

High-resolution mapping and terrain classification of *Halimeda* bioherms in the northern Great Barrier Reef

Zsanett Szilagyi^{a,c,*}, Luke Nothdurft^a, Stephanie Duce^b, Jody M. Webster^c, Mardi McNeil^{d,a}, Robin J. Beaman^e, Juan Carlos Braga^f, Trevor Graham^g, Maria Byrne^h, Amy Nauⁱ, Christopher Berry^j, Victorien Paumard^j, Jeffrey Shragge^k, Catherine Kim^a, Helen Bostock^g

^a School of Earth and Atmospheric Sciences, Queensland University of Technology, Brisbane, QLD, 4000, Australia

^b College of Science and Engineering, James Cook University, Bebegu Yumba Campus, Townsville, QLD 4811, Australia

^c Geocoastal Research Group, School of Geosciences, The University of Sydney, Sydney, NSW 2006, Australia

^d Geoscience Australia, Canberra, ACT, 2601, Australia

^e College of Science and Engineering, James Cook University, Cairns, QLD 4870, Australia

^f Department of Stratigraphy and Palaeontology, University of Granada, Granada, 18071, Spain

^g School of the Environment, University of Queensland, Brisbane, QLD 4072, Australia

^h School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW 2006, Australia

ⁱ Commonwealth Scientific and Industrial Research Organisation (CSIRO), Hobart, TAS 7000, Australia

^j Centre for Energy Geoscience, University of Western Australia, Perth, WA 6009, Australia

^k Department of Geophysics, Colorado School of Mines, Golden, CO 80401, USA

A B S T R A C T

Halimeda is a prolific marine calcifying green alga that forms vast green meadows at mesophotic water depths (20–50 m) on tropical continental shelves. Over time, their carbonate skeletal remains accumulate and build enigmatic interconnected seafloor structures known as bioherms. This study presents the first sub-metre resolution digital elevation model for three sites in the northern Great Barrier Reef, significantly advancing our understanding of their geomorphology since *Halimeda* bioherms were described in the 1970s. These high-resolution data reveal complex bioherm features, including fine-scale characteristics not previously observed. Geomorphometric analysis was used to quantify surface characteristics within, and between the three sites, and produce the first benthic terrain classification identifying benthic structures.

The analysis reveals extensive positive-relief crests encircling hollows, higher prevalence of pinnacles within the hollows, and intricate slope asymmetries suggestive of sediment transport processes. Large internal depressions (150 to 700 m diameter) exhibit weak east-west orientation and increasing irregularity and elongation with size, potentially reflecting the influence of water depth and hydrodynamic conditions on bioherm accumulation over time. Six different bioherm-specific benthic structures were identified including plain, peak or pinnacle, crest, slope, gentle slope, and hollow with a consistent northward shallowing trend across the three sites (15°–13° S latitude). Their relative area coverage mimics the mound-like bioherm structure, while terrain metrics underscore their structural complexity.

These findings reveal that *Halimeda* bioherms are more morphologically complex than previously described and offer new insight into their formation processes. The terrain classification provides a valuable foundation for future benthic habitat mapping, paleo-environmental analysis and management of these important ecosystems.

1. Introduction

Compared with shallow water coral reef systems (0–10 m depth), deeper inter-reef and shelf environments are relatively understudied (Hopley et al., 2007). Significant knowledge gaps persist in our understanding of the geomorphology, physicochemical conditions, ecology, and biodiversity status of many inter-reef habitats. One such underexplored inter-reef habitat is the *Halimeda* bioherms in Australia's northern

Great Barrier Reef (GBR), located at depths of 25–50 m (Davies and Marshall, 1985; Marshall and Davies, 1988; Wolanski et al., 1988; McNeil et al., 2016; McNeil et al., 2021a; McNeil et al., 2021b; McNeil et al., 2022). These bioherms consist of *Halimeda* meadows and mound deposits (Davies and Marshall, 1985; Orme, 1985), which support higher average species richness and biodiversity than neighbouring inter-reef areas (McNeil et al., 2021a).

Halimeda is an important pan-tropical calcareous green macroalgae

* Corresponding author at: School of Earth and Atmospheric Sciences, Queensland University of Technology, Brisbane, QLD 4000, Australia.

E-mail address: zsannett.szilagyi@hdr.qut.edu.au (Z. Szilagyi).

<https://doi.org/10.1016/j.geomorph.2026.110243>

Received 24 October 2025; Received in revised form 18 February 2026; Accepted 19 February 2026

Available online 23 February 2026

0169-555X/© 2026 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

and a major contributor to coral reef and shelf sediments and found in large volumes along the entire GBR (Hopley et al., 2007; Mathews et al., 2007; Rees et al., 2007; Whiteway et al., 2013). In 2016, McNeil et al., published LiDAR bathymetry mapping that highlighted the distinct *Halimeda* bioherms are more extensive features of the seafloor than previously thought. This habitat covers ~26% of the northern shelf of the GBR Marine Park, exceeding >6000 km² (Orme and Salama, 1988; McNeil et al., 2016). Due to their high productivity and rapid calcification, these bioherms are likely to have a significant influence on the shallow marine carbon cycle and make them potential blue and inorganic carbon sinks (Drew, 1983; Hill et al., 2015). Globally *Halimeda* bioherms are estimated to have accumulated a total of ca. 590 Gt net CaCO₃ on shelves throughout the Holocene, including 55 Gt in the northern GBR (Hinestrosa et al., 2022; McNeil et al., 2021b).

Early studies of the *Halimeda* bioherms off Lizard Island (Orme, 1985; Orme et al., 1978a; Orme and Salama, 1988), Cooktown (Davies and Marshall, 1985; Marshall and Davies, 1988), and Lloyd Bay (Skjold, 1988), found that bioherms were up to ~20 m thick and suggested that they formed connected linear ridges and flat-topped mounds in ~20–40 m water depth (Fig. 1a). It was hypothesized that this morphology was formed by the merging of individual lenticular mounds (Marshall and Davies, 1988; Searle and Flood, 1988), surface flora stabilization by trapping and baffling mechanisms (Marshall and Davies, 1988), and/or hydrodynamic processes such as back-reef eddies and seasonal tidal jet upwelling, bringing nutrients to the bioherms (Marshall and Davies, 1988; Wolanski et al., 1988; McNeil et al., 2021c).

The concept of bioherms forming connected linear ridges persisted until 2016 (summarized in Mathews et al., 2007) until the application of new technologies, such as airborne LiDAR bathymetry surveys (Beaman, 2010), revealed that bioherm morphology and seafloor characteristics were more complex (McNeil et al., 2016) (Fig. 1b). Analysis of 3D bathymetric datasets showed honeycomb-like surfaces with circular ring shapes, each up to ~300 m across, with three different morphotypes defined as honeycomb-like (reticulate), smooth circular hollow-centred ring-like (annulate), and sinuous, wave-like (undulate) (McNeil et al., 2016) (Fig. 2).

McNeil et al. (2021b) conducted a preliminary quantitative morphometric analysis on the available airborne LiDAR and multibeam echosounder bathymetry dataset with 30 m spatial resolution (Beaman, 2010, 2017) over *Halimeda* bioherms at Lloyd Bay and Lizard Island. Their study characterised three morphotypes:

- Annulate morphotype: Characterised by high positive reliefs with uniform thickness, smooth ring crests, and a bi-modal slope pattern, referred to as the double ‘halo’ effect, where the inner slopes were three times steeper than the outer slopes.
- Reticulate morphotype: Exhibits more complex surfaces with steeper topographic relief, sharper crests, and variable thickness, but lacked the double slope expression.
- Undulate morphotype: Displays minimal topographic relief and a smooth to wavy surface, resembling the adjacent shelf terrain.

Aspect morphometry analysis revealed that there is no preferred azimuthal orientation in 3D space for any of the morphotypes (McNeil et al., 2021b). In terms of distribution, reticulate morphotypes dominate the eastern side (seaward) of the bioherm complex, while the annulate types are common on the western (inshore) side. Undulate morphotypes are organised between and around the other two. The bioherm boundary is sharply defined, marked by a bathymetric break on the eastern margin. McNeil et al. (2021b) proposed that this cross-shelf variation in morphotype distribution reflects different environmental forcing such as storm wave exposure and proximity to shelf edge barrier reefs that influence growth patterns and morphological development.

The availability of extensive bathymetry coverage at 30 m resolution, together with localized submersible observations, has allowed previous studies to suggest high complexity of benthic structures,

ecology and sediments in the bioherms. However, the lack of sub-meter scale analyses has limited the ability to systematically identify and quantitatively characterise their unique morphology. In this study, we examine the *Halimeda* bioherms in unprecedented detail using the first sub-meter resolution multibeam bathymetry data acquired over these features (Fig. 1c). The data were collected at three targeted sites during Project HALO (IN2022_V07) on the Research Vessel Investigator (Webster et al., 2023). Using these newly acquired high-resolution bathymetric datasets we aim to address the following question: (1) How can *Halimeda* bioherms be identified and differentiated from other geomorphological seafloor features? and (2) What insights can their morphometrics possibly provide into their formation and evolution?.

To achieve this, we present:

- 1) A general geomorphometric analysis of the three targeted sites, and comparison against previously defined annulate, reticulate, and undulate *Halimeda* morphotypes;
- 2) Identification, mapping and quantification of the morphometrics of internal depressions within *Halimeda* bioherms;
- 3) Characterisation of the distinct benthic structures that form *Halimeda* bioherms using novel benthic terrain classification;
- 4) Comparison of the benthic structures morphometrics within and between study sites; and
- 5) Evaluation of morphological similarities and differences between bioherms and other geomorphological seafloor features.

Understanding the surface characteristics provides insights into bioherm formation and evolution and is essential for future studies to remotely identify *Halimeda* bioherms in other regions. Furthermore, benthic terrain classification serves as a powerful tool for capturing the complexity of these features. Precisely targeted surface grabs, vibrocores, and sub-bottom profiles were also collected to support future ground truthing efforts (Webster et al., 2023), however, their presentation and analysis falls beyond the scope of the present study.

2. Materials and methods

2.1. Study sites

The three sites investigated are located 35–50 km from the coast, separated by approximately 1° of latitude on the northern GBR shelf (Fig. 3). For each site targeted a cross-shelf area covering the different bioherm morphotypes defined by McNeil et al. (2016).

- **Site 1** (145.7398 E, 15.4845 S) is located ~50 km offshore of Cooktown stretching in an east – west direction (Fig. 3 b).
- **Site 2** (145.5581 E, 14.6404 S) is on the eastern side of Lizard Island, ~40 km offshore, having a northeast – southwest orientation (Fig. 3 c).
- **Site 3** (143.8693 E, 13.2111 S) is the furthest north, ~ 35 km offshore, east of Night Island and orientated in an east-northeast – west-southwest direction (Fig. 3 d).

All three sites are situated in the lee of elongated shelf edge barrier reefs and enclosed by reef passages roughly on their north and south side.

Site 1 is sheltered by Ribbon Reef No. 3 at the shelf edge on the east and surrounded by drop-shaped crescentic reefs (Hopley et al., 2007; Sansoleimani et al., 2022) on the west (Fig. 3 b). To the north, there is a reef passage that separates Ribbon Reef No. 3 and 4. Site 2 is enclosed by Yonge Reef at the shelf edge and Lizard Island on the southwest and sits between two reef passages (Fig. 3 c). Site 3 is located adjacent to Tjijou Reef, which is more than three times longer than the individual barrier reefs at the other sites, and surrounded to the west-southwest by sub-merged shoal reefs (Hopley et al., 2007; Sansoleimani et al., 2022).

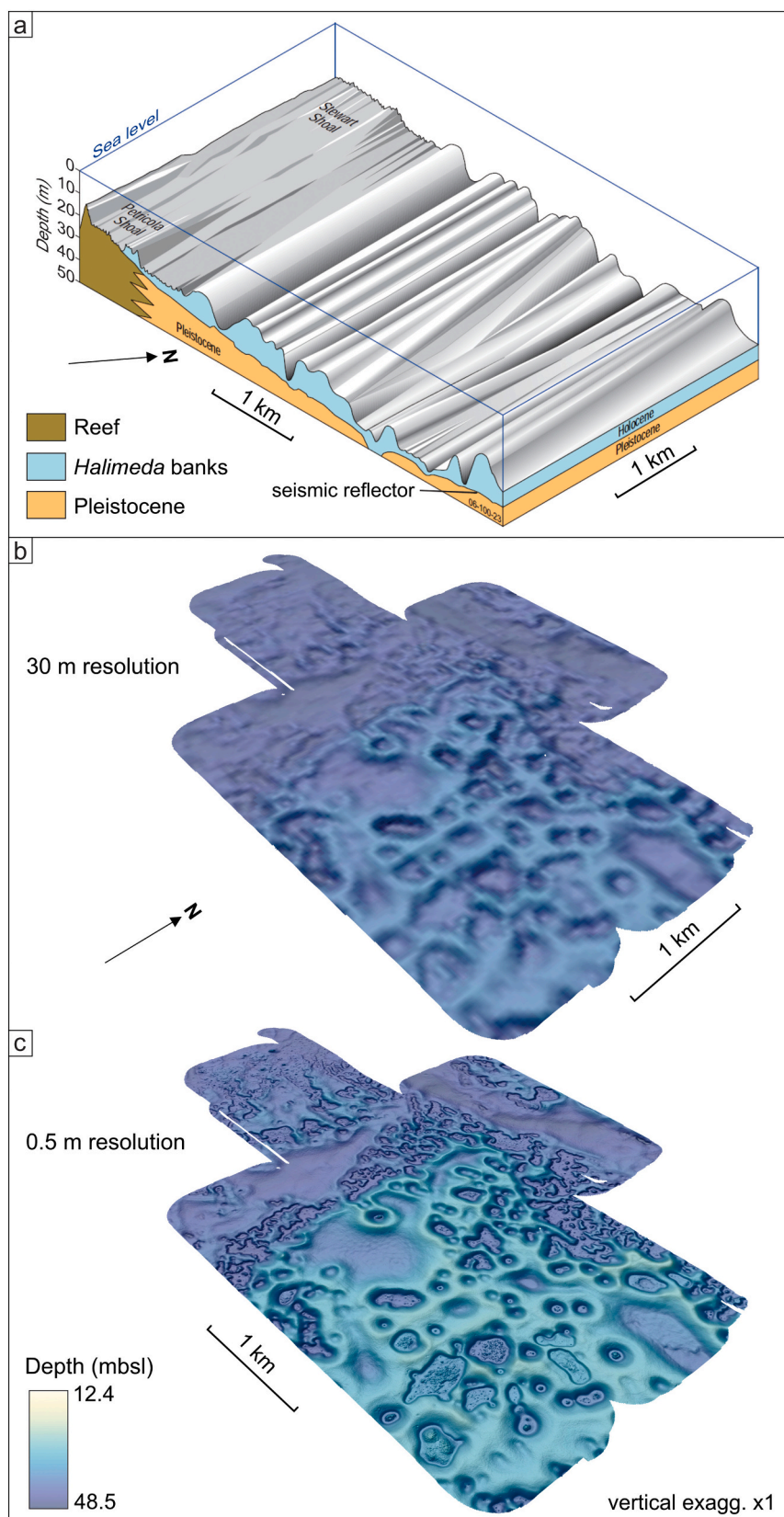


Fig. 1. *Halimeda* bioherm morphology revealed through technology advancement. a) Schematic interpretation of bioherm morphology forming connected linear ridges based on interpolation of parallel sub-bottom profile transects (adapted from Mathews et al., 2007). b) Oblique 3D view of Digital Elevation Model for Site 1 using the compiled data at 30 m resolution (McNeil et al., 2016) and c) the newly acquired 0.5 m resolution multibeam echosounder bathymetric dataset (this study). Both b) and c) illustrate actual complexity of bioherm morphology, with sub-meter resolution multibeam bathymetry data (c) revealing more intricate details.

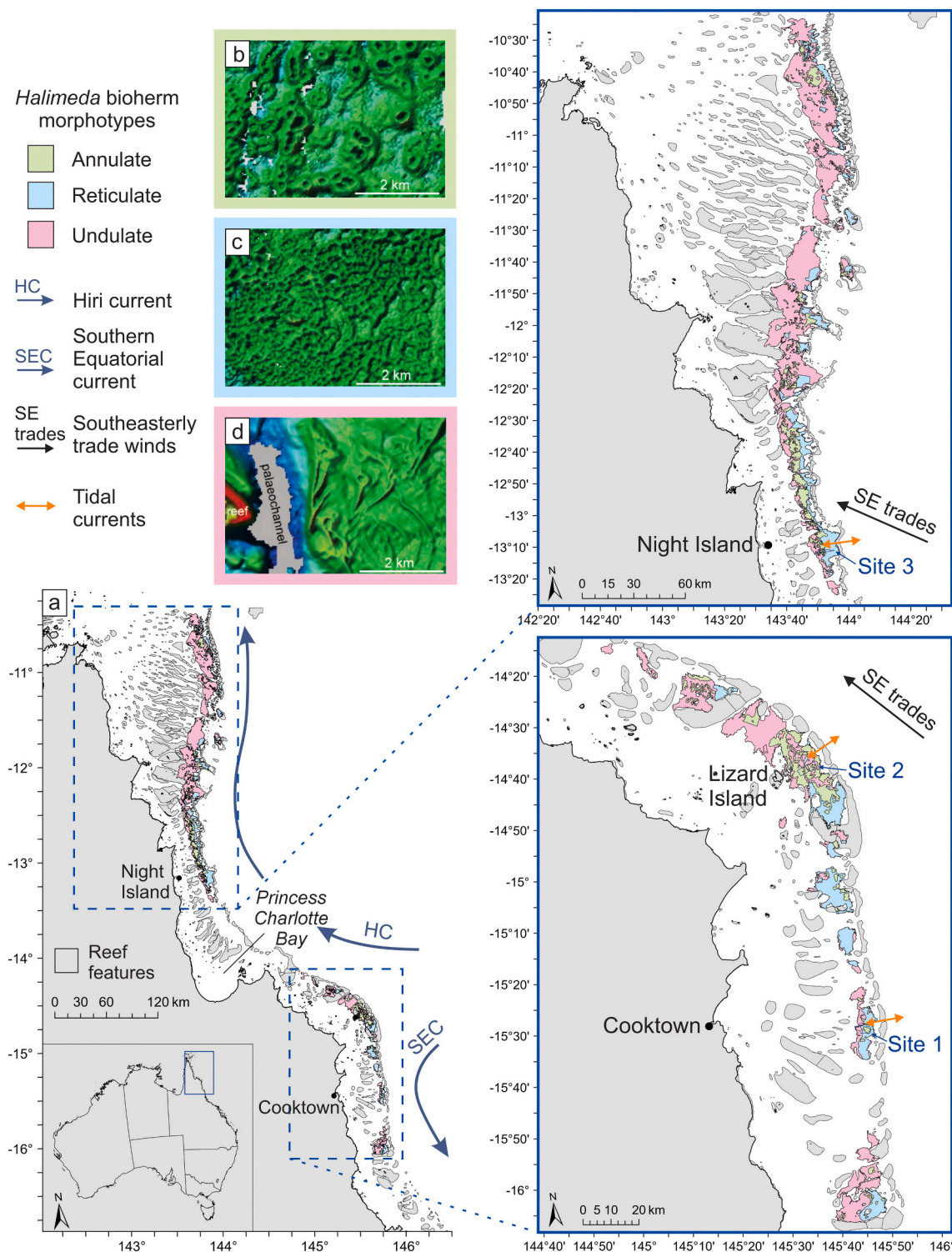


Fig. 2. Map of the northern Great Barrier Reef showing *Halimeda* bioherm morphotypes distribution (modified after McNeil et al., 2016). a) Bioherm morphotypes distribution with zoom-in insets north and south of Princess Charlotte Bay. Local oceanographic drivers such as offshore currents (modified after Sun et al., 2024), southeasterly trade winds (modified after Gallop et al., 2014), and tidal currents (modified after Wolanski et al., 1988; Wolanski et al., 2024) also displayed with blue, black and orange arrows respectively. b) bathymetric model showing the reticulate morphotype characterised by honeycomb-like interconnected ridges and crests. c) Annulate morphotype displaying the hollow-centred, circular ring-like structures. d) Undulate morphotype representing the smooth, wave-like form. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Bathymetric data

Bathymetric data were systematically collected across the three sites using a dual-head Kongsberg EM2040C multibeam echosounder,

mapping over 500 linear kilometres (Webster et al., 2023). The echosounder operated at a 300 kHz central frequency, with positioning and motion correction supported by a Seapath 330+ and MRU 5+. Depths were corrected to Mean Sea Level (MSL) by applying predicted

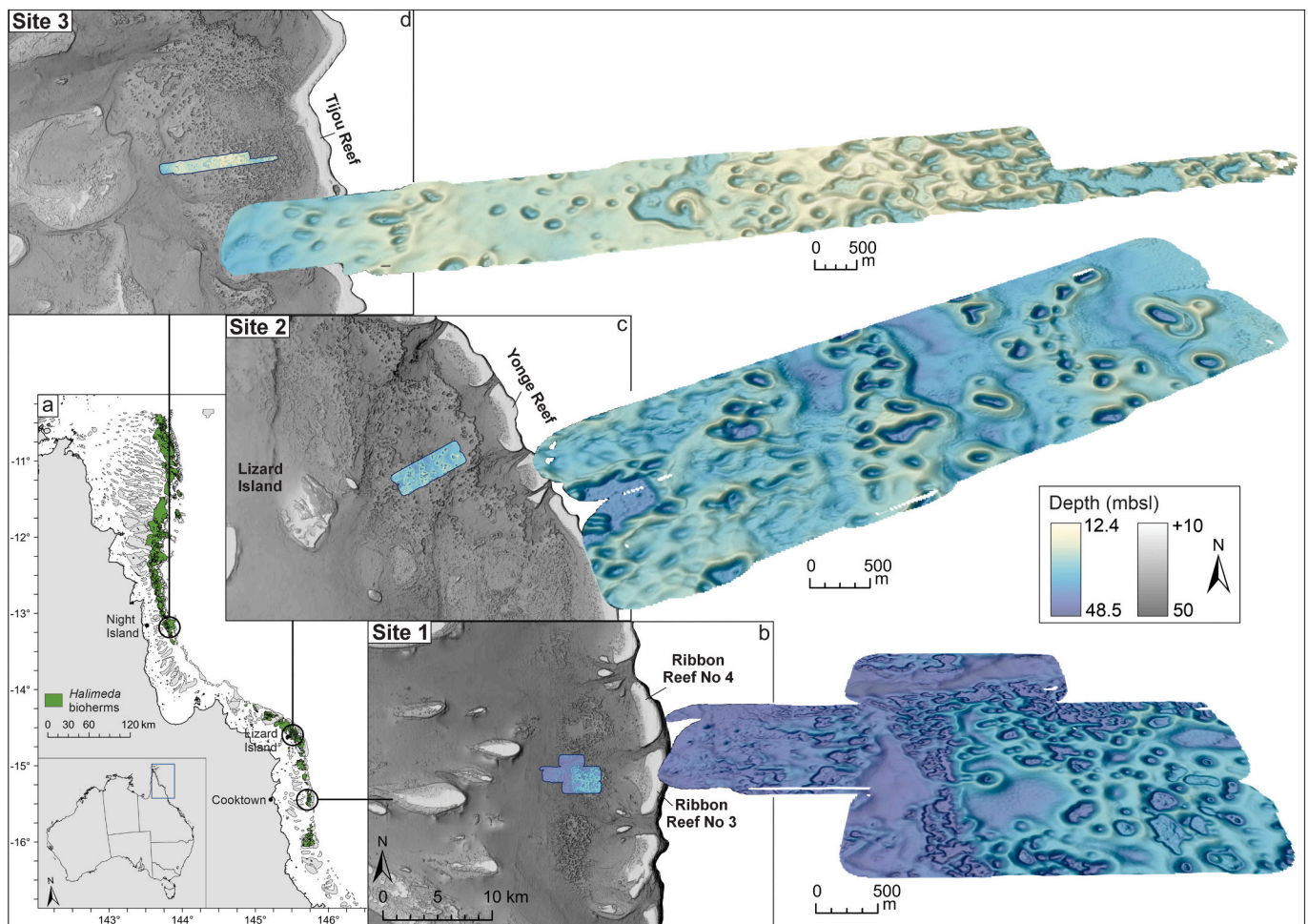


Fig. 3. a) Inter-reef *Halimeda* bioherm coverage over the northern Great Barrier Reef (GBR) and the three visited sites during the HALO voyage: b) Site 1 c) Site 2 and d) Site 3. Each maps display the position of the sites relative to the shelf margin using the 30 m resolution (grey) (Beaman, 2017) and on the right 0.5 m resolution (blue – yellow multipart) bathymetric datasets acquired during this study. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

tides using the AusTides 2022 package for each of the closest tide stations.

Each site has a dataset consisting of a digital elevation model (DEM) with horizontal dimensions of approximately 5.5 km × 3.5 km (Site 1), 6 km × 2 km (Site 2) and 10 km × 1 km (Site 3), with a spatial resolution of 0.5 m. These DEMs were converted to Esri raster formats for further analysis, using the Universal Transverse Mercator (UTM) projected co-ordinate system zone 55S for Sites 1 and 2, and 54S for Site 3.

2.3. Drop camera imaging

Targeted high-resolution imagery of the seafloor was collected across the three sites using a Deep Towed Camera system. The submersible camera platform included a Canon 1DX stills camera fitted with a Zeiss Distagon 18 mm f3.5 lens set at 45° and a Canon C300 high-definition video camera with a Canon EFS 10-18 mm f4.5–5.6 lens set at 45° (Sherlock et al., 2016; Carroll et al., 2020). A pair Laserex 10 mW red lasers spaced 10 cm apart provided a reference scale for image analysis (Sherlock et al., 2016; Carroll et al., 2020).

The camera system was deployed in a vertical, down-facing, drop camera mode and lowered periodically in vertical dips in an ~East-West transect targeting high and low relief features identified on the preliminary DEM. At each drop, continuous high-resolution video (1920 × 1080 at 59.94 frames/s) and still imagery at 2 to 10 s intervals were captured. Images were acquired at a horizontal and vertical resolution of

350 dpi.

2.4. General geomorphometric analysis of *Halimeda* bioherm features

Gridded bathymetry DEMs were analysed using Esri ArcGIS Pro 3.3, beginning with a visual inspection of each site to identify surface morphologies and structural complexities. The dimensions of both large- and small-scale features were recorded using the built-in *Measuring tool* for further analysis of surface characteristics.

Following the visual analysis, terrain attributes and bathymetric derivatives were generated using the *Spatial Analyst toolbox* and *Benthic Terrain Modeler (BTM)* extensions (Lundblad et al., 2006; Walbridge et al., 2018). These tools enabled visualisation, quantification and comparison of the bioherms surface characteristics both within and between sites.

First-order bathymetric derivatives including slope, aspect and profile curvature were calculated using the *Surface Parameter tool* (James et al., 2014; Lundblad et al., 2006; Minár et al., 2020). An adaptive 15 × 15 cell window (3.5 m neighbourhood distance) with quadratic mode was used during their computation as recommended for high-resolution datasets.

- Slope is the measure of steepness at each cell in degrees, with lower values indicating flatter terrain.

- Aspect identifies the compass direction (azimuth) of the downhill slope that the surface is facing, with values ranging from 0^0 to 360^0 . An aspect value of -1 indicates flat surfaces with no downslope.
- Profile curvature indicates whether the surface is concave or convex at each cell in the normal slope line's direction. Positive values refer to convex surfaces, indicating increased surface flow and erosion, while negative values signal concave surfaces associated with reduced surface flow and deposition. Flat surfaces record zero values (James et al., 2014; Minár et al., 2020).

Surface roughness, also referred to as rugosity or topographic roughness, was calculated using the Vector Ruggedness Measure (VRM) within the BTM (Sappington et al., 2007). The metric facilitates comparison with previous studies over reef systems (Asner et al., 2020; Harris et al., 2023; McNeil et al., 2021b; Pascoe et al., 2021; Price et al., 2019). VRM values range between 0 and 1, with higher values indicating greater terrain ruggedness. However, VRM tends to exaggerate roughness in broader-scale calculations, limiting its utility for finer-scale (Lindsay et al., 2019; Sappington et al., 2007). Therefore, to balance resolution and coverage, a filter radius (r) of 20 cells (≈ 10 m) was applied to capture broader-scale features while also summarizing finer-scale variations.

Additionally, the polygon of previously defined *Halimeda* bioherm morphotypes distribution (McNeil et al., 2016) was used to compute average depth and slope values from the 0.5 m resolution grid to facilitate comparison with earlier findings by McNeil et al. (2021b). Further methodological details are provided in Suppl. Material Section 1.1.

2.5. Morphometrics of large-scale internal depressions of *Halimeda* bioherms

A semi-automated workflow was applied to further investigate the distinct morphologies of bioherms and delineate the large-scale internal depressions (i.e. the depressions in the circular-shaped structures) (Fig. 7 c and Table 1). This workflow combines multiple geoprocessing tools (Böttner et al., 2019; Schneider von Deimling et al., 2023).

Depressions were filled with the *Fill* tool to their pouring point (the lowest point of the surrounding crest). The original bathymetric grid was then subtracted from the filled grid and all areas with vertical change of ≥ 0.5 m were retained and reclassified. A minimum vertical change threshold of ≥ 0.5 m was applied because this corresponds to the conservative vertical uncertainty of the multibeam system, ensuring that only geomorphically meaningful depressions were retained.

Areas of polygons representing depressions were calculated, and those smaller than 200 m^2 were excluded to eliminate very small-scale depressions that may represent single-cell pits or noise-related artefacts inherent in very high-resolution datasets. Although this filtering may under-represent the smallest depressions, sensitivity checks confirmed that it does not influence site-scale patterns in depression orientation, size distributions, or depth trends.

For the remaining depression polygons, several morphometric parameters were calculated to characterise their geometry and spatial configuration:

- Minimum internal depth, defined as vertical distance from the lowest point of the crest to the deepest part of the hollow (Fig. 7 c and 10 a).
- Area and perimeter were calculated with *Zonal Geometry* and *Zonal Statistics* tool.
- Length, width and orientation were computed with *Minimum Bounding Geometry* function using rectangle by width geometry type.
- The circularity of single polygons was calculated using the following formula:

$$C = 4\pi \frac{A}{P^2} \quad (1)$$

Table 1

Summary of Geomorphon Landform elements reclassified into bioherm-specific benthic structures including a description of their visual appearance in the high-resolution dataset (this study) in line with existing terminology systems (International Hydrographic Organization, 2019; Dove et al., 2020; Nanson et al., 2023). Feature of large-scale internal depression also defined in this study.

Geomorphon Landform elements (Jasiewicz and Stepinski (2013))	Bioherm-specific benthic structures (this study)	Standardization of undersea feature names (International Hydrographic Organization, 2019; Dove et al., 2020; Nanson et al., 2023)	Visual appearance and feature definition (this study in line with existing definition systems (International Hydrographic Organization, 2019; Dove et al., 2020))
Flat	Plain	Plane	Flat terrain ($< 2^0$) with a smooth, occasionally uneven, texture.
Peak	Peak or Pinnacle	Peak and Pinnacle	Prominent, pointed bathymetric elevation or spire-shaped pillar ($> 2^0$) with a hard outcrop like appearance. Single, multiple or complex peaks/pinnacles.
Ridge Shoulder			Bathymetric high with a line of highest elevation ($> 2^0$). Circular, elongated or merging, reticulate-like appearance.
Spur	Crest	Crest	
Slope			Steeper inclined surface ($> 4^0$) that forms inner and outer slopes of depressions. Inner slopes appear to be steeper than outer slopes.
Hollow	Slope	Slope	
Footslope	Gentle slope	Slope	A moderate slope ($\approx 2^0$) that mostly appears as a continuity of the outer slope and often separates plain from the steeper slope.
Valley			Depressions or bathymetric lows with a closed contour and varying in shape from circular to irregular. Still have a slope $> 2^0$ that continues into the inner slope. It also may contain smaller depressions or hard outcrop (peak or pinnacle).
Pit	Hollow	Depression	
–	Large-scale internal depression	Depression	Depressions or bathymetric lows with a closed contour at the lowest point of the crest. It varies in

(continued on next page)

Table 1 (continued)

Geomorphon Landform elements (Jasiewicz and Stepinski (2013))	Bioherm- specific benthic structures (this study)	Standardization of undersea feature names (International Hydrographic Organization, 2019; Dove et al., 2020; Nanson et al., 2023)	Visual appearance and feature definition (this study in line with existing definition systems (International Hydrographic Organization, 2019; Dove et al., 2020))
			shape from circular to irregular.

where ‘C’ is circularity, ‘A’ is polygon area and ‘p’ is polygon perimeter (Huang et al., 2023) while progressively lower values indicate increasingly irregular or elongate shapes, which is why the constant 4π is used. Values were classified into five categories:

Round	Sub-round	Sub-angular	Angular	Irregular
≥ 0.8	0.6–0.8	0.4–0.6	0.2–0.4	< 0.2

The previously defined polygon of *Halimeda* morphotypes (McNeil et al., 2016) was overlaid onto the mapped large-scale internal depressions. This overlay enabled the classification of depressions by morphotype, allowing for the generation of both site-specific and composite morphometric datasets across the annulate, reticulate, and undulate forms.

