Benthic Faunal Ecology in the Algal Turf Zone of a Bornean Rocky Shore: the Influence of Habitat-Forming Species

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Abstract

Brunei lies within the highly diverse Palawan-North Borneo ecoregion, but taxonomic and ecological assessments of the benthic marine fauna are distinctly lacking. Local intertidal ecosystems are dominated by sandy beaches, mudflats and mangroves, with sparsely distributed rocky shores. We studied the fauna and community ecology associated with the low-shore algal turf zone of the only remaining 'undisturbed' natural rocky shore of Brunei (the Empire). We assessed the macrobenthic invertebrate species and tested whether assemblage structure related to turf habitat complexity (16 samples; 20×20 cm). Comparisons were made between two categories of substratum, (1) finely branched and (2) broadly expanded substrata, determined by the predominance of differently structured coralline and green algae, and sessile animals (sponge and mussels). More than 1099 macrofaunal specimens were retrieved from the samples, comprising 30 families and 46 OTUs (Operational Taxonomic Unit), with the most abundant groups being amphipods (12 OTUs), ostracods (2), tanaidaceans (2), isopods (3), polychaetes (5) and gastropods (22). Multivariate analyses based on 25 common OTUs revealed significant dissimilarity in assemblages associated with the different substrate types. Indicator species analysis identified amphipods (abundant in coralline algae) and tanaidaceans (abundant on flat substrates) as contributing the most to this differentiation (28.63% for three species). The gastropod, *Zafra* cf. *troglodytes* (17.7%) and the ostracod cylindroleberid sp. (14.3%) contributed the most to assemblage similarity of the finely branched and expanded substrates, respectively. The drivers of habitat preference, and local spatial and temporal variation in assemblage structure are discussed. This work adds to our knowledge of local rocky shore benthic ecology but reveals a dire need for dedicated taxonomic work to resolve the species, crucial for appropriate environmental conservation and management.

Index Terms: community structure, coralline algae, macrofauna, rocky shores, tropical ecology

1. Introduction

Algal turfs represent a distinct component of rocky shore ecosystems, constituting dense multi-species assemblages of short-tufted algae, acting as habitat-forming structures.[1] These turfs increase the habitat heterogeneity and not only protect from physical stressors such as wave action or desiccation but also serve as feeding grounds for different motile macroinvertebrates[2]. Although the role of habitat complexity in structuring benthic assemblages is well documented generally,[2] less is known for tropical Southeast Asia. Overall, the ecological interactions between turf-forming species and associated faunal communities remain poorly resolved in local environments of Borneo.

An understudied facet of algal turf ecology is the effect of structural variability of the algae on the faunal distribution.[3-7] Turf habitats cover a continuum of morphological types from minute branched coralline and filamentous algae to broader, bladed macroalgae and mixed substrates with widely spaced sessile invertebrates such as mussels and sponges.[8,9] Such variation in architecture can drive microhabitat availability, resource distribution, and predator–prey interactions with cascading effects on community structure. Few studies, however, have explicitly compared the ways in which structural extremes mediate assemblage organization, particularly at tropical intertidal sites where environmental variation is high, and baseline ecological data are limited.

Although the Palawan–North Borneo ecoregion is considered a global marine biodiversity hotspot,[10-12] the coastal benthic ecosystems in the region are still relatively underexplored compared to other tropical environments (coral reefs and pelagic systems). Within Brunei, coastal habitats mainly comprise soft-sediment systems (mangroves, mudflats, and sandy beaches), with natural rocky shores existing only as small, fragmented outcrops.[13] This paucity of information enhances the ecological significance of surviving rocky environments as vital refugia for specialised intertidal assemblages.[14] Despite their importance, these systems have been largely overlooked from taxonomic and ecological perspectives, leading to gaps in our knowledge of benthic biodiversity distribution and ecosystem functions in the region.

This study investigated the low-shore algal turf zone of the Empire rocky shore, Brunei's last relatively undisturbed natural rocky habitat. We assessed the diversity and composition of the macrobenthic invertebrates associated with this habitat and how assemblage structure changes across substrate characteristics. We tested whether macrofaunal communities are different between two broad categories habitat-forming substrata: (1) finely branched algal turfs and (2) expanded substrata comprising blade-like algae and animal-generated structures. Taxonomic assessment and multivariate community analyses were undertaken to identify key taxa influencing the differences in microhabitat-level structuring of assemblages. The information on benthic faunal ecology for the low rocky shore zone of Brunei Darussalam should contribute to our knowledge on tropical algal turf systems and inform future ecological research by identifying priorities for taxonomic resolution and conservation management in a region where coastal habitats are increasingly vulnerable to environmental change.

2. Methods and Materials

2.1 Study area and sampling

Fieldwork was conducted at the Empire rocky shore on 22 October 2024, between two sites positioned 80 m apart: Site 1 (4°58'9.81"N, 114°51'24.15"E) and Site 2 (4°58'7.54"N, 114°51'20.21"E; see ***Figure 1***). The rocky shoreline constitutes broken and disconnected sandstone blocks, originating from deltaic to shallow marine sandstones, and extending at a near right angle to the coastline running north-westerly towards the islet, Pulau Punyit. The coastline orientation is such that wave exposure of this shore is moderate (not severe). As background, the rock formation outcropping is part of the Jerudong Formation[15] and is of Tortonian age (11.63 to 7.25 Ma). It comprises mudstone, siltstone, and sandstone, with bottomset deposits of mudstone and siltstone and foreset beds that dominate the lower and middle shoreface. Intact beds strike at an angle of around 210 degrees with a dip of approximately 35 to 40 degrees. These beds belong to the limb of the Jerudong anticline, indicating that post-depositional uplift caused the inclination of the strata. Honeycomb weathering and cross stratification, including herringbone cross-stratification, are present and demonstrate tidal influence. The rock mass is jointed, with joints at 90 degrees to the strike formation, resulting in large rock blocks that are broken off at the lower shoreface due to weathering and wave action. The outcropping sandstones at the lower shoreface have been eroded by wave action. Some sandstone blocks display tidal channels that have been washed out and polished by mechanical abrasion. The shoreface strata exhibit a thickening upwards trend demonstrating progradation, with sandstone bed thicknesses ranging from a few centimeters to about 0.5 meters. Tidal pools emerge between the broken rock blocks during low tide. Sediment deposition on the rocks varies seasonally in relation to monsoonal rainfall when nearby seawater becomes highly turbid, as well as to typhoon activity when high wave swell conditions wash out deposited sediment from the turfs.

