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Dramatic Enhancement of Macrozoobenthic Species β-Diversity in Response to Artificial Breakwater Construction Along a Tropical Coastline

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Abstract: The beneficial or detrimental effects of human-built marine structures (piers, breakwaters, and seawalls) on macrozoobenthic assemblages and diversities are currently underexplored. The present study investigated the enhancement of β-diversity of oysterbed-associated species on breakwaters constructed along sandy beaches. We compared habitat complexities and species assemblages among artificial breakwater shores (ABS), a natural rocky shore (NS), and an embayment shore (ES). Oysterbed habitat complexity was found to be greatest on the ABS due to the successional colonization of the reef-forming estuarine oyster, *Saccostrea echinata*, followed by the colonization of boring bivalves and burrowing annelids. High-resolution taxonomic data revealed that the ABS supports the greatest species richness, including 48.1% unique species and 33.3% species shared with the embayment shore. The other shores uniquely or in combination with ABS support up to 11.1% of the total species richness associated with the oysterbeds (n = 81). Taxonomic dominance in terms of species number was Mollusca > Annelida > Arthropoda. This study reveals that ABS enhances β-diversity by ~91% (Jaccard dissimilarity index), which is driven by the sequential cascading events of (1) sheltering of shores, (2) colonization of novel habitat-forming oysters, (3) novel macrozoobenthic species recruitment from adjacent shores and sheltered embayments, including habitat-forming bivalves and annelids, and (4) the recruitment of macrozoobenthic species to boreholes. ABS habitat complexity derives from a spatially distinct, three-tiered ecological engineering system, involving (1) breakwater construction (100 m), (2) reef-forming oysters (10 m), and (3) boring bivalves and burrowing annelids (<10 cm). Irrespective of the purpose of their construction, breakwaters along extended sandy shores can potentially increase the resilience (β-diversity) and regional interconnectivity of hard surface macrozoobenthic species.

Keywords: artificial habitats; biogenic reefs; bivalve borers; breakwaters; ecological engineering; foundation species; habitat facilitators; oysterbeds; oyster reefs; Palawan/North Borneo ecoregion; polychaete burrowers

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1. Introduction

Artificial marine structures, such as piers, breakwaters, and seawalls, are not typically engineered for the purpose of enhancing biodiversity, though they provide a hard

substratum for the colonization of sessile foundation species, such as oysters, mussels, and corals [1]. By modifying the surfaces they colonize, foundation species influence microenvironmental temperature, hydrodynamics, and resource availability [2,3], creating a novel habitat for the colonization of other benthic species and, ultimately, the formation of novel assemblages and communities [4]. Marine structures worldwide have been found to harbor biodiverse assemblages, including coral communities [1,2,5–9], and despite recent trends towards engineering human-made structures that enhance and reclaim species diversity, these initiatives are limited in application [10]. Even though engineered marine structures are widely used in coastal developments to alleviate erosion and sea encroachment, there is little information on their unintended ecological benefits, including the enhancement of local β-species diversity. There are several definitions for β-diversity, but it primarily refers to the variability in species composition or species turnover between samples from an area [11,12]. Such diversity enhancement contributes positively to the integrity, resilience, and functionality of ecosystems [5,13,14]. Furthermore, the successional events and mechanisms (larval settlement, colonization, and ecoengineering) underlying macrozoobenthic diversity enhancement following the building of marine structures are incompletely explored [15].

Oysters are among the primary colonizing organisms of hard substrata on sheltered tropical shores, and their relatively large size and flattened structure makes them effective ecological engineers [3,6,16]. The larvae of both oysters and their associated colonizing species [7,17–20] commonly preferentially settle on oyster shells via the secretion of biomineralization [21–23], resulting in structurally and functionally complex and self-maintaining oyster reefs [16,24]. With time, the stacking of oysters potentially creates a complex 3D habitat in an otherwise 2D seascape [3,21–23]. This structure, together with the filter-feeding effect of oysters, modifies microcurrent flows around an oysterbed, improving sediment trapping and the feeding opportunities of organisms living in the bed [3,7,8,25–28]. Furthermore, the ecological functions of oysterbeds last well beyond the lifetime of individual oysters [20,29]. Even dead oysterbeds support significant species diversities compared to nearby bare rocky shore habitats (without oyster remnants) and are preferred refuges for several marine arthropod species [2,5]. Examples of the role of oysterbeds in enhancing species diversity (richness and abundance) include studies in Australia and Pakistan, showing that local oysterbeds may support up to 300 associated species [5,25,26], surpassing the diversity of key ecosystems, such as seagrasses and mudflats [28–31]. Oysterbeds may support a 20-fold increase in abundance and 5-fold increase in species richness compared to bare rock habitats, through their effect of increasing habitat complexity [3].

Oysterbed complexity may increase with time as a result of the stacking of oysters from different generations. The increase in 3D complexity creates habitats for organisms that typically bore into marine hard substrata (rock, corals, or wood), including other bivalves (Mytillidae, Petricolidae, Pholadidae, Trapezidae, Pholadidae, and Gastrochaenidae) [25,32]. Their colonization, in turn, should contribute to the habitat complexity at a finer scale (that of the borehole) and create refuge for small invertebrates (including crabs and polychaetes). Boreholes also trap sediment and organic matter, which serve as a food resource for members of the assemblage. As an example, the vacated boreholes of *Petricola dactylus* (Veneridae) are known to increase species richness by three times that of similar but unengineered habitats [33]. Whereas infaunal and vagile species use these boreholes, species with strong adhesion mechanisms were more prevalent in unengineered areas [33]. The colonization of oysters on artificial, human-made marine structures, followed by that of boring bivalves, essentially represents a three-tiered ecological engineering system for species diversity enhancement (Figure 1). The reduction in near-surface hydrodynamic forces on the inner surfaces of obtusely angled (relatively to coastline) breakwaters encourage larval settlement (tier 1; Figure 1). Habitat complexity arising from oyster stacking encourages the colonization of boring species (tier 2), which, in turn, enhances habitat complexity in the form of vacated boreholes (tier 3; Figure 1).