A detailed description of the polygon cleaning, smoothing, clipping, and extraction steps is provided in Suppl. Material Section 1.2.

2.6. Benthic terrain classification

This study is the first to apply the Esri *Geomorphon Landforms* tool (Spatial Analyst toolbox) to classify and map benthic structures for geomorphological analyses across *Halimeda* bioherms. This approach uses pattern recognition to identify landform types compared to other methods that rely on differential geometry (Jasiewicz and Stepinski, 2013), offering a new perspective on the structural complexity of these features (Fig. 4). This tool recognises landform elements based on the specific spatial arrangement of elevation values by using the Local Ternary Patterns (LTP) model (Jasiewicz and Stepinski, 2013; Liao, 2010). The resulting model is based on a defined search and skip distance, tailored to the size of the landforms and the study's objectives.

The method detects 498 unique LTPs (called geomorphons) representing both landform types and terrain attributes, with a self-adaptive neighbourhood responsive to the local topography (Jasiewicz and Stepinski, 2013; Julesz, 1981). This technique enables the user to generate a geomorphometric map, with the ten most common landform elements based on a look up table (Jasiewicz and Stepinski, 2013).

A search distance of 500 cells (250 m) and a skip distance of 10 cells (5 m) were applied to classify the different landforms across the three bioherm sites. The 250 m search distance was selected to encompass the full spatial extent of both small and large bioherm features, ensuring that crest-to-crest dimensions and broader morphological patterns were adequately resolved. The 5 m skip distance reduced artefacts associated with sub-metre bathymetric variability while preserving fine-scale structures within internal depressions. Sensitivity testing using smaller (300–400 cells) and larger (600 cells) search distances yielded comparable spatial distributions of the principal landform classes, indicating that the classification is robust to moderate parameter variation.

Built-in landform elements (flat, peak, ridge, shoulder, spur, slope, hollow, footslope, valley, and pit) were reclassified into six bioherm-specific benthic structures - **plain**, **peak** or **pinnacle**, **crest**, **slope**, **gentle slope**, and **hollow**. This terminology aligns with Dove et al.

(2020), Nanson et al. (2023), the International Hydrographic Organization (2019), and Jasiewicz and Stepinski, 2013 (Fig. 4, Fig. 7c and Table 1).

Following reclassification, the benthic structure rasters were smoothed using the *Majority Filter* function to reduce artefacts. In the first step, cells were filtered based on the nearest four cells, with at least half required to share the same value. In the second step, eight neighbouring cells were considered, with the majority required to share the same value. Once filtered, the rasters were converted to multipart polygons using the *Raster to Polygon* function (Fig. 4).

Descriptive summary statistics including area, perimeter, and first-order bathymetric derivatives were calculated for each benthic structure using the *Zonal Statistics* tool. A more detailed description of benthic terrain classification is provided in Suppl. Material Section 1.3.

3. Results

3.1. Geomorphometrics of *Halimeda* bioherm features

3.1.1. Visual analysis

High-resolution bathymetric data revealed a significantly more intricate seabed morphology compared to previous results from 30 m resolution LiDAR images (McNeil et al., 2016; McNeil et al., 2021b) (Fig. 1 b vs. 1 c). While similar features were observed across all three sites, the complexity and character of the benthic structures vary notably between them (Fig. 3, Fig. 5, and Fig. 6).

Mounded structures, commonly referred to as “donuts” (Webster et al., 2023), dominate the seafloor between 12 and 48 m water depth, exhibiting distinct variations within each site. These structures appear as circular (Fig. 5 g), elongated (Fig. 5 c, d, h, i), or irregular forms (Fig. 5 b, f), and are characterised by internal hollows and surrounded by well-defined crests. They range up to 700 m in diameter from crest to crest, with an average width of 250 m.

Prominent positive-relief crests often form singular rings, coalesced rings sharing borders, or a reticulate network where rings merge. Some structures display double rings with hard substrates (identified based on drop camera imagery) or peaks along their outer slope (Fig. 5 d), while others appear as U-shaped half-rings (Fig. 5 a). In some places, structures are connected to deeper zones via elongated, channel-like structures (Fig. 5 c).

Across all sites, regardless of shape, the inner slopes of the hollows are consistently steeper than the outer slopes. Hollow interiors exhibit either flat or more complex morphologies, often containing smaller depressions or pinnacles. Pinnacles vary widely in form, appearing as singular (Fig. 5 g), multiple (Fig. 5 b, c, d, f, h) or complex (Fig. 5 i) but are typically located centrally within the hollows. While individual pinnacles are typically less than 1 m wide, their average width is around 10 m across. Site 2 contains fewer pinnacles compared to Sites 1 and 3.

The texture of the surrounding plains also varies with some areas displaying a smooth surface, while other locations show a distinctly uneven appearance potentially indicative of bioturbation or sediment re-working by benthic or nektonic organisms (Fig. 5 e).

Seafloor depth, varies across the study sites, revealing a clear trend of shallowing from south to north (Figs. 5 and 7 a, b; Suppl. Table 1). The southern-most site, Site 1, shows a bimodal depth distribution with the highest relative area in 43.6 to 44 m water depth. Deeper zones in the north and west portion of Site 1, range from 37 to 48 m below sea level (mbsl), while shallower areas range from 26 to 33 mbsl, separated by a transitional depth zone.

In contrast, Sites 2 and 3 display a unimodal elevation distribution. At Site 2, most of the area sits between 26 and 31 mbsl, with relatively deeper areas progressively shallowing with multiple peaks. The highest relative area is in 29.3 to 29.7 m water depth. Site 3 follows a similar pattern, with most of the area ranging between 18 and 25 mbsl and peaking between 21.5 and 21.8 mbsl, showing a gradual shoaling pattern toward both the western and eastern edges of the site. The

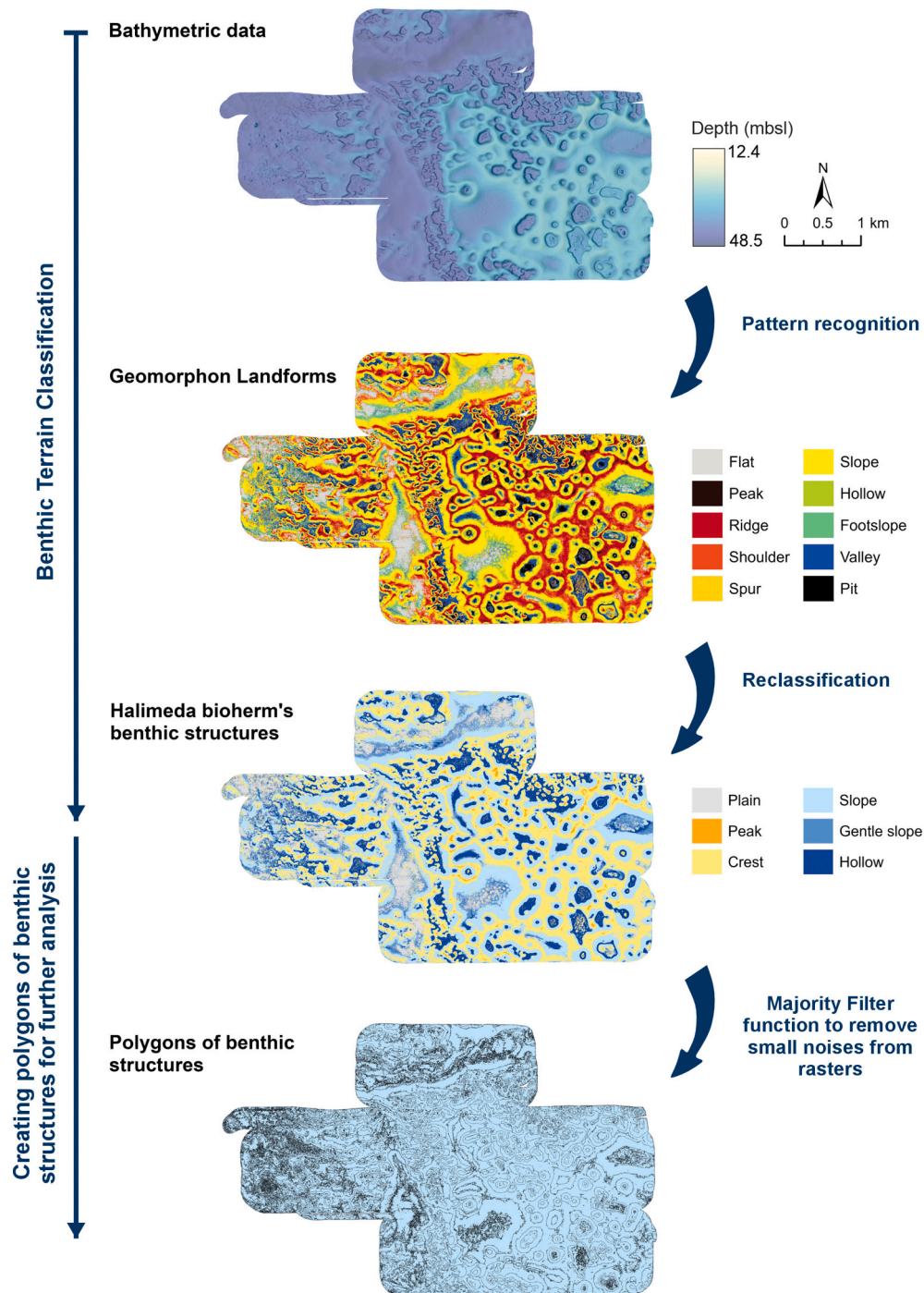


Fig. 4. Workflow of Benthic Terrain Classification over the *Halimeda* bioherms using Site 1 as the example. Pattern recognition was applied over the high-resolution bathymetric grid using the *Esri Geomorphon* tool. Next, the ten computed geomorphon landforms were reclassified into six bioherm-specific benthic structures. The resulting raster was then filtered and vectorized into polygons for further spatial and statistical analysis.

shallowest regions of Site 1 coincide with the mid-depth zones of Site 2, and the shallow areas of Site 2 align with the deepest section of Site 3 (Fig. 7 b).

3.1.2. Surface characteristics and Terrain Attributes

Terrain attributes (slope, aspect, curvature and rugosity) were generated to visualise, describe and compare surface characteristics over the *Halimeda* bioherms. The highest slope values (up to 80°) were observed around the pinnacles within the hollows at all sites, with the steepest at Site 1 and the gentlest at Site 3 (Fig. 8). The double 'halo' effect, as described by McNeil et al. (2021b) referring to the inner and

outer slope relationship at annulate morphotypes, was present at all sites around single hollows and were more complex in areas with merging hollows, particularly on the eastern side of Site 3. The morphology of the inner slopes varies across the sites. Site 1 shows inner slopes with a gradual gradient at the start that steepens sharply, whereas Site 2 and 3 display more moderate gradients. A consistent pattern across all sites is the asymmetry of inner slopes – steeper on the northwest side of hollows, while the southeast side exhibits slightly more gradual gradients (Fig. 8 and cross-section A and B).

Profile curvature analysis reveals higher positive values (convex surfaces) around both the inner and outer slopes, while zero or negative

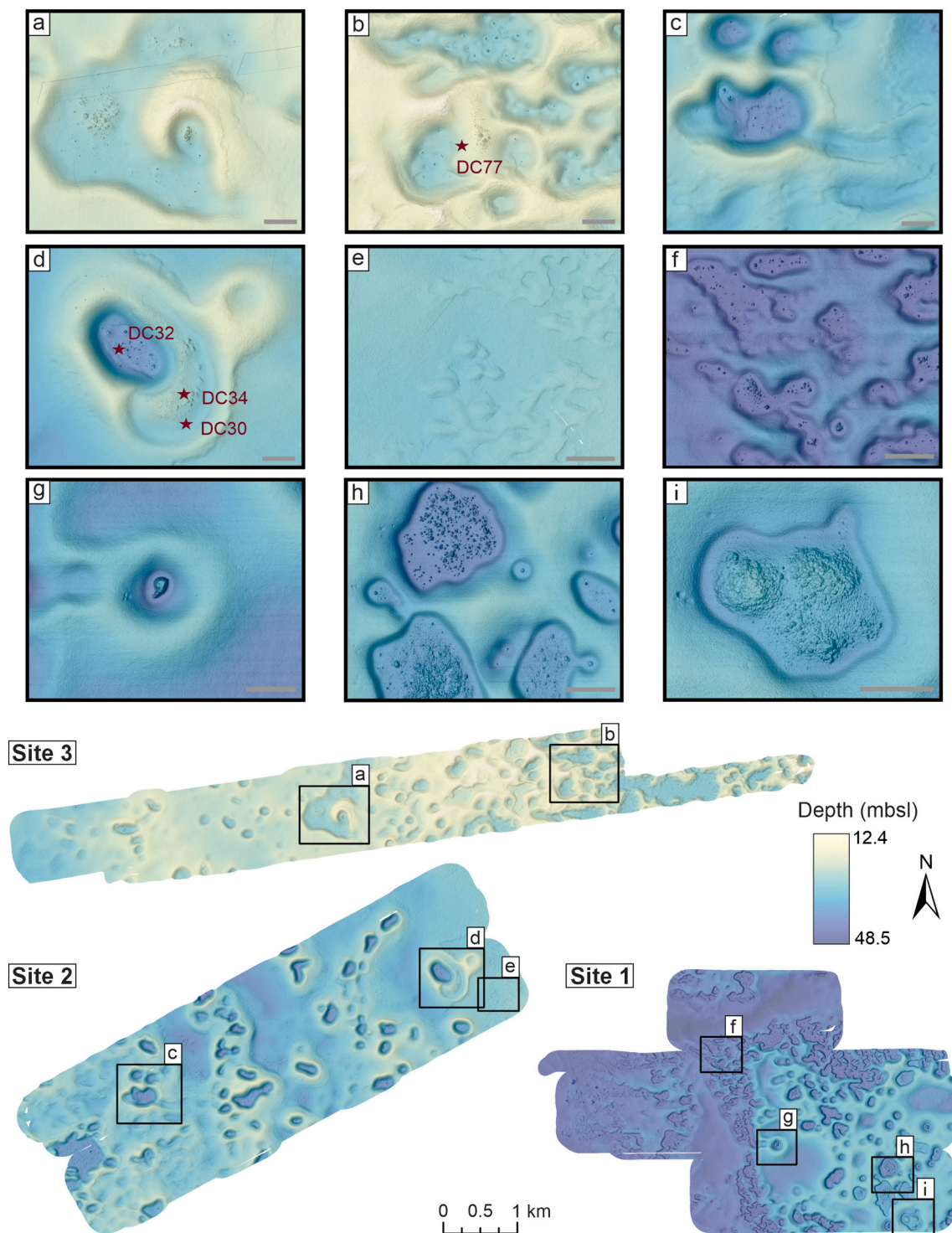


Fig. 5. Bathymetric images showing previously undescribed complexity and variability in seafloor morphology across sites (grey scale bar lines = 100 m). Circular (g), elongated (c, d, h, i) and irregular (b, f) structures with internal hollows and distinct crests dominate both the shallow and deeper regions. Some of these features have double rings with hard substrates on their outer slope (d) or form a U-shaped half-ring (a). In places, elongated, channel-like structures connect them to deeper regions (c). Internal hollows are either flat or contain small depressions or centralised pinnacles, where pinnacles can be singular (g), multiple (b, c, d, f, h), or complex (i). Surrounding plains display smoother or rougher (e) textured appearance. Red stars in panels b and d indicate locations of drop-camera (DC) imagery shown in Fig. 6. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

values (concave surfaces) concentrated within hollows (Suppl. Fig. 1). The presence of pinnacles introduced additional complexity to curvature patterns within the hollows. Aspect analysis showed no preferred orientation of features, with azimuth orientation values randomly distributed (Suppl. Fig. 2).

Rugosity measured using VRM, varies both between and within sites (Fig. 9). Elevated rugosity values were typically located around pinnacles within the hollows, and along outer slopes with peaks that are armoured by hard substrate. Inner slopes of hollows, and in some cases, along the crests, were also typically more rugose. Site 1 recorded the

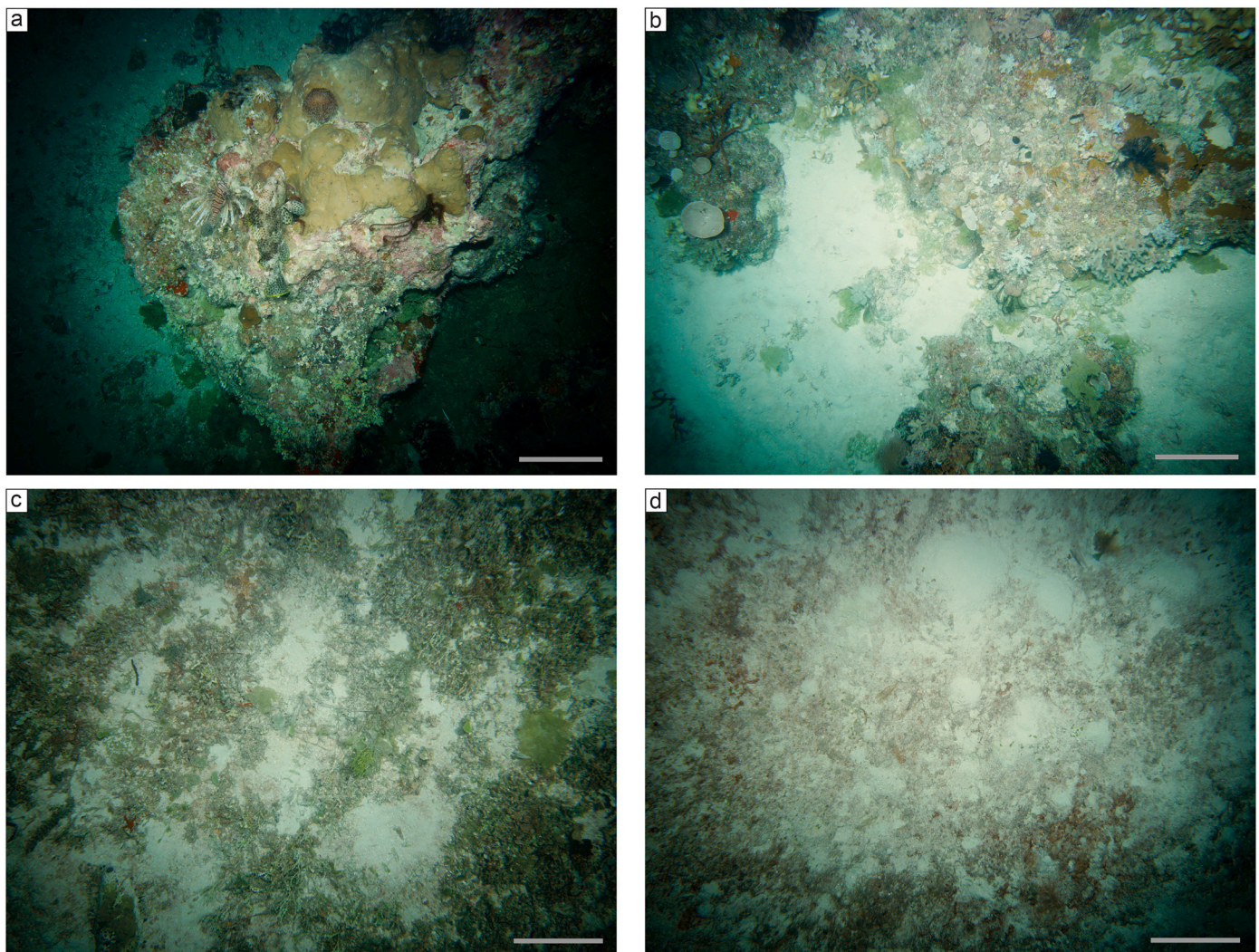


Fig. 6. Drop-camera (DC) images showing the surface complexity of the different *Halimeda* bioherm-specific benthic structures (grey scale bar lines = 10 cm). Image locations correspond to red stars shown in Fig. 5 b and d. a) Pinnacle structure in the hollow (DC32). b) Hard grounds on the outer slope (DC34). c) *Halimeda* meadow on the low gradient section of the outer slope (DC30). d) Bioturbation with sparse live *Halimeda* on the inner slope (DC77). (more details in Suppl. Table 2). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

highest VRM values, reaching 0.15, while Site 3 has the lowest with a maximum value of 0.07.

3.1.3. Morphometrics of large-scale internal depressions

To further investigate the unique morphologies of the *Halimeda* bioherms, large-scale internal depressions were isolated for morphometric analysis. A total of 154 individual depressions were mapped at Site 1, 86 at Site 2 and 85 at Site 3 (Suppl. Table 3). These depressions occur in water depths between 16.9 and 45.4 mbsl, measured from the lowest point of their crest with respect to sea-level (Fig. 10 a). Their minimum internal depth with respect to the crest (distance from the lowest point of the crest to the deepest part of the hollow (Fig. 10 a)) ranges between 0.4 and 10.7 m at Site 1, 0.3 and 14.0 m at Site 2 and 0.3 and 9.2 m at Site 3. Analysis of the relationship between the water depth and minimum internal depth range revealed that depressions located in shallower waters tend to exhibit greater internal depth ranges across all sites. This suggests, greater vertical build up in shallower waters compared to those in deeper settings (Fig. 10 b).

Circularity calculations revealed that depression shapes range from sub-rounded to irregular (Fig. 11), with average values falling within the sub-angular class at all sites (Suppl. Table 3). In addition to shape variability, depressions differ significantly in size. Lengths span between

16.2 and 884.3 m, while widths range from 14.2 to 540.2 m. A spectrum of size is present at all sites, with Site 1 exhibiting both the highest and lowest length-width ratios. A consistent linear trend exists between length-width ratio at all sites (Fig. 11). As the length-width ratio increases, the circularity tends to be more angular and irregular. Conversely, depressions with low length-width ratios are typically smaller in area and exhibit more sub-rounded and sub-angular shapes.

To assess orientation preferences, elongate depressions with ≥ 1.5 length-width ratio were analysed. Most of these features display an approximately E to W orientation, along their long axis across sites, with average of $101^\circ \pm 41$ at Site 1, $80^\circ \pm 35$ and $82^\circ \pm 38$ at Sites 2 and 3, respectively. This orientation is broadly perpendicular to the adjacent ribbon reefs at the shelf edge. However, their orientation patterns are notably more complex at site-level (Suppl. Table 3).

3.1.4. *Halimeda* bioherm morphotypes

The previously defined *Halimeda* bioherm polygon of the three morphotypes – annulate (hollow-centred ring like), reticulate (honeycomb-like), undulate (wave-like) (McNeil et al., 2016) – was overlain at each study site (Figs. 2 and 12).

Annulate morphotypes were most dominant at Site 2, covering 67% of the relative area, and covered around 30% at Sites 1 and 3

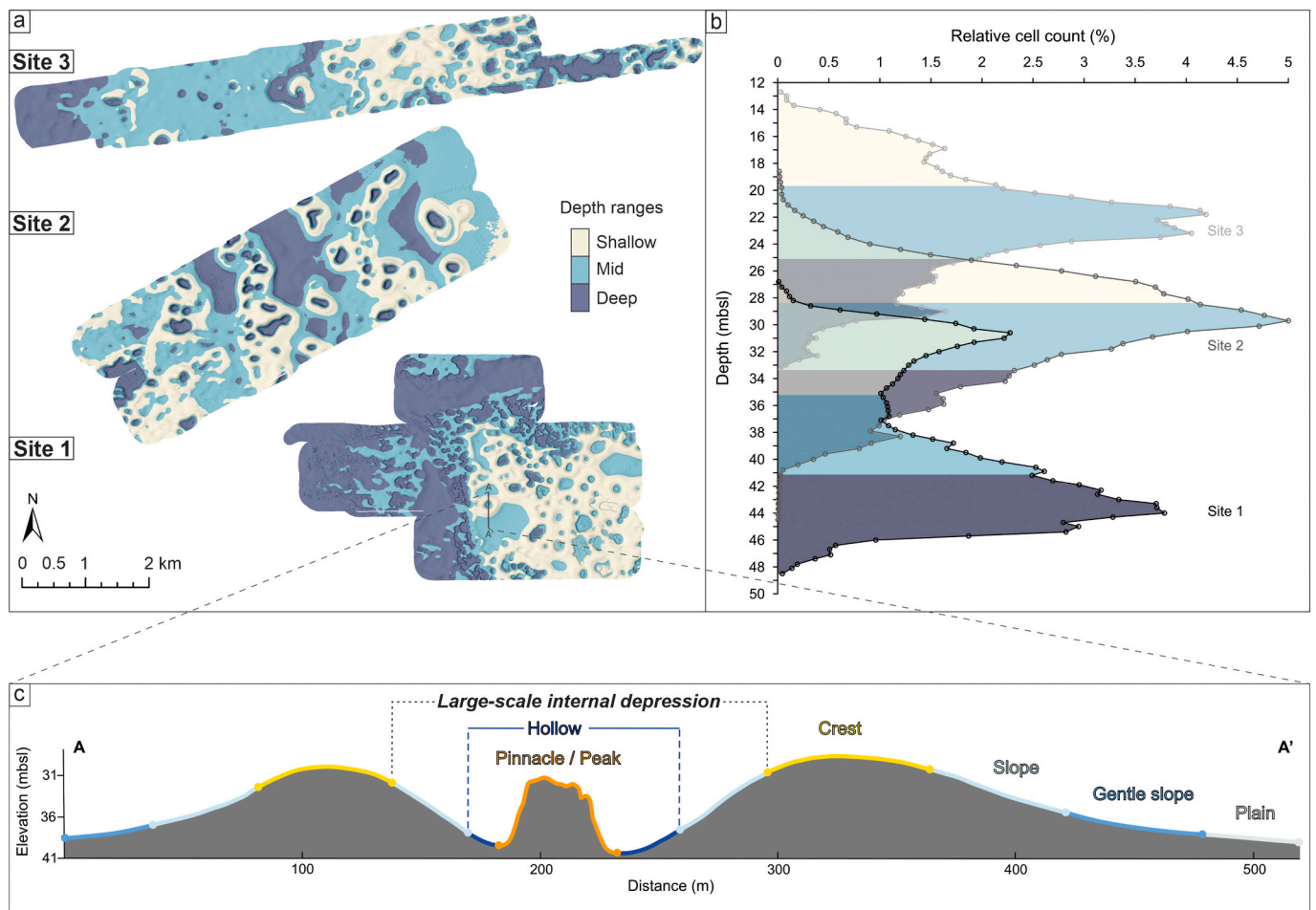


Fig. 7. Hypsometric analysis of the three *Halimeda* bioherm sites. (a) Spatial distribution of relative depth zones across each site, classified into deep (dark blue), middle (light blue), and shallow (yellow) areas using the Natural Breaks (Jenks) method in ArcGIS. (b) Hypsometry curves as a histogram showing the surface area (relative cell count %) at any given depth using 0.3 or 0.4 m bin sizes. Maximum and minimum depths (in meters below mean sea level (mbsl)) are highlighted for each site showing a shallowing trend from south to north. Site 1 represents a bimodal distribution trend while Site 2 and 3 shows unimodal patterns. (c) Classification of six bioherm-specific benthic structures - plain, peak/pinnacle, crest, slope, gentle slope, and hollow - aligning with terminology from [International Hydrographic Organization \(2019\)](#), [Dove et al. \(2020\)](#), and [Nanson et al. \(2023\)](#). The position of large-scale internal depressions is also shown extending horizontally from crest to crest at their lowest point, and vertically from the lowest point of the crest to the deepest point of the hollow. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Table 2). These features had a unimodal elevation distribution, occurring at depths from 21 mbsl (Site 3) to 33 mbsl (Site 1). Average slopes varied across sites, with Site 3 showing the lowest gradient ($2.5^\circ \pm 2.2$). Peaks and pinnacles were common within the annulate rings, and rugosity was locally high around these features in the hollows, and as well as around inner slopes.

Reticulate morphotypes dominated Sites 1 and 3 (37% and 41% of relative area, respectively) but were scarce at Site 2 (1%) (Table 2). They were generally in deeper water depth (mbsl) than annulate morphotypes, except at Site 3, and exhibited a bimodal depth pattern at Sites 1 and 3. Slopes were comparable to annulate types, though Site 2 showed slightly higher gradients. The reticulate morphotype showed complex, merging depressions. Peaks and pinnacles were again common, with additional small depressions (holes) at Site 3. Rugosity was more extensive than in annulate types, especially around outer slopes and crests.

Undulate morphotypes consistently covered $\sim 30\%$ of relative area at all sites and were the deepest features, with average depths between 24 and 43 mbsl (Table 2). Like annulate types, they exhibited a unimodal elevation distribution, though the slope values were generally the lowest, especially at Sites 2 and 3 ($\sim 1.8\text{--}1.9^\circ$). Site 1, however, had steeper gradients ($3.3^\circ \pm 2.9$) and more elongated, wave-like structures.

Surface roughness was typically low, with localized increases around pinnacles and hollows at Sites 1 and 3. A notable half-ring structure at Site 3 was also classified as undulate.

Despite these differences, several consistent traits were observed across all morphotypes: their occurrence at all three sites; commonly featuring peaks and pinnacles; and elevated rugosity around those features in the hollows. Lastly, both undulate and annulate morphotypes shared a unimodal depth distribution, while reticulate morphotypes exhibited bimodality (Suppl. Table 4 and 5).

Analysis of the large-scale internal depressions revealed a total of 154 annulate, 113 reticulate, and 56 undulate features across the three study sites. On average, annulate depressions appear in the shallowest water depths, while undulate forms occur in the deepest waters (Suppl. Table 6 and Fig. 13). Reticulate depressions show the broadest depth range (relative to sea-level), while annulate ones appear in a narrow, restricted depth range (Fig. 13 e).

Morphometric differences among morphotypes were also evident in their average minimum internal depth relative to the surrounding crest. Annulate depressions exhibit the greatest vertical relief (average 5.6 m), followed by reticulate forms (average 3.3 m), and undulate depressions have the smallest internal depth range (average 1.9 m) (Fig. 13 d). A positive correlation is demonstrated between minimum internal depth

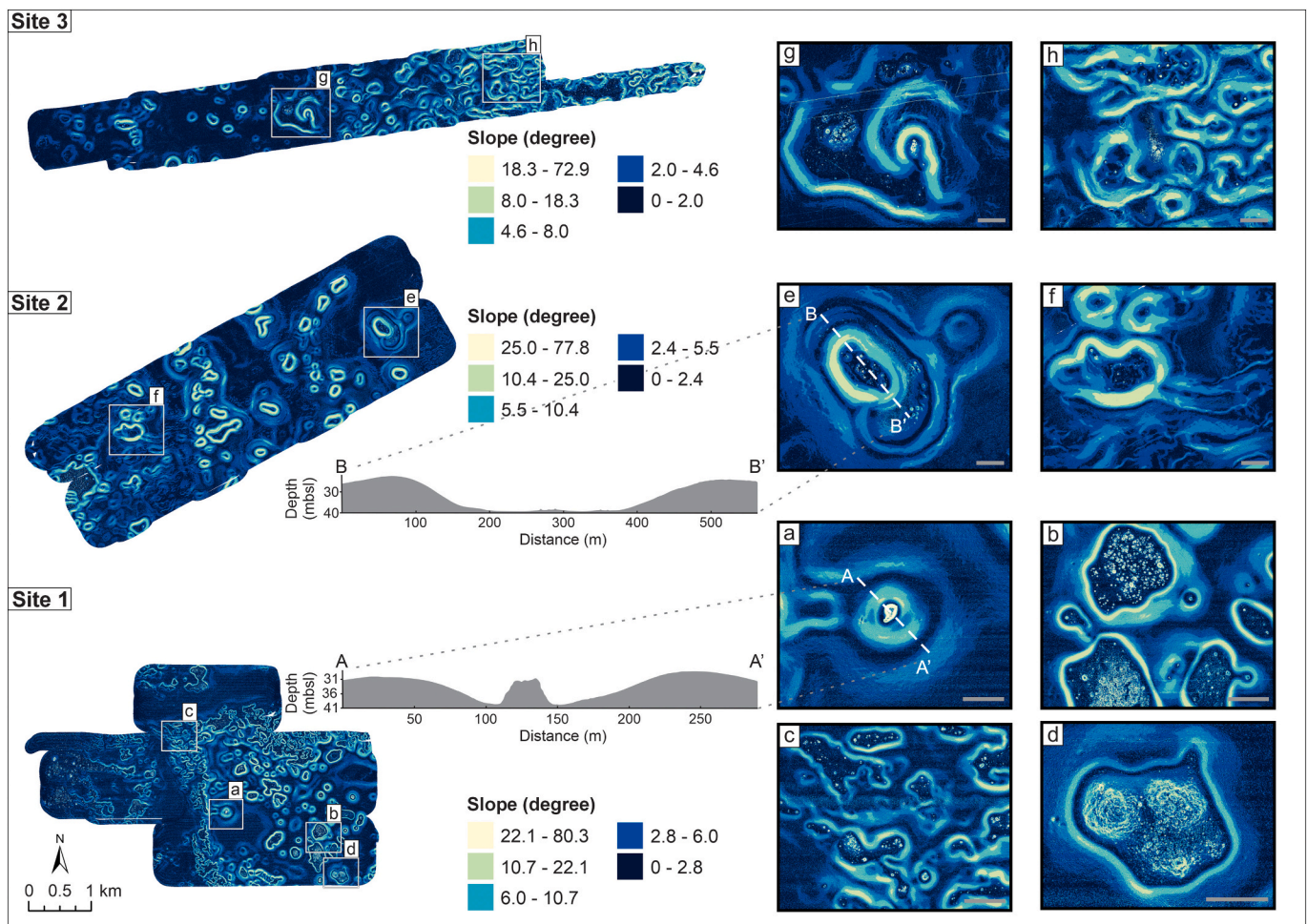


Fig. 8. Slope characters of the seafloor at each site. Panels a-h correspond to previously described seafloor features in Fig. 5, highlighting the distinct slope patterns of associated bioherms morphology. Cross-sectional profiles (A-A' and B-B') are extracted from a) and e), illustrating the asymmetry of inner slopes – steeper gradients on the northwest side and the more gradual gradients on the southeast side of hollows.

range and the water depth ($R^2 = 0.5$ at Site 1, $R^2 = 0.15$ at Site 2, $R^2 = 0.18$ at Site 3) (Suppl. Fig. 3). Notably, reticulate morphotypes occur both in deeper water depths with relatively low internal amplitudes (e.g. Site 1), as well as in shallow waters with relatively high amplitudes (e.g. Site 3). Undulate morphotypes occur in comparatively deeper water depth with low internal amplitude, with occasional exceptions (Suppl. Fig. 3).