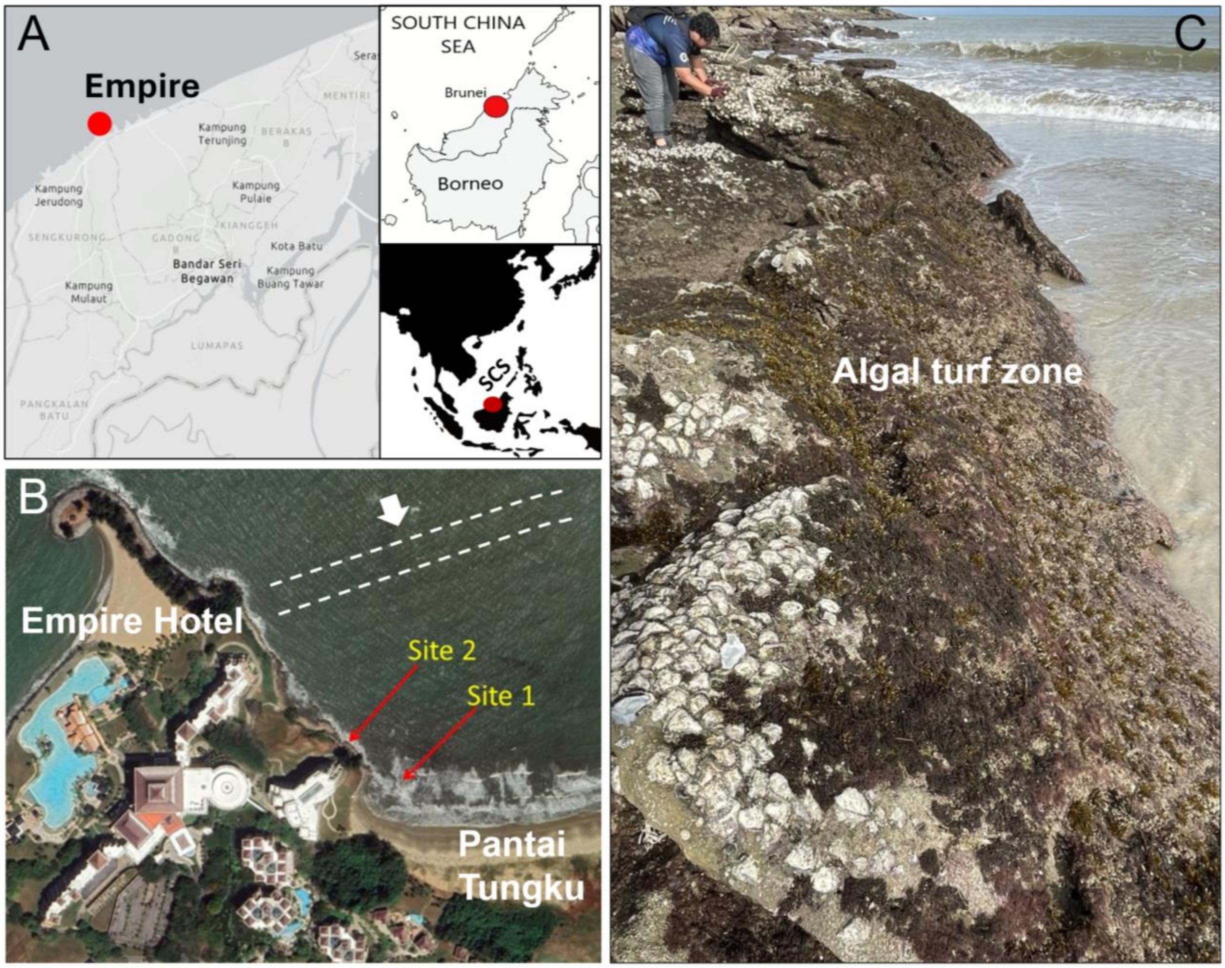

Figure 1. (A) Map showing the location of the study area. (B) Satellite image of the study area, sampling was undertaken between Site 1 and Site 2. (C) Algal turf zone at site 1 (samples were collected from nearby less steeply sloped areas). Arrow and dashed white lines in figure B indicate direction and periodicity of prevailing wavefront at time of photograph.

The Empire shore exhibits distinct biotic zones relating to shore height and characterised by dominant species. The highest level, the supralittoral zone above 2.5 m Chart Datum (CD), is solely inhabited by marine littorinid snails. The high-shore zone below this spans approximately 1.5 to 2.5 m CD and is dominated by gastropods such as *Echinolittorina malaccana*, *E. vidua*, and *Planaxis sulcatus*. The mid-shore zone, ranging from roughly 1.5 to 0.5 m CD, is characterised by the presence of oysters (*Saccostrea scyphophilla*), barnacles (*Chthamalus malayensis*, *Tetraclita kuroshioensis*), and a variety of gastropods including *Planaxis sulcatus*, *Nerita chamaeleon*, *Monodonta labio* and *Cellana testudinaria*.[13,16] The lowest zone, below ~ 0.5 m CD (**see *Figure 1***), constitutes a turf comprising > 30 algal species.[17] Sampling was conducted during low tide on near horizontal broken rock shelves. The algal turf within a 20×20 cm^2 quadrat was scraped off the rocks and collected in labelled plastic bags. For pragmatic reasons 16 samples were collected for this pilot study, haphazardly within the study site zone (see ***Figure 2***).