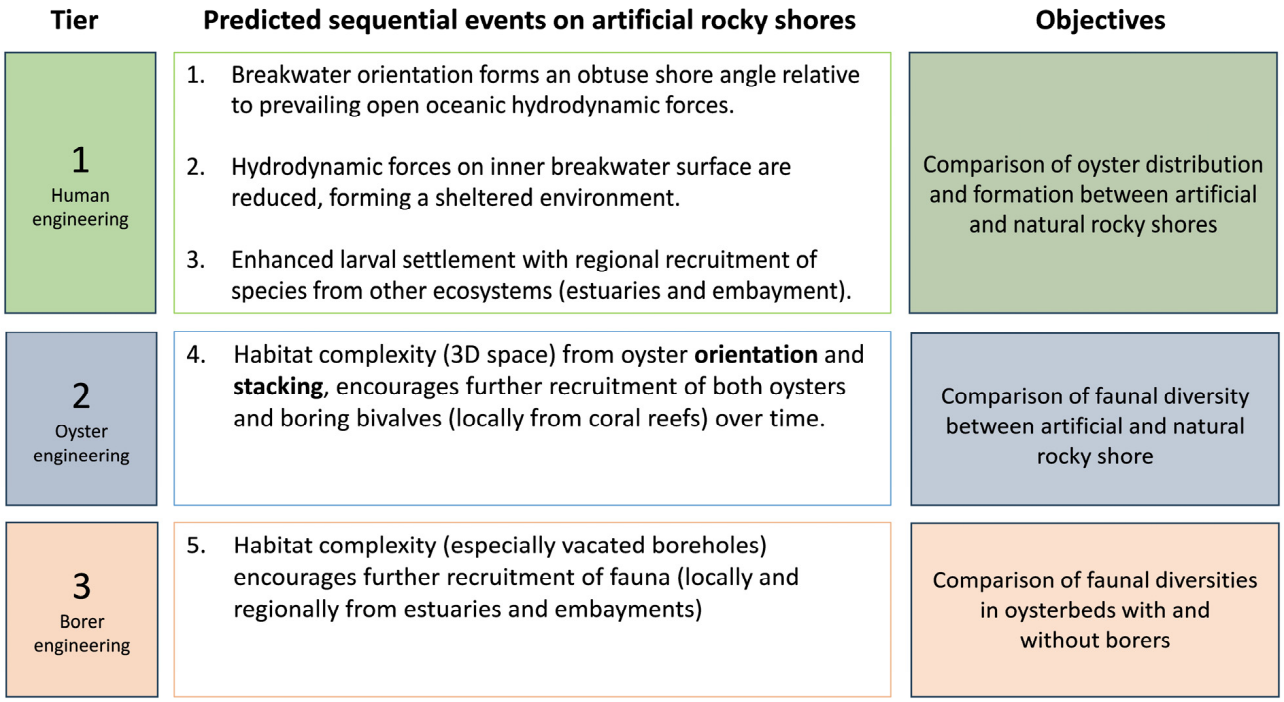


Figure 1. The predicted sequential temporal events associated with the oysterbed community on the breakwaters, the tiers of eco-engineering, and the relevant objectives to test these predictions.

The Brunei shoreline of the South China Sea (SCS) naturally constitutes a linear sandy beach ecosystem with highly limited rocky-shore outcrops [34]. However, extensive coastal development was undertaken in the early 1990s (~30 years old) resulting in the sandy beach being fragmented and replaced with artificial rubble mound breakwater shores (4.3 km sandy shores, 7.9 km artificial breakwaters; Figure 2). These breakwaters were constructed to protect against coastal erosion (Tungku) and to establish a small harbor (Jerudong; Figure 2). There are only two natural rocky protrusions that extend perpendicularly to the coast, along the ~120 km SCS coastline of Brunei [34], and currently, the only undisturbed natural rocky shore is found at the Empire (Figure 2). The breakwaters are constructed from large and irregular boulders (>1–5 m^3), and due to the obtuse angles that form relative to the coastline, their inner intertidal surfaces are sheltered and become heavily encrusted with oysters (Figure 2). Currently, the only published ecological study on the faunas of these artificial shores in Brunei refers to their coral communities [35].

This study aimed to assess the effect of artificial breakwaters on species β-diversity enhancement, by considering the above three-tiered ecological engineering system. We hypothesized that by altering the rocky surface hydrodynamics, breakwaters facilitate the cascading successional colonization of novel habitat-forming species (oysters and borers) and of their macrozoobenthic recruits (Figure 1). As objectives, we investigated the patterns and mechanisms of species diversity enhancement by comparing habitat structure and species assemblages for artificial breakwaters, a natural rocky shore (high energy) and an embayment shore (low energy). Whereas the natural rocky shore comparison primarily informs about larval settlement potential, the embayment shore informs about the recruitment of species that occupy other low-energy hydrodynamic environments.

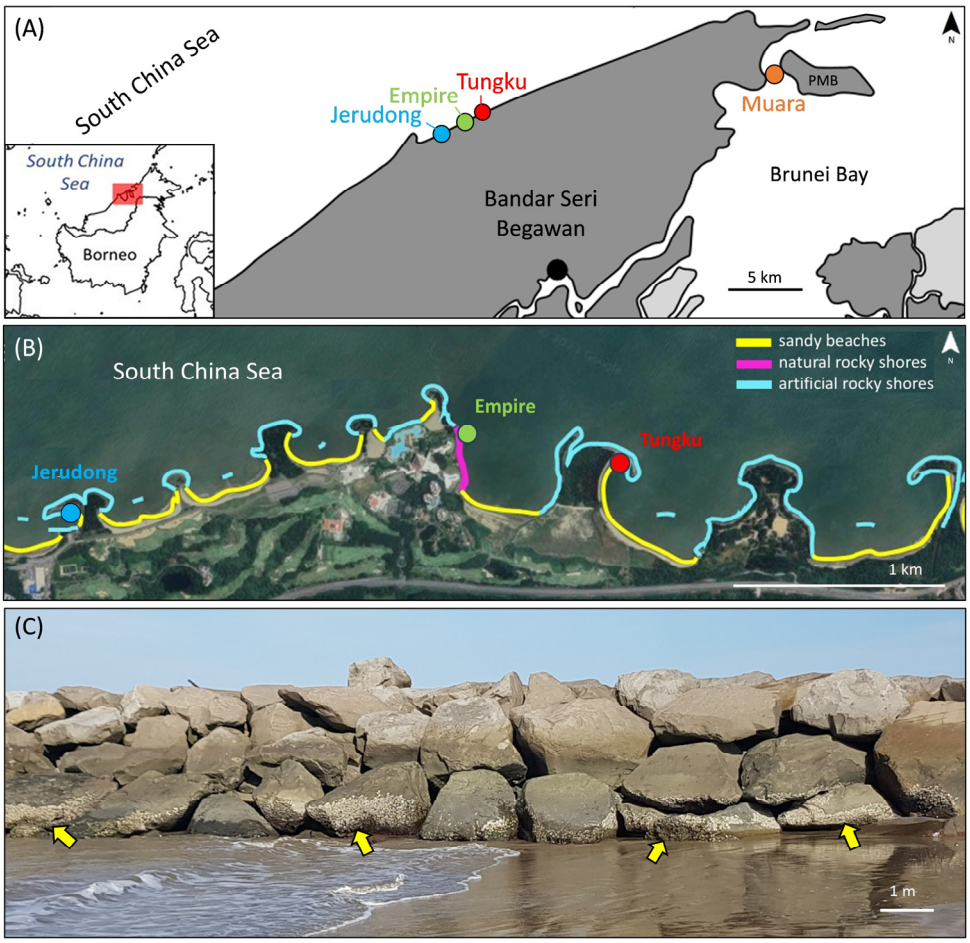


Figure 2. (**A**) Study locations along the South China Sea coastline of Brunei and the Brunei Bay, at Pantai Jerudong, Empire, Pantai Tungku, and Muara. (**B**) Satellite image showing extensive modification of the coastline, and the distribution of sandy beaches, natural rocky shores, and artificial breakwater shores (respectively, outlined in yellow, fuchsia, and cyan). Sampling locations are marked with colored circles. (**C**) Inner breakwater at Pantai Tungku, showing boulders (1–2 m^3) and the establishment of oysterbeds (yellow arrows).

2. Materials and Methods

2.1. Study Sites

The main study sites covered 12.5 km of the SCS shoreline, comprising 4.3 km of sandy beach (34.2%) interspersed with 7.9 km of artificial breakwater shore (63%) and 351 m of natural rocky shore (2.8%) (QGIS, Google Earth Pro 7.3, Figure 2). Observations were made at two artificial breakwater shores, Pantai Jerudong (ABS, 4.959° N, 114.840° E) and Pantai Tungku (ABS, 4.972° N, 114.863° E), and at the natural rocky shore at Empire (NS, 4.969° N, 114.855° E). The embayment study site was located at Pulau Muara Besar (ES, 5.006° N, 115.076° E) in the inner Brunei Bay (Figure 2). The artificial breakwater shores vary in structure and orientation relative to the natural shoreline, with the Tungku ABS oriented southwest and the Jerudong ABS oriented southeast (Figure 2). Also, some breakwaters are attached to the land; whereas, others are unattached and akin to rocky islets (Figures 2 and 3). The present study focused on attached breakwaters, which, along their landward (inner) side, are sheltered from direct wave action and high energy hydrodynamics and, consequently, facilitate oysterbed colonization (Figure 2). The natural rocky shore at Empire constitutes broken, gently sloping rocky formations and a low-lying boulder beach [34]. The embayment site (low wave action) comprises large concrete pillars supporting a bridge that was constructed in 2018 (6 years ago; Figure S1). The oyster zone at all sites is vertically distributed on shores between ~0.05 and 1.2 m Chart Datum [36]. The

salinity and pH of the sites have been previously well studied: SCS (salinity = 20.2–33.2, pH = 7.9–8.5), Brunei Bay (salinity = 19.6–31.2, pH = 7.7–8.3), and Brunei Estuarine System (salinity = 3.6–26.9, pH = 5.8–8.1) [37–39]. Habitat water temperatures typically vary between 27–30 °C, and rock temperatures during air exposure rise to above 51 °C, with daily maximum temperatures recorded in oyster habitats of above 46 °C [40].