In terms of shape and size, depressions across all morphotypes shared similar characteristics, including sub-angular circularity on average. Reticulate depressions recorded the highest length-width ratios with more elongate forms (Fig. 13 b, c). Orientation analysis of the long axis revealed a general E-W alignment, with mean azimuths of $87^\circ \pm 40$ for annulate, $101^\circ \pm 40$ for reticulate, and $77^\circ \pm 32$ for undulate depressions (Fig. 13 a).

3.2. Benthic Terrain Classification

For each benthic structure at all sites (Fig. 7 c, Fig. 14 and Table 1), average area, perimeter, depth and terrain attribute values were calculated (Suppl. Table 7).

Among the classified benthic structures, slope covers the largest relative area, with Site 2 having the highest percentage of slope area (46.5%) and Site 3 the lowest (36.6%) (Fig. 15 d). Crests represent the second largest area, notably occupying 31.5% at Site 1. The highest area of hollows, peaks and pinnacles, are concentrated at Site 1. In contrast, Site 3 has the most extensive areas of plain (18.7%), with Site 1 having

the least (7.1%).

The deepest regions of Site 1 were dominated by plains, while at Sites 2 and 3 hollows occupy the deepest regions (Suppl. Table 7; Fig. 15 c). Conversely, the tops of the peaks and pinnacles occur in the shallowest water depth, showing 7 to 11 m depth difference across sites. When normalised to the average depth of the plain at each site, pinnacles and peaks show the highest positive difference, ranging from 6.6 to 8.1 m above the base level plain across sites. Gentle slope and hollows display the lowest difference, even negative values at Sites 2 and 3. Crest shows the second highest positive values, with a 3 m difference on Site 1 compared to Sites 2 and 3 (Suppl. Table 7).

Slope analysis across benthic structures revealed Site 1 contains the steepest terrain, while Sites 2 and 3 show more variation (Fig. 15 b). The average slope gradient at Site 1 is $5.7^\circ \pm 3.8$, compared to $4.7^\circ \pm 3.7$ and $4.8^\circ \pm 2.9$ at Sites 2 and 3, respectively. The inclines of peaks and pinnacles are more pronounced at Site 1, with gradients exceeding other sites by 2° . Other structures including plains, crests, gentle slopes, and hollows are approximately 1° less steep at Sites 2 and 3 compared to Site 1.

Rugosity, scaled between 0 and 1, show a pattern similar to the slope gradients, with Site 1 displaying the highest rugosity across all benthic structures (Fig. 15 a). As expected, peaks and pinnacles are the most rugose features across the bioherms, though data vary between sites. Crests and slopes also exhibit high rugosity at all sites. Notably, Site 3 shows relatively uniform rugosity values for the peak/pinnacle, crest, slope, gentle slope and hollow structures. Sites 1 and 2 show more

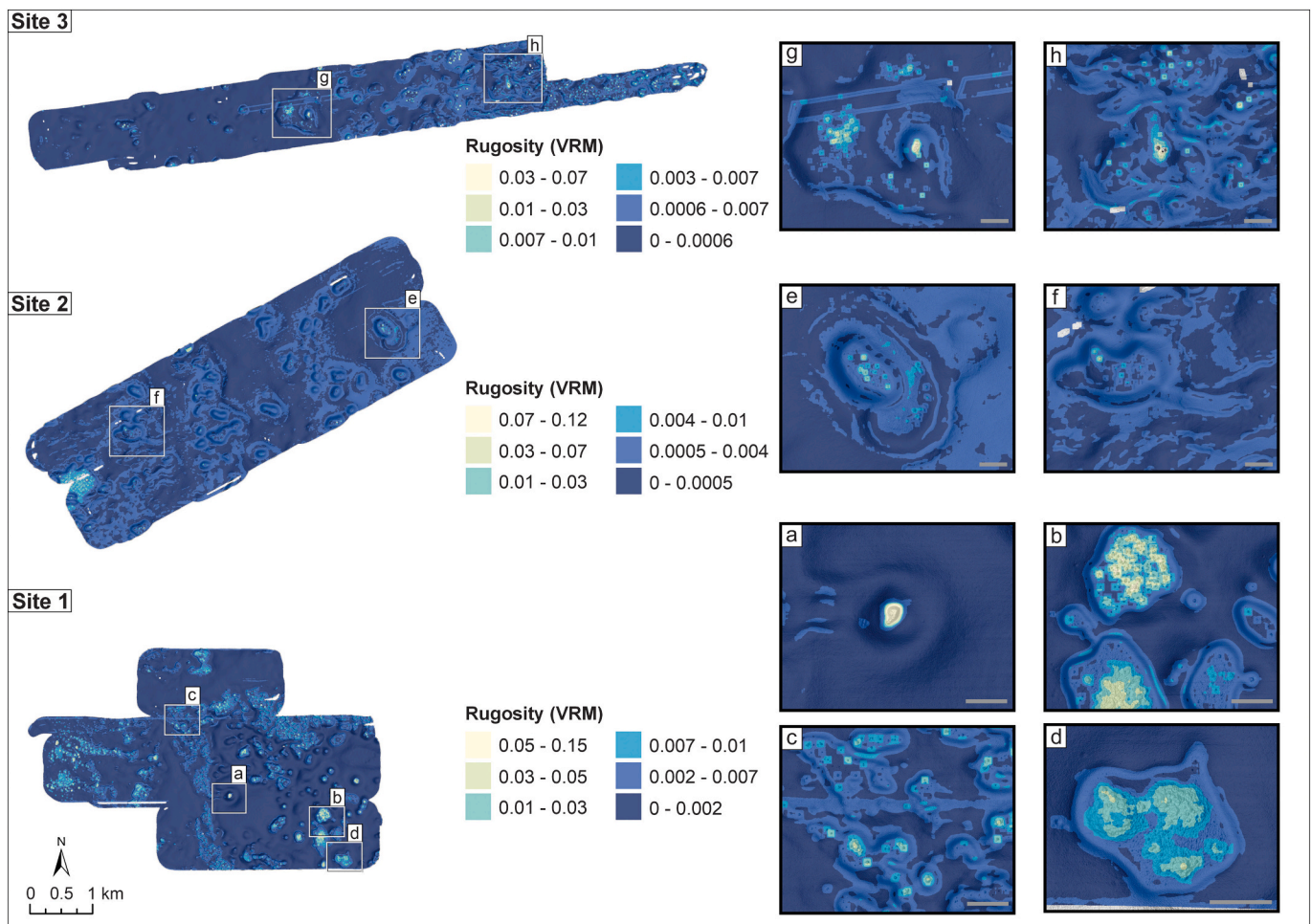


Fig. 9. Rugosity of the seafloor at each site, measured with Vector Ruggedness Measure (VRM). Panels a-h correspond to previously described seafloor features in Fig. 5, highlighting distinct rugosity patterns over the bioherms. Elevated VRM values are associated with internal hollows containing pinnacles, outer slopes with hard substrates, and some crest regions, reflecting structural complexity.

distinct difference in rugosity values between these benthic structures.

4. Discussion

This section integrates geomorphometric analysis and terrain classification to interpret the structural complexity and spatial variability of *Halimeda* bioherms across the three study sites. By combining terrain attributes, morphometric patterns and benthic structures, we discuss how the bioherm morphology records local environmental influences and broader geomorphic processes. These patterns reflect the influence of interacting geomorphic and environmental processes - such as hydrodynamic forcing, sediment redistribution, and antecedent topographic controls which are explored in detail in Section 4.1.2. The improved resolution enables a more nuanced interpretation of bioherm morphology, moving beyond what was previously possible with the lower-resolution dataset (e.g., McNeil et al., 2016; McNeil et al., 2021b).

4.1. The key geomorphic patterns revealed by sub-metre bathymetry

4.1.1. Structural complexity of *Halimeda* bioherms

Visual analyses revealed a diverse array of bioherm morphologies, including circular (ring- or donut-shaped), elongated, and irregular mounds with internal hollows. These hollows exhibit either flat floors or more complex internal structures, such as depressions and single, multiple, or compound pinnacles (Fig. 5). Surrounding crests display high structural complexity, forming rings or interconnected networks.

Integration of morphotype polygons (McNeil et al., 2016) with the new 0.5 m resolution bathymetry provides a more detailed and accurate classification of *Halimeda* bioherm morphotypes. The refined dataset reveals a general depth hierarchy: undulate morphotypes consistently occur at the greatest depths, reticulate forms occupy intermediate depths, and annulate morphotypes are found in the shallowest zones. While this pattern holds across sites, local depth ranges vary. Notably, results from Site 2 (Lizard Island region) align with previous 30 m resolution analyses (McNeil et al., 2021b), whereas at Site 3, reticulate morphotypes are now resolved as shallower than previously reported.

Slope metrics derived from the sub-metre dataset show higher average and maximum values than those from the 30 m grid, with reticulate morphotypes generally exhibiting the steepest gradients. Local slope values reach up to $\sim 80^\circ$, reflecting the presence of fine-scale pinnacles within hollows. These small-scale structures significantly influence mean slope statistics and suggest that morphotype boundaries defined from lower-resolution models may require refinement. Vector ruggedness measure (VRM) further reveals increased complexity with high rugosity values concentrated around pinnacles, internal slopes, and crests.

Morphometric classification of large-scale internal depressions further supports these findings. Annulate morphotypes host the deepest hollows (up to 14 m; mean ≈ 5.6 m), while reticulate forms display variable amplitudes ranging from 6 to 9 m. Collectively, the sub-metre bathymetry reveals greater vertical and spatial heterogeneity than previously recognised, highlighting morphotype-specific relief probably

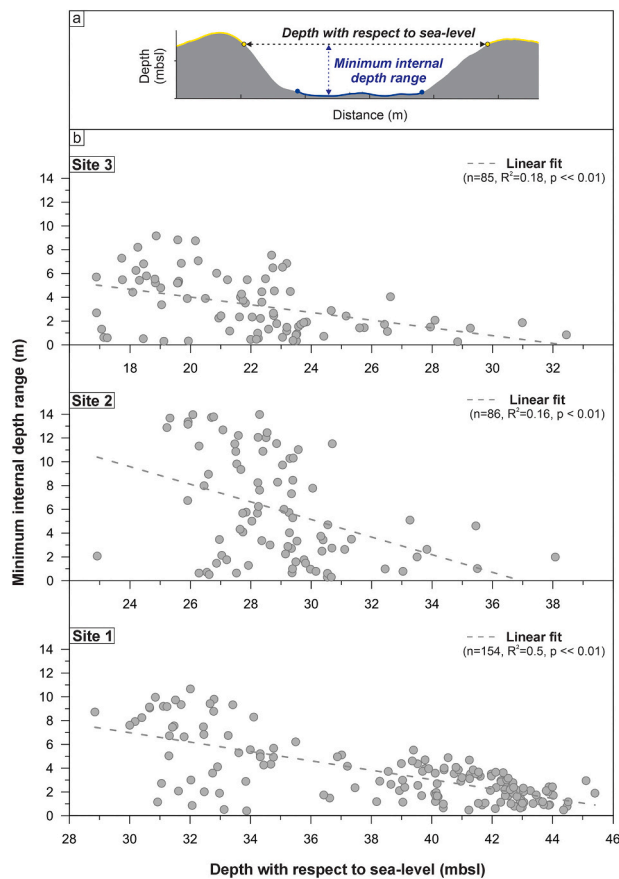


Fig. 10. Relationship between minimum internal depth range of large-scale bioherm depressions and their position in the water column. a) Schematic illustration of measurement points. Depth relative to sea-level was recorded at the lowest point of the crest (yellow dots), while minimum internal depth range was measured as the vertical distance between the lowest point of the crest (yellow dots) and the deepest point of the hollow (blue line). b) Diagrams show how internal depth range relates to occurrence in variable water depth. Note that x-axis scales differ between sites to reflect local bathymetric variability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

shaped by local hydrodynamic conditions.

Our observations also indicate a broader distribution and higher prevalence of pinnacles than previously reported by McNeil et al. (2016), who documented their occurrence exclusively within annulate morphotypes. In contrast, this study identifies pinnacles across both annulate and reticulate forms, including on outer slopes – challenging the notion of smooth annulate crests described by McNeil et al. (2021b). Locally diversified seabed topography associated with submerged pinnacles and non-viable reef structures has been documented using seismic profiling and side-scan sonar to depths of 30 m below present sea level (Orme et al., 1978a, 1978b; McNeil et al., 2021b). Our higher-resolution data extend these observations, revealing fine-scale relief that was previously unresolved.

Historical submersible surveys by Phipps et al. (1985) described *Halimeda* banks behind Ribbon Reefs 4, 5, and 7 as exhibiting consistent ridge-valley morphology, with slopes ranging from 5 to 25° and sharp ecological boundaries between algal-covered ridges and barren sandy valleys. These findings align with our terrain analysis, which reveals steep slope gradients and distinct benthic structures. The presence of conical depressions and cylindrical hollows observed in historical submersible dives – interpreted as bioturbation features – further supports our findings. Such features likely contribute to sediment mixing and nutrient cycling (Riddle, 1988), reinforcing the ecological complexity

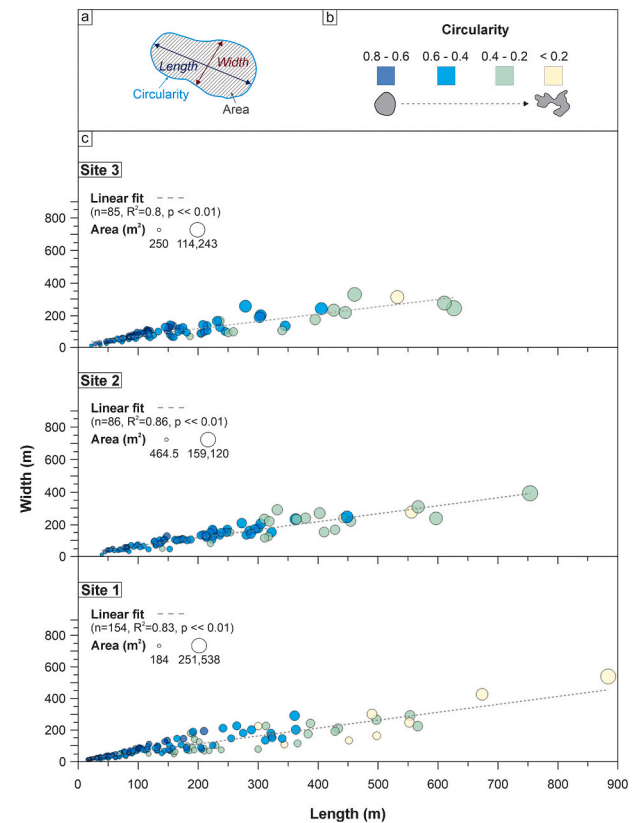


Fig. 11. Morphometric characteristics of large-scale internal depressions across sites. a) Schematic illustration showing measurement of length, width, area and circularity for each depression ranging from sub-rounded to irregular forms. b) Colour-coded classification of depressions by circularity values. c) Scatterplots showing the linear relationship between length and width (x and y axes) across sites. Symbol size represents the depression area, while colour indicating circularity category, and highlighting trends in shape and scale variation.

and functional significance of bioherm habitats.

4.1.2. Process interpretation: Hydrodynamics as a control of complexity?

McNeil et al. (2021b) suggest that the lateral extent of bioherm growth in the GBR is influenced by antecedent topography, current flow, and nutrient availability (Marshall and Davies, 1988; Wolanski et al., 1988; Drew, 2001). Also, storm wave energy may impose an upper growth limit on GBR bioherms, as their consistent depth of ~20–25 mbsl places them within the zone of wave-base influence, potentially restricting vertical accretion despite available accommodation space (McNeil et al., 2021b; Skjold, 1988). Wave energy and tidal currents may play a pivotal role in shaping the morphology and sedimentary dynamics of *Halimeda* bioherms across the GBR shelf. Steeper NW inner slopes and more gradual SE inner slopes (Fig. 8; cross-sections A-B) are consistent with prevailing southeasterly trade winds and wave attenuation/reformation across barrier passages (Fig. 2). This raises important questions about the influence of hydrodynamics on formation processes.

One interesting hypothesis to explain this phenomenon is that a higher energy input from the southeast transports sediment over the southeastern crests, depositing material on the internal southeast slope, while removing sediment from the northwest side of the hollows and redepositing it on their outer slopes. This dynamic aligns with relatively consistent southeasterly trade winds and wind-driven waves over the GBR (Gallop et al., 2014; Hopley et al., 2007; Smith et al., 2023; Wolanski et al., 1988). Waves can break over the shelf edge reef crest, then attenuate but reform in the lagoon, driving currents and reef circulation, therefore affecting sediment transport (Gallop et al., 2014). Seasonal intensification of southeasterly trade winds, driven by the

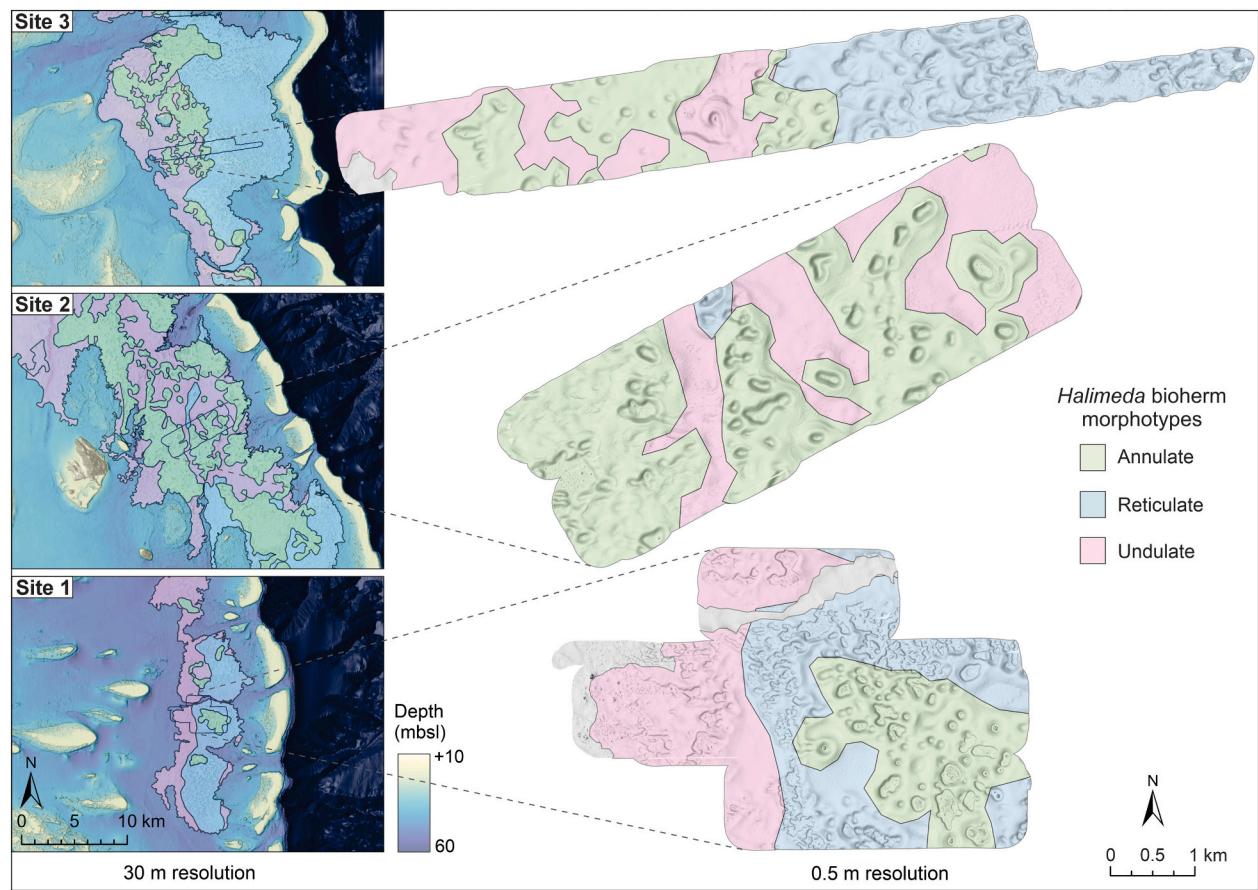


Fig. 12. Distribution of *Halimeda* bioherm morphotypes across study sites (McNeil et al., 2016). Morphotypes are mapped over the high-resolution (0.5 m) bathymetric dataset. Broader morphotype distribution surrounding the study sites is also shown using the 30 m resolution dataset from Beaman (2017) providing regional context for cross shelf variability.

Table 2

Summary table of general morphometrics of *Halimeda* bioherm morphotypes, adapting polygons from McNeil et al. (2016), at each study site using the 0.5 m resolution bathymetric grid (more detailed dataset provided in Suppl. Table 4, 5, and 6). Mean depth and average slope values presented by McNeil et al. (2021b) is also indicated for comparison.

SITES	ANNULATE			RETICULATE			UNDULATE		
	1	2	3	1	2	3	1	2	3
Relative area coverage (%)	29	67	31	38	1	41	33	32	28
Mean depth (mbsl)	33.1 ± 3.4	29.0 ± 3.7	21.6 ± 2.3	38.5 ± 4.4	30.4 ± 4.5	20.9 ± 4.3	42.6 ± 1.9	32.6 ± 3.0	24.5 ± 3.2
Mean depth (mbsl) (McNeil et al., 2021b)*	24.5 ± 3.3			28.6 ± 3.9			25.7 ± 4.7		
Elevation distribution	Unimodal			Bimodal			Unimodal		
Average slope (°)	4.8	4.0	2.5	4.6	5.5	4.3	3.3	1.9	1.8
Average slope (°) (McNeil et al., 2021b)**	1.9			2.7			1.4		
Slope morphometry	Double 'halo' effect (McNeil et al., 2021b)			Complex, merging			Smooth, low gradient		
Surface rugosity	Localized (esp. around pinnacles in hollows)			More extensive			Generally low		

* Combined average depth values from Target Area 1 and 2 by McNeil et al. (2021b) Table S4.

** Slope characteristics from Target Area 1 by McNeil et al. (2021b) Table S3.

northward migration of the modern Intertropical Convergence Zone (ITCZ), generates larger wave events during the dry season, enhancing sediment transport across reef passages and inter-reef zones (Gallop et al., 2014; Smith et al., 2023). Diurnal and semi-diurnal tides further contribute to sediment redistribution, particularly in sheltered lagoonal settings (Hopley et al., 2007; Wolanski and Kingsford, 2024). Our findings on the large-scale internal depressions within *Halimeda* bioherms also suggest potential linkages to local physical oceanographic processes. These depressions show a weak East to West orientation of the long axis. Their orientation follows a perpendicular exposure to the surrounding reef features, except on Site 1 where some depressions have a SE to NW orientation, forming ~45° angles with the adjacent ribbon

reefs. Notably, depressions at shallower water depths (relative to sea-level) show a greater internal vertical depth, suggesting a higher degree of vertical build-up. Furthermore, increasing irregularity is observed as both the area and length-width ratio of the depressions increase, possibly reflecting a space filling or coalescence influenced by sedimentation and local hydrodynamic conditions. The presence of pinnacles may further intensify local flow acceleration and vortex shedding, promoting sediment resuspension and localized erosion – analogous to scour processes observed around offshore structures (Whitehouse and Stroescu, 2023). Recurring super-cyclones at 100–300 year intervals, recorded in mid-Holocene beach ridge sediments along the GBR, are proposed as

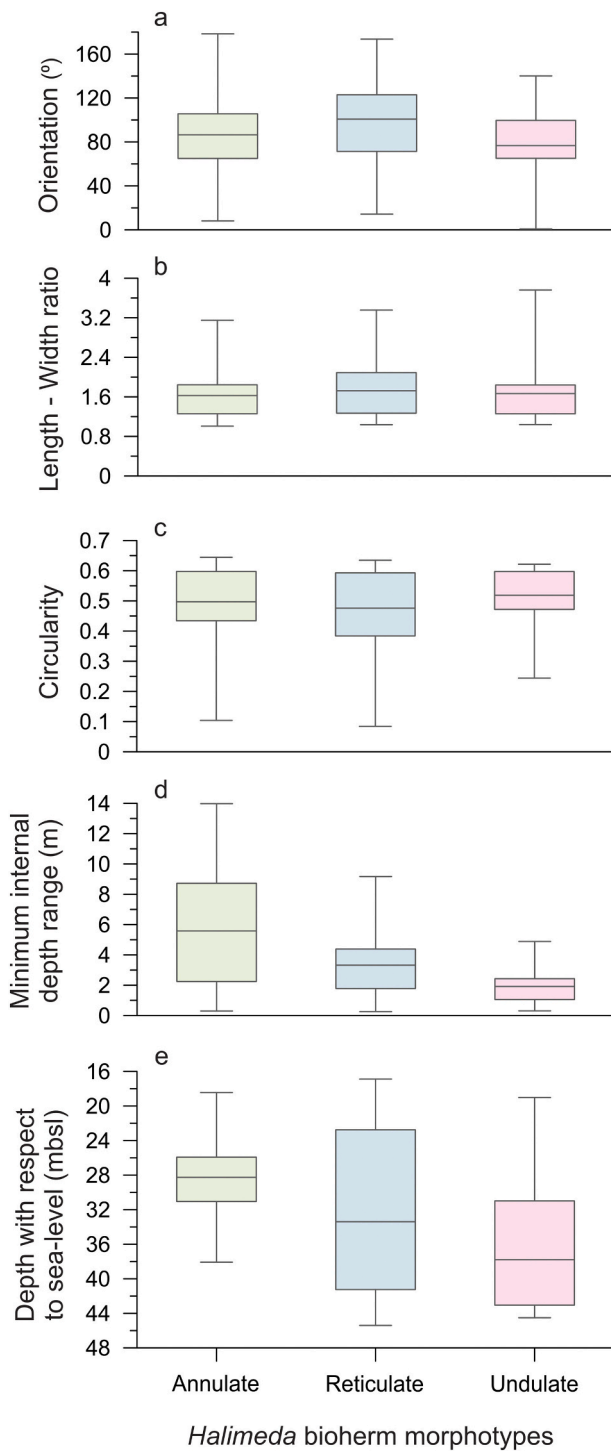


Fig. 13. Morphometric analysis of large-scale internal depressions classified by *Halimeda* morphotypes. Box and whisker plots are showing depressions' orientation (a), length-width ratio (b), circularity (c), minimum internal depth range (d), and depth occurrence relative to sea-level (e) across morphotypes. These plots highlight distinct morphometric signatures associated with annulate, reticulate, and undulate features.

potential drivers of cyclical regime shifts in the *Halimeda* ecosystem (McNeil et al., 2021b). Tropical cyclones are also a common feature of the Austral summer on the GBR shelf. Events such as Cyclone Winifred (1986 – Category 3), have historically mobilized large volumes of sediment, forming storm beds and megaripples across the shelf, just south of this study in the central GBR (Orpin et al., 1999). These episodic

disturbances may contribute to variable accretion and enhanced relief and coalescence of bioherm structures, particularly in shallower zones where internal depressions exhibit greater relief. Previously described cone-like *Halimeda* mounds which occur at depths of 50–65 m on the Queensland Plateau appear to also have asymmetric slopes shaped by alternating fair-weather accumulation and storm-driven sediment redistribution (Reolid et al., 2024). Rapid bioturbation following such events, as observed by Riddle (1988), suggests that sediment reworking and faunal recovery are integral to bioherm resilience and morphological evolution (particular by callianassids shrimp). Drop-camera imagery confirmed bioturbation features and sediment heterogeneity (Fig. 6 d).

An additional complexity not explored in detail here is the influence of shelf-edge reefs in locally redirecting currents. Turbulence modelled by Wolanski et al. (1988) and Wolanski et al. (2024) and wave attenuation studies (Larcombe and Carter, 2004) suggest that these reefs act as partial barriers to storm energy and modulate wave fetch during tidal cycles, potentially limiting sediment transport and shaping bioherm development in ways that are difficult to directly quantify. Regardless, these varying morphologies reinforces that the bioherm development are likely influenced by a combination of differing processes and biophysical feedback mechanisms (McNeil et al., 2021b).

Although the geomorphometry provides valuable insight into bioherm morphology, the age and growth history of the mapped mounds remain unresolved in this study. Earlier work on the northern GBR indicates that *Halimeda* bioherms initiated shortly after post-glacial flooding of the outer shelf (~11.1 cal kyr BP) and have since accreted at rates ranging from ~0.26–1.84 m/kyr, with episodic accelerations occurring when mounds attain favourable light and nutrient conditions (McNeil et al., 2022). Establishing site-specific age-depth relationships for our three study areas will require radiometric dating of the vibrocores collected during the voyage. Until these analyses are completed, constraints on formation depth, temporal variability in accretion rates, and mound evolutionary stages should be considered an important uncertainty in interpreting the observed morphologies.

4.1.3. Site variability vs. shelf structure

Superimposed on these local-scale patterns are broader spatial variations across the study sites. A clear latitudinal gradient in bioherm surface depth was observed, with a south-to-north shallowing trend of approximately 14–15 m. Most depth pixels at Sites 2 and 3 correspond to mid-depth zones, while Site 1 is dominated by deeper regions (Fig. 7 b). Interestingly, the shallow zones of Site 1 align with the mid-depth areas of Site 2, and the shallowest regions of Site 2 correspond to the deepest parts of Site 3. This interconnected depth pattern may reflect progressive sediment accumulation as the shelf flooded during the Holocene transgression and bioherm growth stages, similar to those documented for other reef systems (Hopley, 1982; Sansoleimani et al., 2022).

Sansoleimani et al. (2022) identified a bidirectional shallowing trend along the GBR shelf, with a subsided central region and gradual shallowing toward both the northern and southern zones. Sites 1 and 2 fall within the northern zone, where mature and senile reefs that have grown close to sea level – cover 40% and 31% of the area, respectively. These reef features exhibit polymodal elevation profiles and depth distributions (18–40 mbsl) (Sansoleimani et al., 2022) that closely resemble those of the *Halimeda* bioherms. McNeil et al. (2016) also reported increasing bioherm coverage toward the north, with shelf coverage rising by 4–15%.

