in wave power in the South China Sea," *Journal of Marine Science and Engineering*, 13, 524, 2025.
- [23] A. Brahim *et al.*, "Non-reversible and reversible heat tolerance plasticity in tropical intertidal animals: Responding to habitat temperature heterogeneity," *Frontiers in Physiology*, 9, 2019.
- [24] D. J. Marshall and C. D. McQuaid, "Warming reduces metabolic rate in marine snails: Adaptation to fluctuating high temperatures challenges the metabolic theory of ecology," *Proceedings of the Royal Society B: Biological Sciences*, 278, 281-288, 2011.
- [25] A. Brahim and D. J. Marshall, "Differences in heat tolerance plasticity between supratidal and intertidal snails indicate complex responses to microhabitat temperature variation," *Journal of Thermal Biology*, 91, 102620, 2020.
- [26] G. N. Somero *et al.*, *Biochemical adaptation: Response to environmental challenges, from life's origins to the Anthropocene*, Sinauer Associates, Sunderland (MA), 2017.
- [27] D. J. Marshall and C. D. McQuaid, "Metabolic regulation, oxygen limitation and heat tolerance in a subtidal marine gastropod reveal the complexity of predicting climate change vulnerability," *Frontiers in Physiology*, 11, 1106, 2020.
- [28] D. J. Marshall and A. Rashid, "Organismal responses to coastal acidification informed by interrelating erosion, roundness and growth of gastropod shells," *Zoological Studies*, 62, e41, 2023.
- [29] D. J. Marshall and B. Tsikouras, "Compensatory shell thickening in corrosive environments varies between related rocky-shore and estuarine gastropods," *Marine Environmental Research*, 198, 106536, 2024.
- [30] A. A. Abdelwahab *et al.*, "Hydrogeochemistry of submarine groundwater discharge along a Bruneian coastline: Iron and aluminum enrichment along with coastal acidification," *Environmental Earth Sciences*, 85, 34, 2025.

- [31] Y. Y. Hee and S. Suratman, “Physico-chemical parameters profile during dry and wet seasons in southern South China Sea: Brunei Bay,” *Asian Journal of Chemistry*, 28, 2146-2152, 2016.
- [32] S. S. Lukehurst *et al.*, “Clarifying the identities of *Saccostrea scyphophilla* (Péron & Lesueur, 1807) and *S. mordax* (Gould, 1850) (Bivalvia: Ostreidae) from the Indo-Pacific,” *Zootaxa*, 5799, 1-31, 2026.
- [33] D. J. Marshall *et al.*, “Thermal adaptation in the intertidal snail *Echinolittorina malaccana* contradicts current theory by revealing the crucial roles of resting metabolism,” *Journal of Experimental Biology*, 214, 3649-3657, 2011.
- [34] D. J. Marshall *et al.*, “Supratidal existence drives phenotypic divergence, but not speciation, in tropical rocky-shore snails,” *Biological Journal of the Linnean Society*, 132, 1-16, 2020.
- [35] M. A. Ullah and D. J. Marshall, “Starvation and dormancy in marine gastropods: Taxonomic and ecological patterns, and energetic implications,” *Journal of Molluscan Studies*, 91, eyaf016, 2025.
- [36] T. Chatterjee *et al.*, “New records of *Copidognathus* mites (Acari: Halacaridae) from mangroves in Brunei Darussalam with descriptions of two new species,” *Zootaxa*, 3269, 18-30, 2012.
- [37] V. Pešić *et al.*, “A new marine mite of the genus *Litarachna* Walter, 1925 (Pontarachnidae, Hydrachnidia, Acari) from Brunei Darussalam,” *Ecologica Montenegrina*, 97, 136-142, 2026.
- [38] R. N. Bamber *et al.*, “Inshore apseudomorph tanaidaceans (Crustacea: Peracarida) from Brunei: new records and new species,” *Zootaxa*, 3520, 71-88, 2012.
- [39] T. Chatterjee *et al.*, “New record of *Acineta sulcata* (Ciliophora: Suctorea) epibiont on *Agauopsis* halacarid mite (Acari: Halacaridae) from northwest Borneo, South China Sea,” *Cahiers de Biologie Marine*, 66, 81-86, 2025.
- [40] S. Choy, “The crustacean fauna of Negara Brunei Darussalam,” *Brunei Museum Journal*, 7, 117-153, 1991.
- [41] N. Mustapha *et al.*, “The neritid snails of Brunei Darussalam: Their geographical, ecological and conservation significance,” *Ecologica Montenegrina*, 42, 45-61, 2021.
- [42] S. C. Choy and W. E. Booth, “Prolonged inundation and ecological changes in an *Avicennia* mangrove: implications for conservation and management”. *Hydrobiologia*, 285, 237-247, 1994.
- [43] D. J. W. Lane and D. J. Marshall, “Four new records of *Astropecten* seastar (Asteroidea: Astropectinidae) from Brunei”. *Scientia Bruneiana*, this volume.

Appendix

Appendix Table 1. Algal species recorded at Pulau Punit (Booth et.al 1997)<sup>10</sup>  
MSL, mean seawater level; MLWN, mean low water neap.

Species	Algal group	Shore level
<i>Acanthophora muscooides</i>	Red	MSL
<i>Amphiroa fragilissima</i>	Red	Lower littoral
<i>Centroceras sp.</i>	Red	Below MLWN
<i>Cheilosporum sp.</i>	Red	Near Chart Datum
<i>Gelidiella acerosa</i>	Red	Upper littoral – MSL
<i>Gelidiopsis sp.</i>	Red	Lower littoral
<i>Gracilaria sp.</i>	Red	MLWN , Lower littoral
<i>Grateloupia sp.</i>	Red	Upper littoral - MSL
<i>Herposiphonia sp.</i>	Red	Below MLWN
<i>Hypnea boergesenii</i>	Red	Upper littoral - MSL
<i>Laurencia papillosa</i>	Red	Upper littoral - MSL
<i>Laurencia sp.</i>	Red	Upper littoral - MSL
<i>Peyssonnelia sp.</i>	Red	Near Chart Datum
<i>Porolithon sp.</i>	Red	Below MLWN (rock substrate)
<i>Wurdemannia miniata</i>	Red	Below MLWN
<i>Anadyomene sp.</i>	Green	Lower littoral
<i>Bryopsis pennata</i>	Green	Lower littoral
<i>Caulerpa fergusonii</i>	Green	Lower littoral
<i>Caulerpa microphysa</i>	Green	Lower littoral
<i>Caulerpa racemosa</i>	Green	Lower littoral
<i>Caulerpa sertularioides</i>	Green	Lower littoral
<i>Caulerpa verticillata</i>	Green	Lower littoral
<i>Chaetomorpha sp.</i>	Green	Upper littoral - MSL
<i>Cladophora vagabunda</i>	Green	Upper littoral - MSL