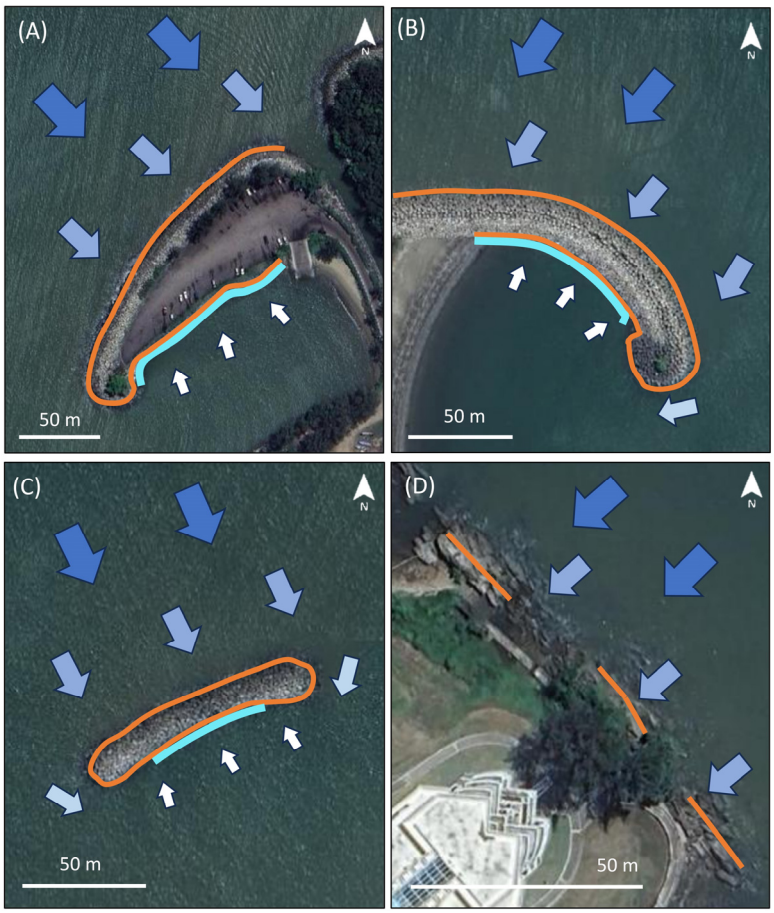


Figure 3. Satellite images showing artificial breakwaters and a natural rocky shore. The distributions *Saccostrea echinata* beds (blue lines) and *Saccostrea mordax* beds (orange lines) at (**A**) Jerudong attached breakwater, (**B**) Tungku attached breakwater, (**C**) Tungku unattached breakwater, and (**D**) the natural rocky shore of Empire. Predicted direction and intensity of ocean currents indicated by gradational blue and white lines, with darker blue indicating strongest intensity eventually reduced to white. This study considered only (**A**,**B**,**D**).

2.2. Oyster Distributions and Habitat (Oysterbed) Structure

Surveys were undertaken to determine the oyster species on the shores and to map their long-shore and within-shore distributions. The cover (density) of the prominent species at the natural shore site (NS), where oysterbeds comprised non-overlapping individuals, was assessed from photographs of quadrats (10 replicates × 50 cm^2) and expressed as the number of oysters per meter square. Surface photographs of quadrats were also taken at the artificial breakwater shores (ABS; 10 replicates × 20 cm^2; Jerudong and Tungku) and the embayment site (ES; 6 replicates × 20 cm^2), where oysterbeds formed vertical stacks of individuals. The oysterbeds of the ABS and ES transects were then prized off the rocky substratum with a hammer and screwdriver, bagged, and returned to the laboratory for further analyses. To study the structural (3D) complexity differences in the oyster stacks between the ABS (30 years of recruitment) and the ES (6 years of recruitment), photographs were taken in the field of all surfaces for representative samples that had been prized off the rocky substratum (iPhone 14 Pro Max). The structural habitat complexity was further

assessed by determining the volume (mL) of fine-grain sediment (180 µm) that accumulates with collected oyster piles (20 cm^2 surface area) in the laboratory, with the assumption that a greater sediment volume indicates greater habitat complexity.

2.3. Species Assemblage Comparisons Across the Shores

In the laboratory, the ABS samples (n = 10 replicates for each site) and ES samples (n = 6 replicates) were immersed in containers of tap water for up to an hour to allow the animals to emerge from crevices under the salinity stress. This also minimized the damage of soft-bodied species (particularly polychaetes and crabs). The oyster piles (stacks) were then broken apart into individual oysters and rinsed at all angles above a stack of 2 mm, 500 µm, and 180 µm brass sieves. The immersion water containing specimens was then passed through the sieve stack. Individual oysters and shell debris fractions from the sieves were examined under a Leica EZ4 microscope for the remaining and attached fauna. Retrieved specimens were sorted into their respective taxonomic classes, photographed (Olympus SZX10 dissecting microscope, DP28 Olympus digital camera, Tokyo, Japan; Olympus cellSens software A2, and Helicon Focus 8.0 photo stacking software), and later, stored in 70% ethanol. Our analysis included only the species that occurred in the 500 µm and larger fractions and excluded microarthropods that were occasionally retrieved in these fractions though were much more common in the 180 µm fraction (amphipods, isopods, tanaidaceans, mites, collembolans, and other hexapods). Likewise, displaced stragglers and species that could only be identified to the level of family were excluded from consideration. Species occurring in the NS habitat were determined from the original photographs taken in the field. Photographs and/or specimens were sent to taxonomic experts for confirmation of the species.

A species list was compiled to compare the presence of species between the three shore types (N, ABS, and ES). The taxonomic representation of species richness was determined for the five main phyla, and the uniqueness (or occupancy) of the species representation within a habitat was assessed; rare species that only occurred once in the overall sampling (n = 1) were omitted from the assessment. Differences in species composition between the three shore types (NS, ABS, and ES) were assessed statistically using the multivariate statistical analysis package PRIMER v7. A PERMANOVA was run on species presence/absence data based on Jaccard similarity, followed by pairwise comparisons between the four sites (N, ABS (T), ABS (J), and ES) and an nMDS was used to visualize the differences as distances between points in a 2D plot. β-diversity, which refers to the differentiation of diversity among local sites, was assessed using the Jaccard similarity index (more similar shores have higher values between 0–100) [11,12]. PERMDISP was also used to assess multivariate dispersions between shore types. To investigate species richness, Margalev's and Brillouin indexes were calculated using the Diverse function.

To assess the utilization by the various species of the borehole habitat, we measured the body sizes (length and width) of several individuals of each borer bivalve and nonborer species. Specimens were selected randomly but included a broad size range. Annelids were excluded, as they can accommodate their body to various crevice shapes and sizes.