Postglacial flooding studies of the GBR shelf (Hinestrosa et al., 2019; Lin et al., 2023) reveal a complex flooding history, with later inundation in the northern GBR (Site 3) and earlier flooding in the northern-central region (Sites 1 and 2). Our depth profiles support this pattern, showing a northward shallowing trend consistent with a progressively elevated Pleistocene surface. Seismic data confirm this gradient, with the antecedent surface located >45 mbsl at Site 1 (McNeil et al., 2022), between 30 and 45 mbsl at Site 2 (McNeil et al., 2021b), and < 30 mbsl at Site 3

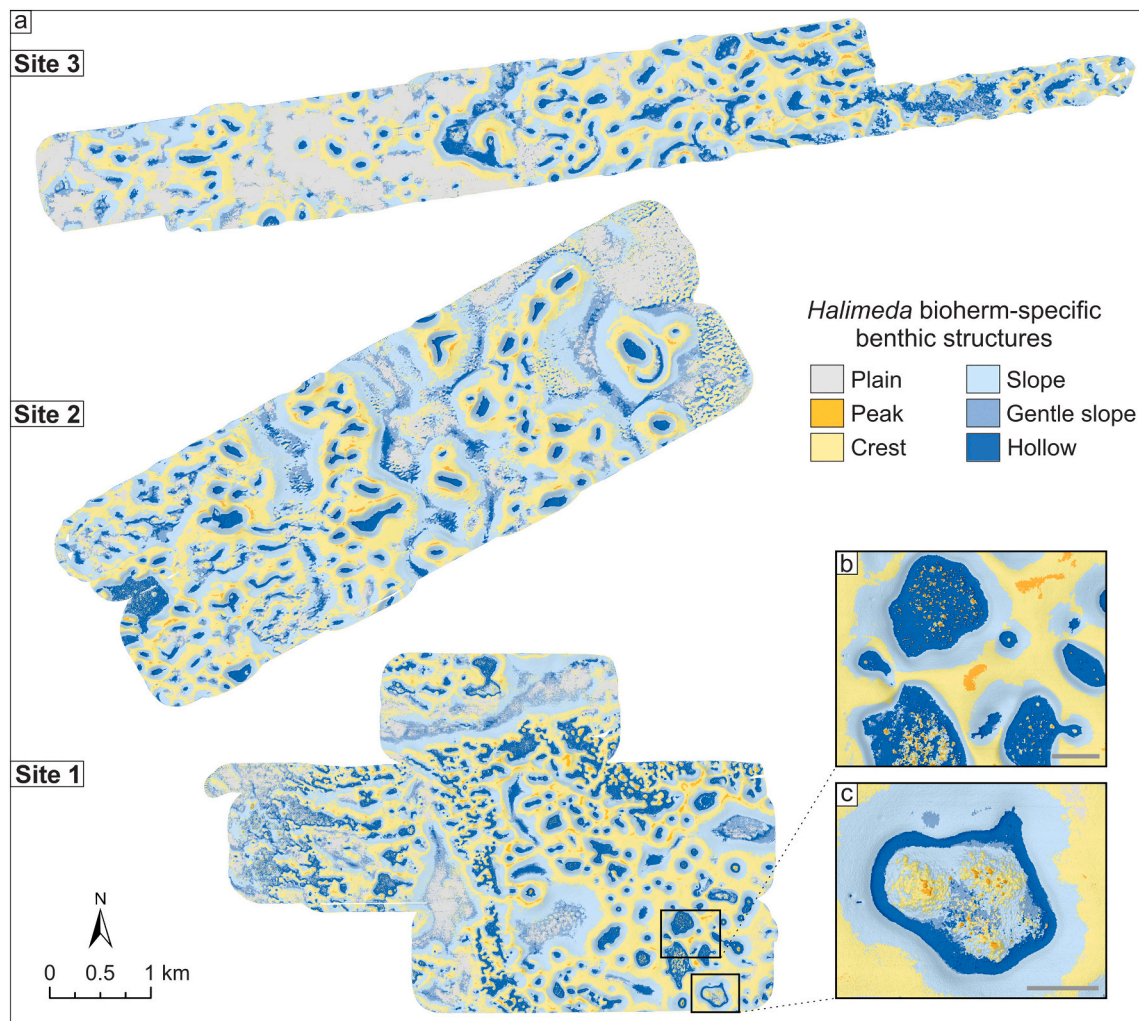


Fig. 14. High-resolution maps showing the distribution of *Halimeda* bioherm-specific benthic structures over the three sites (a). The results highlight the mounded shapes of bioherms, characterised by extensive crest and slope structures interrupted by hollows. These structural patterns underscore the complexity and variability of terrain across the bioherm landscape. Insets b and c correspond to previously described high rugosity seafloor features, such as peaks, shown in Fig. 5 h-i, Fig. 8 b-d, and Fig. 9 b-d; grey scale bar lines in these insets denote 100 m.

(McNeil et al., 2021b).

Expanding on these findings, Sansoleimani et al. (2025) investigated the northernmost GBR, including Site 3, and identified four distinct geomorphic reef zones. Their study suggests that neotectonic reactivation of pre-existing faults may have led to subtle eastward tilting and right-lateral movement of the continental shelf, influencing reef platform morphology. Site 3, surrounded by juvenile reefs and fault lineaments, may be similarly affected. This raises the possibility that *Halimeda* bioherms are shaped not only by sediment dynamics but also by accommodation space, influenced by local tectonic subsidence. Newly acquired high-resolution sub-bottom profiles from our expedition (Webster et al., 2023) may offer further insight into the underlying structure and tectonic influences on bioherm development.

4.2. Benthic Terrain Classification as a framework for habitat interpretation

Benthic terrain classification is increasingly utilized for characterizing seascape features and provides a baseline for targeted geomorphometric analysis and habitat mapping (Jasiewicz and Stepinski, 2013; Lecours et al., 2016; Lundblad et al., 2006). The structural characteristics of the seafloor terrain – such as depth, complexity, morphology, and substrate type – influence species distribution and

diversity (Borland et al., 2021; Duckworth, 2016; Ternon et al., 2022). A complex terrain impacts predator refuge, prey detection, food availability, foraging behaviour, hydrodynamic conditions and nutrient inputs, making seascape metrics crucial for understanding changes in assemblage composition and ecosystem complexity (Borland et al., 2021).

This study presents the first benthic terrain classification of *Halimeda* bioherms representing both large (~100 s of m) and small-scale (~10s of m) features within a single classification framework (Fig. 16). Due to this approach, some misclassification of features is unavoidable within all automated and semi-automated classifications (Fig. 14 b, c). For instance in this study, on large-scale features pinnacle or peak structure were identified on crests due to its pointed elevation (Fig. 14 b), even though visual inspection did not support their presence. Nevertheless, the high-resolution dataset effectively classified small-scale terrain features, such as pinnacles and their associated crest, slope, gentle slope, and even internal hollows within complex pinnacle structures (Fig. 14 c). These classification artefacts may have affected terrain attribute metrics such as slope and rugosity. However, our primary aim was to generate an overall benthic terrain classification to support further research. These limitations do not alter broader spatial interpretations.

The large relative area coverage of slope and crest structures across all sites reflects the mound-like morphology of bioherms, with smaller

proportions of hollow, pinnacle and plain areas (Fig. 15). Notably, a latitudinal trend in benthic structure coverage was observed from south to north, with decreasing proportions of crest, slope and hollow and an increasing presence of plain areas. This spatial pattern may reflect potential accommodation space infilling, as hypothesized above. However, confirming this would require future sedimentological ground-truthing using the collected vibrocores and analysing the internal lithological

build-up of bioherm morphologies along with sub-bottom profiles.

Terrain attribute calculations further underscore the variability between benthic structures across sites. Rugosity and slope are well-established proxies in coral reef studies, where they are often associated with live coral coverage, ecosystem health, fish biomass, and carbonate production (Borland et al., 2021; Darling et al., 2017; Dee et al., 2020; Harris et al., 2023; Perry et al., 2008). When, comparing slope values across all structures and sites, Site 1 emerged as the most structurally complex, whereas Sites 2 and 3 displayed more moderate terrain signatures.

A recent study by Harris et al. (2023) demonstrated that rugosity metrics may reflect morphodynamic processes across multiple spatial scales. Using a 0.25 m DEM over One Tree Island (GBR), they compared two rugosity metrics, Vector Ruggedness (VRM) and *MultiscaleRoughness* (MR) (Lindsay et al., 2019). They found that both techniques detected high rugosity around shallow fore-reef and back-reef slope, and reef crest geomorphic zones – areas that are associated with higher percentage of live coral coverage and structurally complex features.

Previous studies have linked average VRM values ≥ 0.05 to high coral coverage (Fukunaga et al., 2020; Pascoe et al., 2021; Price et al., 2019). While average VRM values for the bioherm benthic structures do not reach this threshold, localized maximum values did – particularly over pinnacle features – signifying high habitat complexity and potential coral colonisation. Similarly, elevated slope and rugosity values recorded for crest and slope structures may reflect the inclusion of complex pinnacle structures within those classifications. Although VRM cannot isolate scale effects, its correlation with ecological proxies supports its use as a first-order habitat indicator. Future analyses integrating MR (Harris et al., 2023) would help disentangle fine- versus broad-scale contributions to terrain complexity.

4.3. Diagnostic traits and habitat significance

A key objective of this study was to compare *Halimeda* bioherms with other seafloor features – both physical and biological – to better understand their geomorphological distinctiveness. While *Halimeda* bioherms exhibit characteristic mound-like and often ring-shaped morphologies, similar forms may arise through various non-biogenic and biogenic processes, complicating their identification without supporting sedimentological and sub-bottom data.

Several physical seabed features resemble *Halimeda* bioherms in form but differ in origin and structure (Suppl. Table 8). Submarine dunes may appear as elongated or crescent-shaped ridges with asymmetric slopes (Ashley, 1990; Cassol et al., 2021; Debes et al., 2016; Di Stefano and Mayer, 2018; Thibaud et al., 2013), yet they lack the circular mound-like forms and internal hollows typical of bioherms. Karst landscapes can produce pinnacles and dolines (Cao et al., 2024; Kan et al., 2015; Micallef et al., 2013; Taviani et al., 2012), but these are dissolution features with negative relief. Pockmarks, found in both shallow and deep settings, are symmetrical depressions without persistent positive relief or internal complexity (Andrews et al., 2010; Böttner et al., 2019; Díaz-Mendoza et al., 2023; Gafeira et al., 2018; Hillman et al., 2023; Picard et al., 2018; Riera et al., 2022; Sun et al., 2011). Circular features like macro-bioturbation pits and grazing halos also lack vertical relief and crest-hollow morphology (Alevizon, 2002; Bilodeau, 2019; Bilodeau et al., 2021; DiFiore et al., 2019; Downie et al., 2013; Madin et al., 2019; Marsh et al., 2018; Schneider von Deimling et al., 2023). Anthropogenic structures such as dredge spoil mounds and explosive craters may mimic bioherm shapes but are typically shallow, small, and lack ecological integration (Díaz-Mendoza et al., 2023). Even archaeological features like the Sapelo Shell Ring (Thompson et al., 2004) share superficial similarities but differ fundamentally in origin and composition.

Biogenic structures also share some morphological traits with bioherms. Seagrass meadows may form shallow semi-circular pools (<1 m depth) (van der Laan and Wolff, 2006; Wolff and Smit, 1990), and oyster

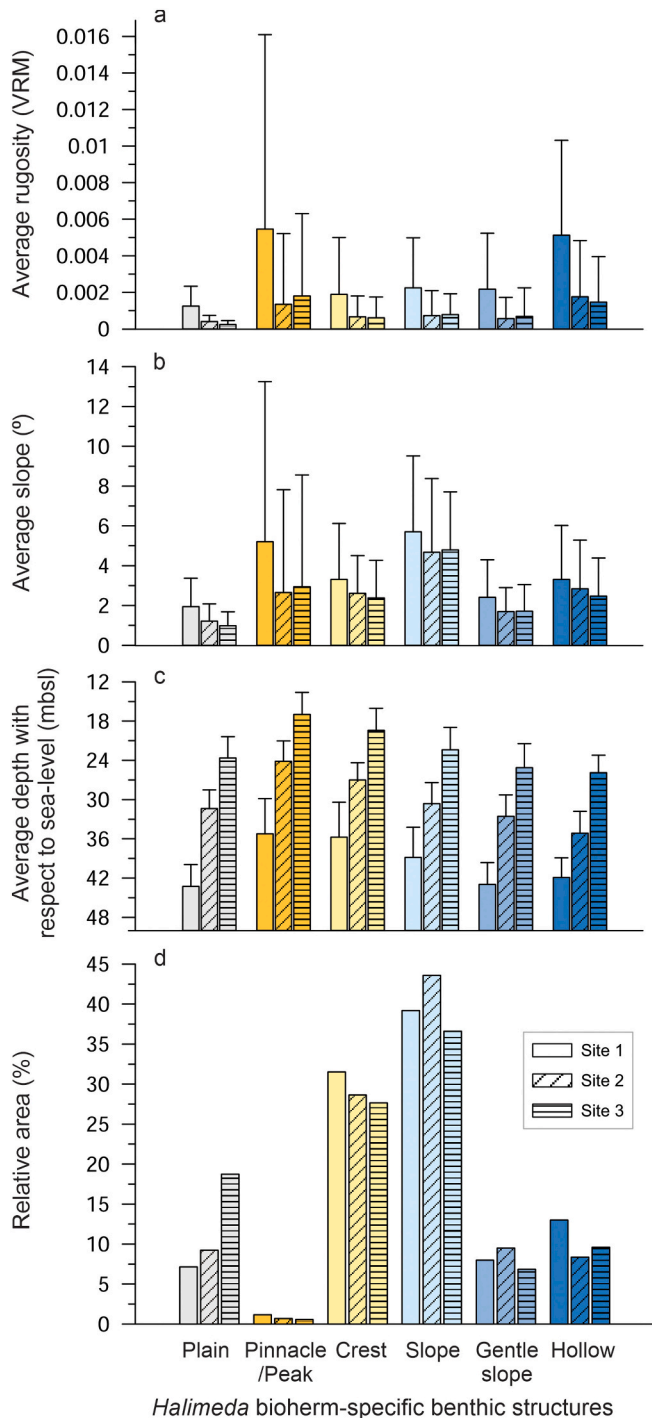


Fig. 15. Morphometric comparison of *Halimeda* bioherm-specific benthic structures by study sites. Column charts summarise site average of classified benthic structures for: rugosity (a), slope (b), depth occurrence relative to sea-level (c), and relative area coverage (d) across the three sites. Error bars are representing the standard deviation of mean values, highlighting variability within each benthic structure type across sites.

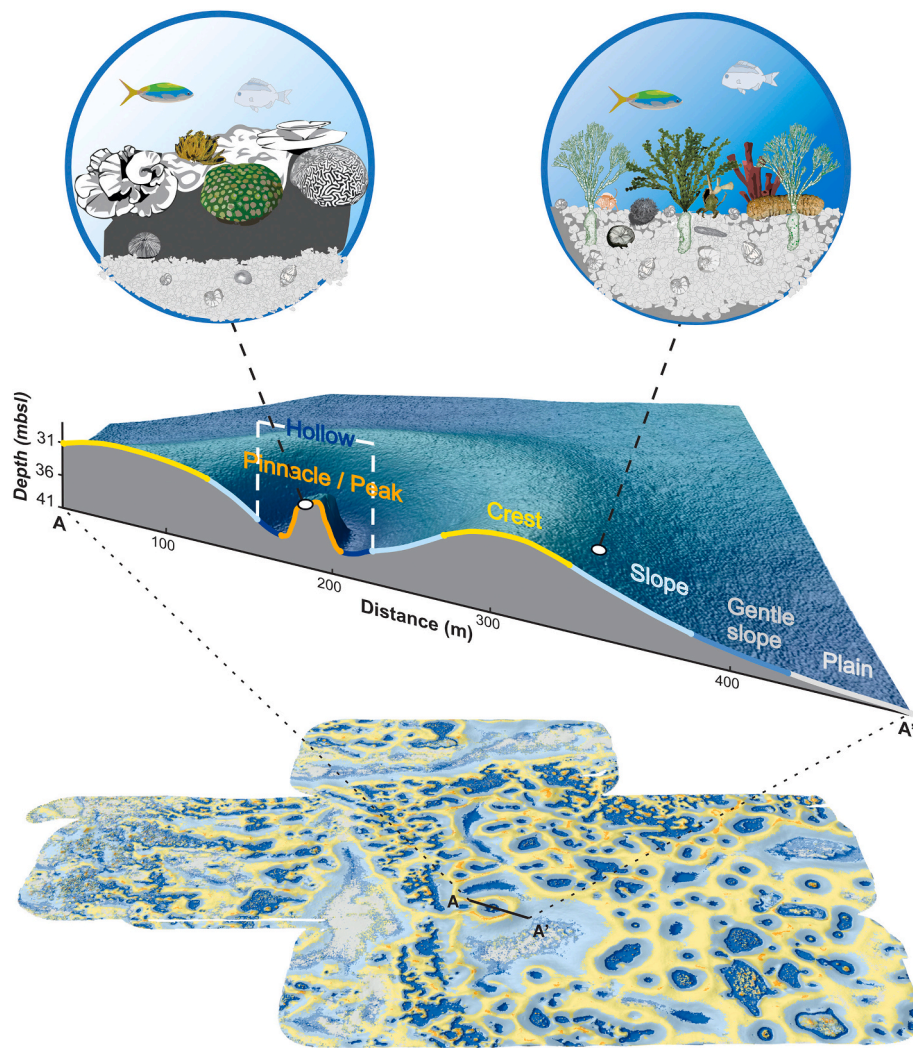


Fig. 16. Benthic terrain classification and habitat complexity across a *Halimeda* bioherm area, illustrating the transition from coral-covered pinnacles to *Halimeda* meadows. This schematic presents a map-scale terrain classification of *Halimeda* bioherms, highlighting distinct high-rugosity features (e.g., coral-covered pinnacles and crests) alongside terrain elements dominated by *Halimeda* meadows (e.g., slopes and flats). The classification framework captures geomorphic and ecological gradients, supporting spatial interpretation of habitat complexity across the bioherm system.

reefs can develop into patchy or elongated formations (Roncolato et al., 2024; Zhuang et al., 2025). Coralligenous algal build-ups in the Mediterranean form squat columns and ridges with relief up to 4 m (Bracchi et al., 2015), while cold-water coral mounds exhibit conical or reticulate morphologies at depths >100 mbsl (Hebbeln and Wienberg, 2025; Wheeler et al., 2007; Wienberg and Titschack, 2017). However, these features typically lack the consistent presence of elevated crests and defined internal hollows that typify *Halimeda* bioherms.

While many seafloor features may mimic aspects of bioherm morphology, most differ in origin, internal structure, relief characteristics, and spatial organization. A defining trait of *Halimeda* bioherms is the combination of well-developed positive-relief crests, internal hollows, and spatial connectivity – likely resulting from in situ biogenic accumulation and feedback mechanisms (Schlager and Purkis, 2015; Xi et al., 2025). Spatial self-organization, driven by hydrodynamic feedback, light availability and metabolic stress, may govern bioherm development, leading to emergent patterns like those observed in coral reef systems (Purkis et al., 2016).

Metrics such as rugosity and slope may reflect different stages of bioherm morphogenesis and ecological maturity. These distinctions, combined with high-resolution terrain mapping, enable clearer differentiation from similar-appearing features and underscore the value of

geomorphometric analysis. Ultimately, this study reinforces the unique nature of *Halimeda* bioherms as distinct geomorphology and habitats. Their structural and ecological significance highlights the need to consider these features as key representative areas for conservation and management within the GBR Marine Park.

4.4. Ecological significance and management implications

The *Great Barrier Reef Outlook Report (2024)* recognises ecological significance of *Halimeda* bioherms directly contributing to the Outstanding Universal Value (OUV) of the Great Barrier Reef World Heritage Area, as recognised by UNESCO. *Halimeda* bioherms are globally significant carbonate-producing ecosystems, covering approximately 6000 km² of the northern GBR shelf (McNeil et al., 2016). Their roles in sediment generation, nutrient cycling, and carbon sequestration make them critical contributors to reef resilience and ecosystem functioning (Rees et al., 2007; Hinestroza et al., 2022; McNeil et al., 2021c). Although, currently assessed as being in ‘very good’ condition, the Outlook Report identifies a lack of systematic monitoring of *Halimeda* habitats. Phipps et al. (1985) reported sparse live *Halimeda* despite abundant *Halimeda*-derived sediment, suggesting seasonal die-off following reproduction, and Marshall and Davies (1988) discussed a

potential ‘boom and bust’ cycle in GBR bioherms ranging from lush, ‘rainforest-like’ growth to barren ‘white desert’ conditions. In addition, McNeil et al. (2021b) imaged localized die-off of *Halimeda* near Lizard Island, following consecutive marine heatwaves in 2016 and 2017, with a recent phase shift to algal mats observed. These factors may influence temporal variability in bioherm productivity and warrants consideration in future monitoring programs. The high-resolution terrain classification developed in this study provides a scalable framework for consistent mapping and long-term ecological assessment, directly supporting benthic habitat inventories and marine spatial planning.

Halimeda meadows, seagrass and other macroalgae habitats are known to provide valuable nursery habitats for reef fish settlement and recruitment (Sambrook et al., 2019; Tang et al., 2020; Sievers et al., 2020; Galbraith et al., 2024) and invertebrates (Webster et al., 2023). These habitats support distinct biotic assemblages, with over 40% of species recorded in bioherm settings not found in adjacent inter-reef zones (McNeil et al., 2021a), reinforcing their status as biodiversity hotspots. Their unique biodiversity, structural complexity, and role in supporting reef resilience underscore the importance of including these habitats in conservation and management frameworks.

Occupying mesophotic depths, *Halimeda* bioherms exhibit pronounced structural complexity, particularly around pinnacles and crests, where elevated rugosity ($VRM \geq 0.05$) may correspond to zones of enhanced biodiversity and live coral cover (Harris et al., 2023). Studies comparing submerged pinnacles to shallow emergent reefs often find that pinnacles possess significantly higher biodiversity metrics, despite their typically smaller size (Galbraith et al., 2023). Submerged pinnacle reefs support greater fish biodiversity than emergent coral reefs primarily due to distinct hydrodynamic regimes associated with their abrupt physical structure and offshore locations, which lead to enhanced nutrient delivery and support robust, diverse fish assemblages (Cresswell et al., 2025). In addition, being remote, isolated and located offshore, these pinnacles are most likely facing reduced exposure to land-based runoff, pollution, and fishing pressure. Despite the pinnacle features being relatively small in area compared to emergent reefs in the region, the unique locations and biophysical conditions suggest that these sites will have high and unique biodiversity. Cooler subsurface waters from marginal upwelling (Wolanski et al., 1988) may also render these systems partial refugia from thermal stress (Galbraith et al., 2023) increasing resilience against climate change impacts (Bongaerts et al., 2017).

Given their ecological distinctiveness and exposure to climate-driven disturbances, *Halimeda* bioherms should be recognised as representative habitats within ecosystem-based management frameworks. Their morphology and dynamics – potentially shaped by alternating phases of algal growth and storm-induced sediment redistribution (McNeil et al., 2021b; Reolid et al., 2024) – highlight both their vulnerability and their importance for climate-resilient conservation planning.

5. Conclusion

This study presents the first sub-metre resolution geomorphometric and terrain classification of *Halimeda* bioherms in the northern Great Barrier Reef, revealing their fine-scale structural complexity and ecological significance.

- Enhanced geomorphological understanding:** *Halimeda* bioherms exhibit diverse mound-like architectures with internal hollows and pinnacles, indicative of complex biogenic accumulation and hydrodynamic shaping. These forms expand on earlier descriptions and align with historical submersible observations (Phipps et al., 1985), suggesting long-term ecological stability and zonation.
- Terrain metrics as ecological proxies:** A clear south-to-north shallowing trend reflects progressive accommodation space infilling. Slope asymmetries and elevated rugosity around pinnacles

indicate zones of sediment redistribution and potentially elevated coral cover.

- Benthic terrain classification:** Six distinct bioherm-specific benthic structures – plain, peak/pinnacle, crest, slope, gentle slope, and hollow – were identified and quantitatively assessed. This classification provides a scalable framework for habitat delineation and integration into marine park monitoring programs and climate-resilience planning.
- Morphometric insights:** Large-scale internal depressions commonly exhibit East to West orientation, often perpendicular to adjacent reef margins. Shallower depressions display greater vertical relief, suggesting advanced build-up stages, while increasing irregularity and elongation with size may reflect coalescence processes and hydrodynamic influence.

Collectively, these findings establish *Halimeda* bioherms as geomorphologically and ecologically distinct features of the GBR shelf. Consistent with the 2024 Outlook Report, this study supports their recognition within regional management frameworks – such as the Reef 2050 Plan – as representative habitats requiring targeted protection and systematic monitoring.

The terrain metrics and morphometric methods developed here offer transferable tools for identifying and assessing bioherms across other tropical shelf systems, as well as other marine seafloor features. Beyond their sedimentary importance, *Halimeda* bioherms may sustain unique benthic communities shaped by depth, substrate, and hydrodynamic gradients – representing both a valuable sedimentary archive and an under-recognised ecological asset within the GBR Marine Park (Webster et al., 2023).

CRedit authorship contribution statement

Zsanett Szilagyi: Writing – original draft, Visualization, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Luke Nothdurft:** Writing – review & editing, Validation, Supervision, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization. **Stephanie Duce:** Writing – review & editing, Validation, Supervision, Software, Methodology, Conceptualization. **Jody M. Webster:** Writing – review & editing, Validation, Supervision, Resources, Funding acquisition, Data curation, Conceptualization. **Mardi McNeil:** Writing – review & editing, Validation, Investigation, Funding acquisition, Data curation. **Robin J. Beaman:** Writing – review & editing, Validation, Data curation. **Juan Carlos Braga:** Writing – review & editing, Validation, Investigation, Data curation. **Trevor Graham:** Writing – review & editing, Validation, Investigation, Funding acquisition, Data curation. **Maria Byrne:** Writing – review & editing, Validation, Investigation, Data curation. **Amy Nau:** Writing – review & editing, Validation, Resources, Methodology, Investigation, Data curation. **Christopher Berry:** Writing – review & editing, Validation, Resources, Methodology, Investigation, Data curation. **Victorien Paumard:** Writing – review & editing, Validation, Conceptualization. **Jeffrey Shragge:** Writing – review & editing, Validation. **Catherine Kim:** Writing – review & editing, Validation, Methodology. **Helen Bostock:** Writing – review & editing, Validation, Supervision, Investigation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT and Co-Pilot in order to improve readability and language. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Funding sources

We acknowledge the use of the CSIRO Marine National Facility (<https://ror.org/01mae9353>) and grant of sea time on RV Investigator in undertaking this research. We also acknowledge funding support from the National Geographic Society and The Ian Potter Foundation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the entire HALO science team, Commonwealth Scientific and Industrial Research Organization (CSIRO) support staff, and the captain and crew of R/V Investigator for their outstanding work on the voyage. We acknowledge the support provided by Geoscience Australia for the voyage.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geomorph.2026.110243>.

Data availability

I have shared my data in Supplementary Material and Tables at the 'Attach Files' step.