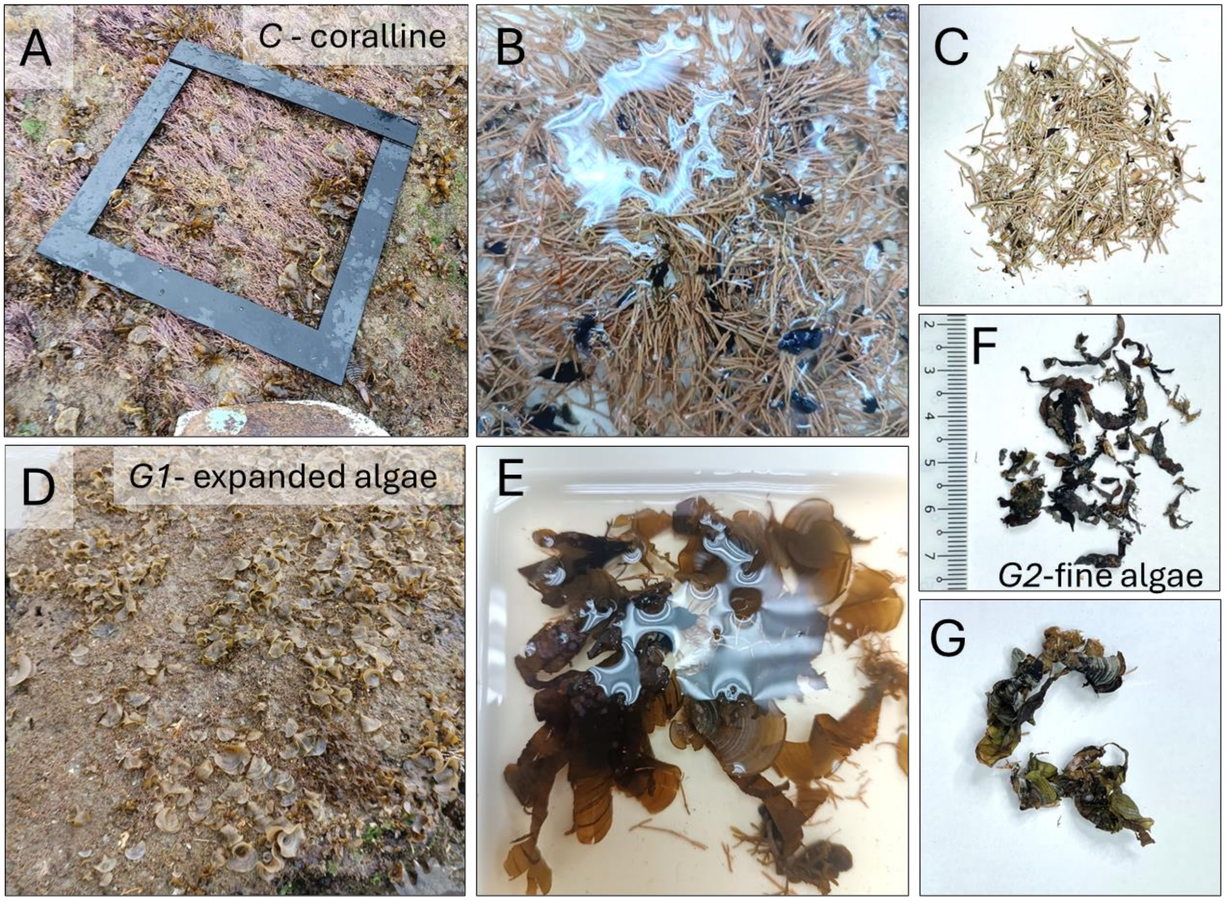

Figure 2. Three dominant structural types of algae. (A,B,C) Finely branched coralline alga, *Amphiroa fragilissma*, in the field, sorted wet in laboratory and after drying, in this order. (D,E,G) The expanded alga, *Padina* sp., as above. (F) Finely-branched green alga, mainly *Sargassum*, dry.

2.2 Faunal taxa and habitat complexity

In the laboratory, the algal and other substrata were washed over a stack of brass sieves with mesh sizes of 2 mm, 500 µm, and 180 µm. The small invertebrates were extracted, and algae were sorted into three groups based on taxonomic and structural features; (1) finely branched coralline algae dominated by *Amphiroa fragilissma*, (2) finely branched green algae containing *Sargassum* sp., and the expanded green algae containing *Padina* sp.) (see ***Figure 2***). Habitat complexity of each algal type was estimated from the ratio of the area to perimeter using photographs of the substratum (DP 28 Olympus digital camera; SZX 10 Olympus microscope; n=60 samples) and Olympus cellSens digital imaging software. The quantity of each substratum in a sample was determined gravimetrically, after oven-drying at 70°C for 24 h. In addition to algal substratum, the sessile mytilid mussel, *Dentimodiolus* sp., was quantified in terms of abundance (density). Another animal substratum in the samples, a sponge (Porifera), was not quantified.

The invertebrates retained in the 500 µm mesh were stored in vials of 70% ethanol and later examined under a Leica EZ4 dissecting microscope. Specimens were isolated, counted and necessarily identified to Operative Taxonomic Units (OTUs), given that the fauna has not been previously taxonomically determined. The 180 µm fraction, containing the meiofauna (mainly harpacticoid copepods and chironomid larvae) was excluded from further consideration. To achieve some level of taxonomic identification, photographic images of OTUs were sent to specialists (SKT, molluscs, KW, amphipods, SNB, ostracods, and MBH, isopods, tanaidaceans and polychaetes). Univariate statistical analyses were performed using SigmaPlot ver.14 (Systat Software Inc.).