<i>Udotea javensis</i>	Green	Near Chart Datum
<i>Dictyopteris delicatula</i>	Brown	More abundant towards MLWN
<i>Dictyopteris membranacea</i>	Brown	More abundant towards MLWN
<i>Dictyota bartayresiana</i>	Brown	More abundant towards MLWN
<i>Dictyota spp.</i>	Brown	More abundant towards MLWN
<i>Lobophora variegata</i>	Brown	More abundant towards MLWN
<i>Padina sp.</i>	Brown	MSL
<i>Sargassum sp.</i>	Brown	MLWN, MSL

**Appendix Table 2.** Preliminary list of marine species associated with Brunei’s rocky shores. JPM, Jerudong Park Medical Centre; PJER, Pantai Jerudong; EMP, Empire; PUN, Punyit; TUN, Pantai Tungku; PEL, Pelumpong; HS, high shore and supratidal; MS, mid shore; LS, low shore; SB, subtidal. \*late entries not included in analysis.\*\*currently under further review.

Taxon	Family	Genus	Species	JPM	PJER	EMP	PUN	TUN	PEL	Habitat
<b>Cnidaria</b>										
Hexacorallia	Sphenopidae	<i>Palythoa</i>	<i>cf. mutuki</i>					1		LS
Hexacorallia	Acroporidae	<i>Acropora</i>	<i>bifurcata</i>			1				LS
Hexacorallia	Acroporidae	<i>Acropora</i>	<i>pulchra</i>						1	SB
Hexacorallia	Acroporidae	<i>Acropora</i>	<i>speciosa</i>						1	SB
Hexacorallia	Acroporidae	<i>Isopora</i>	<i>brueggemanni</i>						1	SB
Hexacorallia	Acroporidae	<i>Montipora</i>	<i>hispida</i>						1	SB
Hexacorallia	Acroporidae	<i>Montipora</i>	<i>cf. efflorescens</i>					1		SB
Hexacorallia	Acroporidae	<i>Montipora</i>	sp.						1	SB
Hexacorallia	Agariciidae	<i>Leptoseria</i>	<i>explanata</i>					1	1	SB
Hexacorallia	Agariciidae	<i>Pavona</i>	<i>decussata</i>						1	SB
Hexacorallia	Agariciidae	<i>Pavona</i>	<i>frondifera</i>						1	SB
Hexacorallia	Agariciidae	<i>Pavona</i>	<i>varians</i>						1	SB
Hexacorallia	Agariciidae	<i>Pectinia</i>	<i>paeonia</i>						1	SB
Hexacorallia	Dendrophylliidae	<i>Turbinaria</i>	<i>mesenterina</i>						1	SB
Hexacorallia	Dendrophylliidae	<i>Duncanopsammia</i>	<i>peltata</i>						1	SB
Hexacorallia	Euphylliidae	<i>Galaxea</i>	<i>cf. fascicularis</i>			1		1	1	SB
Hexacorallia	Fungiidae	<i>Lithophyllon</i>	<i>concinna</i>						1	SB
Hexacorallia	Fungiidae	<i>Lithophyllon</i>	<i>undulatum</i>						1	SB
Hexacorallia	Fungiidae	<i>Fungia</i>	<i>fungites</i>						1	SB
Hexacorallia	Lobophylliidae	<i>Acanthastrea</i>	<i>hemprichii</i>						1	SB
Hexacorallia	Lobophylliidae	<i>Echinophyllia</i>	<i>aspera</i>						1	SB
Hexacorallia	Lobophylliidae	<i>Lobophyllia</i>	<i>hemprichii</i>						1	SB
Hexacorallia	Lobophylliidae	<i>Lobophyllia</i>	<i>recta</i>						1	SB
Hexacorallia	Lobophylliidae	<i>Lobophyllia</i>	sp.					1		SB
Hexacorallia	Merulinidae	<i>Dipsastraea</i>	<i>maritima</i>						1	SB

Hexacorallia	Merulinidae	<i>Dipsastraea</i>	<i>matthaii</i>						1	SB
Hexacorallia	Merulinidae	<i>Favites</i>	<i>flexuosa</i>						1	SB
Hexacorallia	Merulinidae	<i>Merulina</i>	<i>ampliata</i>						1	SB
Hexacorallia	Merulinidae	<i>Favia</i>	<i>matthaii</i>				1	1	1	SB
Hexacorallia	Merulinidae	<i>Favia</i>	<i>veroni</i>			1		1	1	SB
Hexacorallia	Merulinidae	<i>Favites</i>	<i>pentagona</i>					1	1	SB
Hexacorallia	Merulinidae	<i>Mycedium</i>	<i>umbra</i>						1	SB
Hexacorallia	Merulinidae	<i>Platygyra</i>	<i>acuta</i>						1	SB
Hexacorallia	Merulinidae	<i>Platygyra</i>	<i>daedalea*</i>			1				SB
Hexacorallia	Merulinidae	<i>Trachyphyllia</i>	sp.					1		SB
Hexacorallia	Montastraeidae	<i>Montastraea</i>	<i>valenciennesi*</i>			1				SB
Hexacorallia	Montastraeidae	<i>Montastraea</i>	sp.						1	SB
Hexacorallia	Poritidae	<i>Goniopora</i>	<i>stokesi</i>						1	SB
Hexacorallia	Poritidae	<i>Porites</i>	<i>lobata</i>						1	SB
Hexacorallia	Poritidae	<i>Porites</i>	<i>lutea</i>						1	SB
Hexacorallia	Poritidae	<i>Porites</i>	<i>monticulosa</i>						1	SB
Hexacorallia	Poritidae	<i>Porites</i>	sp.				1		1	SB
Hexacorallia	Pocillopora	<i>Pocillopora</i>	<i>damicornis</i>						1	SB
Hexacorallia	Rhizangiidae	<i>Pseudosiderastrea</i>	<i>tayamai</i>						1	SB
Octocorallia	Pennatulidae	<i>Pteroeides</i>	sp.				1			SB
Octocorallia	Subergorgiidae	<i>Subergorgia</i>	<i>suberosa</i>					1		SB
Octocorallia	Ellisellidae	<i>Junceella</i>	sp.					1		SB
<b>Annelida</b>										
Sipuncula	Antillesomatidae	<i>Antillesoma</i>	sp.1		1			1		MS
Sipuncula	Antillesomatidae	<i>Antillesoma</i>	sp.2					1		MS
Sipuncula	Phascolosomatidae	<i>Phascolosoma</i>	cf. <i>agassizii</i>		1					MS
Sipuncula	Phascolosomatidae	<i>Phascolosoma</i>	cf. <i>nigrescens</i>					1		MS
Sipuncula	Phascolosomatidae	<i>Phascolosoma</i>	<i>nigrescens</i>					1		MS
Sipuncula	Phascolosomatidae	<i>Phascolosoma</i>	<i>scolops</i>		1			1		MS
Sipuncula	Themisteidae	<i>Themiste</i>	<i>lageniformis</i>		1			1		MS

