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| Abstract | *Halimeda* bioherms occur as extensive geological structures on the northern Great Barrier Reef (GBR), Australia. We present the most complete, high-resolution spatial mapping of the northern GBR *Halimeda* bioherms, based on new airborne lidar and multibeam echosounder bathymetry data. Our analysis reveals that bioherm morphology does not conform to the previous model of parallel ridges and troughs, but is far more complex than previously thought. We define and describe three morphological sub-types: reticulate, annulate, and undulate, which are distributed in a cross-shelf pattern of reduced complexity from east to west. The northern GBR bioherms cover an area of 6095 km^2, three times larger than the original estimate, exceeding the area and volume of calcium carbonate in the adjacent modern shelf-edge barrier reefs. We have mapped a 1740 km^2 bioherm complex north of Raine Island in the Cape York region not previously recorded, extending the northern limit by more than 1° of latitude. Bioherm formation and distribution are controlled by a complex interaction of outer-shelf geometry, regional and local currents, coupled with the morphology and depth of continental slope submarine canyons determining the delivery of cool, nutrient-rich water upwelling through inter-reef passages. Distribution and mapping of *Halimeda* bioherms in relation to Great Barrier Reef Marine Park Authority bioregion classifications and management zones are inconsistent and currently poorly defined due to a lack of high-resolution data not available until now. These new estimates of bioherm spatial distribution and morphology have implications for understanding the role these geological features play as structurally complex and productive inter-reef habitats, and as calcium carbonate sinks which record a complete history of the Holocene post-glacial marine transgression in the northern GBR. |

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1 **REPORT**

2 # New constraints on the spatial distribution and morphology
3 # of the *Halimeda* bioherms of the Great Barrier Reef, Australia

4 **Mardi A. McNeil[1,2]** (ORCID) · **Jody M. Webster[1]** · **Robin J. Beaman[3]** · **Trevor L. Graham[4,5]**

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Introduction 45

Halimeda sediment is a major contributor to the tropical 46
back-reef carbonate facies (Maxwell 1973; Orme et al. 47
1978; Hopley et al. 2007; Rees et al. 2007), where disag- 48
gregated calcium carbonate (aragonite) *Halimeda* segments 49
can accumulate as thick bank-like structures or bioherms, 50
over millennial time scales. Globally, *Halimeda* bioherms 51
have been described from Kalukalukuang Bank (K-Bank), 52
Eastern Java Sea, Indonesia (Roberts et al. 1987; Phipps 53

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and Roberts 1988; Roberts et al. 1988), Miskito Channel, Nicaraguan Rise, south–west Caribbean Sea (Hine et al. 1988), and reported but not described in detail at Big Bank Shoals, Timor Sea (Heyward et al. 1997; Table 1). Upwelling of cool nutrient-rich water onto the continental shelf from below the adjacent oceanic thermocline has been proposed as a control on the distribution and formation of the *Halimeda* bioherms (Drew 1983; Drew and Abel 1985; Roberts et al. 1987, 1988; Hine et al. 1988; Marshall and Davies 1988; Phipps and Roberts 1988; Wolanski et al. 1988). The reported global distribution appears consistent with this idea (Table 1). In the Great Barrier Reef, the previously known extent, morphology, age, sedimentation rates, and carbonate budget of the *Halimeda* bioherms were based on sediment grabs, vibra and piston coring, and widely spaced seismic profiling and single-beam echo-sounder profiles (Hopley et al. 2007; Rees et al. 2007; Davies 2011). Crucially, descriptions of the spatial distribution and 3D morphology of the bioherms in the GBR have not been reassessed in the 30 years since this early body of work was initiated nor with the benefit of more modern survey technologies, such as airborne lidar bathymetry (ALB) and multibeam echosounders.