2.3 Assemblage structure variation across substrata

To test the effect of habitat substratum complexity on assemblage structure, we compared two substratum categories: 1) the finely branched substratum, including both coralline and green algae and (2) the expanded substratum, including bladelike algae, sponge and small mussels (see above, see ***Figure 2***). Non-metric multidimensional scaling (nMDS) and permutational multivariate analysis of variance analysis (PERMANOVA) were performed on Bray-Curtis similarity matrices for 25 functional OTUs (nMDS, PRIMER v7 software). Faunal species of very low abundance (usually fewer than three specimens in the combined samples) and those that were clearly non-interactive with the floral structural complexity (such as crabs and large snails) were excluded from the analyses. The analyses were run at the OTU level using three differently transformed datasets (untransformed, 4th root transformed and presence-absence). This was necessary given that habitat availability (substratum dry mass) varied among the samples and could likely confound the effect of habitat complexity on faunal abundance. Whereas untransformed data completely incorporates abundance, 4th root transformed data down-weights abundance, and presence-absence data completely excludes abundance. A Similarity Percentages (SIMPER) analysis (PRIMER v7 software) was then run on 4th root transformed data to determine the species' contributions to similarity within the groups and dissimilarity between the groups.

3. Results

3.1 Faunistic composition

The > 1099 macrobenthic invertebrate specimens extracted from the samples comprised > 46 morphospecies (or OTUs) from 30 families (see ***Table 1***). Gastropods (22 OTUs) and amphipods (12 OTUs) were the most species-rich taxa, and the amphipods were the most abundant (474 individuals). Other abundant taxa were ostracods (2 OTUs), tanaidaceans (2), isopods (3) and polychaetes (4) (see ***Table 1*****).** The samples also contained individual brachyuran and anomuran crabs. Whereas the gastropods were mostly resolved to genus or species levels, amphipods and other taxa were more difficult to resolve taxonomically from the photographic images. Only three amphipod genera could be confirmed via photographs, *Ampithoe* (Ampithoidae), *Pariphinotus* (Philantidae) and *Elasmopus* (Maeridae). *Ampithoe* contained the most taxa, and our light microscopic counts did not discriminate additional likely species than the four listed here.

3.2 Habitat complexity and faunal abundance

Habitat complexity varied greatly among the algal substrate types. For coralline algae (0.175; 95% CI = 0.11, 0.23) the substrate was an order of magnitude more complex than that of the expanded algae (1.7; 95% CI = 1.57, 1.83; a smaller ratio indicates greater complexity). The ratio for the finely-branched green alga group was intermediate at 0.78 (95% CI 0.69, 0.88). Because area and perimeter were strongly correlated over a broad size range, no size correction of the measured samples was undertaken. As an example, the linear relationship for the coralline algae was

$$\text{area} = -0.85 + 0.235 \times \text{perimeter}$$

($r = 0.91$; $p < 0.001$) across a 5-60 mm perimeter range.

Table 1. Benthic faunal Operational Taxonomic Units (OTUs) associated with the algal turf at the Empire.

OTU	**Family**
Polychaeta (4 OTUs, 2 families)	
nereidid sp.1	Nereididae
nereidid sp.2	Nereididae
nereidid sp.3	Nereididae
syllid sp.	Syllidae
Gastropoda (22 OTUs, 15 families)	
cerithiid sp.	Cerithiidae
Cerithium cf. *torresi*	Cerithiidae
Clypeomorus bifasciata	Cerithiidae
Rhinoclavis sinensis	Cerithiidae
Joculator sp.	Cerithiopsidae
Zafra cf. *troglodytes*	Columbellidae
Pardalinops testudinarius	Columbellidae
Euplica scripta	Columbellidae
Epitonium cf. *simplex*	Epitoniidae
Echinolittorina vidua	Littorinidae
Volegalea cochlidium	Melongenidae
Arakawania granulata	Muricidae
Drupella margariticola	Muricidae
Cellana testudinaria	Nacellidae
Phyllidiella cf. *nigra*	Phyllidiidae
Odostomella opaca	Pyramidellidae
Retusa sp.	Retusidae
Coriophora fusca	Triphoridae
Trochus radiatus	Trochidae
Turbo articulatus	Turbinidae
Ostracoda (2 OTUs, 2 families)	
cylindroleberidid sp.	Cylindroleberididae
sarsiellid (cf. *Eusarsiella*)	Sarsiellidae
Isopoda (3 OTUs, 1 family)	
Sphaeroma sp.	Sphaeromatidae
sphaeromatid sp.1	Sphaeromatidae
sphaeromatid sp.2	Sphaeromatidae
Amphipoda (12 OTUs, 7 families)	
Ampithoe sp.1	Ampithoidae
Ampithoe sp.2	Ampithoidae
Ampithoe sp.3	Ampithoidae

Ampithoe sp.4	Ampithoidae
aorid sp.	Aoridae
hyalid sp.	Hyalidae
kamakid sp.1	Kamakidae
maerid sp.1	Maeridae
maerid sp.2	Maeridae
Elasmopus sp.	Maeridae
megaluripid sp.	Megaluripidae
Pariphinotus sp.	Phliantidae
Tanaidacea (2 OTUs, 2 families)	
leptocheliid sp.	Leptocheliidae
tanaidid sp.	Tanaididae
Decapoda (3 OTUs, 2 families)	
Clibanarius ransoni	Diogenidae
Diogenes sp.	Diogenidae
Leptodius cf. *gracilis*	Xanthidae

Substrate dry mass varied greatly among the samples, and between the dominant substrate types; from ~40 g (samples N4, N5) to ~2 g (samples N7, N9, N13) (see ***Figure 3***). No algae were collected in sample N16, a dense mussel bed (see ***Figure 3***). The mass of the sponge dominated sample (N8) was ~30 g. The samples could thus be characterised based on the dominant structural algal type; samples N3, N4, N5, N10 were dominated by the coralline alga, *Amphiroa fragilissma*, samples N1, N2 by finely-branched green alga, mainly *Sargassum* sp., and samples N6, N7, N9, N11, N12, N14, N15 by the expanded green alga, *Padina* sp. samples N11, N12, N13 and N16 contained a high proportion of mussels (see ***Figure 3***).