Polychaeta	Eunicidae	<i>Eunice</i>	sp.		1			1		MS
Polychaeta	Eunicidae	<i>Lysidice</i>	sp.					1		MS
Polychaeta	Nereididae	<i>Ceratonereis</i>	<i>perkinsi</i>		1			1		MS
Polychaeta	Nereididae	<i>Neanthes</i>	sp.		1			1		MS
Polychaeta	Nereididae	<i>Perinereis</i>	<i>cultrifera</i>					1		MS
Polychaeta	Nereididae	<i>Perinereis</i>	<i>helleri</i>		1			1		MS
Polychaeta	Nereididae	<i>Perinereis</i>	<i>singaporiensis</i>					1		MS
Polychaeta	Nereididae	<i>Perinereis</i>	<i>vancaurica</i>		1			1		MS
Polychaeta	Nereididae	<i>Perinereis</i>	sp.		1			1		MS
Polychaeta	Nereididae	<i>Pseudonereis</i>	<i>trimaculata</i>		1			1		MS
Polychaeta	Polynoidae	<i>Lepidonotus</i>	sp.		1			1		MS
Polychaeta	Phyllodoceidae	<i>Phyllodoce</i>	sp.		1			1		MS
Polychaeta	Phyllodoceidae	<i>Phyllodoceidae</i>	sp.					1		MS
Polychaeta	Syllidae	<i>Odontosyllis</i>	<i>gravelyi</i>					1		MS
Polychaeta	Syllidae	<i>Syllis</i>	<i>gracilis</i>		1			1		MS
<b>Mollusca - Polyplacophora</b>										
Polyplacophora	Acanthochitonidae	<i>Acanthochitona</i>	<i>gemmata</i>				1			LS
Polyplacophora	Acanthochitonidae	<i>Acanthochitona</i>	sp. 1		1					LS
Polyplacophora	Acanthochitonidae	<i>Acanthochitona</i>	sp. 2					1		LS
Polyplacophora	Acanthochitonidae	<i>Squamopleura</i>	<i>miles</i>		1	1		1		MS
<b>Mollusca - Bivalvia</b>										
Bivalvia	Gryphaeidae	<i>Hyotissa</i>	<i>numisma</i>					1		LS
Bivalvia	Isognomonidae	<i>Isognomon</i>	<i>legumen</i>		1			1		MS
Bivalvia	Isognomonidae	<i>Isognomon</i>	<i>nucleus</i>		1			1		MS
Bivalvia	Modiolidae	<i>Botula</i>	cf. <i>cinnamomea</i>		1			1		MS
Bivalvia	Modiolidae	<i>Vignadula</i>	<i>mangle</i>		1			1		MS
Bivalvia	Modiolidae	<i>Leiosolenus</i>	<i>malaccanus</i>		1			1		MS
Bivalvia	Mytilidae	<i>Lithophaga</i>	sp.		1					MS
Bivalvia	Mytilidae	<i>Septifer</i>	<i>bilocularis</i>		1			1		MS