The spatial distribution limits and the boundaries of individual bioherms in the northern and southern GBR are poorly constrained. A pioneering survey of inter-reef sediments from the GBR (Maxwell 1968, 1973) reported *Halimeda*-rich gravel further north of Raine Island (latitude 11°35′S). However, a later survey (Drew and Abel 1988) recorded a northernmost limit for the *Halimeda* bioherms of 11°30′S but did not locate the area further north described by Maxwell. The southern limit of *Halimeda* bioherms is poorly defined due to a lack of survey data, which is restricted to one survey of the Swain Reefs (Searle and Flood 1988) where seismic profiling showed internal structure similar to the northern GBR bioherms, with vibracoring providing evidence of *Halimeda* bioherms at latitude 21°35′S–21°49′S. The known extent of the northern GBR bioherms is concentrated in two regions: east of Cape York between latitudes 11°30′S–13°26′S (Drew 1983, 1993; Drew and Abel 1985, 1988; Orme 1985; Orme and Salama 1988), and the Ribbon Reefs region east of Cooktown and Lizard Island between latitudes 14°40′S and 16°7′S (Davies and Marshall 1985; Orme 1985; Marshall and Davies 1988; Orme and Salama 1988; Fig. 1). The bioherms lie proximal to the landward side of the Ribbon Reefs at 20–40 m depth, with a maximum vertical thickness up to 20 m. Between these two regions, bioherms are absent in the Princess Charlotte Bay area (latitude 13°42′S). Of the reported global *Halimeda* bioherms, very few descriptions of the total spatial extent (area and volume) have actually been quantified, with only one preliminary estimate for the entire GBR of *c.* 2000 km² (Drew

and Abel 1985, 1988; Table 1) based on extensive grab samples.

Previously, the widely accepted paradigm of bioherm morphology occurs as a series of 5–20 m-thick linear parallel ridges and troughs, sometimes forming hummocky mounds (Table 1). This model was constructed, at the time, by a reasonable interpolation between parallel sub-bottom and single-beam echosounder profiles, forming the linear ridges and mound-like morphology that permeates the literature (Orme and Salama 1988; Mathews et al. 2007; Fig. 2), including the interpretation of analogous *Halimeda* deposits in the geological past (Drew and Abel 1988; Braga et al. 1996; Martín et al. 1997). Some cross-shelf morphological variation was reported, with topographic relief being better developed and more pronounced to eastward, and smaller, less complex mounds on the western half of the outer-shelf (Davies and Marshall 1985; Marshall and Davies 1988; Orme and Salama 1988).

In this study, we use new high-resolution airborne lidar and multibeam bathymetry datasets to better quantify and redefine the spatial distribution and morphologic variation of the northern GBR *Halimeda* bioherms. Our objectives are to (1) accurately map the total spatial extent and boundaries of the bioherms, (2) utilise the new bathymetry datasets to redefine and quantitatively describe the bioherm geomorphology, (3) investigate how their morphology varies spatially at different scales both latitudinally and cross-shelf, (4) propose hypotheses to explain the *Halimeda* bioherm distribution, formation, and morphology, and (5) discuss the management/conservation implications of these findings for better characterising and understanding the inter-reef habitats of the GBR.

Materials and methods

To accurately map the total areal extent and redefine the geomorphology of the GBR bioherms, this study synthesised a range of information derived from new airborne lidar and multibeam bathymetry datasets, seismic profiling data, and combining these with existing sediment sampling surveys, seismic profiles, and vibracores taken from the published literature (Table 2). Comparisons were made between the previously reported *Halimeda* bioherm spatial extent, distribution, and morphology descriptions, and our analysis of the new and existing data.