3. Results

3.1. Oyster Distributions and Habitat (Oysterbed) Structure

The most common oysters occurring on rocky shores of the Brunei coastline are *Saccostrea mordax*, *S. echinata*, *S. spathulata*, and *Magallana bilineata*. Only the former two develop oysterbeds. *Saccostrea mordax* is the only species that colonizes the intertidal zones of the natural rocky shores at the Empire (Figure 3), and *S. echinata* dominates in the high salinity regions of the Brunei Bay. The artificial breakwater shores (ABS) support both *S. mordax* and *S. echinata*, which are spatially separated. Only *S. mordax* is distributed on the outer exposed surfaces of the breakwaters; whereas, on the sheltered inner surfaces where both species cohabit, *S. mordax* occurs higher on the shore, above *S. echinata* (Figure 3). The densities of these oysters and their bed-forming capabilities were found to differ. In the

habitats that are more exposed to wave action, *S. mordax* density declines such that oysters occur singly and separated from their neighbors (Figure 4A), but even when this species forms beds, these comprise a single layer of individuals (Figure 4B). In contrast, *S. echinata* beds on the ABS at Jerudong and Tungku are complex, comprising stacked oysters from multiple generations that had colonized over a 30-year period (Figure 4C). The maximum densities (surface counts) of *S. echinata* on artificial shores averaged at 338 indiv.m^{-2} ($\pm$26.3, n = 5) and of *S. mordax* on natural rocky shores at 151.2 indiv.m^{-2} ($\pm$25.2, n = 5), a difference largely accountable to the maximum individual size difference of the species.

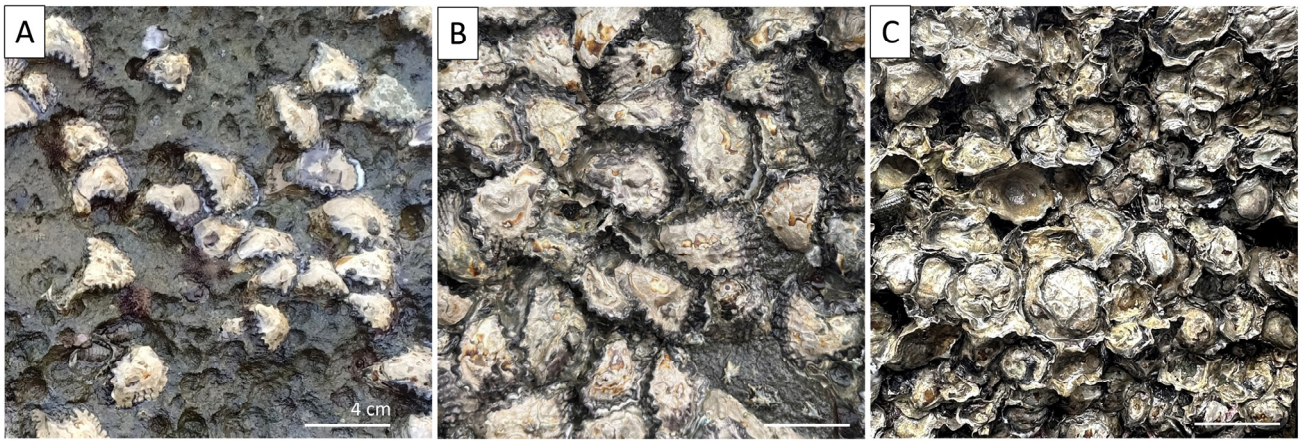


Figure 4. Oyster distributions and bed formation. (**A**) Scattered *Saccostrea mordax* at the natural rocky shore of Empire (NS). (**B**) Single-layered *Saccostrea mordax* bed at the Tungku breakwater (ABS). (**C**) Dense and stacked *Saccostrea echinata* bed at the Tungku breakwater (ABS).

The stacking of oysters in the *S. echinata* beds on the ABSs was random such that oysters grew at different angles to the substratum and, ultimately, produced stacks that were up to 8 cm thick (Figure 5A,B). Vertically, the stacks comprised an outer surface layer of living and nonliving oyster individuals (Figure 5A–C), a middle layer of oyster shells, and a bottom layer attached to the rocky substratum of shell remnants and bioeroded shell fragments (Figure 5C). The angular arrangement of oysters in the stacks created crevices that may become filled with sediment, which sometimes becomes consolidated (Figure 5A–C). Sediment-filled crevices are also sometimes excavated by burrowing species, with some oyster shells (calcium carbonate) possessing multiple boreholes (Figure 5A–C). Thus, there are three functionally different inhabitant types, those occupying the surfaces of the shells (outer surface, crevices, boreholes, and burrows), those creating burrows in the consolidated sediments, and those that bore into the calcium carbonate shells of the oysters. We observed bivalve boring (Figure 5B) and assumed that curved burrows in the consolidated sediment were excavated by soft-bodied organisms, such as polychaetes.

In comparison, the *S. echinata* beds from the embayment were remarkably thinner and less complex (Figure 6A–C). These beds consisted mainly of a single layer of living oysters, with the occasional vertical stacking of individuals and a few crevices (Figure 6B). No boreholes nor polychaete burrows were observed. The bottom view of the oysterbed indicates remnants of barnacle shells, which have been overlaid by the oyster layer and have not yet been bioeroded (Figure 6C). Overall oysterbed habitat complexity and the formation of 3D structuring increased greatly from the *S. mordax* beds on natural rocky shores to *S. echinata* beds in the embayment to *S. echinata* beds on the ABS. The complexity of habitat structure of the ABS oysterbeds was further reflected by their greater fine-grain sediment accumulation (up to nearly 35 mL/100 cm^2) compared to the embayment shore (<7 mL/100 cm^2) (Figure S2).