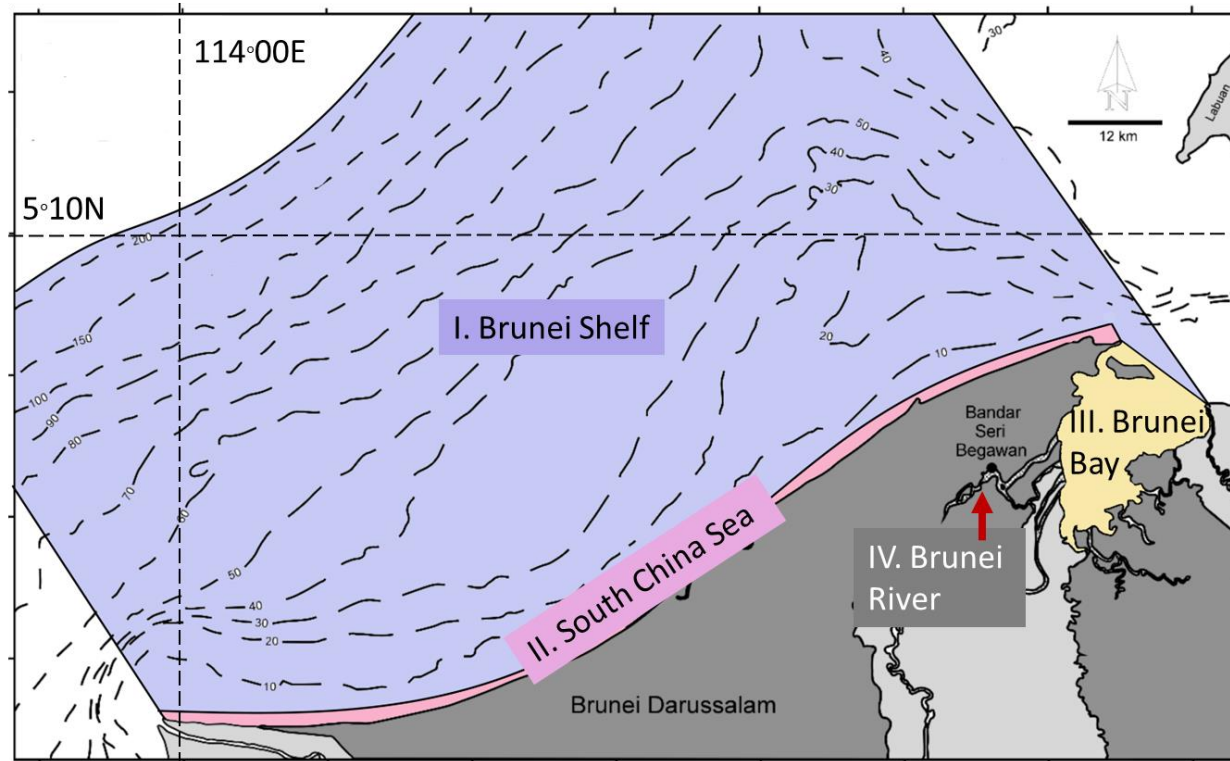
Bivalvia	Mytilidae	<i>Septifer</i>	<i>excisus</i>					1		MS
Bivalvia	Mytilidae	<i>Brachidontes</i>	<i>crebristriatus</i>					1		MS
Bivalvia	Mytilidae	<i>Brachidontes</i>	<i>variabilis</i>		1			1		MS
Bivalvia	Mytilidae	<i>Dentimodiolus</i>	sp.			1		1		LS
Bivalvia	Ostreidae	<i>Saccostrea</i>	<i>echinata</i>		1	1		1		MS
Bivalvia	Ostreidae	<i>Saccostrea</i>	<i>scyphophilla</i>		1	1		1		MS
Bivalvia	Ostreidae	<i>Saccostrea</i>	<i>mordax</i>			1				MS
Bivalvia	Ostreidae	<i>Magellana</i>	<i>bilineata</i>			1				SB
Bivalvia	Petricolidae	<i>Petricola</i>	<i>divergens</i>		1			1		MS
Bivalvia	Pteridae	<i>Pteria</i>	<i>avicular</i>					1		SB
Bivalvia	Pteridae	<i>Pteria</i>	<i>heteroptera</i>					1		SB
Bivalvia	Trapeziidae	<i>Neotrapezium</i>	<i>sublaevigatum</i>		1			1		MS
Bivalvia	Veneridae	<i>Irus</i>	<i>macrophylla</i>		1			1		MS
<b>Mollusca - Gastropoda**</b>										
Gastropoda	Angariidae	<i>Angaria</i>	<i>delphinus</i>				1			MS
Gastropoda	Batillariidae	<i>Batillaria</i>	sp.				1			MS
Gastropoda	Cerithiidae	<i>Clypeomorus</i>	<i>batillariaeformis</i>		1	1				LS
Gastropoda	Cerithiidae	<i>Clypeomorus</i>	<i>bifasciata</i>			1				LS
Gastropoda	Cerithiidae	<i>Rhinoclavis</i>	<i>sinensis</i>			1				LS
Gastropoda	Cerithiidae	<i>Cerithium</i>	cf. <i>torresi</i>			1				LS
Gastropoda	Cerithiopsidae	<i>Joculator</i>	sp.			1				LS
Gastropoda	Columbellidae	<i>Zafra</i>	cf. <i>trolodytes</i>			1				LS
Gastropoda	Columbellidae	<i>Pardalinops</i>	<i>testudinarius</i>			1				LS
Gastropoda	Columbellidae	<i>Euplica</i>	<i>scripta</i>			1	1			LS
Gastropoda	Columbellidae	<i>Pictocolumbella</i>	<i>ocellata</i>				1			LS
Gastropoda	Conidae	<i>Conus</i>	<i>coronatus</i>				1			LS
Gastropoda	Cypraeidae	<i>Maurita</i>	<i>arabica</i>			1	1			LS
Gastropoda	Cypraeidae	<i>Cypraea</i>	<i>tigris</i>					1		SB
Gastropoda	Dialidae	<i>Diala</i>	<i>semistriata</i>		1			1		MS
Gastropoda	Fissurellidae	<i>Montfortula</i>	sp.		1			1		MS

Gastropoda	Littorinidae	<i>Echinolittorina</i>	<i>malaccana</i>	1	1		1	1		HS
Gastropoda	Littorinidae	<i>Echinolittorina</i>	<i>melanacme</i>	1	1		1			HS
Gastropoda	Littorinidae	<i>Echinolittorina</i>	<i>vidua</i>	1	1	1	1	1		HS
Gastropoda	Littorinidae	<i>Littoraria</i>	<i>articulata</i>	1				1		MS
Gastropoda	Littorinidae	<i>Littoraria</i>	<i>intermedia</i>					1		MS
Gastropoda	Littorinidae	<i>Littoraria</i>	sp.				1			MS
Gastropoda	Littorinidae	<i>Peasiella</i>	<i>fasciata</i>	1	1			1		MS
Gastropoda	Littorinidae	<i>Peasiella</i>	<i>lutulenta</i>					1		MS
Gastropoda	Lottiidae	<i>Patelloida</i>	cf. <i>pygmaea</i>		1			1		MS
Gastropoda	Lottiidae	<i>Patelloida</i>	<i>saccharina</i>		1	1	1			MS
Gastropoda	Melongenidae	<i>Volegalea</i>	<i>cochlidium</i>			1				LS
Gastropoda	Muricidae	<i>Mancinella</i>	<i>echinulata</i>		1		1			MS
Gastropoda	Muricidae	<i>Reishia</i>	<i>bitubercularis</i>				1	1		MS
Gastropoda	Muricidae	<i>Indothais</i>	<i>rufotincta</i>				1	1		MS
Gastropoda	Muricidae	<i>Semiricinula</i>	<i>muricoides</i>		1	1				MS
Gastropoda	Muricidae	<i>Semiricinula</i>	sp.	1			1	1		MS
Gastropoda	Muricidae	<i>Arakawania</i>	<i>musiva</i>		1	1	1	1		LS
Gastropoda	Muricidae	<i>Arakawania</i>	<i>granulata</i>			1				LS
Gastropoda	Muricidae	<i>Drupella</i>	<i>margariticola</i>			1				LS
Gastropoda	Muricidae	<i>Purpura</i>	<i>panama</i>			1				MS
Gastropoda	Nacellidae	<i>Cellana</i>	<i>radiata</i>		1			1		MS
Gastropoda	Nacellidae	<i>Cellana</i>	<i>testudinaria</i>	1	1		1	1		MS
Gastropoda	Neritidae	<i>Nerita</i>	<i>albicilla</i>		1	1	1	1		LS
Gastropoda	Neritidae	<i>Nerita</i>	<i>chamaeleon</i>	1	1	1	1	1		MS
Gastropoda	Neritidae	<i>Nerita</i>	<i>histrion</i>			1		1		MS
Gastropoda	Neritidae	<i>Nerita</i>	<i>insculpta</i>			1	1			MS
Gastropoda	Neritidae	<i>Nerita</i>	<i>polita</i>				1			MS
Gastropoda	Neritidae	<i>Nerita</i>	<i>undata</i>	1		1	1			MS
Gastropoda	Neritidae	<i>Nerita</i>	<i>exuvia</i>			1				MS
Gastropoda	Neritidae	<i>Nerita</i>	<i>litterata</i>			1	1			MS