3.3 Assemblage structure variation across substrata

All analyses revealed significantly different assemblages associated with the two habitat types (nMDS, see ***Figure 5***). PERMANOVA statistics for the untransformed data were F = 3.92, p = 0.001, for 4th root data were F = 4.34, p = 0.001, and for presence-absence data were F = 3.62, p = 0.005. The PERMDISP statistics indicated homogeneity of variance in all cases. The significant difference when abundance was excluded confirms species preference for the different habitat types. The assemblage patterns were consistent irrespective of whether mussels were included in the analysis or not; these different analyses were important as mussels can be considered as a substrate (effect) or a coloniser (response). An untransformed PERMANOVA showed that the two major substrate types differed (F= 3.4, p = 0.001) when mussel abundance was excluded from the data matrix.

Similarity Percentages (SIMPER) analyses showed that amphipods, gastropods and ostracods most strongly influenced similarity within the substrate groups and dissimilarity between the groups (see ***Table 2***). 50% of the similarity among the finely branched group was contributed by three species, *Zafra* cf. *troglodytes*, hyalid sp. and cylindroleberid sp. The latter taxon and cerithiid sp. contributed most to the similarity of the expanded substrate groups, whereas hyalid sp., *Ampithoe* sp. 2 and tanaid sp. contributed mostly to the dissimilarity between the groups (see ***Table 2***), cumulatively contributing 28.63%.

4. Discussion

Knowing local species diversities and ecologies underpins understanding and the conservation and management of ecosystems. Such information is limited for the intertidal marine ecosystems of Brunei and the Palawan North Borneo (PNB) ecoregion, a species diverse region at the eastern perimeter of the South China Sea (SCS).[10-12] Aside from taxonomic studies, recent rocky shore work has focused on the ecology and the responses of gastropods to temperature and coastal acidification.[18-22] Intertidal ecological studies are limited to Pulau Punyit and specific shore levels, such as mid-shore oyster reefs[13,16,17] (and see review of Brunei's rocky shores in this journal volume).[23] Algal turf faunal ecology for local ecosystems is currently restricted in study to the Brunei estuarine and bay system.[14] Here, we show that this rocky shore algal turf zone for the SCS coastline supports a rich benthic macrofaunal diversity and forms assemblages relating to the architectural complexity of habitat-forming algae (constituting ~30 species)[17] and other species.

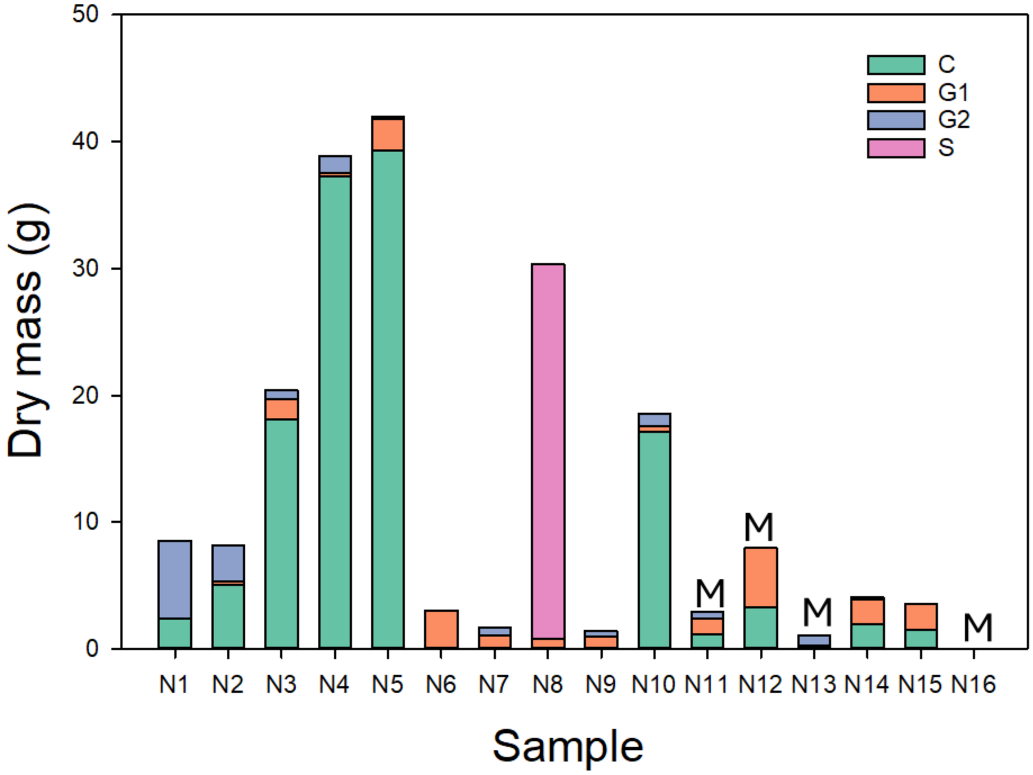

Figure 3. Mass proportions of the three predominant algal types. C, finely branched coralline algae dominated by *Amphiroa fragilissma*, G1, expanded green algae, mainly *Padina* sp., and G2, finely branched green algae dominated by *Sargassum* sp. N1 and N2 possessed comparatively similar amounts of finely branched coralline and green algae. M, abundance of mussels (see ***Figure 5B***), N16 is a dense mussel bed (see ***Figure 5B***). S (NR8) is the sponge substrate.