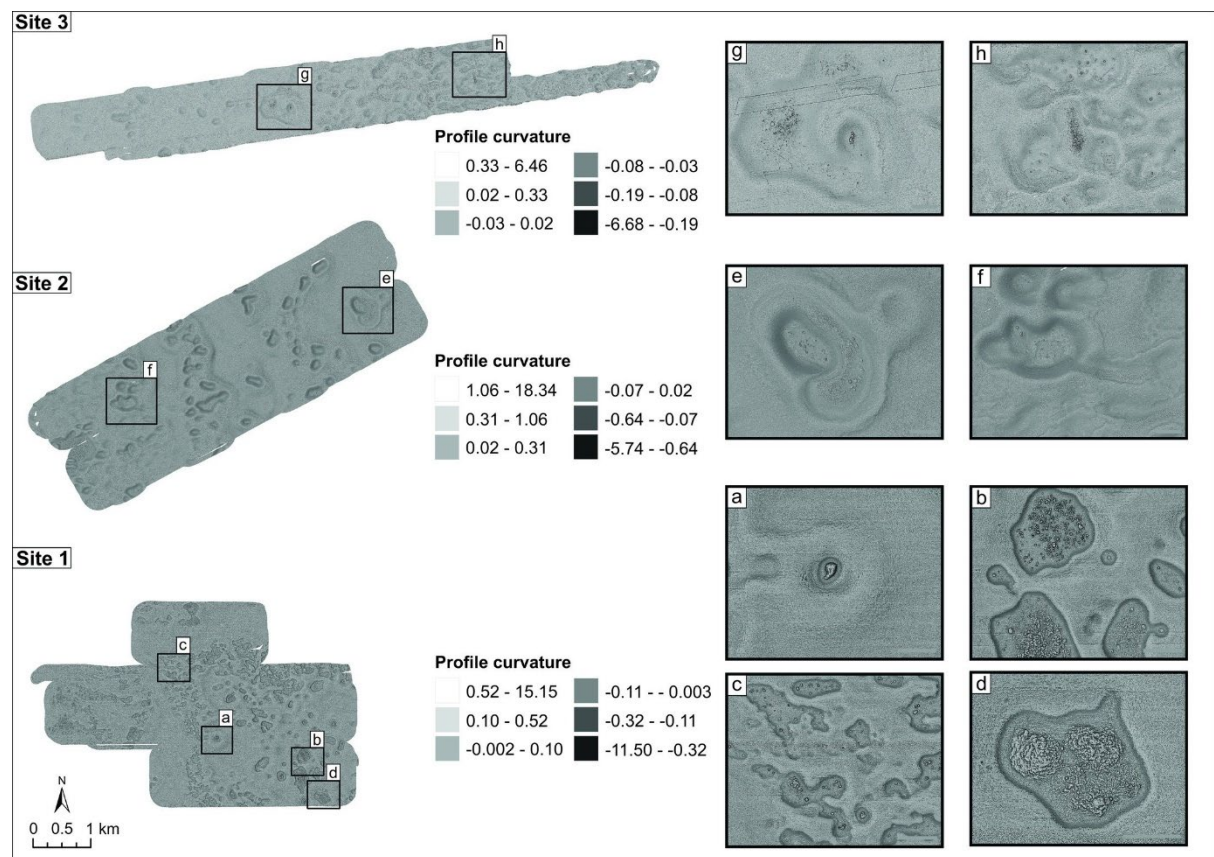
References

- Alevizon, W., 2002. Enhanced seagrass growth and fish aggregations around Bahamian patch reefs: the case for a functional connection. *Bull. Mar. Sci.* 70 (3), 957–966.
- Andrews, B.D., Brothers, L.L., Barnhardt, W.A., 2010. Automated feature extraction and spatial organization of seafloor pockmarks, Belfast Bay, Maine, USA. *Geomorphology* 124 (1), 55–64.
- Ashley, G.M., 1990. Classification of large-scale subaqueous bedforms; a new look at an old problem. *J. Sediment. Res.* 60, 160–172.
- Asner, G.P., Vaughn, N.R., Balzotti, C., Brodrick, P.G., Heckler, J., 2020. High-Resolution Reef Bathymetry and Coral Habitat Complexity from Airborne Imaging Spectroscopy. *Remote Sens.* 12 (2), 310.
- Beaman, R.J., 2010. 3DGBR: a high-resolution depth model for the Great Barrier Reef and Coral Sea: Marine and Tropical Sciences Facility (MTSRF) Project, v. 2, p. 13.
- Beaman, R.J., 2017. High-resolution depth model for the Great Barrier Reef - 30 m. Geoscience Australia, Canberra. <https://doi.org/10.4225/25/5a207b36022d2>.
- Bilodeau, S.M., 2019. Ecological Process in Pattern Generation in Tropical Coral-Seagrass Reefs. Wake Forest University, 125 p.
- Bilodeau, S.M., Layman, C.A., Silman, M.R., 2021. Benthic pattern formation in shallow tropical reefs: does grazing explain grazing halos? *Landsc. Ecol.* 36 (6), 1605–1620.
- Bongaerts, P., Riginos, C., Brunner, R., Englebert, N., Smith, S.R., Hoegh-Guldberg, O., 2017. Deep reefs are not universal refuges: Reseeding potential varies among coral species: *Science. Advances* 3 (2), e1602373.
- Borland, H.P., Gilby, B.L., Henderson, C.J., Leon, J.X., Schlacher, T.A., Connolly, R.M., Pittman, S.J., Sheaves, M., Olds, A.D., 2021. The influence of seafloor terrain on fish and fisheries: a global synthesis. *Fish Fish.* 22 (4), 707–734.
- Böttner, C., Berndt, C., Reinardy, B.T.L., Geersen, J., Karstens, J., Bull, J.M., Callow, B.J., Lichtschlag, A., Schmidt, M., Elger, J., Schramm, B., Haeckel, M., 2019. Pockmarks in the Witch Ground Basin, Central North Sea. *Geochem. Geophys. Geosyst.* 20 (4), 1698–1719.
- Bracchi, V., Savini, A., Marchese, F., Palamara, S., Basso, D., Corselli, C., 2015. Coralligenous habitat in the Mediterranean Sea: a geomorphological description from remote data: *Italian. J. Geosci.* 134 (1), 32–40.
- Cao, H., Xiong, L., Ma, J., Wang, H., Li, S., Yu, F., Wang, P., 2024. Karst landform classification considering surface flow characteristics derived from digital elevation models. *Earth Surf. Process. Landf.* 49 (1), 468–481.
- Carroll, A., Althaus, F., Beaman, R., Friedman, A., Ierodiaconou, D., Ingleton, T., Jordan, A., Linklater, M., Sutherland, M., Monk, J., Post, A., Przeslawski, R., Smith, J., Stowar, M., Tran, M., Tyndall, A., 2020. Marine sampling field manual for towed underwater camera systems. In: Przeslawski, R., Foster, S. (Eds.), *Field Manuals for Marine Sampling to Monitor Australian Waters*, National Environmental Science Programme (NESP).
- Cassol, W.N., Daniel, S., Guilbert, É., 2021. A Segmentation Approach to Identify Underwater Dunes from Digital Bathymetric Models. *Geosciences* 11 (9), 361.
- Cresswell, B.J., Galbraith, G.F., Barnett, A., Harrison, H.B., Jones, G.P., McClure, E.C., Quimpo, T.J.R., Hoey, A.S., 2025. Limited evidence for Depth Specialism in Isolated Seamount Reef Predators. *Ecol. Evol.* 15 (9), e72044.
- Darling, E.S., Graham, N.A.J., Januchowski-Hartley, F.A., Nash, K.L., Pratchett, M.S., Wilson, S.K., 2017. Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs* 36 (2), 561–575.
- Davies, P.J., Marshall, J.F., 1985. Halimeda bioherms—low energy reefs, northern Great Barrier Reef. In: *Proceedings of the 5th International Coral Reef Congress, Tahiti. Volume 5*, p. 1–7.
- Debes, N., Jacq, J.-J., Garlan, T., 2016. Extraction of sandy bedforms features through geodesic morphometry. *Geomorphology* 268, 82–97.
- Dee, S., Cuttler, M., O'Leary, M., Hacker, J., Browne, N., 2020. The complexity of calculating an accurate carbonate budget. *Coral Reefs* 39 (6), 1525–1534.
- Di Stefano, M., Mayer, L.A., 2018. An Automatic Procedure for the Quantitative Characterization of Submarine Bedforms. *Geosciences* 8 (1), 28.
- Diaz-Mendoza, G.A., Krämer, K., von Rönn, G.A., Schwarzer, K., Heinrich, C., Reimers, H.-C., Winter, C., 2023. Circular structures on the seabed: differentiating between natural and anthropogenic origins—examples from the Southwestern Baltic Sea. *Front. Earth Sci.* 11.
- DiFiore, B.P., Queenborough, S.A., Madin, E.M.P., Paul, V.J., Decker, M.B., Stier, A.C., 2019. Grazing halos on coral reefs: predation risk, herbivore density, and habitat size influence grazing patterns that are visible from space. *Mar. Ecol. Prog. Ser.* 627, 71–81.
- Dove, D., Nanson, R., Bjarnadóttir, L.R., Guinan, J., Gafeira, J., Post, A., Dolan, M.F.J., Stewart, H., Arosio, R., Scott, G., 2020. A Two-Part Seabed Geomorphology Classification Scheme (V.2). In: *Part 1: Morphology Features Glossary*, Zenodo.
- Downie, R.A., Babcock, R.C., Thomson, D.P., Vanderklift, M.A., 2013. Density of herbivorous fish and intensity of herbivory are influenced by proximity to coral reefs. *Mar. Ecol. Prog. Ser.* 482, 217–225.
- Drew, E.A., 1983. Halimeda biomass, growth rates and sediment generation on reefs in the central Great Barrier Reef province. *Coral Reefs* 2 (2), 101–110.
- Drew, E.A., 2001. Ocean Nutrients to Sediment Banks via Tidal jets and Halimeda Meadows. In: Wolanski, E. (Ed.), *Oceanographic Processes of Coral Reefs Physical and Biological Links in the Great Barrier Reef*. CRC Press LLC, Boca Raton, USA, pp. 1–348.
- Duckworth, A.R., 2016. Substrate type affects the abundance and size of a coral-reef sponge between depths. *Mar. Freshw. Res.* 67 (2), 246–255.
- Fukunaga, A., Burns, J.H.R., Pascoe, K.H., Kosaki, R.K., 2020. Associations between Benthic Cover and Habitat Complexity Metrics Obtained from 3D Reconstruction of Coral Reefs at Different Resolutions. *Remote Sens.* 12 (6), 1011.
- Gafeira, J., Dolan, M.F.J., Monteys, X., 2018. Geomorphometric Characterization of Pockmarks by using a GIS-Based Semi-Automated Toolbox. *Geosciences* 8 (5), 154.
- Galbraith, G.F., Cresswell, B.J., McCormick, M.L., Jones, G.P., 2023. Strong hydrodynamic drivers of coral reef fish biodiversity on submerged pinnacle coral reefs. *Limnol. Oceanogr.* 68 (11), 2415–2430.
- Galbraith, G.F., Cresswell, B.J., McClure, E.C., Hoey, A.S., 2024. Tropical seamounts as stepping-stones for coral reef fishes: range extensions and new regional distributions from mesophotic ecosystems in the Coral Sea, Australia. *Mar. Biodivers.* 54 (2), 17.
- Gallop, S.L., Young, I.R., Ranasinghe, R., Durrant, T.H., Haigh, I.D., 2014. The large-scale influence of the Great Barrier Reef matrix on wave attenuation. *Coral Reefs* 33 (4), 1167–1178.
- Great Barrier Reef Marine Park Authority, 2024. Great Barrier Reef Outlook Report 2024, Reef Authority, Townsville. URL: <https://hdl.handle.net/11017/4069>.
- Harris, D.L., Webster, J.M., Vila-Concejo, A., Duce, S., Leon, J.X., Hacker, J., 2023. Defining multi-scale surface roughness of a coral reef using a high-resolution LiDAR digital elevation model. *Geomorphology* 439, 108852.
- Hebbeln, D., Wienberg, C., 2025. Unravelling the enigma of discontinuous sedimentary deposits in cold-water coral mounds in the Atlantic Ocean. *Front. Mar. Sci.* 12, 2025.
- Hill, R., Bellgrove, A., Macreadie, P.I., Petrou, K., Beardall, J., Steven, A., Ralph, P.J., 2015. Can macroalgae contribute to blue carbon? An Australian perspective. *Limnol. Oceanogr.* 60 (5), 1689–1706.
- Hillman, J.L.T., Watson, S.J., Maier, K.L., Hoffmann, J.J.L., Bland, K.J., Warnke, F., Pecher, I.A., Gorman, A.R., Davy, B., Bull, S., Woelz, S., 2023. The diverse morphology of pockmarks around Aotearoa New Zealand. *Front. Mar. Sci.* 10.
- Hinestroza, G., Webster, J.M., Beaman, R.J., 2019. Spatio-temporal patterns in the postglacial flooding of the Great Barrier Reef Shelf, Australia. *Cont. Shelf Res.* 173, 13–26.
- Hinestroza, G., Webster, J.M., Beaman, R.J., 2022. New constraints on the postglacial shallow-water carbonate accumulation in the Great Barrier Reef. *Sci Rep* 12, 924. <https://doi.org/10.1038/s41598-021-04586-w>.
- Hopley, D., 1982. *The Geomorphology of the Great Barrier Reef*. Wiley, New York.
- Hopley, D., Smithers, S.G., Parnell, K., 2007. *The Geomorphology of the Great Barrier Reef: Development, Diversity and Change*. Cambridge University Press, Cambridge.
- Huang, Z., Nanson, R., McNeil, M., Wenderlich, M., Gafeira, J., Post, A., Nichol, S., 2023. Rule-based semi-automated tools for mapping seabed morphology from bathymetry data. *Front. Mar. Sci.* 10.
- International Hydrographic Organization, 2019. Standardization of Undersea Feature Names— Guidelines, proposal form, terminology (Edition 4.2.0 - Oct., 2019) (No. IHO Publication B-6). International Hydrographic Bureau, Monaco.
- James, D.E., Tomer, M.D., Porter, S.A., 2014. Trans-scalar landform segmentation from high-resolution digital elevation models. In: *Poster Presented at: ESRI Annual Users Conference: San Diego, California*.
- Jasiewicz, J., Stepinski, T.F., 2013. Geomorphons — a pattern recognition approach to classification and mapping of landforms. *Geomorphology* 182, 147–156.
- Julesz, B., 1981. Textons, the elements of texture perception, and their interactions. *Nature* 290 (5802), 91–97.

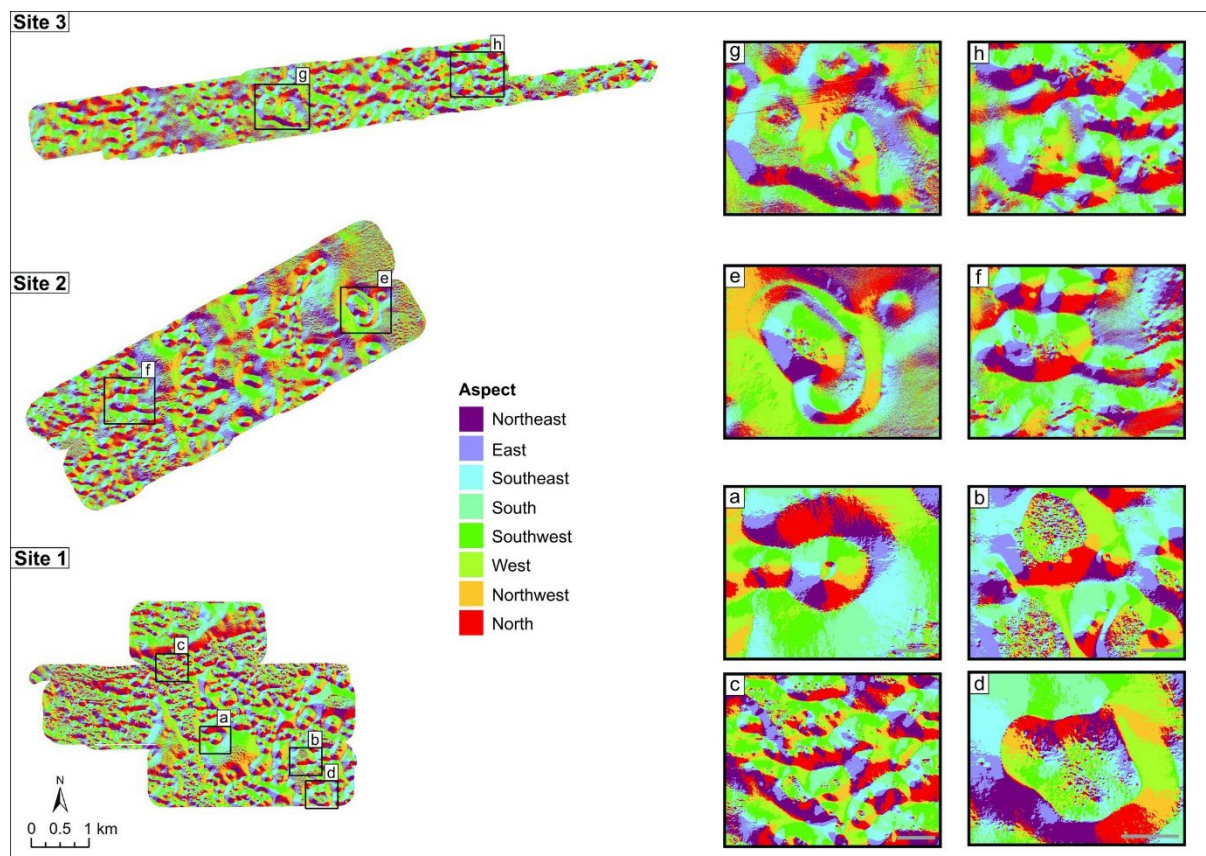
- Kan, H., Urata, K., Nagao, M., Hori, N., Fujita, K., Yokoyama, Y., Nakashima, Y., Ohashi, T., Goto, K., Suzuki, A., 2015. Submerged karst landforms observed by multibeam bathymetric survey in Nagura Bay, Ishigaki Island, southwestern Japan. *Geomorphology* 229, 112–124.
- van der Laan, B.B.P.A., Wolff, W.J., 2006. Circular pools in the seagrass beds of the Banc d'Arguin, Mauritania, and their possible origin. *Aquat. Bot.* 84 (2), 93–100.
- Larcombe, P., Carter, R.M., 2004. Cyclone pumping, sediment partitioning and the development of the Great Barrier Reef shelf system: a review. *Quaternary Science Reviews* 23 (1), 107–135.
- Lecours, V., Dolan, M.F.J., Micallef, A., Luciere, V.L., 2016. A review of marine geomorphometry, the quantitative study of the seafloor. *Hydrol. Earth Syst. Sci.* 20 (8), 3207–3244.
- Liao, W.H., 2010. Region description using extended local ternary patterns. In: *Proceedings 2010 20th International Conference on Pattern Recognition* 23–26 Aug. 2010, pp. 1003–1006.
- Lin, Y., Whitehouse, P.L., Hibbert, F.D., Woodroffe, S.A., Hinestroza, G., Webster, J.M., 2023. Relative Sea level response to mixed carbonate-siliciclastic sediment loading along the Great Barrier Reef margin. *Earth Planet. Sci. Lett.* 607, 118066.
- Lindsay, J.B., Newman, D.R., Francioni, A., 2019. Scale-Optimized Surface Roughness for Topographic Analysis. *Geosciences* 9 (7), 322.
- Lundblad, E.R., Wright, D.J., Miller, J., Larkin, E.M., Rinehart, R., Naar, D.F., Donahue, B.T., Anderson, S.M., Battista, T., 2006. A benthic terrain classification scheme for American Samoa. *Mar. Geod.* 29 (2), 89–111.
- Madin, E.M.P., Precoda, K., Harborne, A.R., Atwood, T.B., Roelfsema, C.M., Luiz, O.J., 2019. Multi-Trophic Species Interactions Shape Seascape-Scale Coral Reef Vegetation patterns. *Front. Ecol. Evol.* v. 7.
- Marsh, L., Huvenne, V.A.L., Jones, D.O.B., 2018. Geomorphological evidence of large vertebrates interacting with the seafloor at abyssal depths in a region designated for deep-sea mining. *R. Soc. Open Sci.* 5 (8), 180286.
- Marshall, J.F., Davies, P.J., 1988. Halimeda bioherms of the northern Great Barrier Reef. *Coral Reefs* 6, 139–148.
- Mathews, E., Heap, A., Woods, M., 2007. Inter-Reefal Seabed Sediments and Geomorphology of the Great Barrier Reef, a Spatial Analysis. *Geoscience Australia*, p. 140.
- McNeil, M., Firn, J., Nothdurft, L.D., Pearse, A.R., Webster, J.M., Roland Pitcher, C., 2021a. Inter-reef Halimeda algal habitats within the Great Barrier Reef support a distinct biotic community and high biodiversity. *Nature Ecology & Evolution*.
- McNeil, M., Nothdurft, L.D., Dyriw, N.J., Webster, J.M., Beaman, R.J., 2021b. Morphotype differentiation in the Great Barrier Reef Halimeda bioherm carbonate factory: Internal architecture and surface geomorphometrics: the Depositional. *Record* 7, 176–199.
- McNeil, M., Nothdurft, L.D., Erler, D.V., Hua, Q., Webster, J.M., 2021c. Variations in mid- to late Holocene nitrogen supply to northern Great Barrier Reef *Halimeda* macroalgal bioherms. *Paleoceanogr. Paleoclimatol.* 36 (2).
- McNeil, M., Nothdurft, L.D., Hua, Q., Webster, J.M., Moss, P., 2022. Evolution of the inter-reef *Halimeda* carbonate factory in response to Holocene Sea-level and environmental change in the Great Barrier Reef. *Quat. Sci. Rev.* 277.
- McNeil, M.A., Webster, J.M., Beaman, R.J., Graham, T.L., 2016. New constraints on the spatial distribution and morphology of the *Halimeda* bioherms of the Great Barrier Reef, Australia. *Coral Reefs* 35 (4), 1343–1355.
- Micallef, A., Foglini, F., Le Bas, T., Angeletti, L., Maselli, V., Pasuto, A., Taviani, M., 2013. The submerged paleolandscape of the Maltese Islands: Morphology, evolution and relation to Quaternary environmental change. *Mar. Geol.* 335, 129–147.
- Minár, J., Evans, I.S., Jenčo, M., 2020. A comprehensive system of definitions of land surface (topographic) curvatures, with implications for their application in geoscience modelling and prediction. *Earth Sci. Rev.* 211, 103414.
- Nanson, R., Arosio, R., Gafeira, J., McNeil, M., Dove, D., Bjarnadóttir, L., Dolan, M., Guinan, J., Post, A., Webb, J., Nichol, S., 2023. A Two-Part Seabed Geomorphology Classification Scheme; Part 2: Geomorphology Classification Framework and Glossary (Version 1.0). *Mareano-Infomare-Maremap-Geoscience Australia*, Zenodo.
- Orme, G.R., 1985. The sedimentological importance of Halimeda in the development of back reef lithofacies, Northern Great Barrier Reef (Australia), in *Proceedings the Fifth International Coral Reef Symposium* 1985, Volume 5, p. 31–37.
- Orme, G.R., Salama, M.S., 1988. Form and seismic stratigraphy of Halimeda banks in part of the northern Great Barrier Reef Province. *Coral Reefs* 6 (3), 131–137.
- Orme, G.R., Flood, P.G., Sargent, G.E.G., 1978a. Sedimentation trends in the lee of outer (ribbon) reefs, Northern Region of the Great Barrier Reef Province. *Phil. Trans. R. Soc. Lond.* 291, 85–99.
- Orme, G.R., Webb, J.P., Kelland, N.C., Sargent, G.E.G., 1978b. Aspects of the geological history and structure of the northern Great Barrier Reef. *Philos. Trans. R. Soc. Lond. Ser. A Math. Phys. Sci.* 291 (1378), 23–35.
- Orpin, A.R., Ridd, P.V., Stewart, L.K., 1999. Assessment of the relative importance of major sediment-transport mechanisms in the central Great Barrier Reef lagoon. *Aust. J. Earth Sci.* 46 (6), 883–896.
- Pascoe, K.H., Fukunaga, A., Kosaki, R.K., Burns, J.H.R., 2021. 3D assessment of a coral reef at Lalo Atoll reveals varying responses of habitat metrics following a catastrophic hurricane. *Sci. Rep.* 11 (1), 12050.
- Perry, C.T., Spencer, T., Kench, P.S., 2008. Carbonate budgets and reef production states: a geomorphic perspective on the ecological phase-shift concept. *Coral Reefs* 27 (4), 853–866.
- Phipps, C.V., Davies, P.J., Hopley, D., 1985. The morphology of Halimeda banks behind the Great Barrier Reef east of Cooktown, QLD, in *Proceedings Proceedings of the Fifth International Coral Reef Congress* 1985, 5, p. 27–30.
- Picard, K., Radke, L., Williams, D., Nicholas, W., Siwabessy, P., Howard, F., Gafeira, J., Przeslawski, R., Huang, Z., Nichol, S., 2018. Origin of high density seabed pockmark fields and their use in inferring bottom currents. *Geosciences* 8 (6).
- Price, D.M., Robert, K., Callaway, A., Lo Iacono, C., Hall, R.A., Huvenne, V.A.I., 2019. Using 3D photogrammetry from ROV video to quantify cold-water coral reef structural complexity and investigate its influence on biodiversity and community assemblage. *Coral Reefs* 38 (5), 1007–1021.
- Purkis, S.J., Koppel, J.V.D., Burgess, P.M., 2016. Spatial Self-Organization in Carbonate Depositional Environments. In: *Autogenic Dynamics and Self-Organization in Sedimentary Systems*, pp. 53–66.
- Rees, S., Opdyke, B., Wilson, P., Henstock, T., 2007. Significance of *Halimeda* bioherms to the global carbonate budget based on a geological sediment budget for the Northern Great Barrier Reef, Australia. *Coral Reefs* 26 (1), 177–188.
- Reolid, J., Bialik, O.M., Lindhorst, S., Eisermann, J.O., Petrovic, A., Hincke, C., Beaman, R.J., Webster, J.M., Betzler, C., 2024. A new type of *Halimeda* bioherm on the Queensland Plateau, NE Australia. *Coral Reefs* 43, 801–821.
- Riddle, M.J., 1988. Cyclone and bioturbation effects on sediments from coral reef lagoons: Estuarine. *Coastal and Shelf Science* 27 (6), 687–695.
- Riera, R., Paumard, V., de Gail, M., Saqab, M.M., Lebre, U., Lang, S.C., Lane, A., 2022. Origin of seafloor pockmarks overlying submarine landslides: Insights from semi-automated mapping of 3D seismic horizons (North West Shelf, Australia). *Mar. Pet. Geol.* 136, 105453.
- Roncolato, F., Fellowes, T.E., Duce, S., Mora, C., Johansson, O., Strachan, I., Bugnot, A. B., Erickson, K., Figueira, W., Gribben, P.E., Pine, C., Morgan, B., Vila-Concejo, A., 2024. Ecomorphodynamics of oyster reefs and their influence on oyster reef morphology. *Geomorphology* 456, 109213.
- Sambrook, K., Hoey, A.S., Andréfouët, S., Cumming, G.S., Duce, S., Bonin, M.C., 2019. Beyond the reef: the widespread use of non-reef habitats by coral reef fishes. *Fish. Fish.* 20 (5), 903–920.
- Sansoleimani, A., Webb, G.E., Harris, D.L., Phinn, S.R., Roelfsema, C.M., 2022. Antecedent topography and active tectonic controls on Holocene reef geomorphology in the Great Barrier Reef. *Geomorphology* 413, 108354.
- Sansoleimani, Atefeh, Webb, Gregory E., Harris, Daniel L., Phinn, Stuart R., Roelfsema, Chris M., 2025. The impact of neotectonics on the geomorphology of the northern Great Barrier Reef. *Coral Reefs* 44 (3), 775–789.
- Sappington, J.M., Longshore, K.M., Thompson, D.B., 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *J. Wildlife Manag.* 71 (5), 1419–1426, 1418.
- Schlager, W., Purkis, S., 2015. Reticulate reef patterns—antecedent karst versus self-organization. *Sedimentology* 62 (2), 501–515.
- Schneider von Deimling, J., Hoffmann, J., Geersen, J., Koschinski, S., Lohrberg, A., Gilles, A., Belkin, I., Böttner, C., Papenmeier, S., Krastel, S., 2023. Millions of seafloor pits, not pockmarks, induced by vertebrates in the North Sea. *Commun. Earth Environ.* 4 (1), 478.
- Searle, D. E., and Flood, P., 1988, *Halimeda bioherms of the Swains Reefs - Southern Great Barrier Reef*, in *Proceedings Proceedings of the International Coral Reef Symposium, Australia, Volume 3*, p. 139–144.
- Sherlock, M., Marouchos, A., Williams, A., Tyndall, A., 2016. A Vessel Towed Platform for Deepwater High Resolution Benthic Imaging: OCEANS 2016 - Shanghai, p. 1–6.
- Sievers, K.T., McClure, E.C., Abesamis, R.A., Russ, G.R., 2020. Non-reef habitats in a tropical seascape affect density and biomass of fishes on coral reefs. *Ecol. Evol.* 10 (24), 13673–13686.
- Skjold, L.J., 1988. A Seismic and Sedimentary Study of the Late Quaternary Development of the Lloyd Bay Area, Northern Great Barrier Reef, Australia. PhD: University of Queensland, 355 p.
- Smith, C., Vila-Concejo, A., Salles, T., 2023. Offshore wave climate of the Great Barrier Reef. *Coral Reefs* 42 (3), 661–676.
- Sun, C., Steinberg, C., Klein Salas, E., Mellin, C., Babcock, R.C., Schiller, A., Cantin, N.E., Stella, J.S., Baird, M.E., Condie, S.A., Hobday, A.J., Herzfeld, M., Jones, N.L., Zhang, X., Chamberlain, M.A., Fiedler, R., Green, C., Steven, A.D.L., 2024. Climate refugia in the Great Barrier Reef may endure into the future: Science. *Advances v. 10*, no. 48 p. ead06884.
- Sun, Q., Wu, S., Hovland, M., Luo, P., Lu, Y., Qu, T., 2011. The morphologies and genesis of mega-pockmarks near the Xisha Uplift. *South China Sea: Marine and Petroleum Geology* 28 (6), 1146–1156.
- Tang, S., Graba-Landry, A., Hoey, A.S., 2020. Density and height of Sargassum influence rabbitfish (f. Siganidae) settlement on inshore reef flats of the Great Barrier Reef. *Coral Reefs* 39 (2), 467–473.
- Taviani, M., Angeletti, L., Campiani, E., Ceregato, A., Foglini, F., Maselli, V., Morsilli, M., Parise, M., Trincardi, F., 2012. Drowned karst landscape offshore the Apulian margin (southern Adriatic Sea, Italy). *J. Cave Karst Stud.* 74 (2), 197–212.
- Ternon, Q., Danet, V., Thiriet, P., Ysnel, F., Feunteun, E., Collin, A., 2022. Classification of underwater photogrammetry data for temperate benthic rocky reef mapping: Estuarine. *Coastal and Shelf Science* 270, 107833.
- Thibaud, R., Del Mondo, G., Garland, T., Mascaret, A., Carpentier, C., 2013. A spatio-temporal graph model for marine dune dynamics analysis and representation. *Trans. GIS* 17 (5), 742–762.
- Thompson, V.D., Reynolds, M.D., Haley, B., Jefferies, R., Johnson, J.K., Humphries, L., 2004. The Sapelo Shell Ring Complex: shallow geophysics on a Georgia Sea Island. *Southeastern Archaeol.* 192–201.
- Walbridge, S., Slocum, N., Pobuda, M., Wright, D.J., 2018. Unified Geomorphological Analysis Workflows with Benthic Terrain Modeler. *Geosciences* 8 (3), 94.
- Webster, J., McNeil, M., Bostock, H., Nothdurft, L., Byrne, M., 2023. Making sense of the Great Barrier Reef's mysterious green donuts. *Eos* 104.
- Wheeler, A.J., Beyer, A., Freiwald, A., de Haas, H., Huvenne, V.A.I., Kozachenko, M., Olu-Le Roy, K., Operbecke, J., 2007. Morphology and environment of cold-water coral carbonate mounds on the NW European margin. *Int. J. Earth Sci.* 96 (1), 37–56.
- Whitehouse, R.J.S., Stroescu, E.I., 2023. Scour depth development at piles of different height under the action of cyclic (tidal) flow. *Coastal Eng.* 179, 104225.

- Whiteway, T., Smithers, S.G., Potter, A., Brooke, B., 2013. Geological and Geomorphological features of outstanding universal value in the Great Barrier Reef World Heritage Area. In: Report prepared for SEWPaC.: Coastal Marine and climate Change Group, Geoscience Australia and School of Earth and Environmental Sciences, James Cook University, 192220188X.
- Wienberg, C., Titschack, J., 2017. Framework-Forming Scleractinian Cold-Water Corals through Space and Time: A late Quaternary North Atlantic Perspective. In: Rossi, S., Bramanti, L., Gori, A., Orejas, C. (Eds.), *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots*. Springer International Publishing, Cham, pp. 699–732.
- Wolanski, E., Kingsford, M.J., 2024. *Oceanographic Processes of Coral Reefs: Physical and Biological Links in the Great Barrier Reef*. CRC Press, Boca Raton.
- Wolanski, E., Drew, E., Abel, K.M., O'Brien, J., 1988. Tidal jets, nutrient upwelling and their influence on the productivity of the alga *Halimeda* in the Ribbon Reefs. *Great Barrier Reef: Estuarine, Coastal and Shelf Science* 26 (2), 169–201.
- Wolanski, E., De Le Court, M., Lambrechts, J., Kingsford, M., 2024. Mechanisms enabling the self-recruitment of passive larvae in the Great Barrier Reef: Estuarine. *Coastal and Shelf Science* 309, 108976.
- Wolff, W., Smit, C., 1990. The Banc d'Arguin, Mauritania, as an environment for coastal birds. *Ardea* 78 (1), 17–38.
- Xi, H., Dong, X., Chirayath, V., Gleason, A.C.R., Purkis, S.J., 2025. Emergent coral reef patterning via spatial self-organization. *Coral Reefs* 44 (1), 273–289.
- Zhuang, J., Yu, Q., Guo, Y., Peng, Y., Li, Y., Wang, Y., 2025. Decoding intertidal oyster reef morphology: Insights from UAV photogrammetry and deep learning. *Mar. Geol.* 480, 107462.

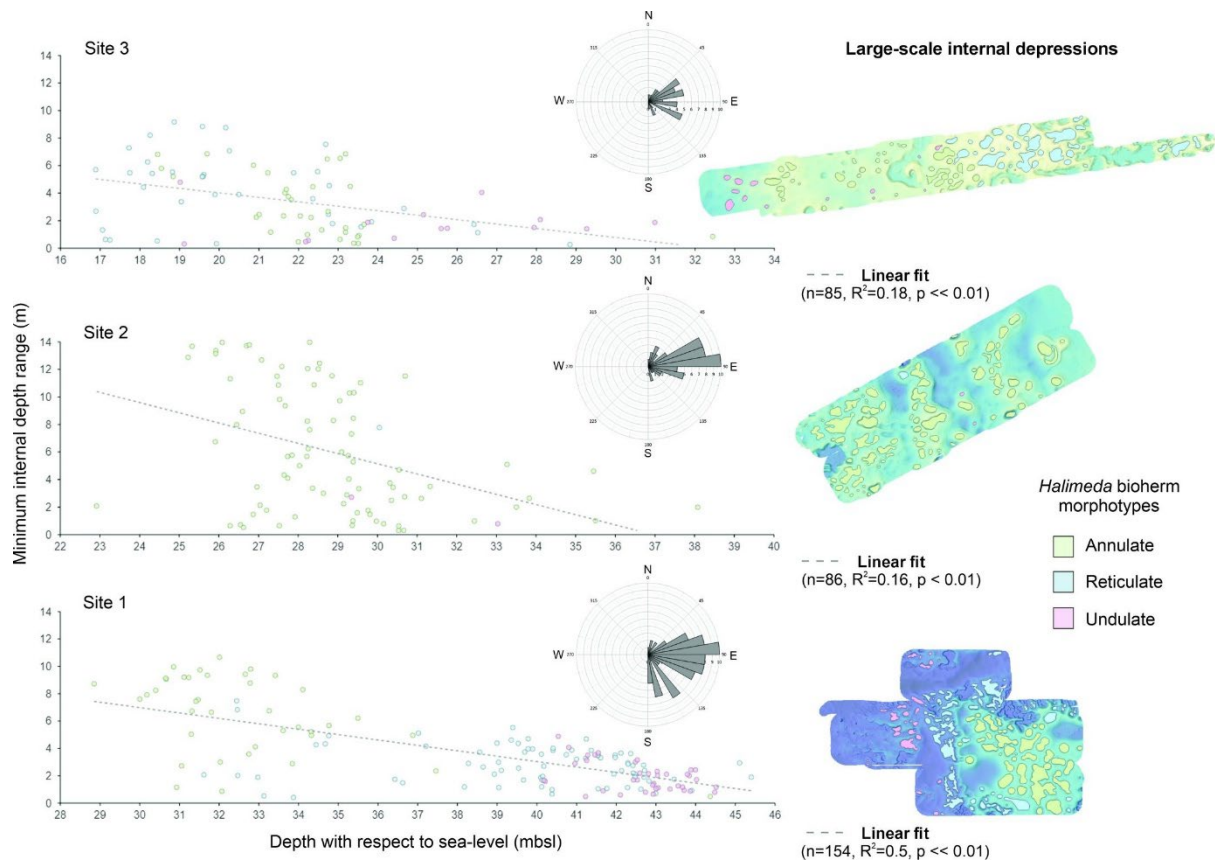
Appendix A. Supplementary data



Supplementary Fig. 1. Profile curvature of the seafloor at each site. Previously presented seafloor features from [Fig. 5](#) were used to show curvature characteristics over the bioherms (a-h).



Supplementary Fig. 2. Aspect metrics of the seafloor at each site. Previously presented seafloor features from [Fig. 5](#) were used to show aspect values over the bioherms (a-h).



Supplementary Fig. 3. Relationship between internal depth range of large-scale internal depressions and their position in the water column classified into *Halimeda* bioherm morphotypes at each site. Rose-diagrams are showing orientation values, while maps are displaying the location and morphotype classification of depressions.

High-Resolution Mapping and Terrain Classification of *Halimeda* Bioherms in the Northern Great Barrier Reef

Zsanett Szilagyi^{1,3*}, Luke Nothdurft¹, Stephanie Duce², Jody M. Webster³, Mardi McNeil^{4,1}, Robin J. Beaman⁵, Juan Carlos Braga⁶, Trevor Graham⁷, Maria Byrne⁸, Amy Nau⁹, Christopher Berry⁹, Victorien Paumard¹⁰, Jeffrey Shragge¹¹, Catherine Kim¹, Helen Bostock⁷

*Corresponding author, zsanett.szilagyi@hdr.qut.edu.au

Supplementary Materials

Supplementary Material. Section 1. Additional information of methods for general geomorphometric analysis (Section 1.1), large-scale internal depression analysis (Section 1.2), and Benthic Terrain Classification of bioherms (Section 1.3).

Section 1: Material and Methods

Section 1.1 Additional information for General geomorphometric analysis of *Halimeda* bioherm features

1. Comparison with previous dataset

- The original *Halimeda* morphotypes' polygon (McNeil et al., 2016) was clipped to the extent of each site.
- Bathymetric data, from the clipped areas, were extracted with *Extract by Mask* function using both the new high-resolution (0.5 m) dataset and the previously available 30 m resolution dataset (Beaman, 2017) for comparative analysis.
- Slope values were computed with *Surface Parameters* tool using the 0.5 m resolution grid to allow comparison with earlier findings by McNeil et al. (2021b).

Section 1.2 Workflow for morphometrics of large-scale internal depressions of *Halimeda* bioherms

To isolate and analyse large-scale internal depressions within *Halimeda* bioherms, the following geoprocessing workflow was applied using ArcGIS Pro 3.3.