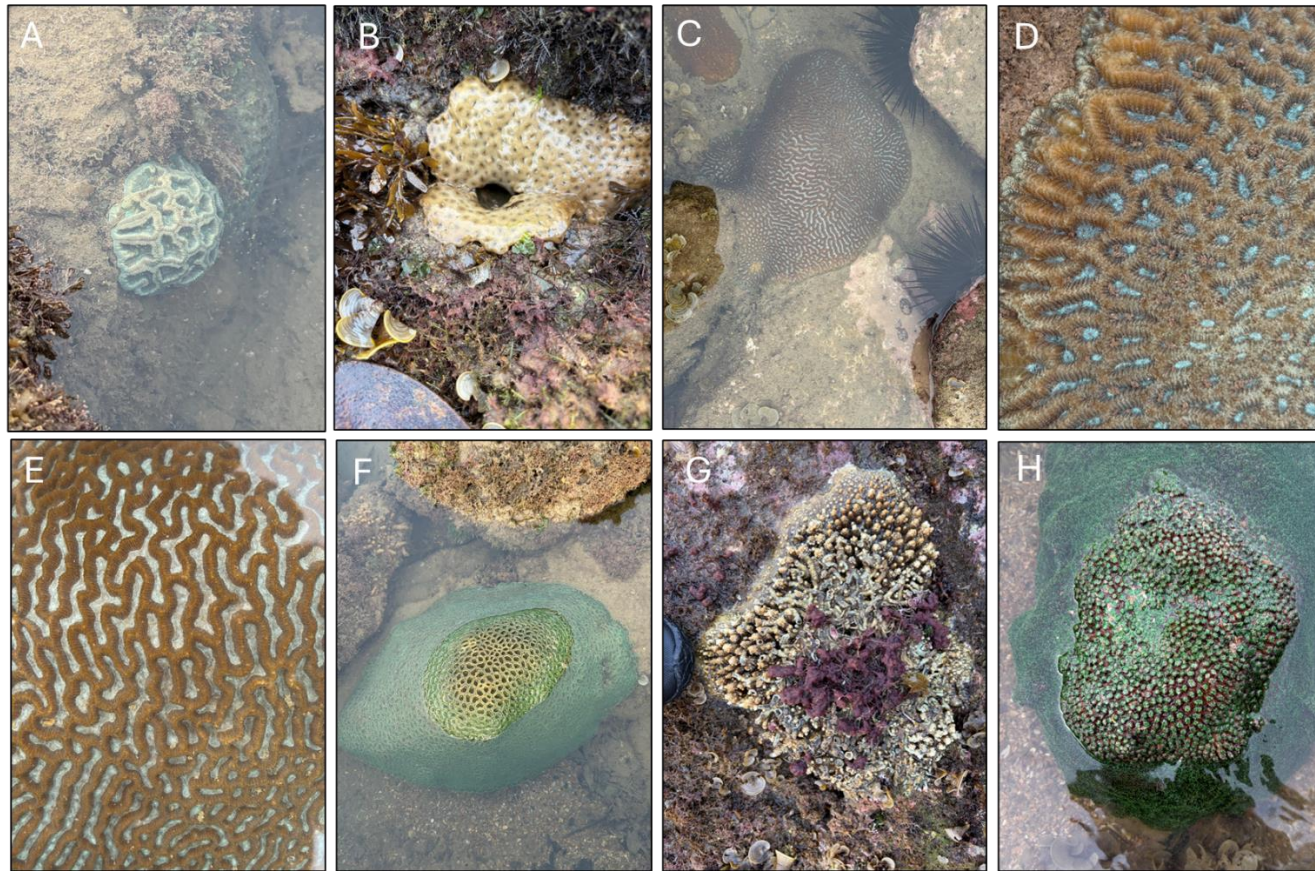
Gastropoda	Neritidae	<i>Nerita</i>	<i>patula</i>			1				MS
Gastropoda	Phyllidiidae	<i>Phyllidiella</i>	<i>cf. nigra</i>			1				LS
Gastropoda	Planaxidae	<i>Planaxis</i>	<i>sulcatus</i>		1	1	1	1		MS
Gastropoda	Planaxidae	<i>Fossarus</i>	<i>trochlearis</i>		1			1		MS
Gastropoda	Pyramidellidae	<i>Boonea</i>	sp.					1		MS
Gastropoda	Pyramidellidae	<i>Odostomella</i>	<i>opaca</i>			1				LS
Gastropoda	Retusidae	<i>Retusa</i>	sp.			1				LS
Gastropoda	Siphonariidae	<i>Siphonaria</i>	<i>guamensis</i>		1			1		MS
Gastropoda	Siphonariidae	<i>Siphonaria</i>	<i>javanica</i>		1		1			MS
Gastropoda	Trimusculidae	<i>Trimusculus</i>	<i>cf. kurodai</i>		1					LS
Gastropoda	Triphoridae	<i>Coriophora</i>	<i>fusca</i>			1				LS
Gastropoda	Trochidae	<i>Monodonta</i>	<i>labio</i>			1				MS
Gastropoda	Trochidae	<i>Trochus</i>	<i>radiata</i>	1	1	1	1			LS
Gastropoda	Turbinidae	<i>Turbo</i>	<i>articulatus</i>		1	1	1			LS
Gastropoda	Turbinidae	<i>Lunella</i>	<i>cinerea</i>			1				MS
<b>Crustacea - Decapoda</b>										
Anomura	Diogenidae	<i>Clibanarius</i>	<i>ransonii</i>			1				LS
Anomura	Diogenidae	<i>Clibanarius</i>	<i>merguiensis</i>			1				MS
Anomura	Diogenidae	<i>Clibanarius</i>	<i>rutilus</i>			1				LS
Anomura	Diogenidae	<i>Clibanarius</i>	<i>striolatus</i>				1			MS
Anomura	Diogenidae	<i>Diogenes</i>	sp. 1			1				LS
Anomura	Diogenidae	<i>Diogenes</i>	sp. 2			1				LS
Anomura	Diogenidae	<i>Dardanus</i>	<i>megistos</i>						1	SB
Anomura	Paguridae	<i>Pagurus</i>	<i>kulkarnii</i>						1	SB
Brachyura	Carpiliidae	<i>Carpilius</i>	<i>maculatus</i>						1	LS
Brachyura	Eriphiidae	<i>Eriphia</i>	<i>laevimana</i>						1	LS
Brachyura	Eriphiidae	<i>Eriphia</i>	<i>sebana</i>				1			LS
Brachyura	Gecarcinidae	<i>Cardisoma</i>	<i>carnifex</i>				1			LS
Brachyura	Grapsidae	<i>Grapsus</i>	sp.			1	1		1	MS
Brachyura	Grapsidae	<i>Metopograpsus</i>	<i>frontalis</i>		1					MS