Despite our pragmatic selection of a few habitat types based on structural complexity, and the spatial limitation of the sampling (6400 cm^2), more than 1099 macroinvertebrates comprising above 46 OTUs from 30 families (see ***Table 1***) were collected. In similarity with other studies, amphipods and gastropods were the most species-rich taxa.[3-8] Furthermore, the amphipod families, Ampithoidae, Aoridae, Hyalidae, and Maeridae, including the genus *Elasmopus*, which contributed to our assemblages, commonly inhabit rocky shore algal turf communities.[7,8] The high gastropod diversity (double the number of amphipod species) observed here is consistent with the findings of coralline turfs of another study.[3] Compared to previously published gastropod lists, at least eight species represent new records for the Empire location and Brunei (*Cerithium* cf. *torresi*, *Rhinoclavis sinensis*, *Zafra* cf. *troglodytes*, *Pardalinops testudinarius*, *Epitonium* cf. *simplex*, *Volegalea cochlidium*, *Odostomella opaca*, and *Coriophora fusca*) (see ***Table 1***).[13,16] *V. cochlidium* represents the first observation on the rocky shore of a live individual of a species commonly found locally in the mangroves. The observation of two tanaidacean species, complies with a Brazilian study also reporting two species from different families (Leptochelidae and Tanaididae).[8] The most abundant OTU was the cylindroleberidid ostracod, which recorded ~200 individuals in all samples combined.

In accordance with our prediction, the algal turf complexity structured the benthic motile invertebrate assemblages (see ***Figure 5***). Previous studies have shown that relatively finely branched coralline algal substrates influence invertebrate assemblages by offering shelter from wave action, protecting against predation, and providing preferential food.[4-8] The rich amphipod fauna in coralline algal substrata is suggested to relate to the mesograzing of epiphytes on these surfaces.[7] Amphipod OTUs (hyalid sp. and *Ampithoe* sp. 2) were found to contribute the most to both assemblage similarity of the finely branched algal substratum group (including the coralline alga) and dissimilarity between the different algal substratum groups (see ***Table 2*** and ***Figure 4***). Tanaidacean abundance served as another primary source of dissimilarity between the habitat substrate types, being particularly high in the broadly flattened (expanded) habitat (see ***Table 2*** and ***Figure 4***). Generality of habitat use, reported elsewhere for tanaidaceans, suggests that these animals may be outcompeted by amphipods in the coralline habitats of the present study.[7,8] A fourth important taxon differentiating the assemblages associated with structurally different substrata were the gastropods, particularly cerithiid sp. These were especially abundant in the broadly flattened habitats (including the mussel and sponge substrates), which may relate to their generalist detritivorous/herbivorous surface scaping feeding behaviour. Polychaetes were likewise largely restricted to these sedentary animal substrata, whose expanded surfaces accumulate sediments and support microbial films. The assemblage defining ostracod, cylindroleberidid sp., however, showed little preference for either structural habitat type (see ***Table 2***), as did the isopods.

Whereas we considered 'microscale' (centimeters) habitat complexity, rocky shores characteristically exhibit extreme habitat heterogeneity over a wide range of spatial scales. For a shoreline scale (10s of meters), the angle of the coast at the Empire habitat leads to the deflection of the prevailing wavefronts, resulting in a moderately-protected shoreline (see ***Figure 1***). Likewise, the low shore algal turf zone experiences similar tidal exposure across its vertical height, suggesting that desiccation plays a minor role in structuring assemblages. However, the algal composition was observed to be patchy at meter scales, varying relative to the slope of the broken rock blocks at the lower shoreface, and with respect to the trapping of water bodies on their upper surfaces. Our study focused on the flatter near horizontal surfaces, with sample collections based on observable dominant algae, suggesting that more extensive meter-scale sampling incorporating greater habitat heterogeneity should better represent the shoreline diversity. A second limitation refers to the temporal sampling protocol of the study, confined to a few days. Despite wave action being highly subdued for most of the year, this moderately exposed shoreline experiences powerful wave forces during high seas in the typhoon season, potentially causing sand scouring of the algal turf. Wave action nonetheless washes out the finer muddy sediment particles accumulating in the turfs under excessive turbidity loading during the monsoonal rainfall periods; this predictably negatively impacts the benthic communities by smothering the algal turf. In summary, despite the informative findings of the present study, they represent a snapshot of an expected much more complex structural and functional ecology. An understanding of the overall regional diversity should also consider the extensive artificial rocky shore constructions along the coastline, including in the vicinity of the Empire. These shores present different orientations to the wave fronts, enabling the colonization of organisms specially adapted to withstand powerful wave exposure, and ultimately driving greater assemblage diversity.

Table 2. SIMPER analysis showing OTUs that contribute most to the similarity within each group and the dissimilarity between the groups (A, finely branched algae, and B, expanded substrates).