1. Depression filling and Raster differencing

- *Fill* tool was used to identify depressions.
- A difference raster was generated by subtracting the original bathymetry from the filled grid.
- Areas showing of ≥ 0.5 m of vertical change were reclassified. This threshold was set based on the vertical uncertainty of the multibeam echosounder system.

2. Polygon generation and cleaning

- Utilizing the newly computed difference raster, the *Raster to Polygon* function was used to draw polygons around the classified areas.
- Polygons < 200 m² were removed to eliminate very small features considered to be noise at this spatial resolution.
- Additional manual polygon removal was then undertaken with the following rules:
 - 1) Polygons that did not encircle bioherm morphologies were removed;
 - 2) Polygons that were on the edges of the study sites were removed;
 - 3) Polygons that were erroneously created because they did not have distinct crests to be filled up until their pouring point were removed.
 - 4) Polygons that partially filled up depressions were removed.

Due to the complexity of bioherm morphologies, polygons were kept that defined smaller depressions within the entire larger scale, complex depressions.

3. Polygon refinement

- The *Eliminate Polygon Part* tool was used to remove empty areas within polygons with a condition namely eliminate polygon parts when their area is less than half of the entire polygon. This removed any noise within the single depressions.
- Following, polygon outlines were smoothed with the *Smooth Polygon* tool using the polynomial approximation with exponential kernel (PEAK) algorithm and 50 m smoothing tolerance. Using this tolerance preserved the complex shapes of depressions while smoothing the perimeters of the polygons.

4. Morphometric analysis

- Internal depth (distance from the lowest point of the crest to the deepest part of the hollow), using *Zonal Statistics*

Table S1 Summary dataset of hypsometric curves at each site.

Table S2 Summary information of Drop Camera images used in this study.

Table S3 Summary of large-scale internal depressions at each site and their statistical analysis.

Table S4 Summary dataset of hypsometry curves of Halimeda bioherm morphotypes at each site using the 0.5 m resolution bathymetric dataset.

Table S5 Summary dataset of bathymetry and slope metrics of Halimeda bioherm morphotypes at each site.

Table S6 Summary of large-scale internal depressions by Halimeda bioherm morphotypes at each site.

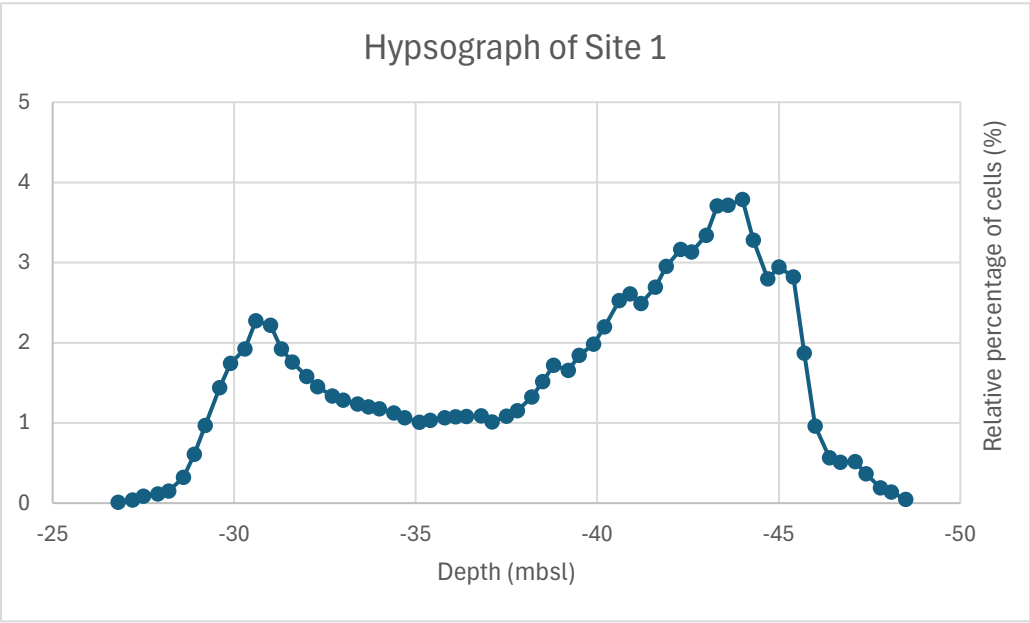
Table S7 Summary dataset of terrain metrics of Halimeda bioherm-specific benthic structures at each site.

Table S8 Summary of biogenic, physical, and Anthropogenic seafloor features.

Site 1					
Min of_Depth	Max of_Depth	Label	Count	Relative percentage of cells	
-48.5	-48.1	-0.4	25110	0.045326999	
-48.1	-47.8	-0.3	76963	0.138928787	
-47.8	-47.4	-0.4	106006	0.191355392	
-47.4	-47.1	-0.3	202603	0.365726247	
-47.1	-46.7	-0.4	286782	0.517680905	
-46.7	-46.4	-0.3	281549	0.508234622	
-46.4	-46	-0.4	313787	0.56642864	
-46	-45.7	-0.3	531685	0.959764463	
-45.7	-45.4	-0.3	1035387	1.869015767	
-45.4	-45	-0.4	1563129	2.821662573	
-45	-44.7	-0.3	1631559	2.945188123	
-44.7	-44.3	-0.4	1548766	2.795735385	
-44.3	-44	-0.3	1817977	3.281698221	
-44	-43.6	-0.4	2097643	3.786533769	
-43.6	-43.3	-0.3	2057154	3.713445562	
-43.3	-43	-0.3	2053061	3.706057135	
-43	-42.6	-0.4	1849504	3.338608787	
-42.6	-42.3	-0.3	1735257	3.132377258	
-42.3	-41.9	-0.4	1753791	3.165833674	
-41.9	-41.6	-0.3	1635486	2.952276897	
-41.6	-41.2	-0.4	1492202	2.693629594	
-41.2	-40.9	-0.3	1379632	2.490425281	
-40.9	-40.6	-0.3	1446010	2.610246689	
-40.6	-40.2	-0.4	1399893	2.526999169	
-40.2	-39.9	-0.3	1216755	2.196409921	
-39.9	-39.5	-0.4	1099254	1.984304475	
-39.5	-39.2	-0.3	1020699	1.842501909	
-39.2	-38.8	-0.4	917780	1.656718976	
-38.8	-38.5	-0.3	952580	1.719537756	
-38.5	-38.2	-0.3	840391	1.5170212	
-38.2	-37.8	-0.4	733454	1.323985225	
-37.8	-37.5	-0.3	638030	1.151731796	
-37.5	-37.1	-0.4	601191	1.085232341	
-37.1	-36.8	-0.3	560223	1.011279473	
-36.8	-36.4	-0.4	603272	1.088988832	
-36.4	-36.1	-0.3	599257	1.081741205	
-36.1	-35.8	-0.3	596097	1.076036971	
-35.8	-35.4	-0.4	590015	1.065058126	
-35.4	-35.1	-0.3	571998	1.032534966	
-35.1	-34.7	-0.4	559250	1.009523074	
-34.7	-34.4	-0.3	590211	1.065411933	
-34.4	-34	-0.4	622941	1.124494079	
-34	-33.7	-0.3	651820	1.176624641	
-33.7	-33.4	-0.3	665506	1.201329751	
-33.4	-33	-0.4	684400	1.235436016	
-33	-32.7	-0.3	710352	1.282282941	

-32.7	-32.3	-0.4	739131	1.33423299
-32.3	-32	-0.3	804040	1.451402651
-32	-31.6	-0.4	874932	1.57937245
-31.6	-31.3	-0.3	974502	1.759109978
-31.3	-31	-0.3	1065205	1.922841353
-31	-30.6	-0.4	1228041	2.216782701
-30.6	-30.3	-0.3	1260311	2.275034484
-30.3	-29.9	-0.4	1064509	1.921584977
-29.9	-29.6	-0.3	966039	1.7438331
-29.6	-29.2	-0.4	797405	1.439425565
-29.2	-28.9	-0.3	537325	0.969945438
-28.9	-28.6	-0.3	337813	0.609798871
-28.6	-28.2	-0.4	178408	0.322050948
-28.2	-27.9	-0.3	84245	0.152073798
-27.9	-27.5	-0.4	63996	0.115521571
-27.5	-27.2	-0.3	47828	0.08633611
-27.2	-26.8	-0.4	21963	0.039646232
-26.8	-26.5	-0.3	5341	0.009641239

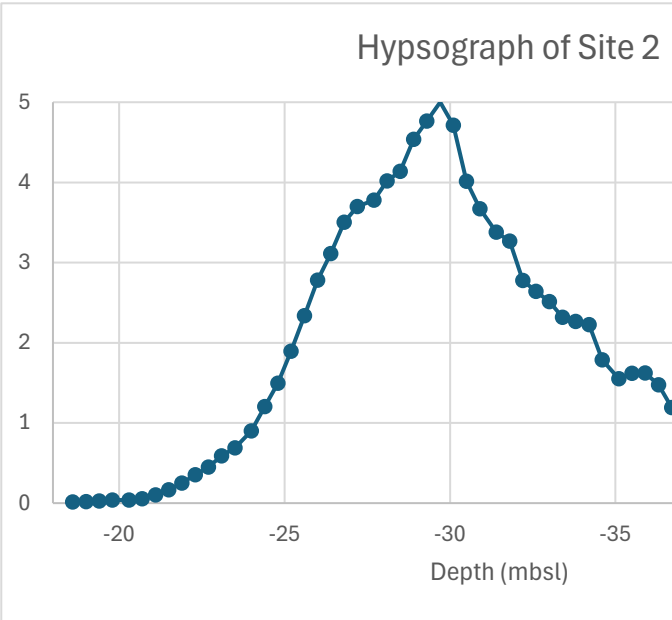
SUM		55397446	100
PEAK	-44	2097643	



Site 2			
Min of_Depth	Max of_Depth	Label	Count
-44.5	-44.1	-0.4	1359
-44.1	-43.7	-0.4	1778
-43.7	-43.3	-0.4	3206
-43.3	-42.9	-0.4	3494
-42.9	-42.5	-0.4	6917
-42.5	-42.1	-0.4	6824
-42.1	-41.6	-0.5	5637
-41.6	-41.2	-0.4	9121
-41.2	-40.8	-0.4	16783
-40.8	-40.4	-0.4	31961
-40.4	-40	-0.4	120889
-40	-39.6	-0.4	213823
-39.6	-39.2	-0.4	285170
-39.2	-38.8	-0.4	488521
-38.8	-38.3	-0.5	560405
-38.3	-37.9	-0.4	734289
-37.9	-37.5	-0.4	557033
-37.5	-37.1	-0.4	606738
-37.1	-36.7	-0.4	635835
-36.7	-36.3	-0.4	729741
-36.3	-35.9	-0.4	903248
-35.9	-35.5	-0.4	994566
-35.5	-35.1	-0.4	991015
-35.1	-34.6	-0.5	950612
-34.6	-34.2	-0.4	1094869
-34.2	-33.8	-0.4	1363127
-33.8	-33.4	-0.4	1386512
-33.4	-33	-0.4	1418087
-33	-32.6	-0.4	1537943
-32.6	-32.2	-0.4	1615845
-32.2	-31.8	-0.4	1700382
-31.8	-31.4	-0.4	1999932
-31.4	-30.9	-0.5	2068556
-30.9	-30.5	-0.4	2247030
-30.5	-30.1	-0.4	2456140
-30.1	-29.7	-0.4	2885487
-29.7	-29.3	-0.4	3060658
-29.3	-28.9	-0.4	2916631
-28.9	-28.5	-0.4	2777744
-28.5	-28.1	-0.4	2531993
-28.1	-27.7	-0.4	2459682
-27.7	-27.2	-0.5	2313495
-27.2	-26.8	-0.4	2263439
-26.8	-26.4	-0.4	2145518
-26.4	-26	-0.4	1905697
-26	-25.6	-0.4	1701170

-25.6	-25.2	-0.4	1430230
-25.2	-24.8	-0.4	1160941
-24.8	-24.4	-0.4	915996
-24.4	-24	-0.4	736275
-24	-23.5	-0.5	552450
-23.5	-23.1	-0.4	421457
-23.1	-22.7	-0.4	360279
-22.7	-22.3	-0.4	274325
-22.3	-21.9	-0.4	215557
-21.9	-21.5	-0.4	152574
-21.5	-21.1	-0.4	101839
-21.1	-20.7	-0.4	62233
-20.7	-20.3	-0.4	32754
-20.3	-19.8	-0.5	24414
-19.8	-19.4	-0.4	22975
-19.4	-19	-0.4	16623
-19	-18.6	-0.4	12082
-18.6	-18.2	-0.4	9432

SUM		61211338
PEAK	-29.7	3060658



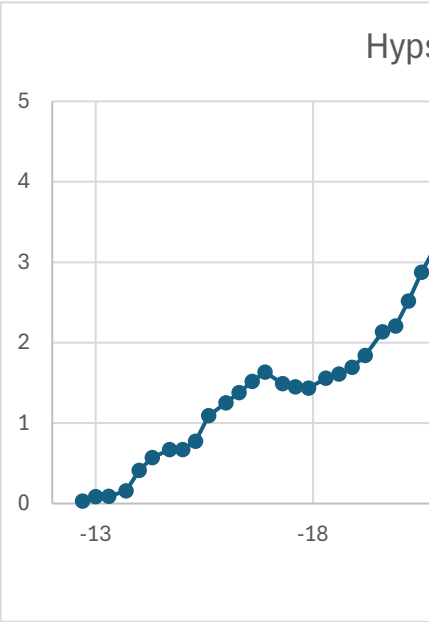
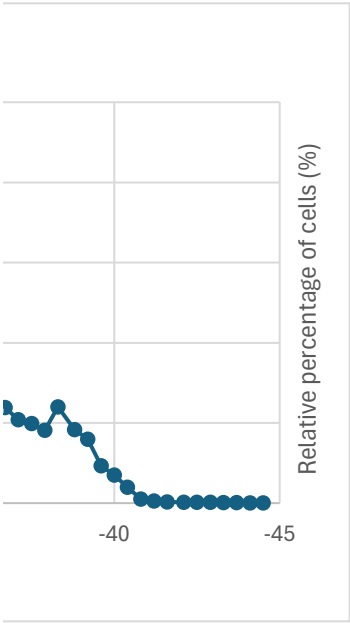
Relative percentage of cells	Min of_Depth	Max of_Depth
0.002220177	-33.3	-33
0.002904691	-33	-32.6
0.005237592	-32.6	-32.3
0.005708093	-32.3	-32
0.011300194	-32	-31.7
0.011148261	-31.7	-31.3
0.009209078	-31.3	-31
0.014900834	-31	-30.7
0.027418123	-30.7	-30.3
0.052214183	-30.3	-30
0.197494458	-30	-29.7
0.349319272	-29.7	-29.4
0.465877743	-29.4	-29
0.798089073	-29	-28.7
0.915524833	-28.7	-28.4
1.199596388	-28.4	-28.1
0.91001605	-28.1	-27.7
0.991218326	-27.7	-27.4
1.038753637	-27.4	-27.1
1.192166392	-27.1	-26.8
1.475622049	-26.8	-26.4
1.624806829	-26.4	-26.1
1.619005616	-26.1	-25.8
1.552999871	-25.8	-25.4
1.788670262	-25.4	-25.1
2.226919137	-25.1	-24.8
2.265122844	-24.8	-24.5
2.316706425	-24.5	-24.1
2.512513286	-24.1	-23.8
2.639780558	-23.8	-23.5
2.777887325	-23.5	-23.2
3.267257448	-23.2	-22.8
3.379367398	-22.8	-22.5
3.670937564	-22.5	-22.2
4.012557281	-22.2	-21.8
4.713974721	-21.8	-21.5
5.000148829	-21.5	-21.2
4.764854184	-21.2	-20.9
4.537956677	-20.9	-20.5
4.136477134	-20.5	-20.2
4.018343791	-20.2	-19.9
3.779520389	-19.9	-19.6
3.697744689	-19.6	-19.2
3.505099006	-19.2	-18.9
3.113307211	-18.9	-18.6
2.779174669	-18.6	-18.3

2.336544253	-18.3	-17.9
1.896611049	-17.9	-17.6
1.496448256	-17.6	-17.3
1.202840885	-17.3	-16.9
0.902528875	-16.9	-16.6
0.688527671	-16.6	-16.3
0.588582135	-16.3	-16
0.448160437	-16	-15.6
0.35215208	-15.6	-15.3
0.249257744	-15.3	-15
0.166372772	-15	-14.7
0.101669073	-14.7	-14.3
0.053509695	-14.3	-14
0.039884768	-14	-13.7
0.037533896	-13.7	-13.3
0.027156734	-13.3	-13
0.019738173	-13	-12.7
0.01540891	-12.7	-12.4

100

SUM
PEAK

-21.8



Site 3

Label	Count	Relative number of cells
-0.3	12103	0.028155398
-0.4	34449	0.080139248
-0.3	90563	0.210678124
-0.3	166161	0.386542934
-0.3	127243	0.296007382
-0.4	110975	0.258162879
-0.3	127626	0.296898361
-0.3	160375	0.373082872
-0.4	135127	0.314348054
-0.3	188231	0.43788472
-0.3	273560	0.636386908
-0.3	330842	0.769642921
-0.4	630210	1.466067383
-0.3	704446	1.638763751
-0.3	605625	1.408874913
-0.3	502220	1.168322243
-0.4	490705	1.141534719
-0.3	525434	1.222325335
-0.3	519337	1.208141788
-0.3	590886	1.374587346
-0.4	655161	1.524111285
-0.3	663899	1.544438631
-0.3	637259	1.482465582
-0.4	655121	1.524018232
-0.3	737723	1.716176557
-0.3	848403	1.973653173
-0.3	884084	2.056658441
-0.4	961962	2.237827251
-0.3	1104426	2.569243483
-0.3	1236418	2.876298538
-0.3	1610458	3.746433642
-0.4	1740997	4.05010856
-0.3	1669759	3.884386486
-0.3	1633448	3.799915638
-0.4	1596418	3.71377217
-0.3	1802894	4.194100519
-0.3	1777489	4.13500047
-0.3	1650319	3.83916291
-0.4	1405837	3.270420608
-0.3	1235998	2.875321485
-0.3	1082083	2.517266613
-0.3	948610	2.206766284
-0.4	917310	2.133952605
-0.3	791735	1.841825518
-0.3	727676	1.692804064
-0.3	692451	1.610859595

-0.4	670414	1.559594577
-0.3	616010	1.433033701
-0.3	623796	1.451146394
-0.4	639900	1.488609382
-0.3	702372	1.633938973
-0.3	652125	1.51704859
-0.3	593359	1.380340325
-0.4	538794	1.253404912
-0.3	468944	1.090911764
-0.3	331960	0.772243742
-0.3	287881	0.669702074
-0.4	287825	0.669571801
-0.3	245726	0.571636238
-0.3	177575	0.413095501
-0.4	67786	0.157691632
-0.3	37847	0.088044068
-0.3	37480	0.08719031
-0.3	12578	0.029260398

42986428

100

1802894

sograph of Site 3

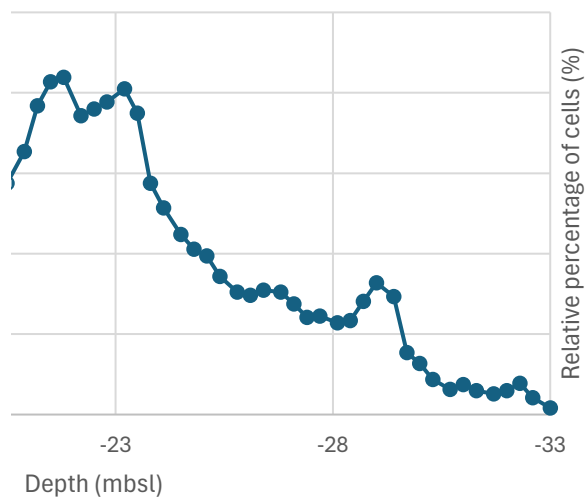
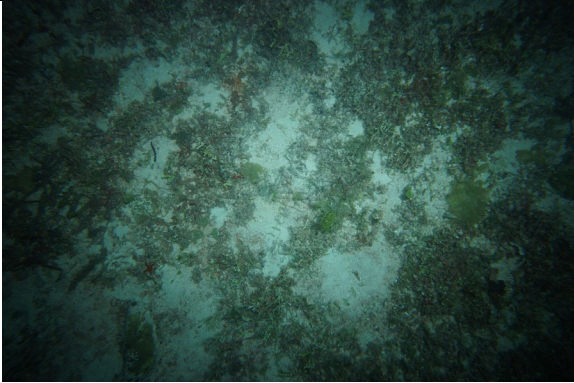
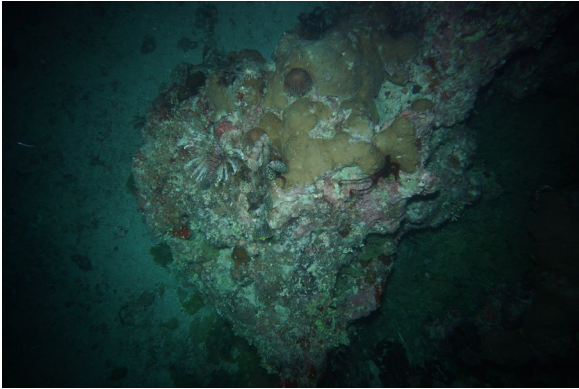
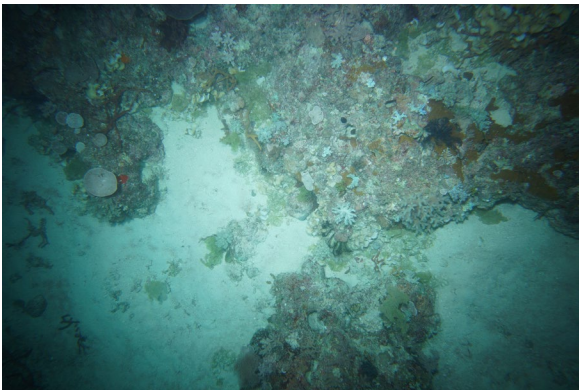
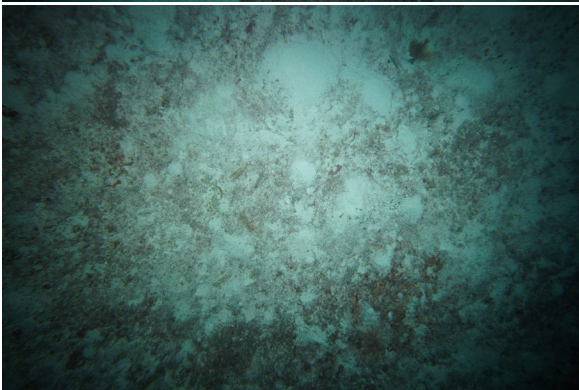


Image ID	High-resolution image	Site	Benthic structure
DC30		2	Slope (outer)
DC32		2	Pinnacle
DC34		2	Hard outcrop on outer slope
DC77		3	Slope (inner)

Longitude	Latitude	Depth with respect to sea-level (mbsl)
-----------	----------	--

145.5807514	-14.63345749	29.4
-------------	--------------	------

145.5785673	-14.63102666	38.8
-------------	--------------	------

145.58065	-14.63252883	25.1
-----------	--------------	------

143.8948343	-13.20850754	21.1
-------------	--------------	------

Site 1	MIN	MAX	AVERAGE
Internal depth range (m)	0.41	10.67	3.54
Area (m2)	184.00	251538.00	
Circularity	0.08	0.63	0.48
Length (m)	16.2	884.3	161.6
Width (m)	14.4	540.2	93.5
Length/Width ratio	1.01	3.76	1.71
Depth with respect to sea-level (mbsl)*	45.4	28.8	38.7
*the lowest point of the crest			
Orientation (°)**	22.4	177.9	102.8
**≥2 Length/ Width ratio			
Orientation (°)***	4.7	177.9	101
***≥1.5 Length/ Width ratio			

Site 2	MIN	MAX	AVERAGE
Internal depth range (m)	0.3	14.0	5.9
Area (m2)	464.5	159120.0	
Circularity	0.17	0.64	0.49
Length (m)	39.2	753.6	216.6
Width (m)	15.4	392.9	128.0
Length/Width ratio	1.10	3.06	1.68
Depth with respect to sea-level (mbsl)*	38.1	22.9	28.9
*the lowest point of the crest			
Orientation (°)*	26.4	105.6	72.4
*≥2 Length/Width ratio			
Orientation (°)**	8.1	167.4	80
* ≥1.5 Length/Width ratio			

Site 3	MIN	MAX	AVERAGE
Internal depth range (m)	0.3	9.2	3.4
Area (m2)	919.5	93077.0	
Circularity	0.10	0.62	0.52

Length (m)	22.7	627.2	170.7
Width (m)	14.2	331.7	105.3
Length/Width ratio	1.03	3.15	1.57
Depth with respect to sea-level (mbsl)*	32.4	16.9	22.0

*the lowest point of the crest

Orientation (°)*	47.8	178.4	89.2
-------------------------	------	-------	-------------

* ≥ 2 Length/Width ratio

Orientation (°)*	0.8	178.4	82
-------------------------	-----	-------	-----------

* ≥ 1.5 Length/Width ratio

STD	STE	Number of polygons
2.53	0.20	154
0.14	0.01	
144.7	11.7	
79.9	6.4	
0.60	0.05	
4.5	0.4	
36.3	2.9	
41	3.3	

STD	STE	Number of polygon
4.4	0.4	86
0.12	0.01	
140.0	11.3	
74.2	6.0	
0.42	0.03	
2.4	0.2	
21.0	1.7	
35	2.8	

STD	STE	Number of polygon
2.4	0.2	85
0.11	0.01	

127.5	10.3
64.7	5.2
0.47	0.04
3.2	0.3

34.0	2.7
------	-----

38	3.1
----	-----

Depth (mbsl) vs Internal depth range (m)

Fit Results

Linear Fit - RR_filled_depth_vs_range

Data Source Plot = RR_filled_depth_vs_range

Equation $Y = -0.39480739 * X + 18.828958$

Number of data points used = 154

Average X = 38.73054

Average Y = 3.5378545

Residual sum of squares = 492.59387

Regression sum of squares = 489.26303

Coefficient of determination, R-sq'd = 0.49830381

Correlation coefficient, R = 0.70590637

Residual mean square, sigma-hat-sq'd = 3.2407491

P-Value = Less than 0.0001

Standard error of intercept (A) = +/-1.2529132

Standard error of slope (B) = +/-0.032131928

Depth (mbsl) vs Internal depth range (m)

Fit Results

Linear Fit - RR_filled_depth_vs_range

Data Source Plot = CR_filled_depth_vs_range

Equation $Y = -0.74060145 * X + 27.365214$

Number of data points used = 86

Average X = 28.921323

Average Y = 5.9460398

Residual sum of squares = 1411.945

Regression sum of squares = 268.55714

Coefficient of determination, R-sq'd = 0.15980767

Correlation coefficient, R = 0.39975952

Residual mean square, sigma-hat-sq'd = 16.808869

P-Value = 0.0001371476

Standard error of intercept (A) = +/-5.3768342

Standard error of slope (B) = +/-0.18528295

Depth (mbsl) vs Internal depth range (m)

Fit Results

Linear Fit - TR_filled_depth_vs_range

Data Source Plot = TR_filled_depth_vs_range

Equation $Y = -0.32447861 * X + 10.510292$

Number of data points used = 85

Average X = 21.964329

Average Y = 3.3833372

Residual sum of squares = 407.15438

Regression sum of squares = 91.277984

Coefficient of determination, $R\text{-sq'd} = 0.18313013$

Correlation coefficient, $R = 0.42793706$

Residual mean square, $\sigma\text{-hat-sq'd} = 4.9054745$

P-Value = Less than 0.0001

Standard error of intercept (A) = ± 1.6695695

Standard error of slope (B) = ± 0.075221772

Length (m) vs Width (m)

Fit Results

Linear Fit - MBG_Width

Data Source Plot = RR_Length vs Width

Equation $Y = 0.50132578 * X + 12.490607$

Number of data points used = 154

Average X = 161.64188

Average Y = 93.525851

Residual sum of squares = 171200.34

Regression sum of squares = 810941.63

Coefficient of determination, R-sq'd = 0.82568677

Correlation coefficient, R = 0.90867308

Residual mean square, sigma-hat-sq'd = 1126.318

P-Value = Less than 0.0001

Standard error of intercept (A) = +/-4.0539201

Standard error of slope (B) = +/-0.018683394

Length (m) vs Width (m)

Fit Results

Linear Fit - CR_Length vs Width

Data Source Plot = CR_Length vs Width

Equation $Y = 0.49090992 * X + 21.619552$

Number of data points used = 86

Average X = 216.60971

Average Y = 127.95541

Residual sum of squares = 66493.774

Regression sum of squares = 406376.59

Coefficient of determination, R-sq'd = 0.85938266

Correlation coefficient, R = 0.92702894

Residual mean square, sigma-hat-sq'd = 791.59255

P-Value = Less than 0.0001

Standard error of intercept (A) = +/-5.5884169

Standard error of slope (B) = +/-0.021666478

Length (m) vs Width (m)

Fit Results

Linear Fit - TR_Length vs Width

Data Source Plot = TR_Length vs Width

Equation $Y = 0.45436776 * X + 27.735882$

Number of data points used = 85

Average X = 170.70129

Average Y = 105.29705

Residual sum of squares = 70220.86

Regression sum of squares = 285095.62

Coefficient of determination, $R\text{-sq'd} = 0.80237094$

Correlation coefficient, $R = 0.89575161$

Residual mean square, $\sigma\text{-hat-sq'd} = 846.03446$

P-Value = Less than 0.0001

Standard error of intercept (A) = ± 5.2730747

Standard error of slope (B) = ± 0.02475177

UNDULATE

Min of_Depth	Max of_Depth	Label	Count	Relative percentage of cells
-47.7	-47.5	-0.2	1301	0.002583383
-47.5	-47.3	-0.2	5706	0.011330349
-47.3	-47.1	-0.2	12816	0.025448607
-47.1	-46.9	-0.2	15263	0.030307591
-46.9	-46.7	-0.2	27530	0.054666055
-46.7	-46.5	-0.2	39797	0.079024518
-46.5	-46.4	-0.1	51779	0.102817059
-46.4	-46.2	-0.2	63873	0.126831998
-46.2	-46	-0.2	70625	0.140239379
-46	-45.8	-0.2	93131	0.184929325
-45.8	-45.6	-0.2	144750	0.287428674
-45.6	-45.4	-0.2	220192	0.437233123
-45.4	-45.2	-0.2	327998	0.651302454
-45.2	-45	-0.2	409360	0.81286219
-45	-44.8	-0.2	434496	0.862774502
-44.8	-44.6	-0.2	436354	0.866463914
-44.6	-44.4	-0.2	440777	0.875246623
-44.4	-44.2	-0.2	508465	1.009654029
-44.2	-44.1	-0.1	555353	1.102759077
-44.1	-43.9	-0.2	640093	1.271026475
-43.9	-43.7	-0.2	687413	1.364989341
-43.7	-43.5	-0.2	671605	1.333599548
-43.5	-43.3	-0.2	687593	1.365346765
-43.3	-43.1	-0.2	668613	1.327658363
-43.1	-42.9	-0.2	674604	1.339554633
-42.9	-42.7	-0.2	626304	1.243645791
-42.7	-42.5	-0.2	592729	1.176976238
-42.5	-42.3	-0.2	582125	1.155919978
-42.3	-42.1	-0.2	587032	1.165663761
-42.1	-42	-0.1	570126	1.13209368
-42	-41.8	-0.2	529998	1.052411899
-41.8	-41.6	-0.2	451902	0.897337428
-41.6	-41.4	-0.2	422172	0.838302854
-41.4	-41.2	-0.2	396660	0.787643923
-41.2	-41	-0.2	353898	0.702731833
-41	-40.8	-0.2	356423	0.707745701
-40.8	-40.6	-0.2	344422	0.683915432
-40.6	-40.4	-0.2	329502	0.654288932
-40.4	-40.2	-0.2	282166	0.560294295
-40.2	-40	-0.2	239216	0.475008896
-40	-39.8	-0.2	219619	0.436095323
-39.8	-39.7	-0.1	217260	0.431411079
-39.7	-39.5	-0.2	197851	0.392870816
-39.5	-39.3	-0.2	180697	0.358808284
-39.3	-39.1	-0.2	147751	0.293387731

-39.1	-38.9	-0.2	130441	0.259015431
-38.9	-38.7	-0.2	121073	0.240413484
-38.7	-38.5	-0.2	109380	0.217194807
-38.5	-38.3	-0.2	100305	0.199174668
-38.3	-38.1	-0.2	85006	0.168795591
-38.1	-37.9	-0.2	65157	0.129381624
-37.9	-37.7	-0.2	51406	0.102076397
-37.7	-37.6	-0.1	37375	0.074215176
-37.6	-37.4	-0.2	38320	0.076091653
-37.4	-37.2	-0.2	32422	0.064380052
-37.2	-37	-0.2	21282	0.042259461
-37	-36.8	-0.2	18309	0.036356004
-36.8	-36.6	-0.2	15553	0.030883442
-36.6	-36.4	-0.2	9876	0.019610678
-36.4	-36.2	-0.2	6739	0.013381567
-36.2	-36	-0.2	6931	0.01376282
-36	-35.8	-0.2	6852	0.01360595
-35.8	-35.6	-0.2	3026	0.006008699
-35.6	-35.4	-0.2	1162	0.002307372