Brachyura	Grapsidae	<i>Pachygrapsus</i>	<i>minutus</i>		1					MS
Brachyura	Macrophthalmidae	<i>Macrophthalmus</i>	sp.			1				LS
Brachyura	Majidae	cf. <i>Hyastenus</i>	sp.					1		SB
Brachyura	Ocypodidae	<i>Ocypode</i>	<i>sinensis</i>			1				LS
Brachyura	Ocypodidae	<i>Ocypode</i>	sp.			1				LS
Brachyura	Oziidae	<i>Ozius</i>	<i>guttatus</i>			1				LS
Brachyura	Oziidae	<i>Epixanthus</i>	<i>frontalis</i>			1				LS
Brachyura	Pilumnidae	<i>Cryptopilumnus</i>	<i>changensis</i>		1					MS
Brachyura	Pilumnidae	<i>Heteropanope</i>	<i>glabra</i>		1					MS
Brachyura	Plagusiidae	<i>Plagusia</i>	<i>squamosa</i>			1				LS
Brachyura	Portunidae	<i>Thalamita</i>	sp.*			1				LS
Brachyura	Sesarmidae	<i>Nanosesarma</i>	<i>minutum</i>		1					MS
Brachyura	Sesarmidae	<i>Parasesarma</i>	cf. <i>eumolpe</i>			1				LS
Brachyura	Sesarmidae	<i>Sesarma</i>	sp.			1				LS
Brachyura	Varunidae	<i>Hemigrapsus</i>	sp.					1		LS
Brachyura	Xanthidae	<i>Leptodius</i>	cf. <i>gracilis</i>			1				LS
Brachyura	Xanthidae	<i>Macromedaeus</i>	sp.			1				LS
Brachyura	Xanthidae	<i>Chlorodiella</i>	sp.						1	LS
Caridea	Palaemonidae	<i>Anchistus</i>	sp.						1	LS
Caridea	Palaemonidae	<i>Coralliocaris</i>	sp.						1	LS
Caridea	Palaemonidae	<i>Pontonia</i>	sp.						1	LS
Caridea	Stenopodidae	<i>Stenopus</i>	<i>hispidus</i>						1	LS
Pleocyemata	Palinuridae	<i>Panulirus</i>	<i>vesicolor</i>					1		SB
Pleocyemata	Palinuridae	<i>Panulirus</i>	<i>ornatus</i> (carapace)					1		SB
<b>Crustacea - Other</b>										
Amphipoda	Phliantidae	<i>Pariphinotus</i>	sp.			1				LS
Amphipoda	Maeridae	<i>Elasmopus</i>	sp.			1				LS
Isopoda	Ligiidae	<i>Ligia</i>	<i>exotica</i>						1	LS
Isopoda	Limnoriidae	<i>Limnoria</i>	sp.						1	LS
Isopoda	Sphaeromatidae	<i>Sphaeroma</i>	sp.			1			1	LS