Group A						
Average similarity: 51.61						
OTU	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Zafra cf. *troglodytes*	1.41	9.15	7.6	17.72	17.72	
hyalid sp.	1.76	8.7	1.26	16.87	34.59	
cylindroleberidid sp.	1.54	8.08	1.34	15.66	50.25	
Ampithoe sp.2	1.56	7.11	1.29	13.78	64.03	
kamakid sp.	1.4	7.1	1.34	13.75	77.78	
Group B						
Average similarity: 51.87						
OTU	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Dentimodiolus sp.	1.77	7.44	1.65	14.33	14.33	
cylindroleberidid sp.	1.58	7.24	4.43	13.96	28.29	
cerithiid sp.	1.37	6.49	1.74	12.51	40.8	
Pariphinotus sp.	1.27	5.66	1.58	10.9	51.71	
Zafra cf. *troglodytes*	1.13	3.96	1.2	7.63	59.34	
Ampithoe sp.1	0.91	2.85	0.89	5.5	64.84	
kamakid sp.	1.03	2.85	0.88	5.49	70.33	
Groups A & B						
Average dissimilarity = 58.42						
	Group A	Group B				
OTU	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Dentimodiolus sp.	0.45	1.77	4.72	1.61	8.09	8.09
hyalid sp.	1.76	0.61	4.54	1.56	7.77	15.85
Ampithoe sp.2	1.56	0.44	4.13	1.51	7.07	22.92
tanaid sp.	0.17	1.04	3.33	1.11	5.7	28.63
cerithiid sp.	0.5	1.37	3.27	1.51	5.59	34.22
kamakid sp.	1.4	1.03	3.06	1.22	5.23	39.45
Pariphinotus sp.	0.5	1.27	3.05	1.22	5.23	44.68
sarsiellid (cf. *Eusarsiella*)	0.17	0.99	2.83	1.3	4.85	49.53
Ampithoe sp.1	0.17	0.91	2.71	1.29	4.64	54.17
cylindroleberidid sp.	1.54	1.58	2.52	1.51	4.31	58.48
Ampithoe sp.3	0.75	0.49	2.49	1.1	4.26	62.74
sphaeromatid sp.1	0.65	0.68	2.47	1.1	4.24	66.98
nereidid sp.2	0.6	0.81	2.39	1.13	4.09	71.07

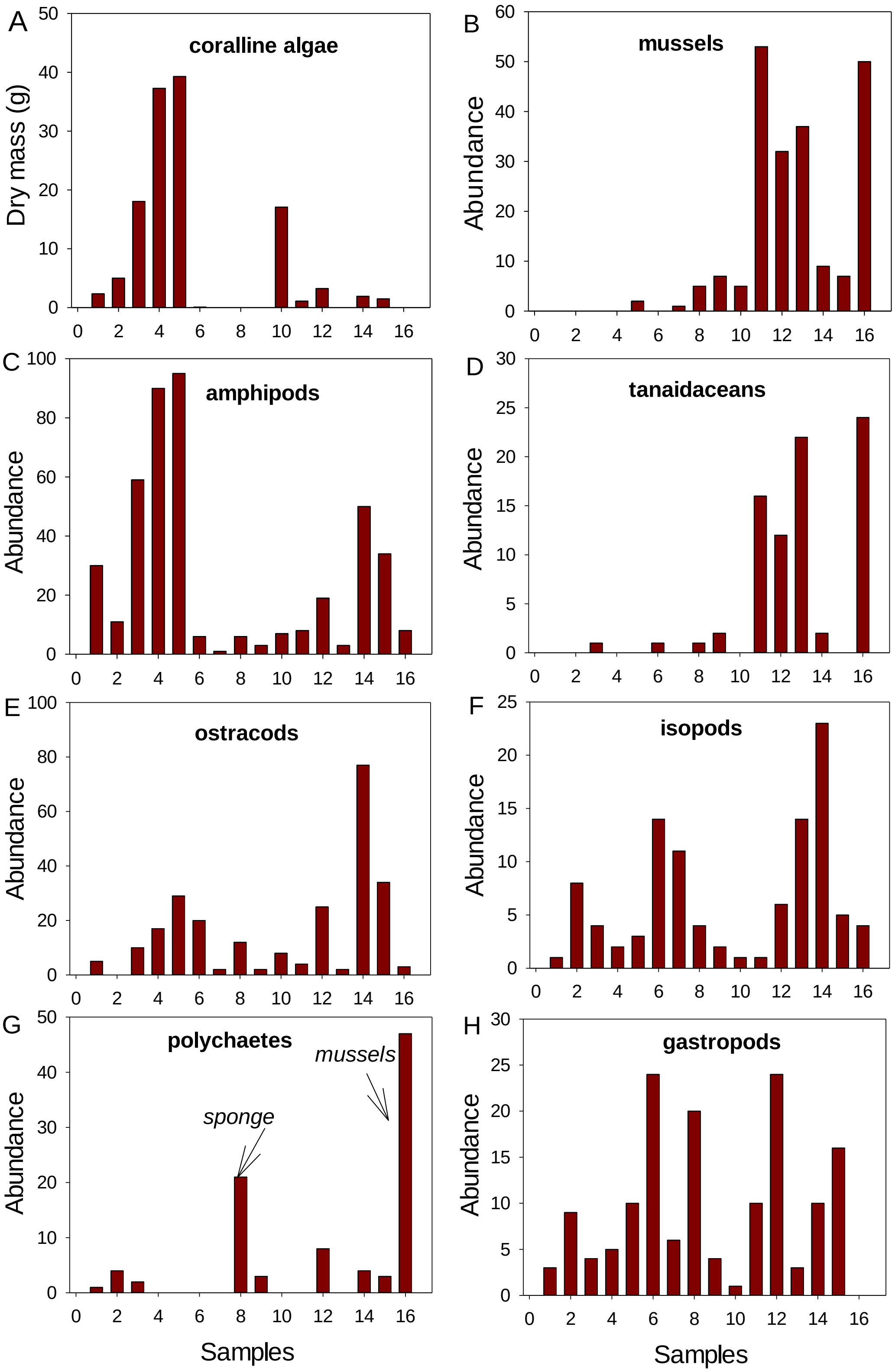

Figure 4. Habitat availability for two dominant substratum taxa (A, coralline algae; B, mussels), and abundances (or density, 400 cm^2) the major faunal groups (C-H) in each sample. A total of 1099 specimens were counted for 25 species. The mussels (B) represent loose specimens collected in the sieve, whereas abundance was vastly greater for the byssus adhered mussels in the bed (NR16).