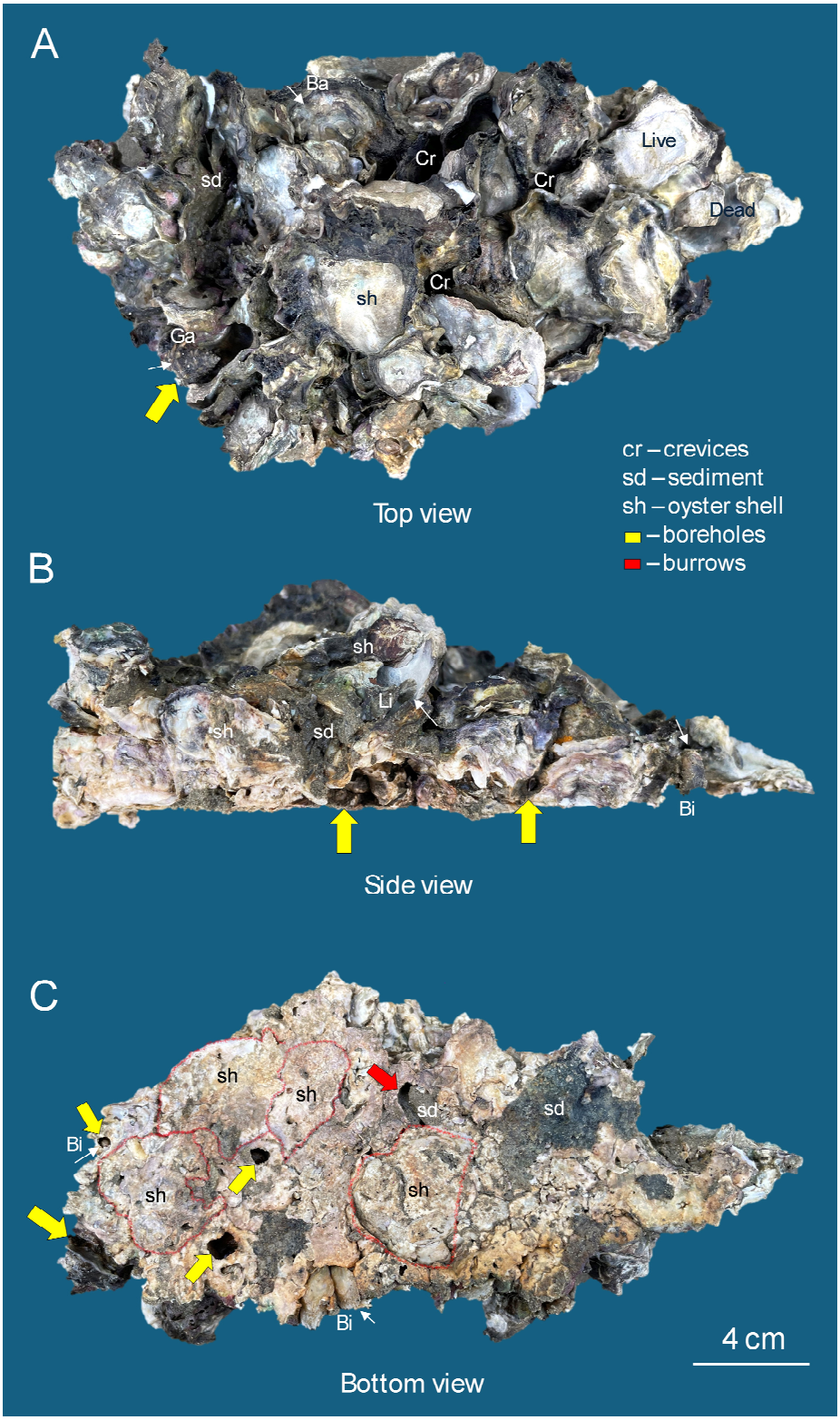


Figure 5. Section of *Saccostrea echinata* bed from an artificial breakwater viewed from (**A**) above, (**B**) side and (**C**) bottom. Successional settlement results in live (Live) and dead (Dead) oysters arranged vertically or horizontally within pile at the surface and middle layer. Crevices (Cr), boreholes (yellow arrows), and burrows (red arrow) can be observed within the pile and may be occupied by borers or nonborers. Fauna, such as bivalves (Bi), gastropod (Ga), barnacles (Ba), and limpets (Li), are indicated by white arrows. Bioeroded oyster shells (sh) and sediment (sd) are observed at the rocky substratum and become reconsolidated and compacted at the bottommost layer (red outlines).

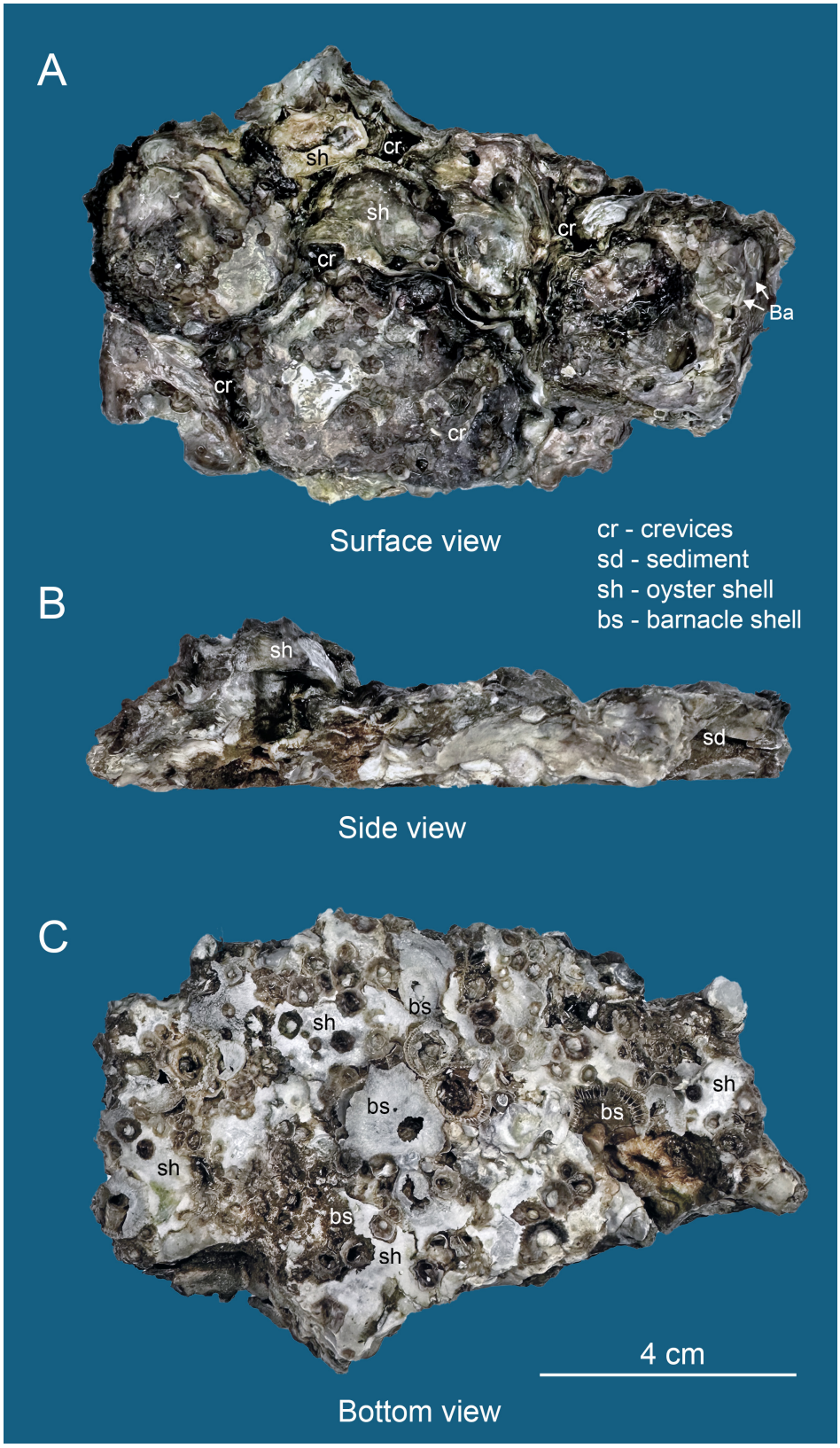


Figure 6. Section of *Saccostrea echinata* bed from the embayment viewed from (**A**) above, (**B**) side and (**C**) bottom. Live and dead oysters are arranged vertically or horizontally within the pile, which is thinner and less complex than that of the breakwater in Figure 5A,B. No boreholes are observed. Oyster and barnacle shells are intact at the rocky substratum and have yet to be bioeroded and reconsolidated at the bottommost layer (see Figure 5C). Live barnacles (Ba) indicated by white arrows.

3.2. Species Assemblage Comparisons Across the Shores

A total of 81 species were found to be associated with the oysterbeds (Table A1, Figures 7 and 8). In addition, 29 species, including displaced stragglers, taxa unresolved to family, or those occurring in the smaller size fraction, were collected in the samples but were not considered further (Table S1). Most of the species were mollusks (46.9%), then annelids (30.9%), and then, arthropods (12.3%), with low numbers of cnidarians and chordates (Figure 7A). The number of species associated with oysterbeds at the ABS (n = 77) was nearly six times that of the natural shore (NS; n = 13) and more than twice that of the embayment shore (ES; n = 32) (Table A1, Figure 7A).