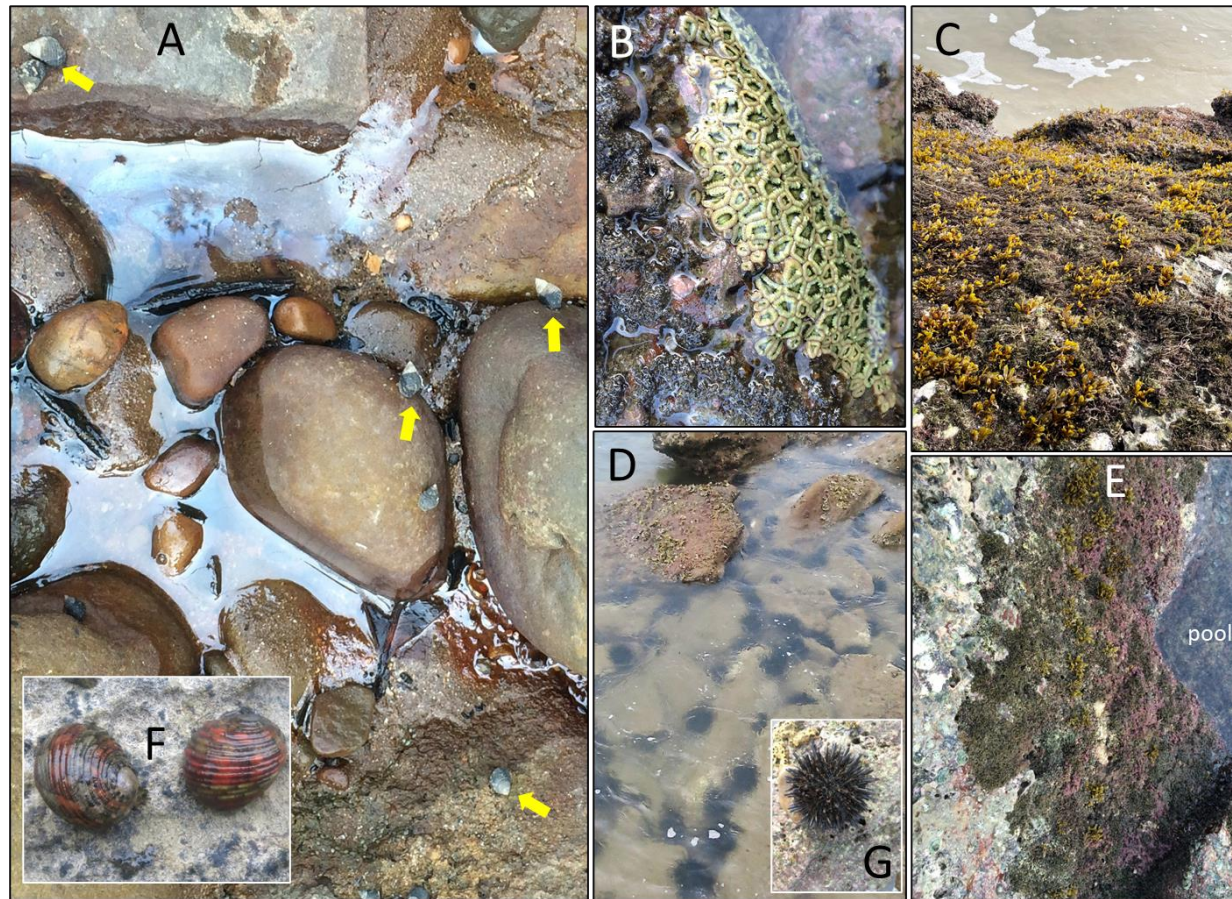
Isopoda	Idoteidae	<i>Idotea</i>	sp.						1	LS
Stomatopoda	Gonodactylidae	<i>Gonodactylus</i>	sp.						1	LS
Stomatopoda	Lysiosquillidae	<i>Lysiosquilla</i>	sp.						1	LS
Thecostraca	Chthamalidae	<i>Caudoeuraphia</i>	<i>caudata</i>					1		MS
Thecostraca	Chthamalidae	<i>Chthamalus</i>	<i>malayensis</i>			1	1	1		HS
Thecostraca	Iblidae	<i>Ibla</i>	<i>cumingi</i>		1	1				MS
Thecostraca	Pollicipedidae	<i>Capitulum</i>	<i>mitella</i>			1				MS
Thecostraca	Tetraclitidae	<i>Tetraclita</i>	<i>kuroshioensis</i>			1	1			LS
Thecostraca	Tetraclitidae	<i>Yamaguchiella</i>	<i>coerulescens</i>			1				LS
<b>Echinodermata</b>										
Asteroidea	Asterinidae	<i>Cryptasterina</i>	sp.			1				LS
Crinoidea	Colobometridae	<i>Colobometra</i>	<i>perspinosa</i>				1			LS
Crinoidea	Thalassometridae	<i>Stephnometra</i>	sp.					1		SB
Echinoidea	Stomopneustidae	<i>Stomopneustes</i>	<i>variolaris</i>			1		1		LS
Echinoidea	Diadematidae	<i>Diadema</i>	<i>setosum</i>					1		SB
Holothuroidea	Holothuriidae	<i>Holothuria</i>	<i>leucospilota</i>			1		1		LS



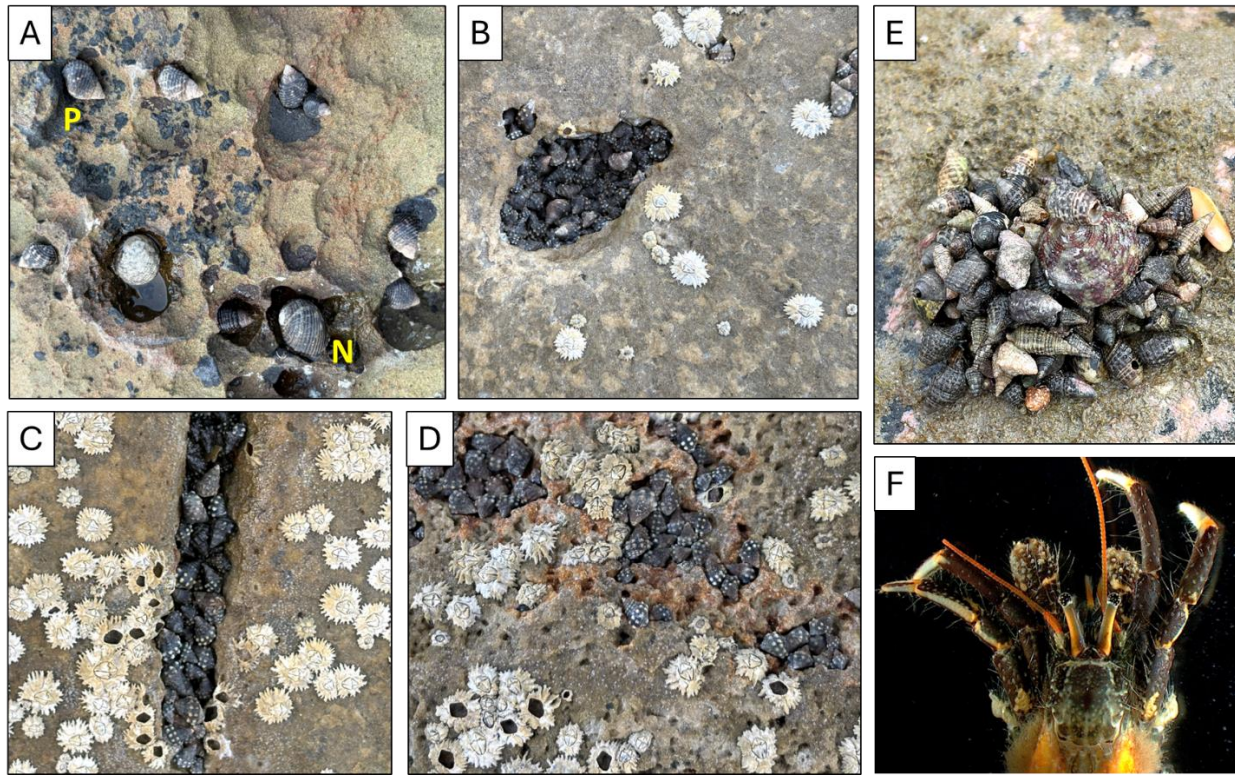
**Appendix Figure 1.** Map showing regions (1-IV) supporting the major marine biomes of Brunei. The South China Sea (coastline II) includes a shoreline biome (MT1), which constitutes rocky shoreline (MT1.1), sandy shoreline (MT1.2), boulder shoreline (MT1.4) and artificial shoreline (MT3.1) functional ecosystems (Keith et al. 2020). Natural rocky shores are spatially highly restricted along the coastline.