GIS methods

Airborne lidar bathymetry (ALB) data were collected by the Royal Australian Navy and supplied by the Australian Hydrographic Service using a lowest astronomical tide (LAT) vertical datum and a WGS84 horizontal datum, with

Table 1 Summary of reported global *Halimeda* bioherm distribution and morphology descriptions

Location	Depth to mound tops (m)	Adjacent basin depth (m)	Morphology descriptions	Area (km²)	Thickness (m)	References
Kalukalukuang Bank, (K Bank) Eastern Java Sea, Indonesia	20–40	800–1000 m strait of Makassar, near vertical slope edge, thermocline at ~70 m	Elongate ridges and valleys, to hummocky mounds 10–30 m across, to broad undulating areas	Not quantified	20–50	Roberts et al. (1987, 1988), Phipps and Roberts (1988)
Nicaraguan Rise, Miskito Channel, Southwest Caribbean	40–50	Cayman trough 1000 m	Mounds with lens-like geometry	Not quantified	20–30, Max 140	Hine et al. (1988)
Big Bank Shoals, Timor Sea	28–45	300 m depth to base of shoal	Distinct hummocks, <150 m across	Not quantified		Heyward et al. (1997)
Lizard Island region, northern Great Barrier Reef	25–40	Queensland Trough 1–2000 m, thermocline at ~80 m	Banks and ridges, troughs and hollows, irregular form and size	184	5–19	Orme et al. (1978), Orme (1985), Orme and Salama (1988), Rees et al. (2007)
Cooktown region, northern Great Barrier Reef	30–50	Queensland Trough 1–2000 m	Mounds, often elongate; ridges and valleys, 3 m high-eroded limestone pinnacles in valleys.	118	10–15	Davies and Marshall (1985), Phipps et al. (1985), Marshall and Davies (1988), Rees et al. (2007)
Whole northern Great Barrier Reef	20–40	Queensland Trough 1–2000 m	Discrete circular mounds, and parallel ridges and valleys.	~2000	5–20	Drew and Abel (1985), Drew and Abel (1988), Drew (1993)
Swain Reefs, southern Great Barrier Reef	20–32	Capricorn Channel 1–3000 m in Cato Trough	Morphology not described	Not quantified	Up to 14	Searle and Flood (1988)

Fig. 1 Regional map of northern Great Barrier Reef (GBR) with comparison of previous and new (this study) *Halimeda* bioherm distribution in relation to the Cape York and Ribbon Reefs regions and surrounding reefs. Locations of figures referred to in this study are *marked* for geographical reference
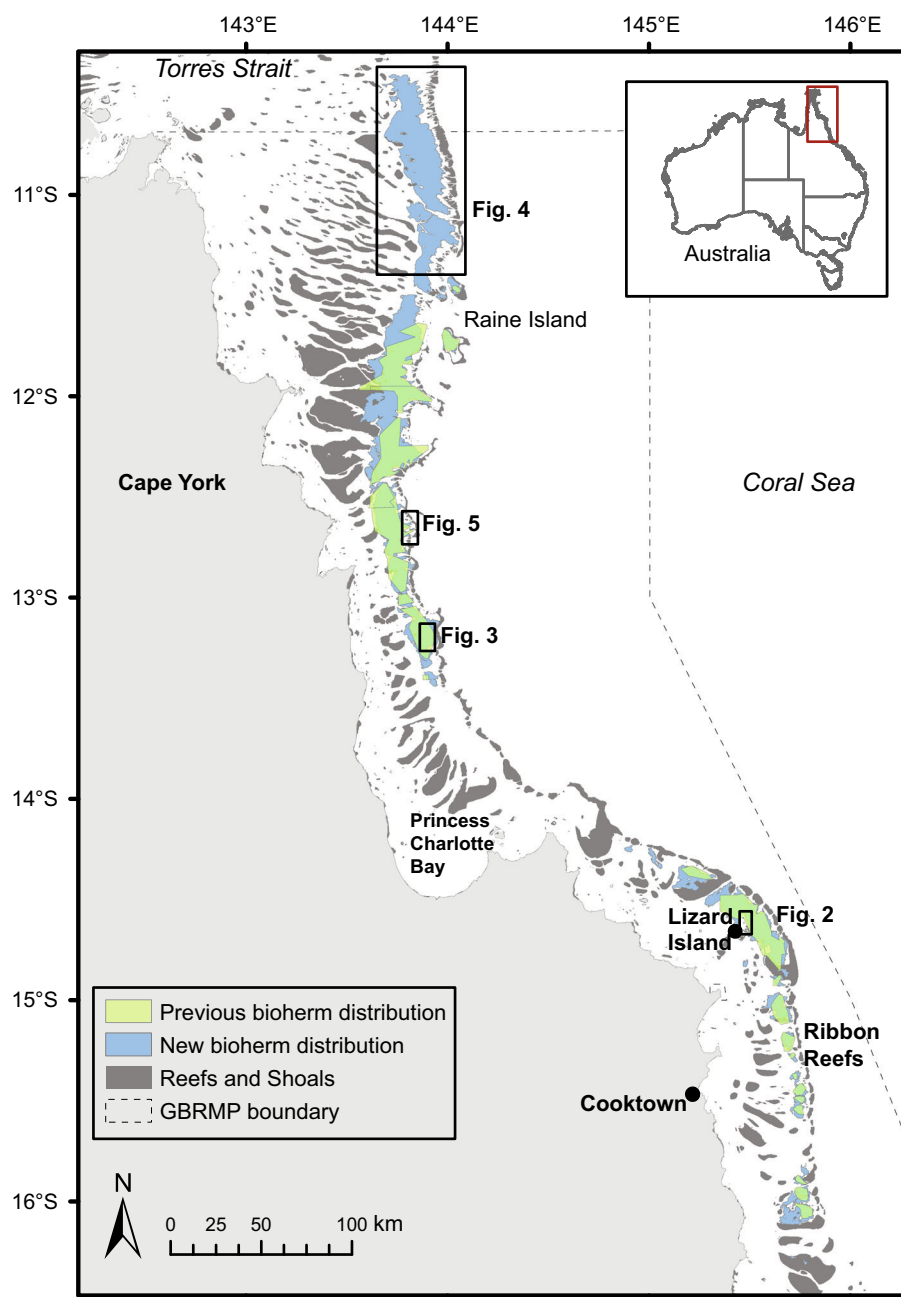