	All cell count
SUM	50360320

UNDULATE

-36.5	-36.3	-0.2	286922	0.468769902
-36.3	-36.1	-0.2	357710	0.584422531
-36.1	-35.8	-0.3	370214	0.604851424
-35.8	-35.6	-0.2	400696	0.654652569
-35.6	-35.4	-0.2	406804	0.66463175
-35.4	-35.1	-0.3	389564	0.636465234
-35.1	-34.9	-0.2	338345	0.552784214
-34.9	-34.6	-0.3	347154	0.567176258
-34.6	-34.4	-0.2	382468	0.62487187
-34.4	-34.2	-0.2	463761	0.757687449
-34.2	-33.9	-0.3	558898	0.913121198
-33.9	-33.7	-0.2	555237	0.907139898
-33.7	-33.5	-0.2	500359	0.817480846
-33.5	-33.2	-0.3	478745	0.782168138
-33.2	-33	-0.2	472889	0.772600672
-33	-32.8	-0.2	442897	0.723600083
-32.8	-32.5	-0.3	484113	0.790938316
-32.5	-32.3	-0.2	451183	0.737137656
-32.3	-32	-0.3	444887	0.726851323
-32	-31.8	-0.2	450203	0.735536543
-31.8	-31.6	-0.2	487662	0.796736631
-31.6	-31.3	-0.3	571227	0.933264178
-31.3	-31.1	-0.2	504276	0.823880396
-31.1	-30.9	-0.2	451438	0.737554272
-30.9	-30.6	-0.3	476159	0.777943161
-30.6	-30.4	-0.2	500912	0.818384331
-30.4	-30.2	-0.2	565250	0.923499024
-30.2	-29.9	-0.3	635686	1.03857656
-29.9	-29.7	-0.2	758914	1.239905065
-29.7	-29.5	-0.2	723589	1.182191482
-29.5	-29.2	-0.3	608688	0.994467534
-29.2	-29	-0.2	500451	0.817631154
-29	-28.7	-0.3	399696	0.653018781
-28.7	-28.5	-0.2	340358	0.556073031
-28.5	-28.3	-0.2	274484	0.448448839
-28.3	-28	-0.3	219689	0.358925391
-28	-27.8	-0.2	166295	0.27169088
-27.8	-27.6	-0.2	131515	0.214867712
-27.6	-27.3	-0.3	100916	0.164875413
-27.3	-27.1	-0.2	59953	0.09795053
-27.1	-26.9	-0.2	38891	0.063539674
-26.9	-26.6	-0.3	25556	0.041753102
-26.6	-26.4	-0.2	15905	0.025985408
-26.4	-26.1	-0.3	5666	0.009257046

PEAK

-29.9

758914

All cell count

SUM

61207428

UNDULATE

Min of_Band_1	Max of_Band_1	Label	Count	Relative percentage of cells
-32.5	-32.2	-0.3	1821	0.004311403
-32.2	-31.9	-0.3	13428	0.031792159
-31.9	-31.6	-0.3	21429	0.050735343
-31.6	-31.3	-0.3	28688	0.067921766
-31.3	-31	-0.3	40316	0.095452241
-31	-30.7	-0.3	58025	0.137380105
-30.7	-30.4	-0.3	57532	0.136212877
-30.4	-30.2	-0.2	100306	0.237484684
-30.2	-29.9	-0.3	188791	0.446981946
-29.9	-29.6	-0.3	244354	0.578533014
-29.6	-29.3	-0.3	195733	0.463417838
-29.3	-29	-0.3	235421	0.557383226
-29	-28.7	-0.3	261639	0.619457015
-28.7	-28.4	-0.3	251350	0.595096758
-28.4	-28.1	-0.3	249602	0.59095819
-28.1	-27.8	-0.3	214159	0.507043273
-27.8	-27.5	-0.3	262783	0.622165551
-27.5	-27.2	-0.3	218607	0.517574366
-27.2	-26.9	-0.3	238966	0.565776375
-26.9	-26.6	-0.3	279417	0.661548243
-26.6	-26.4	-0.2	289359	0.685086942
-26.4	-26.1	-0.3	292674	0.692935542
-26.1	-25.8	-0.3	276444	0.654509362
-25.8	-25.5	-0.3	271799	0.643511851
-25.5	-25.2	-0.3	323602	0.766160736
-25.2	-24.9	-0.3	452183	1.070589366
-24.9	-24.6	-0.3	378385	0.895865075
-24.6	-24.3	-0.3	392478	0.92923169
-24.3	-24	-0.3	401878	0.951487149
-24	-23.7	-0.3	478483	1.132857299
-23.7	-23.4	-0.3	489258	1.15836821
-23.4	-23.1	-0.3	545182	1.290773983
-23.1	-22.8	-0.3	506136	1.198328596
-22.8	-22.5	-0.3	387412	0.917237419
-22.5	-22.3	-0.2	310025	0.734015804
-22.3	-22	-0.3	339436	0.803649346
-22	-21.7	-0.3	402031	0.951849392
-21.7	-21.4	-0.3	444902	1.053350856
-21.4	-21.1	-0.3	360524	0.853577336
-21.1	-20.8	-0.3	318221	0.75342067
-20.8	-20.5	-0.3	231947	0.549158177
-20.5	-20.2	-0.3	145084	0.343501166
-20.2	-19.9	-0.3	112299	0.265879335

-19.9	-19.6	-0.3	80639	0.190921056
-19.6	-19.3	-0.3	69315	0.164110331
-19.3	-19	-0.3	56529	0.133838172
-19	-18.7	-0.3	52842	0.125108824
-18.7	-18.5	-0.2	54451	0.128918295
-18.5	-18.2	-0.3	53471	0.126598046
-18.2	-17.9	-0.3	50176	0.118796797
-17.9	-17.6	-0.3	43358	0.102654487
-17.6	-17.3	-0.3	37135	0.0879209
-17.3	-17	-0.3	32269	0.076400148
-17	-16.7	-0.3	28972	0.068594165
-16.7	-16.4	-0.3	27308	0.064654475
-16.4	-16.1	-0.3	26976	0.063868431
-16.1	-15.8	-0.3	18999	0.04498207
-15.8	-15.5	-0.3	10690	0.025309665
-15.5	-15.2	-0.3	6699	0.015860566
-15.2	-14.9	-0.3	5625	0.013317761
-14.9	-14.7	-0.2	4335	0.010263555
-14.7	-14.4	-0.3	4396	0.010407978
-14.4	-14.1	-0.3	4256	0.010076514
-14.1	-13.8	-0.3	2586	0.006122619

PEAK	-23.4	545182
------	-------	--------

	All cell count
SUM	42236829

Site 1_0.5m

RETICULATE

Min of_Depth	Max of_Depth	Label	Count	Relative percentage of cells
-48.1	-47.7	-0.4	3514	0.006977716
-47.7	-47.4	-0.3	5365	0.010653229
-47.4	-47	-0.4	4288	0.00851464
-47	-46.7	-0.3	9047	0.01796454
-46.7	-46.4	-0.3	12349	0.02452129
-46.4	-46	-0.4	23660	0.046981433
-46	-45.7	-0.3	36777	0.073027733
-45.7	-45.4	-0.3	75021	0.148968474
-45.4	-45	-0.4	124143	0.246509554
-45	-44.7	-0.3	208040	0.413103014
-44.7	-44.4	-0.3	293260	0.582323544
-44.4	-44	-0.4	441927	0.877530167
-44	-43.7	-0.3	539024	1.07033474
-43.7	-43.3	-0.4	585232	1.162089518
-43.3	-43	-0.3	617855	1.226868693
-43	-42.7	-0.3	617942	1.227041449
-42.7	-42.3	-0.4	588950	1.169472315
-42.3	-42	-0.3	576561	1.144871597
-42	-41.7	-0.3	601357	1.194108775
-41.7	-41.3	-0.4	619997	1.231122042
-41.3	-41	-0.3	626956	1.244940461
-41	-40.6	-0.4	665388	1.321254511
-40.6	-40.3	-0.3	757279	1.503721581
-40.3	-40	-0.3	691419	1.372944016
-40	-39.6	-0.4	583056	1.157768656
-39.6	-39.3	-0.3	557839	1.107695503
-39.3	-39	-0.3	549920	1.091970821
-39	-38.6	-0.4	580819	1.153326667
-38.6	-38.3	-0.3	545055	1.082310438
-38.3	-38	-0.3	472096	0.937436458
-38	-37.6	-0.4	422908	0.839764322
-37.6	-37.3	-0.3	377314	0.749228758
-37.3	-36.9	-0.4	326834	0.64899111
-36.9	-36.6	-0.3	292133	0.580085671
-36.6	-36.3	-0.3	263948	0.524118989
-36.3	-35.9	-0.4	252464	0.501315321
-35.9	-35.6	-0.3	247280	0.491021503
-35.6	-35.3	-0.3	240746	0.478047002
-35.3	-34.9	-0.4	233568	0.463793717
-34.9	-34.6	-0.3	230558	0.457816789
-34.6	-34.2	-0.4	240348	0.477256697
-34.2	-33.9	-0.3	249150	0.494734744
-33.9	-33.6	-0.3	255885	0.508108368
-33.6	-33.2	-0.4	240140	0.476843674
-33.2	-32.9	-0.3	242066	0.480668113

-32.9	-32.6	-0.3	245775	0.488033039
-32.6	-32.2	-0.4	254854	0.506061121
-32.2	-31.9	-0.3	271978	0.540064082
-31.9	-31.6	-0.3	281258	0.558491288
-31.6	-31.2	-0.4	329818	0.65491641
-31.2	-30.9	-0.3	319987	0.635395089
-30.9	-30.5	-0.4	325879	0.647094776
-30.5	-30.2	-0.3	288093	0.572063482
-30.2	-29.9	-0.3	166437	0.33049234
-29.9	-29.5	-0.4	119522	0.237333679
-29.5	-29.2	-0.3	61775	0.12266602
-29.2	-28.9	-0.3	57714	0.114602131
-28.9	-28.5	-0.4	52990	0.10522173
-28.5	-28.2	-0.3	44488	0.088339391
-28.2	-27.8	-0.4	42658	0.084705578
-27.8	-27.5	-0.3	42470	0.084332268
-27.5	-27.2	-0.3	37690	0.074840668
-27.2	-26.8	-0.4	17814	0.035373087
-26.8	-26.5	-0.3	5138	0.010202477
-40.6			757279	

Site 2_0.5m

RETICULATE

Min of_Depth	Max of_Depth	Label	Count	Relative percentage of cells
-44.5	-44.2	-0.3	1130	0.001846181
-44.2	-43.8	-0.4	1234	0.002016095
-43.8	-43.5	-0.3	2324	0.003796925
-43.5	-43.2	-0.3	2678	0.004375286
-43.2	-42.8	-0.4	3114	0.005087618
-42.8	-42.5	-0.3	6136	0.010024927
-42.5	-42.1	-0.4	5802	0.009479242
-42.1	-41.8	-0.3	4152	0.00678349
-41.8	-41.4	-0.4	3348	0.005469924
-41.4	-41.1	-0.3	2595	0.004239681
-41.1	-40.8	-0.3	2334	0.003813263
-40.8	-40.4	-0.4	2168	0.003542054
-40.4	-40.1	-0.3	1952	0.003189155
-40.1	-39.7	-0.4	1912	0.003123804
-39.7	-39.4	-0.3	1876	0.003064987
-39.4	-39.1	-0.3	1822	0.002976763
-39.1	-38.7	-0.4	1802	0.002944087
-38.7	-38.4	-0.3	1711	0.002795412
-38.4	-38	-0.4	1761	0.002877102
-38	-37.7	-0.3	7118	0.011629307

-37.7	-37.3	-0.4	11940	0.019507436
-37.3	-37	-0.3	8984	0.014677957
-37	-36.7	-0.3	7554	0.012341639
-36.7	-36.3	-0.4	7143	0.011670152
-36.3	-36	-0.3	7078	0.011563956
-36	-35.6	-0.4	7166	0.011707729
-35.6	-35.3	-0.3	7332	0.011978938
-35.3	-35	-0.3	7314	0.01194953
-35	-34.6	-0.4	7548	0.012331837
-34.6	-34.3	-0.3	7491	0.012238711
-34.3	-33.9	-0.4	7676	0.012540962
-33.9	-33.6	-0.3	8058	0.013165069
-33.6	-33.3	-0.3	8367	0.013669909
-33.3	-32.9	-0.4	8567	0.013996667
-32.9	-32.6	-0.3	9203	0.015035757
-32.6	-32.2	-0.4	9512	0.015540597
-32.2	-31.9	-0.3	10320	0.016860699
-31.9	-31.5	-0.4	12021	0.019639773
-31.5	-31.2	-0.3	13683	0.02235513
-31.2	-30.9	-0.3	15462	0.02526164
-30.9	-30.5	-0.4	17504	0.028597836
-30.5	-30.2	-0.3	20599	0.033654412
-30.2	-29.8	-0.4	24839	0.040581676
-29.8	-29.5	-0.3	27508	0.044942258
-29.5	-29.2	-0.3	31859	0.052050872
-29.2	-28.8	-0.4	47322	0.077314146
-28.8	-28.5	-0.3	47410	0.077457919
-28.5	-28.1	-0.4	40481	0.066137398
-28.1	-27.8	-0.3	39145	0.063954656
-27.8	-27.4	-0.4	24613	0.04021244
-27.4	-27.1	-0.3	25863	0.042254675
-27.1	-26.8	-0.3	24577	0.040153623
-26.8	-26.4	-0.4	24996	0.040838181
-26.4	-26.1	-0.3	17987	0.029386956
-26.1	-25.7	-0.4	12544	0.020494245
-25.7	-25.4	-0.3	9918	0.016203916
-25.4	-25.1	-0.3	8566	0.013995033
-25.1	-24.7	-0.4	7788	0.012723946
-24.7	-24.4	-0.3	7184	0.011737138
-24.4	-24	-0.4	6721	0.010980693
-24	-23.7	-0.3	6605	0.010791174
-23.7	-23.3	-0.4	6356	0.010384361
-23.3	-23	-0.3	7819	0.012774593
-23	-22.7	-0.3	5885	0.009614846
-28.8			47410	

Site 3_0.5m

RETICULATE

Min of_Band_1	Max of_Band_1	Label	Count	Relative percentage of cells
-30.2	-30	-0.2	11483	0.027187174
-30	-29.7	-0.3	26461	0.062649116
-29.7	-29.4	-0.3	63359	0.150008894
-29.4	-29.1	-0.3	296580	0.702183395
-29.1	-28.8	-0.3	331622	0.785148904
-28.8	-28.6	-0.2	318445	0.753951013
-28.6	-28.3	-0.3	222522	0.526843528
-28.3	-28	-0.3	165794	0.392534203
-28	-27.7	-0.3	173023	0.409649598
-27.7	-27.4	-0.3	176602	0.418123245
-27.4	-27.2	-0.2	201172	0.476295226
-27.2	-26.9	-0.3	195044	0.461786561
-26.9	-26.6	-0.3	217703	0.515434054
-26.6	-26.3	-0.3	220537	0.522143838
-26.3	-26	-0.3	232158	0.549657741
-26	-25.8	-0.2	223258	0.528586083
-25.8	-25.5	-0.3	236899	0.560882542
-25.5	-25.2	-0.3	230675	0.546146587
-25.2	-24.9	-0.3	208565	0.493798907
-24.9	-24.6	-0.3	209288	0.495510683
-24.6	-24.4	-0.2	221025	0.523299228
-24.4	-24.1	-0.3	224577	0.53170895
-24.1	-23.8	-0.3	216517	0.512626078
-23.8	-23.5	-0.3	220365	0.52173661
-23.5	-23.3	-0.2	233537	0.552922664
-23.3	-23	-0.3	243982	0.577652266
-23	-22.7	-0.3	261909	0.620096267
-22.7	-22.4	-0.3	286862	0.679175039
-22.4	-22.1	-0.3	317198	0.750998613
-22.1	-21.9	-0.2	332712	0.78772959
-21.9	-21.6	-0.3	364893	0.86392139
-21.6	-21.3	-0.3	374268	0.886117658
-21.3	-21	-0.3	392364	0.928961784
-21	-20.7	-0.3	392082	0.92829412
-20.7	-20.5	-0.2	389999	0.923362405
-20.5	-20.2	-0.3	398803	0.944206773
-20.2	-19.9	-0.3	404781	0.958360297
-19.9	-19.6	-0.3	397704	0.941604778
-19.6	-19.3	-0.3	414504	0.981380491
-19.3	-19.1	-0.2	390038	0.923454741
-19.1	-18.8	-0.3	379384	0.89823031
-18.8	-18.5	-0.3	371141	0.878714167
-18.5	-18.2	-0.3	364691	0.863443134

-18.2	-17.9	-0.3	357463	0.846330107
-17.9	-17.7	-0.2	345374	0.817708166
-17.7	-17.4	-0.3	365319	0.864929988
-17.4	-17.1	-0.3	393486	0.931618233
-17.1	-16.8	-0.3	471333	1.115928944
-16.8	-16.6	-0.2	500705	1.18547015
-16.6	-16.3	-0.3	466209	1.103797352
-16.3	-16	-0.3	425061	1.006375266
-16	-15.7	-0.3	385006	0.911540968
-15.7	-15.4	-0.3	358372	0.848482257
-15.4	-15.2	-0.2	291675	0.690570308
-15.2	-14.9	-0.3	239495	0.567028836
-14.9	-14.6	-0.3	222077	0.525789945
-14.6	-14.3	-0.3	222060	0.525749696
-14.3	-14	-0.3	186255	0.440977707
-14	-13.8	-0.2	152669	0.361459427
-13.8	-13.5	-0.3	86765	0.205424986
-13.5	-13.2	-0.3	33164	0.078519152
-13.2	-12.9	-0.3	32480	0.076899712
-12.9	-12.6	-0.3	31841	0.075386815
-12.6	-12.4	-0.2	8270	0.019580068
-16.8			500705	

ANNULATE

Min of_Depth	Max of_Depth	Label	Count	Relative percentage of cells
-44.8	-44.5	-0.3	1712	0.003399502
-44.5	-44.2	-0.3	4816	0.009563085
-44.2	-43.9	-0.3	6830	0.013562265
-43.9	-43.7	-0.2	7849	0.015585683
-43.7	-43.4	-0.3	6644	0.013192926
-43.4	-43.1	-0.3	5048	0.010023765
-43.1	-42.8	-0.3	7691	0.015271944
-42.8	-42.5	-0.3	10233	0.020319569
-42.5	-42.3	-0.2	39306	0.078049544
-42.3	-42	-0.3	75344	0.149609852
-42	-41.7	-0.3	99033	0.19664887
-41.7	-41.4	-0.3	94870	0.188382441
-41.4	-41.1	-0.3	89967	0.178646601
-41.1	-40.9	-0.2	78845	0.156561753
-40.9	-40.6	-0.3	91782	0.182250629
-40.6	-40.3	-0.3	82967	0.164746769
-40.3	-40	-0.3	102346	0.203227462
-40	-39.7	-0.3	111636	0.221674525
-39.7	-39.5	-0.2	110757	0.219929103
-39.5	-39.2	-0.3	109520	0.217472804
-39.2	-38.9	-0.3	101275	0.201100787
-38.9	-38.6	-0.3	115782	0.229907197
-38.6	-38.3	-0.3	120558	0.239390854
-38.3	-38.1	-0.2	125175	0.248558786
-38.1	-37.8	-0.3	128252	0.254668755
-37.8	-37.5	-0.3	128621	0.255401475
-37.5	-37.2	-0.3	142901	0.283757133
-37.2	-36.9	-0.3	155259	0.308296294
-36.9	-36.7	-0.2	204446	0.405966443
-36.7	-36.4	-0.3	247539	0.491535796
-36.4	-36.1	-0.3	267110	0.530397742
-36.1	-35.8	-0.3	267144	0.530465255
-35.8	-35.6	-0.2	277573	0.55117402
-35.6	-35.3	-0.3	271356	0.538828983
-35.3	-35	-0.3	265189	0.526583231
-35	-34.7	-0.3	267227	0.530630067
-34.7	-34.4	-0.3	284713	0.565351848
-34.4	-34.2	-0.2	298492	0.592712675
-34.2	-33.9	-0.3	313267	0.62205125
-33.9	-33.6	-0.3	324921	0.645192485
-33.6	-33.3	-0.3	343841	0.682761746
-33.3	-33	-0.3	361269	0.717368357
-33	-32.8	-0.2	373018	0.740698232
-32.8	-32.5	-0.3	386844	0.768152387
-32.5	-32.2	-0.3	409315	0.812772834

-32.2	-31.9	-0.3	446487	0.886584914
-31.9	-31.6	-0.3	490395	0.973772605
-31.6	-31.4	-0.2	526229	1.044927832
-31.4	-31.1	-0.3	568785	1.129430869
-31.1	-30.8	-0.3	679916	1.35010262
-30.8	-30.5	-0.3	762143	1.513379979
-30.5	-30.2	-0.3	766690	1.522408912
-30.2	-30	-0.2	716858	1.423457992
-30	-29.7	-0.3	684588	1.359379766
-29.7	-29.4	-0.3	639794	1.270432753
-29.4	-29.1	-0.3	527197	1.04684998
-29.1	-28.8	-0.3	327218	0.649753616
-28.8	-28.6	-0.2	220423	0.437691818
-28.6	-28.3	-0.3	124236	0.246694223
-28.3	-28	-0.3	41340	0.082088438
-28	-27.7	-0.3	24094	0.047843223
-27.7	-27.4	-0.3	12188	0.024201594
-27.4	-27.2	-0.2	6899	0.013699278
-27.2	-26.9	-0.3	2786	0.005532133
-30.5			766690	

ANNULATE

Min of_Depth	Max of_Depth	Label	Count	Relative percentage of cells
-42.3	-41.9	-0.4	282	0.000460728
-41.9	-41.5	-0.4	2865	0.004680804
-41.5	-41.1	-0.4	4425	0.007229515
-41.1	-40.8	-0.3	5198	0.008492433
-40.8	-40.4	-0.4	19149	0.031285418
-40.4	-40	-0.4	62245	0.101695173
-40	-39.6	-0.4	98021	0.160145595
-39.6	-39.3	-0.3	124587	0.203548824
-39.3	-38.9	-0.4	193669	0.31641421
-38.9	-38.5	-0.4	277712	0.453722708
-38.5	-38.1	-0.4	446997	0.730298617
-38.1	-37.8	-0.3	388181	0.634205705
-37.8	-37.4	-0.4	244991	0.400263511
-37.4	-37	-0.4	210926	0.344608501
-37	-36.6	-0.4	209614	0.34246497
-36.6	-36.2	-0.4	228246	0.37290572
-36.2	-35.9	-0.3	239089	0.39062089
-35.9	-35.5	-0.4	262988	0.429666804
-35.5	-35.1	-0.4	278883	0.455635875
-35.1	-34.7	-0.4	314780	0.514283985

-34.7	-34.4	-0.3	335426	0.548015185
-34.4	-34	-0.4	346330	0.565830017
-34	-33.6	-0.4	398385	0.650876884
-33.6	-33.2	-0.4	469035	0.766304051
-33.2	-32.9	-0.3	596935	0.975265616
-32.9	-32.5	-0.4	680978	1.112574114
-32.5	-32.1	-0.4	760492	1.242483184
-32.1	-31.7	-0.4	838704	1.37026506
-31.7	-31.4	-0.3	965968	1.578187536
-31.4	-31	-0.4	1089267	1.779632041
-31	-30.6	-0.4	1268824	2.072990226
-30.6	-30.2	-0.4	1328073	2.169790569
-30.2	-29.9	-0.3	1444876	2.360621982
-29.9	-29.5	-0.4	1602850	2.618718107
-29.5	-29.1	-0.4	1723265	2.815450765
-29.1	-28.7	-0.4	1924358	3.143994222
-28.7	-28.4	-0.3	1889442	3.086948859
-28.4	-28	-0.4	1883563	3.077343815
-28	-27.6	-0.4	1973854	3.224860224
-27.6	-27.2	-0.4	1925763	3.146289695
-27.2	-26.8	-0.4	1969359	3.217516345
-26.8	-26.5	-0.3	1922701	3.141287035
-26.5	-26.1	-0.4	1745796	2.852261657
-26.1	-25.7	-0.4	1594640	2.605304703
-25.7	-25.3	-0.4	1364671	2.229583965
-25.3	-25	-0.3	1172259	1.915223427
-25	-24.6	-0.4	931215	1.52140848
-24.6	-24.2	-0.4	747207	1.220778302
-24.2	-23.8	-0.4	618110	1.009861091
-23.8	-23.5	-0.3	458819	0.749613266
-23.5	-23.1	-0.4	368328	0.601770099
-23.1	-22.7	-0.4	316620	0.517290156
-22.7	-22.3	-0.4	251511	0.410915812
-22.3	-22	-0.3	202413	0.330700058
-22	-21.6	-0.4	148969	0.243383859
-21.6	-21.2	-0.4	105582	0.172498671
-21.2	-20.8	-0.4	68515	0.111939028
-20.8	-20.5	-0.3	40158	0.065609684
-20.5	-20.1	-0.4	24233	0.0395916
-20.1	-19.7	-0.4	22498	0.036756977
-19.7	-19.3	-0.4	18936	0.030937422
-19.3	-18.9	-0.4	14042	0.02294166
-18.9	-18.6	-0.3	10966	0.017916126
-18.6	-18.2	-0.4	8444	0.013795711

ANNULATE

Min of_Band_1	Max of_Band_1	Label	Count	Relative percentage of cells
-30	-29.8	-0.2	17	4.02492E-05
-29.8	-29.5	-0.3	62	0.000146791
-29.5	-29.3	-0.2	2123	0.005026419
-29.3	-29	-0.3	9698	0.022961004
-29	-28.8	-0.2	15773	0.037344186
-28.8	-28.5	-0.3	14051	0.033267175
-28.5	-28.2	-0.3	13698	0.032431412
-28.2	-28	-0.2	18739	0.044366494
-28	-27.7	-0.3	29020	0.068707809
-27.7	-27.5	-0.2	26934	0.063768992
-27.5	-27.2	-0.3	31962	0.075673295
-27.2	-27	-0.2	37594	0.089007629
-27	-26.7	-0.3	51194	0.121207016
-26.7	-26.5	-0.2	53663	0.127052625
-26.5	-26.2	-0.3	55359	0.131068078
-26.2	-25.9	-0.3	50248	0.118967264
-25.9	-25.7	-0.2	52636	0.124621098
-25.7	-25.4	-0.3	57982	0.137278298
-25.4	-25.2	-0.2	65869	0.155951575
-25.2	-24.9	-0.3	82279	0.194803923
-24.9	-24.7	-0.2	106026	0.251027368
-24.7	-24.4	-0.3	198230	0.469329741
-24.4	-24.1	-0.3	216821	0.513345829
-24.1	-23.9	-0.2	247674	0.586393453
-23.9	-23.6	-0.3	289015	0.684272486
-23.6	-23.4	-0.2	431032	1.020512217
-23.4	-23.1	-0.3	618081	1.4633698
-23.1	-22.9	-0.2	686354	1.62501309
-22.9	-22.6	-0.3	702036	1.662141824
-22.6	-22.4	-0.2	775382	1.835795959
-22.4	-22.1	-0.3	663527	1.570967839
-22.1	-21.8	-0.3	645385	1.528014804
-21.8	-21.6	-0.2	675693	1.599772085
-21.6	-21.3	-0.3	699341	1.655761137
-21.3	-21.1	-0.2	703151	1.6647817
-21.1	-20.8	-0.3	596202	1.411569036
-20.8	-20.6	-0.2	523456	1.239335462
-20.6	-20.3	-0.3	473426	1.120884335
-20.3	-20.1	-0.2	430523	1.019307108
-20.1	-19.8	-0.3	346725	0.820906797
-19.8	-19.5	-0.3	297888	0.705280219
-19.5	-19.3	-0.2	287814	0.681428996
-19.3	-19	-0.3	243235	0.575883668

-19	-18.8	-0.2	198165	0.469175847
-18.8	-18.5	-0.3	168216	0.398268535
-18.5	-18.3	-0.2	158089	0.37429183
-18.3	-18	-0.3	157741	0.373467904
-18	-17.7	-0.3	127564	0.302020779
-17.7	-17.5	-0.2	125573	0.297306884
-17.5	-17.2	-0.3	105159	0.248974657
-17.2	-17	-0.2	77151	0.18266286
-17	-16.7	-0.3	67227	0.159166778
-16.7	-16.5	-0.2	61787	0.146287024
-16.5	-16.2	-0.3	53267	0.126115055
-16.2	-16	-0.2	56790	0.134456116
-16	-15.7	-0.3	63394	0.15009176
-15.7	-15.4	-0.3	49020	0.116059849
-15.4	-15.2	-0.2	36432	0.086256475
-15.2	-14.9	-0.3	17189	0.04069671
-14.9	-14.7	-0.2	15867	0.037566741
-14.7	-14.4	-0.3	17657	0.041804748
-14.4	-14.2	-0.2	19104	0.045230668
-14.2	-13.9	-0.3	17376	0.041139452
-13.9	-13.7	-0.2	5402	0.012789786
-22.6			775382	

Site 1

	Area (m ²)	Relative area (%)	Perimeter	COUNT
Annulate	3725390.0	29.4	10404.2	14886549.0
Reticulate	4806370.0	37.9	22862.5	19095816.0
Undulate	4149480.0	32.7	15020.1	16377955.0

SUM 12681240

CR site

	Area (m ²)	Relative area (%)	Perimeter	COUNT
Annulate	10367300.0	67.3	33595.4	41185228.0
Reticulate	186690.0	1.2	1781.5	733477.0
Undulate	4855900.0	31.5	29641.5	19288723.0

SUM 15409890

Site 3

	Area (m ²)	Relative area (%)	Perimeter	COUNT
Annulate	3314730.0	30.8	19416.8	13124088.0
Reticulate	4410310.0	41.0	13806.9	17129605.0
Undulate	3033930.0	28.2	19521.2	11983136.0

SUM 10758970

Bathymetry						
AREA_1	MIN	MAX	RANGE	MEAN	STD	SUM
3721637.3	-44.8	-26.9	17.9	-33.1	3.4	-492462823.6
4773954.0	-48.1	-26.5	21.6	-38.5	4.4	-735942587.8
4094488.8	-47.7	-35.4	12.2	-42.6	1.9	-697532891.4

Bathymetry						
AREA_1	MIN	MAX	RANGE	MEAN	STD	SUM
10296307.0	-42.3	-18.2	24.1	-29.0	3.7	-1194873740.7
183369.3	-44.5	-22.7	21.9	-30.4	4.5	-22300325.0
4822180.8	-41.3	-26.1	15.1	-32.6	3.0	-629389665.8

Bathymetry						
AREA_1	MIN	MAX	RANGE	MEAN	STD	SUM
3281022.0	-30.0	-13.7	16.4	-21.6	2.3	-283086129.5
4282401.3	-30.2	-12.4	17.9	-20.9	4.3	-358063641.1
2995784.0	-32.5	-13.8	18.7	-24.5	3.2	-293415464.4

		Slope				
MEDIAN	PCT90	COUNT_1	AREA_12	MIN_1	MAX_1	RANGE_1
-32.1	-29.5	14882280.0	3720570.0	0.0	76.2	76.2
-39.5	-31.5	19077029.0	4769257.3	0.0	73.8	73.8
-42.8	-39.9	16359241.0	4089810.3	0.0	80.3	80.3

		Slope				
MEDIAN	PCT90	COUNT_1	AREA_12	MIN_1	MAX_1	RANGE_1
-28.5	-24.9	41145896.0	10286474.0	0.0	77.8	77.8
-29.1	-25.9	732041.0	183010.3	0.0	71.9	71.9
-32.4	-29.1	19270264.0	4817566.0	0.0	23.0	23.0

		Slope				
MEDIAN	PCT90	COUNT_1	AREA_12	MIN_1	MAX_1	RANGE_1
-21.7	-18.6	13109465.0	3277366.3	0.0	72.9	72.9
-20.4	-15.6	17098103.0	4274525.8	0.0	71.3	71.3
-24.2	-20.8	11969478.0	2992369.5	0.0	59.6	59.6

MEAN_1	STD_1	SUM_1	MEDIAN_1	PCT90_1
4.8	3.9	71764218.5	3.7	10.1
4.6	3.6	88319028.5	3.6	9.8
3.3	2.9	54276297.9	2.6	6.4

MEAN_1	STD_1	SUM_1	MEDIAN_1	PCT90_1
4.0	3.4	162738801.2	2.9	8.6
5.5	4.6	3991942.1	4.1	11.9
1.9	1.3	35976854.9	1.5	3.6

MEAN_1	STD_1	SUM_1	MEDIAN_1	PCT90_1
2.5	2.2	32168743.8	1.8	5.5
4.3	3.0	72796057.4	3.6	8.3
1.8	1.8	21728445.1	1.3	3.5

	Annulate			
	MIN	MAX	AVERAGE	STD
Internal depth range (m)	0.30	13.98	5.58	3.87
Circularity	0.10	0.64	0.50	0.13
Length (m)	33.13	884.33	214.67	146.20
Width (m)	15.44	540.21	129.82	77.53
Length/Width ratio	1.01	3.15	1.63	0.46
Depth with respect to sea-level (mbsl)*	38.08	18.45	28.26	4.16