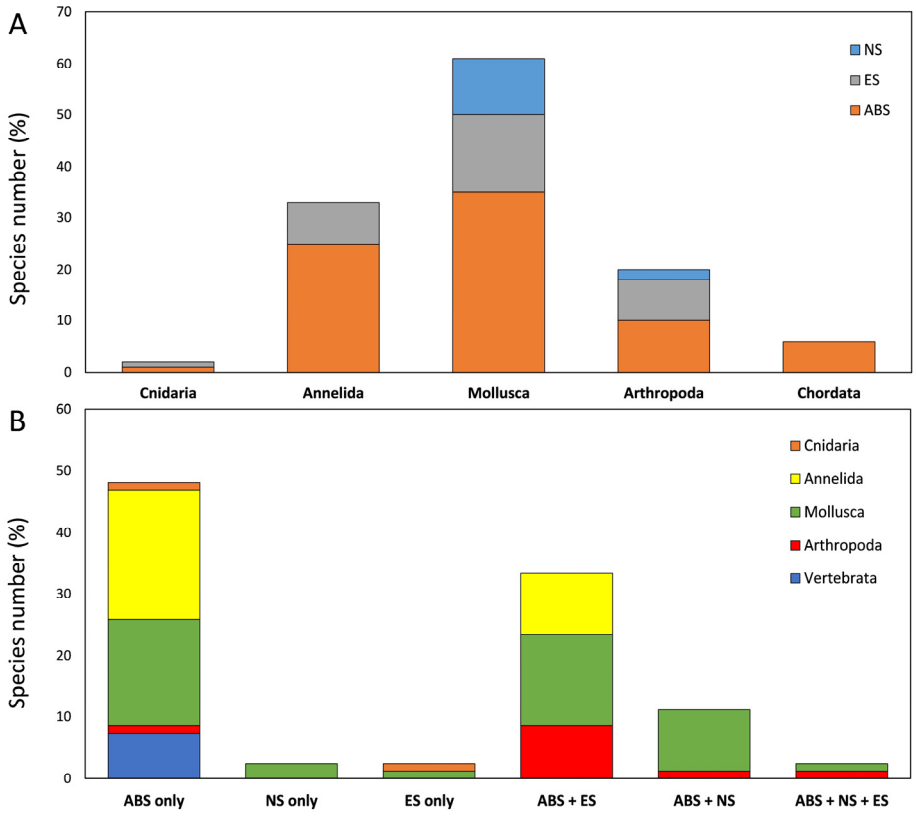


Figure 7. Species number associated with oysterbeds (**A**) grouped by phylum (**B**) at a combination of localities, ABS—breakwaters, NS—natural shore, and ES—embayment.

Importantly, 39 species (48.1%) were uniquely found in the ABS, two (2.5%) species were found to uniquely occur at each of the NS and ES, with the remaining 38 species (46.9%) occupying more than one habitat (Figure 7B).

The ABS uniquely supported six species of fishes, seventeen annelids (of which two are burrowers), six bivalves (of which three are borers), eight other mollusks, one crab, and one cnidarian (Table A1, Figure 8). Out of twelve bivalves found at the ABS, four were categorized as borers (*Leiosolenus malaccanus*, *Botula* cf *cinnamomea*, *Neotrapezium sublaevigatum*, and *Ptericola divergens*) (Figure 8). Though *N. sublaevigatum* was also found at the ES, its occurrence there was uncommon (n = 3, six transects), and all were juveniles (<1 cm). Three burrowing annelid worms were found at the ABS, *Lysidice* sp., *Eunice* sp., and *Phascolosoma scolops*; the latter also occurred at the ES. Only four species comprising mollusks and cnidarians from the master list (n = 81) were not found at the ABS, of which two (*Monodonta labio* and *Cellana testudinaria*) were unique to the NS and the remaining two (Actiniidae sp. 2 and *Indothais gradata*) unique to the ES. The chitons were only found at the ABS and the NS, while the cnidarians were only found on the ABS and the ES; although, species between both localities differ. The ABS and the ES also shared many common mollusks, annelids, and arthropods (33.3%).



Figure 8. A selection of species associated with artificial breakwater oysterbeds (stars indicate species unique to the artificial breakwaters). (1) *Leiosolenus malaccanus*, (2) *Neotrapezium sublaevigatum*, (3) *Botula* cf *cinnamomea*, (4) *Brachidontes crebristriatus*, (5) *Brachidontes variabilis*, (6) *Septifer excisus*, (7) *Septifer bilocularis*, (8) *Petricola divergens*, (9) *Irus macrophylla*, (10) *Isognomon nucleus*, (11) *Isognomon legumen*, (12) Actiniidae sp. 1, (13) *Cryptopilumnus changensis*, (14) *Heteropanope glabra*, (15) *Pachygrapsus minutus*, (16) *Metopograpsus frontalis*, (17) *Nanosesarma minutum*, (18) *Patelloida pygmaea*, (19) *Cellana radiata*, (20) *Montfortula* sp., (21) *Tenguella musiva*, (22) *Littoraria articulata*, (23) *Nerita chamaeleon*, (24) *Squamopleura miles*, (25) *Acanthochitona* sp. 1, (26) *Acanthochitona* sp. 2, (27) *Tetraclita kuroshioensis*, (28) *Balanus amphitrite*, (29) *Ibla cumingi*, (30) *Themiste lageniformis*, (31) *Antillesoma* sp., (32) *Phascolosoma scolops*, (33) *Eunice* sp., (34) *Lysidice* sp., (35) Hesionidae sp., (36) *Omobranchus obliquus*, (37) *Omobranchus elongatus*, (38) *Ecsenius trilineatus*, (39) *Laiphognatus multimaculatus*, (40) *Istiblennius dussumieri*, and (41) *Praealticus striatus*.

Statistical comparisons using PERMANOVA revealed that the species composition of the three shores differed significantly from one another (Pseudo-F = 19.251, p = 0.001; Table 1). Pairwise comparisons showed that all four sites significantly differed in species composition (p = 0.001), except between the two ABS, Tungku and Jerudong (p = 0.077; Table 1). The multivariate dispersions were mostly homogenous, except for the comparisons between ES and ABS (T) and ES and ABS (J) (F = 3.75, p = 0.056; Table S2). The average Jaccard similarity within groups varied between 64.1% (ES) and 41.6% (Jerudong ABS) (Table 1). The similarity in the species composition between the NS and ABS was low, varying between 6.7% and 8.9%, while the similarity between the NS and ES was low at 4.4% (Table 1). Thus, the dissimilarity between the NS and ABS, which explains the enhancement of β-diversity caused by breakwater construction along the sandy beaches, was ~91%.

Table 1. Test of variance between three shore types (NS—natural shore, ES—embayment shore, ABS—artificial breakwater shore, T—Pantai Tungku, J—Pantai Jerudong) using PERMANOVA.

PERMANOVA						
Source	**df**	**SS**	**MS**	**Pseudo-F**	***p* (Perm)**	**Unique Perms**
Error	2	54,177	27,088	19.251	0.001	999
Res	33	46,436	1407.1			
Total	35	1.0061×10^5				
Pairwise comparisons						
Groups	t	*p* (perm)	Unique perms			
NS, ES	5.0924	0.001	937			
NS, ABS (T)	4.752	0.001	992			
NS, ABS (J)	4.2747	0.001	995			
ES, ABS (T)	2.9745	0.001	936			
ES, ABS (J)	3.9939	0.001	942			
ABS (T), ABS (J)	1.2202	0.077	994			
Average similarity between/within groups						
	NS	ES	ABS (T)	ABS (J)		
NS	51.52					
ES	4.44	64.12				
ABS (T)	6.73	31.98	47.23			
ABS (J)	8.92	26.84	42.87	41.55		

Jaccard similarity index values are typically used to explain β-diversity in the case of species richness [11,12]. Notably, there was a 26.8% and 32.0% average similarity, respectively, in the comparisons between the ES and ABS (J) and ABS (T) sites (Table 1). These pattern differences are depicted in the nMDS (Figure 9). Species diversity and species richness (Brillouin and Margalev's indexes) were highest at the ABS of Tungku (H = 4.26, d = 16.42) and Jerudong (H = 4.11, d = 14.60) compared to the NS (H = 2.57, d = 4.68) and ES (H = 3.47, d = 8.95). All animals were of a body size range that was smaller or equal to the size of borer bivalves, with the exception of the fishes (Figure S3). Furthermore, some very common species to the oyster zones of both the ABS and the natural shore (*Monodonta labio*, *Capitulum mitella*, and *Clibanarius ransonii*) were missing from the samples studied, implying that they avoid *S. echinata* surfaces or only temporally interact with these.