point spacing varying between 6 and 30 m. LAT to MSL (Mean Sea Level) vertical adjustment was made to the bathymetry data to give a MSL vertical datum. Maximum depths for ALB data vary due to clarity of water but may be up to 50 m depth on the outer-shelf. Fledermaus 3D visualisation software was used to edit the data of noise then generate a compiled digital elevation model (DEM) with a 0.00025 arc degree ($\sim$25 m) pixel size and a corresponding hillshaded geotif image (Fig. 3). The resulting DEM was converted to an ESRI raster grid for further spatial analysis in ArcGIS 10.1 software. Because of the relatively shallow depth limit of the ALB data, an additional 0.0005 arc degree ($\sim$50 m) DEM was generated for the northern GBR, combining all available bathymetry data, including the new ALB and multibeam data and the older single-beam survey data. This regional-scale seamless DEM across the shelf and into the adjacent continental slope revealed the deeper inter-reef passages and upper-slope canyons of the northern GBR. The 50 m DEM was then analysed with the ArcGIS Benthic Terrain Modeller (BTM) plug-in (Wright et al. 2005) to derive a slope model (in degrees) and a rugosity model (measure of terrain complexity) to visualise the bioherm morphology and distribution limits within the adjacent landscape features.

Fig. 2 a Bioherm morphology conceptual diagram derived by interpolating between parallel echo-sounder profiles (adapted from Mathews et al. 2007), **b** new 3D view of lidar bathymetry for the same 5.6 × 3.6 km area showing their actual complex reticulate morphology. See Fig. 1 for location
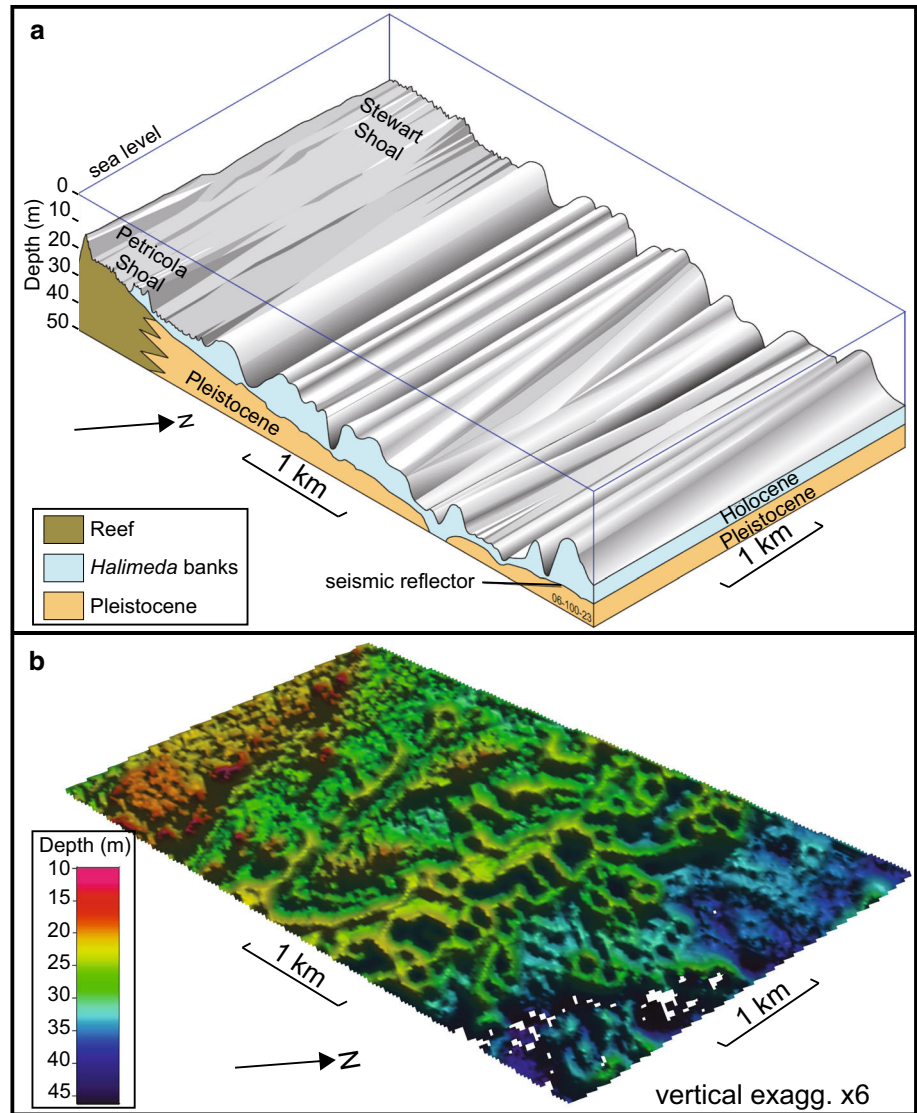
Using these derived models, the characteristic geomorphology of the *Halimeda* bioherms was clearly distinguishable from coral reefs, inter-reef passages, and deeper palaeochannels. Care was taken to avoid false-positive identification of bioherms and a conservative approach was taken when comparing different sized DEMs and their derived models.

An ArcGIS polyline shapefile was created by hand digitising polygons over the 25 m hillshade image and 50 m slope and rugosity models to delineate the boundaries of the bioherms at 1:25,000 scale. The new polygons were cross-referenced against existing seismic profiles (Davies and Marshall 1985; Drew and Abel 1985, 1988; Phipps et al. 1985; Marshall and Davies 1988; Webster et al. 2012) and the original maps of bioherm distribution (Drew and Abel 1985; Drew 1993). A second shapefile was created from the original maps (Drew and Abel 1985, 1988; Drew

1993) to quantify the previously known distribution and compare to the areal extent of the new map. The ArcMap Calculate Geometry Tool was used to calculate the 2-D surface area of both shapefiles. Defining the three morphological sub-type boundaries required a broader-scale approach and was manually digitised in ArcMap at 1:100,000 scale.