To conclude, this study presents novel taxonomic and ecological information for local and regional low shore algal turf benthic faunal assemblages. Though this is useful for comparisons with the structural and functional aspects of other rocky shore habitat types, the study reveals a serious knowledge gap in terms of the resolution of the taxa. Determining the species names of the macrobenthic fauna is crucial to future research and conservation management practices.

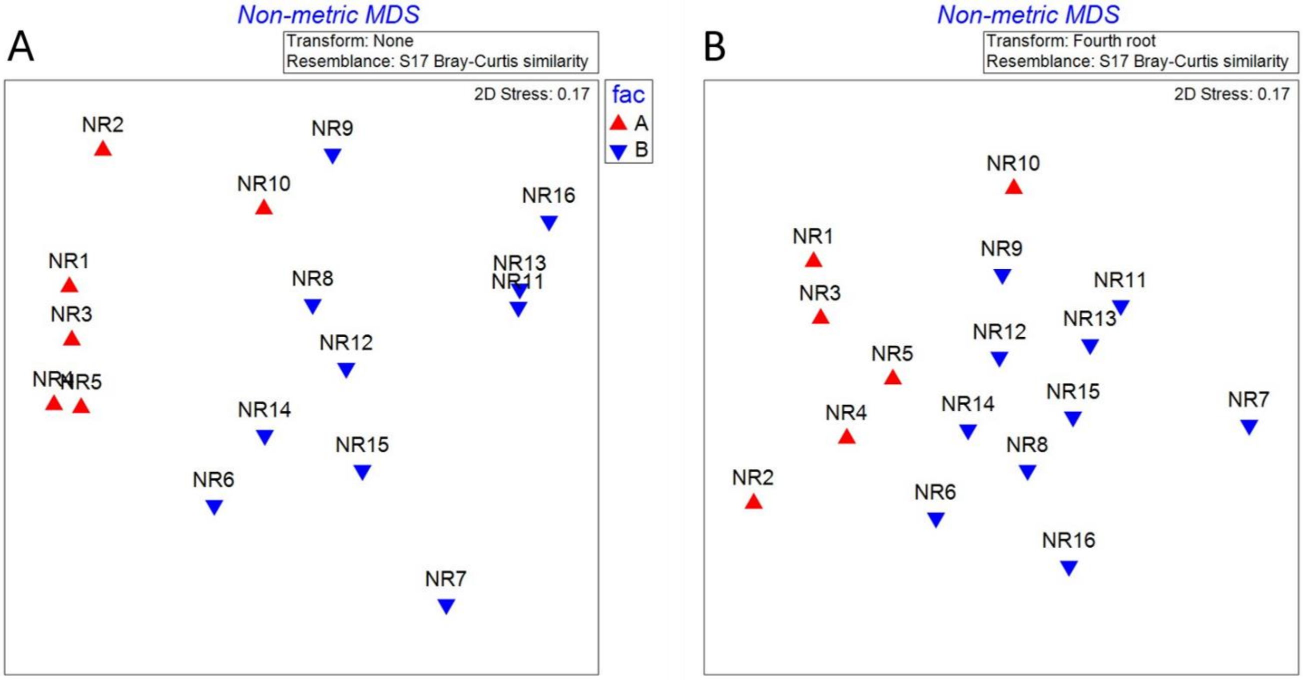

Figure 5. Non-metric Multi-Dimensional Scaling (nMDS) plots showing invertebrate assemblages based on (A) untransformed Bray Curtis similarity, and (B) fourth root similarity matrix. There was clear separation between assemblages for substrates dominated by finely branched algae (Factor A, red symbols: coralline and green algae, C and G2, ***Figure 4***) and those dominated by expanded green algae and mussels (Factor B, blue symbols). NR8 is the sponge substrate. The untransformed plot completely reflects abundance, whereas abundance is down-weighted in the fourth root plot. NR (1-16) refers to N (1-16) samples in ***Figure 3***.

Acknowledgements

We are grateful to Dr Md. Shiblur Rahaman for reviewing the paper. Natasha Khairul is thanked for helping to prepare the reference list.

This research was supported by grants UBD/RSCH/1.4/FICBF/2025/004 and UBD/RSCH/URC/NIG(b)/10.0/2022/001 awarded to DJM and SG, respectively.

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Appendix

Appendix Figure 1. Selected algal turf invertebrates, excluding molluscs and decapods. ***Table 1*** gives a complete list of the taxa. A, *Ampithoe* sp.1; B, *Ampithoe* sp.2; *Ampithoe* sp.3; D, *Elasmopus* sp.; E, maerid sp.1; F, *Elasmopus* sp.; G, aorid sp; H, kamakid sp.1; I, *Pariphinotus* sp.; J, *Sphaeroma* sp.; K, hyalid sp.; L, megaluripid sp.; M, leptocheliid sp.; N, sphaeromatid sp.1; O, sphaeromatid sp.2; P, tanaidid sp.; Q, nereidid ; R, sarsiellid (cf. *Eusarsiella*); S, cylindroleberidid sp.; T, syllid sp.; U, nereidid sp.2; V, nereidid sp.3

Appendix Figure 2. Gastropods found in the algal turf. A, *Zafra* cf. *troglodytes;* B, cerithiid sp.*;* C, *Joculator* sp.*;* D, *Retusa* sp., E, *Odostomella opaca;* F, *Euplica scripta;* G, *Pardalinops testudinarius;* H, *Epitonium* cf. *simplex;* I, *Volegalea cochlidium;* J, *Coriophora fusca;* K, *Cerithium* cf. *torresi;* L, *Clypeomorus bifasciata;* M, *Rhinoclavis sinensis;* N, *Arakawania granulata;* O, *Turbo articulatus;* P, *Clypeomorus batillariaeformis* (juvenile)*;* Q, *Phyllidiella* cf. *nigra*. Asterisk indicates species used in the statistical analyses.