**Appendix Figure 2.** Coral forms in low tide natural pools or partly exposed in air at the Empire (section D, adjacent to the artificial headland, Figure 5). A, *Favia veroni*, B, zoanthid (probably *Palythoa* cf. *mutuki*), C-E, *Platygyra daedalea*, F, *Montastrea valenciennesi*, G, *Acropora* sp., and H, *Galaxea* sp.



**Appendix Figure 3.** Horizontal rocks and pools on the natural rocky shore (Empire). (A) Boulder beach mid-shore tidal pool receives acidified groundwater discharge, characterised by oily surface microbial biofilm and rusty coloured deposits of  $\text{Fe}(\text{OH})_2$ , a product of pyrite oxidation. Yellow arrows indicate the common gastropod *Planaxis sulcatus*, showing shell dissolution. (B) Low-shore pool framed with the yellowish zoanthid species, *Palythoa* cf. *mutuki*. (C) Low-shore algal turf abutting sandy substratum. (D) Flat rocks in low-shore pool forming ideal habitat for the black sea urchin, *Stomopneustes variolaris* (G). (E) Thick algal turf fringing a low shore pool. (F) *Nerita chamaeleon*, a common gastropod of the boulder shore – the specimen shown was collected away from acidified water exposure and shows no shell dissolution.



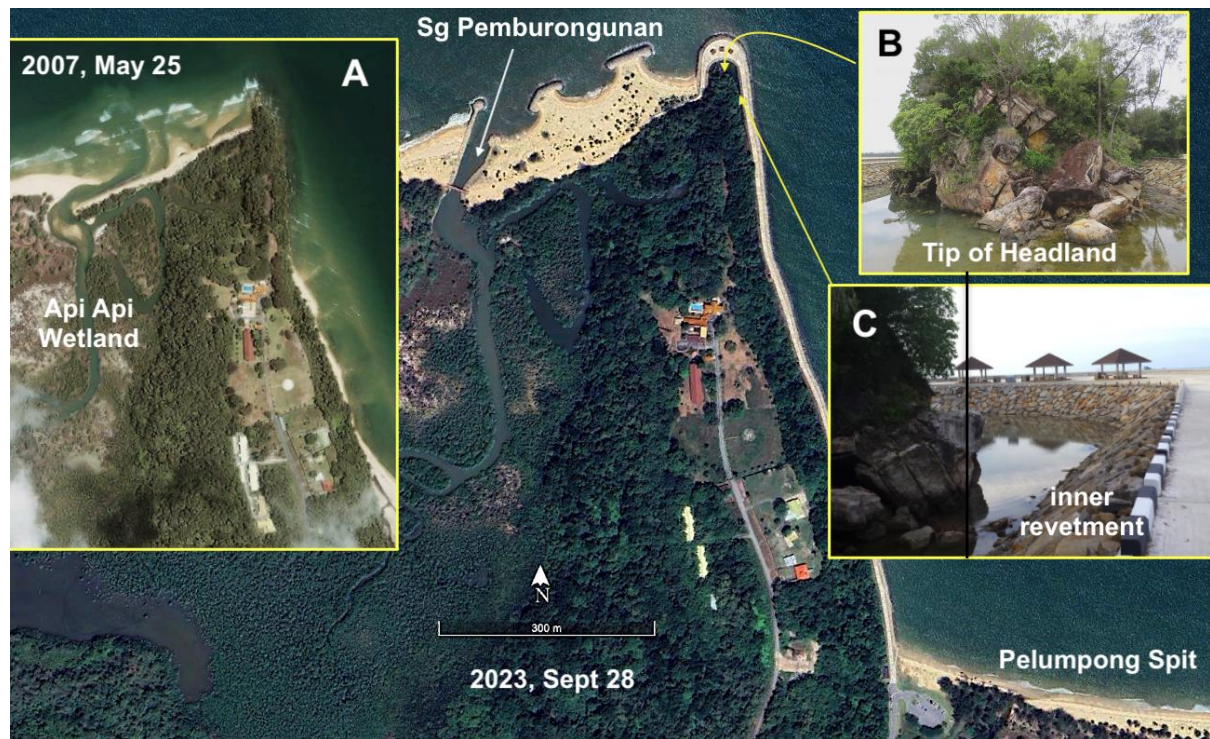
**Appendix Figure 4.** Natural rocky shore (Empire) substratum and crab behaviour. Weathering forms depressions, crevices and pits, providing microrefugia for gastropods. (A) Mid-shore depressions in rock surface occupied by *Planaxis sulcatus* (P) and *Nerita chamaeleon* (N). (B) High-shore depression occupied by *Echinolittorina malaccana* snails, surrounded by the barnacle, *Chthamalus malayensis*. (C) *E. malaccana* huddled in rocky crevice. (D) Fine-scale pitting of the rock substratum, sometimes the same size as an individual snail. (E) Low shore aggregation of hermit crabs (*Clibanarius merguiensis*) inhabiting gastropod shells. (F) This species can be distinguished from its mid-shore congener, *C. ransoni*, by cream-coloured dactylus of pereopods I and II.



**Appendix Figure 5.** Selected invertebrates from the rocky shores of Brunei. Top row (left to right), hermit crab *Pagurus kulkarnii* (Empire, uncommon), cryptic star *Cryptasterina* sp. (Empire, uncommon), sea cucumber *Holothuria leucospilota* (yellow arrow, Empire, uncommon), sea fan *Suberegorgia suberosa* (Tungku, common). Bottom row (left to right), spider crab *Hyastenus* sp. with two barnacles on carapace (Tungku, associated with sea fan, uncommon), feather star *Colobometra perspinosa* (Empire, uncommon), sea urchin *Diadema setosum* (Tungku, common), and sea pen *Pteroeides* sp. (Empire, uncommon).



*Appendix Figure 6.* Low shore Empire. White bleached coralline algae shown on midground rocky block.



**Appendix Figure 7.** Tg Batu Headland and Coastal Development. The image compares Tg Batu before and after construction of coastal protection and recreational amenities. (A) Natural headland and the Api-Api wetland. Note the unstable mouth of Sg Pemburungan. (B) Tip of Tg Batu headland, surrounding by promenade and rock-armoured revetment. (C) Inner revetment and enclosed non-marine pool that formed as a consequence of the development, and recreational amenities (Pelumpong Spit now referred to as Pantai Muara).