Results

Based on a comprehensive analysis of the new and existing high-resolution bathymetry datasets, we have quantified the spatial distribution and morphologic variation of bioherms across the entire northern GBR (Table 3). We have included the estimate of the small (73 km²) area previously reported in the Swain Reefs from the southern GBR within

Table 2 Summary of new and existing data sources used to delineate new *Halimeda* bioherm boundaries and distribution

Data	Source	Description	References
Aerial photographs CAB-7082 RUN 16 Frame 234 + 236, RUN 17 Frame 215 + 217, RUN 18 Frame 170 + 172, RUN 19 Frame 189, RUN 20 Frame 145, RUN 21 Frame 127 + 129, RUN 22 Frame 032, RUN 23 Frame 048	Geoscience Australia	August 1972 routine aerial photography flight over Hibernia Entrance and Second Three-Mile Opening. *Halimeda* banks clearly visible to ~25 m depth	Drew and Abel (1988), Drew (1993)
Airborne lidar bathymetry	Royal Australian Navy Australian Hydrographic Service	Nov 1993 to Sep 2013 LADSI & II system, Mean Sea Level (MSL) vertical datum; WGS84 horizontal datum	Beaman (2010)
Multibeam bathymetry	Australian Hydrographic Service Multiple survey cruises	Multiple surveys forming gbr100 DEM	Beaman (2010)
Previous *Halimeda* survey maps	Ed Drew *Halimeda* Atlas 1983 HMAS Kimbla, RV The Harry Messel	Original distribution map, based on sediment grabs and survey tracks (echosounder). Georeferenced in ArcMap to determine area	Davies and Marshall (1985), Drew and Abel (1985), Marshall and Davies (1988)
Sediment grab sample stations	Ed Drew *Halimeda* Atlas 1983 HMAS Kimbla, RV The Harry Messel	Includes lat/long, depth (m), living *Halimeda* by species (g m^{-2}), sediment *% Halimeda*	Drew (1983), Drew (1993), Drew and Abel (1985)
Sediment grab sample stations	Geoscience Australia and CSIRO	Great Barrier Reef Seabed Biodiversity Project	Pitcher et al. (2007)
Seismic profiles	Australian Hydrographic Service	Lizard Island region, northern GBR 14°27′S–15°02′S	Orme et al. (1978), Orme (1985), Orme and Salama (1988)
Seismic profiles	Geoscience Australia 1984 RV James Kirby	Cooktown region, northern GBR 15°10′S–15°46′S	Davies and Marshall (1985), Phipps et al. (1985), Marshall and Davies (1988)
Seismic profiles	Geological Survey of Queensland	Swain Reefs, southern GBR 20°53′S–22°24′S	Searle and Flood (1988)
Vibracores	Geoscience Australia 1984 RV James Kirby	Cooktown region, northern GBR 15°10′S–15°46′S	Davies and Marshall (1985), Marshall and Davies (1988)
Vibracores	Geological Survey of Queensland	Swain Reefs, southern GBR 20°53′S–22°24′S	Searle and Flood (1988)