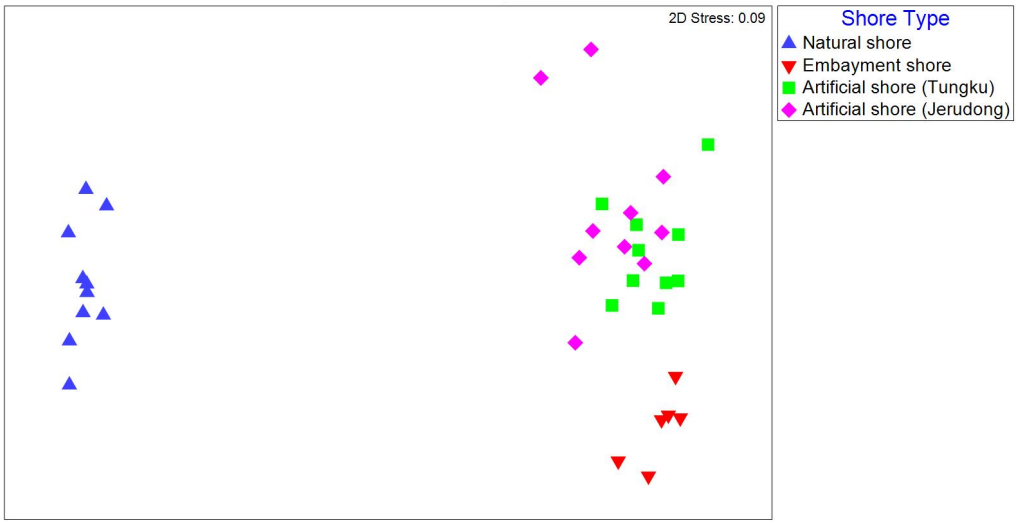


Figure 9. nMDS based on presence/absence data of species associated with oysterbeds from the three shore types.

4. Discussion

The present study reveals that the building of artificial breakwaters to protect coastal erosion along an extended sandy beach produces the unintentional beneficial effect of enhancing rocky shore β-diversity. We show dramatic enhancement of the macrozoobenthic species diversity in the oysterbeds colonizing artificial breakwaters. Our data support our hypothesis that mechanisms of diversity enhancement operate over several spatial and temporal scales (Figure 1). This enhancement specifically derives from sequential, time-related, cascading events that (1) create sheltered low-energy shore surfaces, (2) encourage the colonization of novel habitat-forming oysters (*Saccostrea echinata*), which (3) facilitate further recruitment and the colonization of novel species, including habitat-forming boring bivalves or burrowing polychaetes. These, in turn, (4) promote further habitat complexity and the recruitment of species to vacated boreholes. The habitat complexity can be spatially contextualized as a three-tiered ecological engineering system involving (1) the breakwater construction (operating at arbitrary spatial scales of 100 m), (2) reef-forming oysters (at a 10 m scale), and (3) boring bivalves or burrowing polychaetes (at a <10 cm scale) (Figure 1).

Rocky shores are typically acutely angled to natural coastlines, and the prevailing oceanic wave forces and current systems, such that they limit larval settlement to species adapted to these conditions [41–44]. *Saccostrea mordax* is the only oyster species that commonly colonizes the natural intertidal zone of the open sandy shore coastline of Brunei and occurs as solitary individuals or single-layered beds varying negatively in density to wave exposure (Figures 3 and 4). The attenuation of hydrodynamic forces on the sheltered inner surfaces of the artificial breakwaters facilitates the larval settlement of ecologically novel (to the open shore) species, and results in the robust colonization of the typically estuarine oyster, *Saccostrea echinata* (Figures 3 and 4) [45–47]. This species outcompetes *S. mordax* on the inner breakwater surfaces, such that *S. mordax* occupies a vertically higher shore position where their distributions overlap. The colonization of bed-forming *S. echinata* at the ABS study sites over 30 years has resulted in a complex three-dimensional structure. This structural complexity derives from both horizontal oyster stacking and the random angular arrangement of the oysters within the stacks [3,7,8,25,48]. The combination of hydrodynamically low-energy surfaces and the new *S. echinata* oysterbed habitat drives the larval settlement and the colonization of a variety of novel macrozoobenthic species. Sequential events of colonization and habitat complexity creation have enhanced species richness on the artificial breakwaters (n = 77 species) compared to the natural rocky (NS) shore (n = 13 species). These breakwaters share low similarity in species composition with the NS (Jaccard similarity = 6.7–8.9%; Table 1) and add 39 unique species to the open sandy

shore coastline of Brunei (Table A1). Despite the proximity of the ABS on either side of the NS along the SCS coastline, and their distant location from the embayment site (ES, Figure 2) at Brunei Bay, ABS species compositions were more similar to that of the ES.

The similarity in *S. echinata* oysterbed species composition between the ABS and the ES (Jaccard similarity = 26.8–32.0%; Table 1) implies the significant recruitment to ABS of calmer water estuarine species. Species composition differences between the ABS and ES sites is probably partly explained by their temporal differences in successional development and habitat complexity (Figures 5 and 6), considering that the former is 30 years old, and the latter is only 6 years old. Differences could also relate to different salinity tolerances of the species forming the assemblages, given the instability of the embayment salinity [39]. Several brachyuran crabs, polychaetes, and cnidarians (33.3%) were common to both the ABS and the embayment shore (Table A1, Figure 7). However, other than recruitment from sheltered embayment systems, the possibility exists for novel ABS species to be recruited from other nearby reef systems, such as coral reefs [35,49]. This is supported by the occurrence in the ABS oysterbeds of six fish species, five bivalve species and five annelid species, which are commonly associated with coral reefs. Differences in species composition between the ABS sites (Jaccard similarity = 42.9%; Table 1) seemingly relate to Tungku ABS being a deeper water structure that uniquely supports a coral reef system. Three of the fish species only occurred at the Tungku ABS (Table A1), and some of the bivalve borers are also known to bore into the hard calcium carbonate skeletons of corals [32,35,49–51].

Much of the novel recruitment to and colonization of the ABS oysterbeds occurs in response to habitat-facilitating boring and burrowing species, not commonly found in the embayment oysterbeds. This adds to the habitat facilitated by the crevices formed by the irregular stacking of oysters and the deposition and accumulation of sediment in the stack, which, in both loose and agglutinated forms, recruit burrowing polychaetes [3,7,52–56]. In effect, the borers and burrower function to enhance habitat complexity at a fine spatial scale (<10 cm). This successional habitat modification ultimately attracts novel species that inhabit vacated boreholes and burrows [9,57,58]. With respect to the boring bivalves, three species uniquely occurred at the ABS (*L. malaccanus*, *B.* cf *cinnamomea*, and *P. divergens*); whereas, only juveniles of *N. sublaevigatum* were rarely found at the ES. It should be noted, nonetheless, that the bivalve *B.* cf *cinnamomea* has been found to bore into the shells of *Saccostrea spathulata* (Figure S4) at a nearby rocky outcrop (Bedukang), suggesting that the full complement of borer species might not have been reached in the less successionally developed ES oysterbeds. Whether the polychaetes excavate burrows or whether they occupy existing cervices is unclear. Irregular burrow holes within agglutinated sediments occupied by polychaetes in the ABS beds (Figure 5C) indeed suggest that these worms can modify the habitat [59,60]. *Eunice* sp. and *Lysidice* sp. observed in the ABS beds (Table A1) are suggested to be hard substrate burrowers and have serrated jaws that functionally support scraping and burrowing activities [53–56]. *Perinereis cultrifera* and *Leocrates* sp. (Tables A1 and S1) have been reported as coral burrowers [53–55]; however, their jaw structure is inconsistent with burrowing activity [56]. *Phyllodoce* sp. (Table A1) has been observed to produce viscous material when disturbed, which facilitates the gathering and adherence of sediment around it as camouflage and to line its crevices; this possibly contributes to habitat modification through biogenic agglutination. A body size structure analysis suggested that all taxa excluding the fishes could inhabit the small-sized boreholes and burrows (Figure S3). The fishes preferred vacant oysters rather than boreholes and crevices.