*the lowest point of the crest

Orientation (°)***	8.1	178.4	86.5	39.8
---------------------------	-----	-------	-------------	------

*** ≥ 1.5 Length/ Width ratio

		Reticulate					
STE	Number of polygons	MIN	MAX	AVERAGE	STD	STE	
0.31	154	0.26	9.17	3.32	2.04	0.16	
0.01		0.08	0.63	0.48	0.14	0.01	
11.78		16.17	674.07	168.16	142.70	11.50	
6.25		14.21	426.92	94.86	74.30	5.99	
0.04		1.04	3.36	1.72	0.56	0.04	
0.33		45.40	16.88	33.40	9.53	0.77	
3.21		14.3	173.6	100.8	39.6	3.19	

	Undulate				
Number of polygons	MIN	MAX	AVERAGE	STD	STE
113	0.31	4.88	1.92	1.11	0.09
	0.24	0.62	0.52	0.11	0.01
	18.42	387.77	104.14	75.86	6.11
	15.56	243.02	63.72	45.23	3.64
	1.04	3.76	1.67	0.62	0.05
	44.52	19.02	37.79	7.93	0.64
	0.8	140.1	76.7	32.1	2.59

Site 1						
Benthic structure	gridcode	Area	Relative area	Perimeter	OID_	
Plain	1	988898	7.1	644291		0.0
Pinnacle/Peak	2	161022	1.2	118556		1.0
Crest	3	4364590	31.5	1279320		2.0
Slope	4	5427940	39.2	1509960		3.0
Gentle slope	5	1105090	8.0	1162290		4.0
Hollow	6	1799740	13.0	586355		5.0
SUM		13847280				

Site 2						
Benthic structure	gridcode	Area	Relative area	Perimeter	OID_	
Plain	1	1413650	9.2	590397		0.0
Pinnacle/Peak	2	105558	0.7	54840		1.0
Crest	3	4381010	28.6	1092240		2.0
Slope	4	6669780	43.6	1298770		3.0
Gentle slope	5	1452460	9.5	981128		4.0
Hollow	6	1279270	8.4	364960		5.0
SUM		15301728				

Site 3						
Benthic structure	gridcode	Area	Relative area	Perimeter	OID_	
Plain	1	2015440	18.7	417844		0.0
Pinnacle/Peak	2	60625.3	0.6	37257.30078		1.0
Crest	3	2973000	27.7	720903		2.0
Slope	4	3934740	36.6	722513		3.0
Gentle slope	5	734945	6.8	519981		4.0
Hollow	6	1032390	9.6	236068		5.0
SUM		10751140				

Id_1	COUNT	AREA_1	MIN	MAX	RANGE	MEAN
1.0	3955432.0	988858.0	-48.4	-28.5	19.9	-43.3
2.0	644088.0	161022.0	-46.0	-26.5	19.5	-35.2
3.0	17458143.0	4364535.8	-48.0	-26.5	21.5	-35.7
4.0	21711713.0	5427928.3	-48.0	-27.7	20.2	-38.8
5.0	4420150.0	1105037.5	-48.4	-29.4	19.0	-43.0
6.0	7198955.0	1799738.8	-48.5	-29.9	18.6	-41.9

Id_1	COUNT	AREA_1	MIN	MAX	RANGE	MEAN
1.0	5654504.0	1413626.0	-42.6	-22.6	20.0	-31.4
2.0	422231.0	105557.8	-39.8	-18.2	21.6	-24.2
3.0	17523856.0	4380964.0	-40.4	-18.3	22.1	-27.0
4.0	26679095.0	6669773.8	-44.4	-19.5	24.9	-30.6
5.0	5809682.0	1452420.5	-44.5	-22.8	21.7	-32.5
6.0	5117049.0	1279262.3	-44.5	-23.3	21.2	-35.1

Id_1	COUNT	AREA_1	MIN	MAX	RANGE	MEAN
1.0	8057366.0	2014341.5	-33.2	-13.0	20.2	-23.6
2.0	242407.0	60601.8	-32.1	-12.4	19.8	-17.0
3.0	11886427.0	2971606.8	-32.7	-12.4	20.3	-19.4
4.0	15731998.0	3932999.5	-33.0	-12.8	20.2	-22.4
5.0	2938236.0	734559.0	-33.2	-13.8	19.4	-25.1
6.0	4127859.0	1031964.8	-33.3	-15.3	18.0	-25.9

Bathymetry						
Normalised to "Plain"			STD	SUM	MEDIAN	PCT25
			3.3	-171155412.2	-44.2	-45.20295
8.1			5.4	-22682258.1	-36.2	-40.04391
7.5			5.3	-623920987.0	-35.1	-40.75833
4.4			4.6	-843253102.5	-39.7	-42.86758
0.3			3.3	-189928729.4	-43.7	-45.20997
1.4			3.0	-301702751.0	-43.0	-44.0871

Bathymetry					
Normalised to "Plain"		STD	SUM	MEDIAN	PCT25
		2.8	-177365619.8	-31.0	-33.48122
7.2		3.1	-10198479.3	-23.8	-25.13506
4.4		2.6	-473094471.1	-26.8	-28.53345
0.7		3.2	-816984264.8	-30.2	-32.66033
-1.2		3.3	-189101717.4	-32.2	-35.1037
-3.8		3.3	-179795555.3	-35.6	-38.1275

Bathymetry					
Normalised to "Plain"		STD	SUM	MEDIAN	PCT25
		3.2	-190326118.4	-23.0	-24.35619
6.6		3.4	-4115067.3	-16.6	-18.65821
4.2		3.4	-230888676.1	-19.4	-21.34671
1.2		3.4	-352273421.5	-22.1	-24.63924
-1.5		3.7	-73791757.6	-25.0	-28.27229
-2.3		2.7	-106819625.4	-26.3	-27.92877

		Std						
PCT75	PCT90	OID_1	Id_12	COUNT_1	AREA_12	MIN_1	MAX_1	RANGE_1
-42.23756	-40.4	0	1	3942132	985533	0.000885	65.34668	65.34579
-29.93881	-28.3	1	2	644088	161022	0.001252	80.31718	80.31592
-30.52478	-29.5	2	3	17444573	4361143	0.000887	79.83365	79.83276
-34.66278	-32.1	3	4	21706999	5426750	0.001467	80.24529	80.24382
-41.57161	-38.5	4	5	4406771	1101693	0.00101	79.45092	79.44991
-40.10337	-36.9	5	6	7198126	1799532	0.000568	80.15266	80.1521

		Std						
PCT75	PCT90	OID_1	Id_12	COUNT_1	AREA_12	MIN_1	MAX_1	RANGE_1
-29.59393	-27.8	0	1	5636295	1409074	0.000511	60.81034	60.80983
-22.22432	-21.1	1	2	422217	105554.3	0.003704	77.05636	77.05265
-25.33357	-23.9	2	3	17504766	4376192	0.000678	77.82116	77.82048
-28.36452	-26.8	3	4	26675006	6668752	0.00058	76.32344	76.32286
-29.90629	-28.6	4	5	5795866	1448967	0.001016	69.22805	69.22703
-32.44484	-30.3	5	6	5116837	1279209	0.000663	73.99219	73.99152

		Std						
PCT75	PCT90	OID_1	Id_12	COUNT_1	AREA_12	MIN_1	MAX_1	RANGE_1
-21.76207	-20.9	0	1	8037365	2009341	0.000205	58.67931	58.67911
-14.46847	-13.6	1	2	242402	60600.5	0.001267	72.68118	72.67992
-16.73385	-15.2	2	3	11864177	2966044	0.000646	66.36031	66.35967
-20.06067	-18.0	3	4	15727087	3931772	0.001128	69.23605	69.23492
-22.46564	-21.0	4	5	2925780	731445	0.000641	66.59393	66.59329
-23.92711	-22.0	5	6	4127740	1031935	0.001217	72.89048	72.88926

pe								
MEAN_1	STD_1	SUM_1	MEDIAN_1	PCT25_1	PCT75_1	PCT90_1	OID_12	Id_12_13
1.9	1.4	7664103	1.615602	0.890563	2.667191	3.812571	0	1
5.2	8.0	3352826	2.421293	1.38697	4.398839	14.35272	1	2
3.3	2.8	57758061	2.673151	1.613847	4.167512	6.144542	2	3
5.7	3.8	1.24E+08	4.738159	2.784849	7.830909	11.27509	3	4
2.4	1.9	10626724	1.977141	1.17284	3.160875	4.563096	4	5
3.3	2.7	23823571	2.686374	1.566301	4.291823	6.328207	5	6

pe								
MEAN_1	STD_1	SUM_1	MEDIAN_1	PCT25_1	PCT75_1	PCT90_1	OID_12	Id_12_13
1.2	0.9	6844089	1.018191	0.633457	1.564823	2.265462	0	1
2.7	5.2	1120833	1.73422	1.066334	2.620658	3.76901	1	2
2.6	1.9	45673629	2.209108	1.365549	3.380749	4.77484	2	3
4.7	3.7	1.25E+08	3.456043	2.133862	5.873999	10.54869	3	4
1.7	1.2	9788500	1.450958	0.942327	2.137499	3.011106	4	5
2.8	2.4	14536309	2.117208	1.245531	3.687966	6.015735	5	6

pe								
MEAN_1	STD_1	SUM_1	MEDIAN_1	PCT25_1	PCT75_1	PCT90_1	OID_12	Id_12_13
1.0	0.7	7943033	0.835899	0.531087	1.265833	1.809661	0	1
2.9	5.6	712051.7	1.595426	0.976907	2.497512	4.091123	1	2
2.4	1.9	28284013	1.894757	1.179554	3.026686	4.673491	2	3
4.8	2.9	75451096	4.340371	2.373373	6.787096	8.799295	3	4
1.7	1.3	5004324	1.400917	0.91244	2.128827	3.120764	4	5
2.5	1.9	10204171	2.07449	1.235076	3.254973	4.595575	5	6

Aspect								
COUNT_12	AREA_12_1	MIN_12	MAX_12	RANGE_12	MEAN_12	STD_12	SUM_12	MEDIAN_12
3944021	986005.3	-1	360	361	183.1908	103.1853	7.23E+08	186.5868
644088	161022	-1	359.9998	360.9998	178.2019	101.5184	1.15E+08	176.9405
17445880	4361470	-1	360	361	181.2804	104.6944	3.16E+09	183.1827
21707367	5426842	-1	360	361	183.1551	107.9956	3.98E+09	186.5142
4408480	1102120	-1	360	361	182.3241	104.1569	8.04E+08	185.2675
7198230	1799558	-1	360	361	182.947	100.9209	1.32E+09	185.9108

Aspect								
COUNT_12	AREA_12_1	MIN_12	MAX_12	RANGE_12	MEAN_12	STD_12	SUM_12	MEDIAN_12
5636295	1409074	-1	359.9999	360.9999	184.0438	102.6328	1.04E+09	186.1044
422217	105554.3	-1	359.9991	360.9991	178.8225	107.3245	75501889	171.7049
17504766	4376192	-1	360	361	182.7357	103.7561	3.2E+09	179.8657
26675006	6668752	-1	360	361	182.0957	108.4109	4.86E+09	183.6707
5795866	1448967	-1	360	361	182.9821	103.8887	1.06E+09	184.4458
5116837	1279209	-1	360	361	180.1091	102.4104	9.22E+08	179.0419

Aspect								
COUNT_12	AREA_12_1	MIN_12	MAX_12	RANGE_12	MEAN_12	STD_12	SUM_12	MEDIAN_12
8037365	2009341	-1	360	361	181.875	103.7776	1.46E+09	182.0223
242402	60600.5	-1	359.999	360.999	177.1303	103.0201	42936742	171.7508
11864177	2966044	-1	360	361	187.536	101.5099	2.22E+09	188.7879
15727087	3931772	-1	360	361	189.0972	104.5174	2.97E+09	186.7072
2925780	731445	-1	360	361	187.0857	104.0513	5.47E+08	188.4733
4127740	1031935	-1	360	361	180.2014	103.4758	7.44E+08	181.6773

	Profile Curvature							
PCT90_12	OID_12_13	Id_12_13_1	COUNT_12	AREA_12_1	MIN_12_13	MAX_12_13	RANGE_12	MEAN_12_13
323.8866	0	1	19726	4931.5	-0.59676	0.565203	1.161965	-0.00683
322.5839	1	2	10894	2723.5	-1.41041	2.100312	3.510727	0.031084
326.4377	2	3	532894	133223.5	-1.05331	2.949896	4.003207	0.008229
333.3858	3	4	563000	140750	-2.172	1.245048	3.417053	-0.00035
325.7607	4	5	26038	6509.5	-1.26321	1.883507	3.146718	-0.01255
321.8335	5	6	111723	27930.75	-1.89494	2.320918	4.215853	-0.02267

	Profile Curvature							
PCT90_12	OID_12_13	Id_12_13_1	COUNT_12	AREA_12_1	MIN_12_13	MAX_12_13	RANGE_12	MEAN_12_13
324.8991	0	1	5636295	1409074	-2.02579	1.198086	3.223876	0.001485
332.3521	1	2	422217	105554.3	-3.17324	18.34389	21.51713	0.024536
327.2554	2	3	17504766	4376192	-5.73709	5.01616	10.75325	0.006885
328.9414	3	4	26675006	6668752	-4.94472	4.65663	9.601348	-0.00104
325.7722	4	5	5795866	1448967	-2.66475	1.350394	4.015145	-0.00702
322.4267	5	6	5116837	1279209	-2.91038	5.89521	8.805594	-0.0144

	Profile Curvature							
PCT90_12	OID_12_13	Id_12_13_1	COUNT_12	AREA_12_1	MIN_12_13	MAX_12_13	RANGE_12	MEAN_12_13
324.907	0	1	8037365	2009341	-2.01014	1.647314	3.657457	0.001009
328.1688	1	2	242402	60600.5	-3.79675	5.203887	9.000637	0.032853
326.5724	2	3	11864177	2966044	-3.89775	4.156576	8.054322	0.005966
332.8624	3	4	15727087	3931772	-6.15953	3.803064	9.962599	-0.0015
327.8805	4	5	2925780	731445	-2.98419	6.463369	9.447563	-0.00572
323.5816	5	6	4127740	1031935	-6.68421	4.636637	11.32084	-0.01203

STD_12_13	SUM_12_13	MEDIAN_12	PCT90_12	OID_12_13	Id_12_13_1	COUNT_12	AREA_12_1	MIN_12_13
0.106953	-134.673	-0.00113	0.122504	0	1	3819998	954999.5	0.000132
0.141152	338.6315	0.00364	0.136627	1	2	641023	160255.8	0.000332
0.103088	4385.137	0.002223	0.134416	2	3	17171595	4292899	0.000159
0.093823	-199.065	0.001254	0.099856	3	4	21360329	5340082	0.000146
0.107945	-326.838	-0.00245	0.113855	4	5	4279103	1069776	0.000139
0.110211	-2532.36	-0.00736	0.089563	5	6	7114775	1778694	0.000147

STD_12_13	SUM_12_13	MEDIAN_12	PCT90_12	OID_12_13	Id_12_13_1	COUNT_12	AREA_12_1	MIN_12_13
0.04444	8369.413	0.000433	0.049393	0	1	5499294	1374824	9.18E-05
0.117091	10359.67	0.005529	0.06994	1	2	419031	104757.8	0.000114
0.052887	120518.8	0.001982	0.058567	2	3	17158881	4289720	0.000101
0.053148	-27816.4	0.000159	0.037804	3	4	26167440	6541860	9.25E-05
0.050532	-40661.2	-0.0014	0.038493	4	5	5668950	1417238	9.09E-05
0.058299	-73657.9	-0.00403	0.017151	5	6	5028142	1257036	9.11E-05

STD_12_13	SUM_12_13	MEDIAN_12	PCT90_12	OID_12_13	Id_12_13_1	COUNT_12	AREA_12_1	MIN_12_13
0.041793	8109.911	0.000138	0.046363	0	1	7842500	1960625	6.74E-05
0.14029	7963.691	0.006679	0.083664	1	2	239334	59833.5	0.000152
0.050538	70775.89	0.001506	0.053561	2	3	11521831	2880458	7.72E-05
0.048739	-23582.9	0.000159	0.033231	3	4	15201078	3800270	6.77E-05
0.055418	-16737.4	-0.00104	0.040121	4	5	2800132	700033	6.48E-05
0.064254	-49672.5	-0.00291	0.033259	5	6	4066538	1016635	7.4E-05

Rugosity							
MAX_12_13	RANGE_12_13	MEAN_12_13	STD_12_13	SUM_12_13	MEDIAN_12_13	PCT25_12_13	PCT75_12_13
0.064998	0.064866	0.001248	0.001088	4766.752	0.001101	0.000835	0.001399
0.146613	0.146282	0.005466	0.01063	3503.691	0.001722	0.001129	0.004601
0.144426	0.144267	0.001894	0.003096	32529.31	0.001279	0.000964	0.001741
0.1135	0.113353	0.002252	0.002736	48112.28	0.001497	0.001125	0.002456
0.078648	0.078509	0.002174	0.003065	9304.09	0.001275	0.000964	0.001725
0.08965	0.089503	0.005127	0.005184	36475.5	0.003701	0.002015	0.006123

Rugosity							
MAX_12_13	RANGE_12_13	MEAN_12_13	STD_12_13	SUM_12_13	MEDIAN_12_13	PCT25_12_13	PCT75_12_13
0.035595	0.035503	0.000402	0.000342	2209.038	0.000316	0.000234	0.000467
0.120367	0.120253	0.001346	0.003865	563.912	0.000781	0.000532	0.001153
0.11185	0.111749	0.000661	0.00114	11341.35	0.000523	0.00037	0.000749
0.110078	0.109985	0.000733	0.001365	19179.21	0.000537	0.000311	0.00091
0.052575	0.052485	0.000563	0.00116	3189.146	0.000331	0.000228	0.000622
0.056899	0.056808	0.001757	0.003073	8836.952	0.000778	0.000394	0.00152

Rugosity							
MAX_12_13	RANGE_12_13	MEAN_12_13	STD_12_13	SUM_12_13	MEDIAN_12_13	PCT25_12_13	PCT75_12_13
0.027683	0.027616	0.000238	0.000222	1862.863	0.000209	0.000166	0.000261
0.072944	0.072792	0.001801	0.004505	430.9328	0.000711	0.000469	0.001296
0.073492	0.073415	0.000612	0.001138	7051.519	0.000378	0.000254	0.000686
0.072851	0.072783	0.000778	0.001145	11827	0.000528	0.000289	0.000935
0.068577	0.068512	0.000689	0.001553	1930.55	0.000291	0.000186	0.000576
0.072354	0.07228	0.001471	0.002481	5980.6	0.000752	0.000446	0.001377

PCT90_12_13_14
0.001675725
0.014075267
0.003049672
0.004271686
0.004595149
0.010372102

PCT90_12_13_14
0.000726163
0.001674831
0.001078665
0.001336396
0.001017928
0.004044533

PCT90_12_13_14
0.000337958
0.002440357
0.001136184
0.00147748
0.001218736
0.003104705

Features	
Biogenic features	Seagrass
	Oyster reefs
	Coralligenous algal reefs
	Cold-water coral mounds
	live <i>Halimeda</i> algae on coral reef
	<i>Halimeda</i> bioherms
	Karst pinnacles (on land)

Physical features

Submerged karst formations

Submarine dunes

Pockmarks

Seafloor pits / Macro-bioturbation

Patch reef "halos" or "grazing halos"

Anthropogenic features

Location

Banc d'Arguin, Mauritania

Botany Bay, Port Hacking, and
Crookhaven River estuary,
Australia

Liyashan oyster reef, Haimen,
Jiangsu, China

Torre Guaceto Marine
Protected Area and Ugento
coast, Apulia region,
Mediterranean Sea, Italy

Atlantic Ocean

Palmira Atoll, US

Kalukalukuang Bank (K-Bank),
Easter Java, Sea, Indonesia

Nicaraguan Rise, Miskito
Channel, Southwest
Caribbean

Big Bank Shoals, Timor Sea,
Australia

Northern Great Barrier Reef,
Australia

Guilin, China

Nagura Bay, Ishigaki Island,
southern Ryukyu Islands,
Japan

Apulian Margin, southern
Adriatic Sea, Italy

Maltese Islands, offshore north
Gozo to south-east Malta

Northern Traverse of Saint-
Lawrence river, Quebec,
Canada
Lézardrieux bank, north
Brittany, France
Great South Channel,
Georges Bank, Gulf of Mexico,
USA
middle of the Dover Strait,
between France and Great
Britain

Bonaparte Basin, western
Timor Sea, northwest
Australia, Oceanic Shoals
Australian MP

Xisha Uplift, northern South
China Sea

Belfast Bay, Maine, USA

around Aotearoa, New
Zealand

Witch Ground Basin, North
Sea, UK

Malin Basin, Ireland

Barents Sea, Norway

Witch Ground Basin, central
North Sea

Gorgon Pockmark Field,
Australian Northwest shelf

Carnarvon Pockmark Field,
Australian Northwest shelf

southeastern North Sea

Flensburg Fjord and Lübeck
Bay, southwestern German
Baltic Sea

Sylt Outer Reef, German
Bight, southeastern North Sea

Clarion–Clipperton Zone
(CCZ), Northeast Pacific
Ocean

Lighthouse Reef Atoll, Belize

Heron Island, Australia

Little Bahama Bank, The
Bahamas

Ningaloo Reef, Australia

Florida Keys Natinal Marine
Sanctuary, USA

Sout Water Caye Marine
Reserve, Belize

Fehmarn Island and Lübeck
Bay, southwestern German
Baltic Sea

Flensburg Fjord, Lübeck Bay
and Gelting Bay, southwestern
German Baltic Sea

Flensburg Fjord, Lübeck Bay
and Gelting Bay, southwestern
German Baltic Sea

Kiel Bight and Fehmam Belt,
southwestern German Baltic
Sea

Sapelo Island, McIntosh
County, Georgia, USA

Shape description

Circular to semi-circular pools

Sparse reefs aligned with tidal current (patch reef), broken up barriers semi-aligned with tidal current (string reef), forming barrier in low hydrodynamic conditions (fringing reef)

Ring-shaped, string-shaped, and patch-shaped reefs

Squat columns that are randomly scattered or field of squat columns that are coalescent or forming large ridges that are circular to elongated or irregular with channels.

Diverse morphologies: conical, oval, elongated, ridge-like, V-shape; individual mounds or arranged in clusters, sometimes merged into reticular structures

Polygonal pattern of live veneers

Small or hummocky mounds with no evidence of pinnacles in topographic lows

Undulating, elongated ridges and valley ('hay-stack' features)

Rounded topographic mounds with lens like geometry

Distinct hummocks

Lizard Island region - Parallel mounds/banks and ridges separated by hollows and channels with rocky features; some isolated mounds

Cooktown region - Subconical, often elongated mounds with pinnacles up to 3 m

Whole northern GBR - circular mounds, and parallel ridges and valleys

Whole northern GBR - three sub-morphotypes: annulate (circular ring-shaped), reticulate (honeycomb-like), undulate (wave-like)

Fenglin (isolated pinnacle)

Fengcong (Pinnacles with common base)

Fluviokarst (crescent-shaped, closed depression)

Doline karst (plateaus with concordant ridge elevation and bowl-shaped basins)

Cockpit karst (polygonal karst, conical hills with steep-sided enclosed lobate depressions)

Polygonal karst with central hill (cellular network)

Uvalas & mega-dolines

Dolines (circular depressions)

Complex, rough topography with small grooved relief

Karstified limestone plateau (irregular surfaces like fissures, pools, clints, grykes)

Sinkholes (circular to ellipsoidal depressions)

Identification by crest line, stoss trough, lee through. Linear to asymmetric crest line.

Sinuous or straight isolated dunes or in fields

Crest line from linear ridge to crescent shapes

Ripples, mega-ripples and sand dunes. Straight to sinuous crest line

Very elongated, more or less linear shape

Pockmark -circular to elongated

Scoured pockmark - circular to elongated with a 'v'-shaped depression

Circular, elliptical, crescentic in plan view; 'U'-shaped, asymmetrical in cross-section

Circular to elongated

Rounded to irregular and elongated

Circular to elongated with mostly 'v'-shaped depression, sometime 'u' or 'w'-shaped

Elongated

Rounded to elongated

rounded to elongated

Circular to elongated, and cauliflower (irregular) shape

Circular to elliptical depressions

Peculiar shape: non-circular or half-moon or crescent dune -like or irregular; 'w'-shaped cross-section with furrows and concentric high in the pit, and mounds on the rims

Elongated depressions forming curvilinear tracks

Circular with feature in their centre (patch reef)

Circular with feature in their centre

Circular with feature in their centre

Circular with feature in their centre (patch reef - high: 4m, diameter: 10m)

Circular with feature in their centre

Circular with feature in their centre

Dumping rings - positive relief, ring-shaped with internal elevations

Random dumping spots - positive or slightly negative relief; circular structures

Strings of dumping spots - flat areas with strings of rounded spots

Craters/ ammunitions blasting - U-shaped craters without elevated rims

The Sapelo Shell ring complex - large ring-shaped shell mounds with possible internal shell deposits and small amorphous shell middens

Depth to feature tops (mbsl)	Diameter (m)
Intertidal with tidal range of 1.5 - 2	2-25
0.17 - 0.59 with tidal range of 0.2 - 1.9	NA
Intertidal with tidal range of 2.5 - 6	NA
5 - 100	width: 1 - 5
Both shallow (> 50 m) and deep (up to > 1000 m)	from 10s of centimeters up to 100s to 1000s of meters
10	3-4
20 - 40	~10 - 20 ~100
40 - 50	NA
28 - 45	width: up to 100; length: up to 150
25 - 40	NA
30 - 50	width: 100 -250; length: 150
20 - 40	NA
12 - 49	200 -250 (generally); up to 500
	width: 68-1454; length: 130-1635

2-50	width: 150-200; length: 500-800 80-100 70-100 up to 500 width: 400; length: 650
50-105	50-155
27	width: 2000; length: 5800
11-20	60-270
Shallow marine environments, estuaries, deltas and river channels	wavelength (width): 0.6 - >100
10.5 - 23.5	wavelength (width): ~20 - 60; length: ~30 - 400 m
12 - 27	length: ~ 50 - 600
52 - 82	length: up to 500
20 - 35	wavelength (width): several hundreds of meters; length: 350 - 3000
94-146	10 - 30
94-146	10 - 30 but extend up to 200 with depression
~ 400	width: 200 - 400
~ 750	1000 - 2500 (max. 3210)
9.5 - 25.7	15.9 - 302
6 - 2572	few 10s to few 100s of meters
120 - 150	
126 - 177	40 - 850
255 - 305	25 - 220
144 - 155	length: 250 - 1106; width: 75 - 464 length: 26 - 140; width: 14 - 57
210 - 480	150 - 200

680 - 930	250 - 300
20 - 45	length: 1 - 30; width: 1 - 20
13 - 24	6 - 29
28 - 28.5	< 50; mean diameter: 19.4
3999 - 4258 (Abyssal depth)	width: 0.97, length: 2.57
Lagoon	width: 5 - 15
Lagoon	width: 5 - 14
Lagoon	width: 1 - 2
3 - 8	width: > 90
Lagoon	width: < 1 - 69.7
Lagoon	width: < 1 - 20
24	20 - 49
22	30 - 77
22 - 23	8 - 29
9 - 21	6 - 24
NA	50 - 90

Internal depth (m)	Reference
0.11-1	Wolff & Smit, 1990; van der Laan & Wolff, 2006
NA	Roncolato et al. 2024
NA	Zhuang et al., 2025
0.5 - 4 (topographic relief)	Bracchi et al., 2015
height: few meter to 100s of meters (in shallow shelf environment restricted to 30-40m)	Wheeler et al., 2007; Wienber and Titschack, 2017; Hebbeln and Wienberg, 2025
	Sadin et al., 2022
10 -12 (topographic relief)	Roberts et al., 1987a; Roberts et al., 1987b; Roberts et al., 1988; McNeil et al., 2016; McNeil et al., 2021
2 - 5 (topographic relief)	
20 - 30 (topographic relief)	Hine et al., 1988; McNeil et al., 2016; McNeil et al., 2021
NA	Heyward et al., 1997; McNeil et al., 2016; McNeil et al., 2021
NA	Orme et al, 1978; Orme, 1985; Orme and Salma, 1988; Rees et al., 2007
15 - 20 (topographic relief)	Davies and Marshall, 1985; Phipps et al., 1985; Marshall and Davies, 1988;Rees et al., 2007
NA	Drew and Abel, 1985; Drew and Abel, 1988; Drew, 1993
NA	McNeil et al., 2016; McNeil et al., 2021
NA	
NA	Cao et al., 2024

41	
8-18	
NA	Kan et al., 2015
40	
41	
0.5-20	Taviani et al., 2012
NA	
	Micallef et al., 2013
4-11	
height: 0.075 - > 5	Ashley, 1990; Cassol et al., 2021
height: ~0.2 - 3	Cassol et al., 2021
	Debese et al., 2016
height: > 2	Di Stefano and Mayer, 2018
height: up to several meters	Thibaud et al., 2013
0.5 - 2	
	Picard et al., 2018
0.5 - 2	
up to 10	
60 - 140 (max. 165.2)	Sun et al., 2011
0.5 - 25.4	Amdreus et al. 2010
NA	Hillman et al., 2023
1 - 18	
0.3 - 8.5	Gafeira et al. 2018
2 - 7	
6 - 17.8	
0.9 - 3.1	Böttner et al., 2019
< 37	
	Piera et al. 2022

< 35

0.15 - 1.5

Böttner et al., 2024

0.1 - 1.4

Díaz-Mendoza et al., 2023

0.05 - 0.2

Schneider von Deimling et al., 2023

0.13

Marsh et al., 2018

NA

Bilodeau et al., 2019; Bilodeau et al., 2021

NA

Madin et al., 2019b

NA

Alevizon, 2002

NA

Downie et al., 2013

NA

Di Fiore et al., 2019

NA

up to 3

up to 0.8

Díaz-Mendoza et al., 2023

NA

0.3 - 1.7

NA

Thompson et al., 2004

- Area and perimeter, using *Zonal Geometry* and *Zonal Statistics*
- Orientation, length and width with *Minimum Bounding Geometry* function using rectangle by width geometry type
- Circularity, calculated with: $C = 4\pi \frac{A}{p^2}$

where 'C' is circularity, 'A' is polygon area and 'p' is polygon perimeter.

Round	Sub-round	Sub-angular	Angular	Irregular
≥ 0.8	0.6-0.8	0.4-0.6	0.2-0.4	< 0.2

5. Comparison with previous dataset

- The original *Halimeda* morphotypes' polygon (McNeil et al., 2016) was clipped to the extent of each site.
- Large-scale internal depression polygons on each site were reclassified into bioherm morphotypes.
- Site-specific and combined morphotype dataset was created.

However, it is important to acknowledge the limitations of the geoprocessing tools used in this study, particularly: 1) lack of filling mechanism to the pouring point of disclosed depressions, and 2) the overfilling of depressions that share a lower-relief crest with adjacent features than their surrounding topography.

Section 1.3 Workflow for Benthic Terrain Classification of *Halimeda* bioherms

To conduct the first benthic terrain classification over *Halimeda* bioherms, the following geoprocessing workflow was applied using ArcGIS Pro 3.3.

1. Using *Geomorphon Landforms* tool

- Before terrain classification, benthic features from crest to crest were measured to generate an average size of bioherms.
- A search distance of 500 cells (250 m) was used due to average size of bioherms. This value enabled to capture both large- and small-scale features.
- A skip distance of 10 cells (5 m) was applied after several trials that minimised noise on the bathymetric dataset.

2. Reclassification of built-in landform elements

- *Reclassify* tool was used on the newly generated geomorphon raster

- Previously decided 6 benthic structures were applied based on visual and general geomorphometric analysis.

3. Smoothing of reclassified raster

- *Majority Filter* function enabled us to reduce noise on the new raster
- Firstly, a filtering of Four 'Number of neighbours to use' with Half 'Replacement threshold' was applied. New raster was saved.
- Secondly, on the newly saved raster a filtering of Eight 'Number of neighbours to use' with Majority 'Replacement threshold' was applied. New raster was saved and ready to create polygons.

4. Creating polygons for further analysis

- Multipart polygons were created by each benthic structure for further summary statistics.
- *Raster to Polygon* function was used with 'do not simplify' and 'create multipart features'. This step enables us to have combined polygons for each benthic structure.

5. Summary statistics of bioherm-specific benthic structures

- *Zonal Statistics* tool enabled us to create summary statistics of previously acquired bathymetry, slope, aspect, profile curvature and rugosity rasters on each site by each benthic structure, using the multipart polygons.