In summary, breakwaters can function to increase hard benthic species diversities. The taxonomic and functional complexity of the breakwater ecosystem is time dependent, relating to two significant cascading colonization events that modify habitat complexity: the colonization of the breakwaters by oysters followed by the colonization of oysters by boring and burrowing species. Consequently, the artificial breakwater shores (ABS) were found to support nearly six times the oysterbed species richness of the natural rocky shore (NS). Many of the novel species in the breakwater habitats originated from nearby coral

and estuarine/embayment ecosystems. This pattern of events implies that breakwaters can serve as steppingstones for species and increase interconnectivity between ecosystems and coastal regions, which is especially important along extended linear soft benthic coastlines (sandy beaches and mudflats) common to many tropical regions. The extent to which these observations generalize to subtropical or more temperate ecosystems is currently unknown. Notably, however, many of the inhabitant species (bivalves, polychaetes, and fishes) of the ABS derive from tropical coral ecosystems, suggesting that the circumstances described here may be unique to subtropical or tropical shores where coral ecosystems are found to occur.

5. Conclusions

This study demonstrates the effects of two fundamental processes in enhancing species diversity when artificial marine structures are built: (1) improved larval settlement and, hence, the colonization of novel species due to lowered near-substratum hydrodynamics and (2) the creation of increased habitat complexity. With reference to living seawall programs, ideal diversity-enhancing circumstances could be produced through the orientation of the marine structures (in relation to the coastline), in addition to the careful design of components, surfaces, and materials used in their construction. Whereas these often present practical and financial constraints, especially the manufacturing of fine-scaled habitat complexity, this constraint can be overcome through biotic action and allowing nature to take its course, though this is a severely time-constrained option (decades). We believe that the findings of this study will be valuable to various stakeholders, including scientists, ecologists, conservationists, and managers of marine coastal systems.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16120742/s1, Figure S1. (A) Pulau Muara Besar bridge at Muara within Brunei Bay. (B) Dense and single-layered *S. echinata* beds at the embayment. (C) A section of the embayment walls encrusted with *S. echinata* beds. (D) The embayment. Figure S2. Sediment accumulation in *S. echinata* oyster beds between the artificial breakwaters at Pantai Tungku and Pantai Jerudong and the embayment at Pulau Muara Besar of Brunei Bay. Figure S3. The frequency distribution categorized by body sizes between the boring bivalves and other crevice occupants in the artificial breakwater oysterbeds. Figure S4. *Saccostrea spathulata* from inner Brunei Bay near the embayment infested with *Botula* cf *cinnamomea* (red arrows). Table S1. List of other fauna found associated with oysterbeds, oyster patches, or oyster encrusted rocks. Table S2: Test of homogeneity of multivariate dispersions using PERMDISP.

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Conflicts of Interest: All authors declare no conflicts of interest.

Appendix A

Table A1. List of fauna (identified up to family) associated with oysterbeds and commonness at each locality. Pink, white, light grey, and dark grey cells, respectively, indicate rare species (n = 1 in overall sampling), uncommon species occasionally present in some transects (n < 5), common species present in all transects (n < 5), and very common species abundant in all transects (n > 5).

No.	Species	Presence (/)			
		Jerudong ABS	Tungku ABS	Empire NS	Brunei Bay ES
	Phylum Cnidaria				
1	Actiniidae sp. 1	/	/		
2	Actiniidae sp. 2				/
	Phylum Annelida				
3	*Antillesoma* sp.		/		
4	*Ceratonereis perkinsi*	/	/		
5	*Eunice* sp.		/		
6	*Lepidonotus* sp.	/	/		/
7	*Lysidice* sp.		/		
8	*Neanthes* sp.	/	/		
9	*Odontosyllis gravelyi*		/		
10	*Perenereis helleri*	/	/		
11	*Perinereis cultrifera*		/		
12	*Perinereis singaporiensis*		/		
13	*Perinereis* sp.	/	/		
14	*Perinereis vancaurica*	/	/		
15	*Phascolosoma* cf *agassizii*	/			
16	*Phascolosoma* cf *nigrescens*		/		
17	*Phascolosoma nigrescens*		/		
18	*Phascolosoma scolops*	/	/		/
19	*Phyllodoce* sp.	/	/		/
20	Phyllodocidae sp.		/		
21	*Pseudonereis trimaculata*	/	/		
22	Serpulidae sp.	/	/		/
23	Syllinae sp. 1	/	/		/
24	Syllinae sp. 2	/	/		/
25	Syllinae sp. 3	/	/		/
26	*Syllis gracilis*	/	/		/
27	*Themiste lageniformis*	/	/		
	Phylum Mollusca: Class Polyplacophora				
28	*Acanthochitona* sp. 1	/	/		
29	*Acanthochitona* sp. 2		/		
30	*Squamopleura miles*	/	/	/	
	Phylum Mollusca: Class Bivalvia				
31	*Botula* cf *cinnamomea*	/	/		
32	*Brachidontes crebristriatus*		/		/
33	*Brachidontes variabilis*	/	/		/
34	*Irus macrophylla*	/	/		
35	*Isognomon legumen*	/	/		/
36	*Isognomon nucleus*	/	/		/
37	*Leiosolenus malaccanus*	/	/		
38	*Neotrapezium sublaevigatum*	/	/		/

Table A1. *Cont.*

No.	Species	Presence (/)			
		Jerudong ABS	**Tungku ABS**	**Empire NS**	**Brunei Bay ES**
39	*Petricola divergens*	/	/		
40	*Septifer bilocularis*	/	/		
41	*Septifer excisus*		/		
42	*Vignadula mangle*				/
	Phylum Mollusca: Class Gastropoda				
43	*Boonea* sp.		/		
44	*Cellana radiata*	/	/		/
45	*Cellana testudinaria*			/	
46	*Clypeomorus batillariaeformis*	/			
47	*Diala semistriata*	/	/		/
48	*Echinolittorina vidua*		/	/	/
49	*Fossarus trochlearis*	/	/		/
50	*Indothais gradata*				/
51	*Littoraria articulata*		/		/
52	*Littoraria intermedia*		/		
53	*Monodonta labio*			/	
54	*Montfortula* sp.	/	/		
55	*Nerita albicilla*	/	/		
56	*Nerita chamaeleon*		/	/	
57	*Nerita histrio*		/		
58	*Patelloida pygmaea*	/	/		/
59	*Patelloida saccharina*	/	/	/	/
60	*Peasiella fasciata*	/	/		/
61	*Peasiella lutulenta*		/		/
62	*Planaxis sulcatus*		/	/	
63	*Semirinicula muricoides*	/		/	
64	*Siphonaria guamensis*	/	/		
65	*Tenguella musiva*	/	/	/	
	Phylum Arthropoda: Class Brachyura				
66	*Cryptopilumnus changensis*	/	/		
67	*Heteropanope glabra*	/	/		/
68	*Metopograpsus frontalis*	/	/		/
69	*Nanosesarma minutum*	/	/		/
70	*Pachygrapsus minutus*	/	/		/
	Phylum Arthropoda: Class Cirripedia				
71	*Balanus amphitrite*		/		/
72	*Chthamalus malayensis*		/	/	/
73	*Caudoeuraphia caudata*		/		/
74	*Ibla cumingi*	/	/		/
75	*Tetraclita kuroshioensis*		/	/	
	Phylum Chordata: Class Osteichthyes				
76	*Ecsenius trilineatus*		/		
77	*Istiblennius dussumieri*		/		
78	*Laiphognathus multimaculatus*	/	/		
79	*Omobranchus obliquus*		/		
80	*Omobranchus elongatus*	/	/		
81	*Praealticus striatus*	/			
Total species count per site		**61**	**71**	**13**	**32**

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