Fig. 3 Three-dimensional view of the northern Cape York area, with **a** 2 m multibeam data (*rainbow scale*) overlaid on 25 m lidar data (*grey scale*), **b** sub-bottom profile between points $Z - Z'$ shows distinct *Halimeda* bioherm morphology accreting above a prominent seismic reflector. **c** The 25 m lidar data across the same area clearly delineates bioherms, reefs, and palaeochannels. See Fig. 1 for location
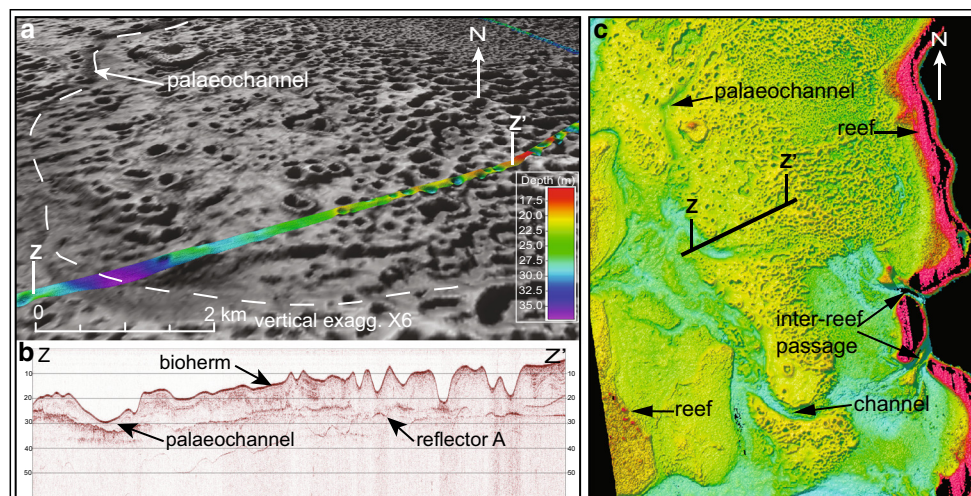

Table 3 Spatial distribution, two dimensional surface area, and proportion of continental shelf covered by the new *Halimeda* bioherm map

Region	Latitude °S	Bioherm northern limit	Bioherm southern limit	Latitudinal distance (km)	Continental shelf area (km^2)[b]	Bioherm area (km^2)	Bioherm shelf area (%)
Northern GBR							
Cape York	10–11	10°24′S	13°26′S	347	6434	1104	17.2
	11–12				12,719	1630	12.8
	12–13				6312	1563	24.8
	13–14				6366	408	6.4
					31,831	4705	14.8
Ribbon Reefs	14–15	14°14′S	16°7′S	187	10,017	864	8.6
	15–16				5624	373	6.6
	16–17				6810	153	2.3
					22,451	1390	6.2
Northern GBR total		10°24′S	16°7′S	534	54,282	6095	11.2
Swain Reefs[a]		21°35′S	21°9′S	34		72	
Total GBR				568		6167	

All dimensions are based on calculations of digitised polygon shapefiles in ArcMap

[a] Preliminary estimate based on limited available data (southern GBR)

[b] *Data source* Lewis and Hutchinson (2001)

Table 3; however, it should be noted that the density of lidar and multibeam surveys do not exist in the southern GBR, and so we do not change this estimate in this current work.

Northern GBR spatial distribution and coverage

The newly mapped *Halimeda* bioherms cover a total area of 6167 km^2 (Table 3) spanning the entire northern GBR (6095 km^2) and including the smaller area estimate from the Swain Reefs in the southern GBR (72 km^2). In the northern GBR, bioherms span 534 km in distance from latitude 10°24′S–16°7′S. Distributed in two distinct regions, Cape York and the Ribbon Reefs, the near-continuous bioherms are separated by a region of absence in the Princess Charlotte Bay region (13°26′S–14°14′S). The Cape York region is the largest region, running continuously for 347 km from latitudes 10°24′S–13°26′S, spanning up to 35 km in width to within 6 km of the shelf break. The Ribbon Reefs region spans 187 km from latitudes 14°14′S–16°7′S, lying proximal to the Ribbon Reefs and within 4 km of the shelf break. In this region, there is a small break in bioherm continuity between latitudes 15°35′S and 15°48′S. The previously known *Halimeda* meadow distribution (Drew and Abel 1988) based on original maps and sediment grabs of living *Halimeda* covers 3474 km^2 (Fig. 1), with locations of bioherms generally consistent to this new map, with the exception

Fig. 4 Map of the northern Cape York region showing extensive bioherms north of Raine Island not previously mapped, and their relationship to the Great Barrier Reef Marine Park Authority (GBRMPA) General Use zone (hatched) and marine park boundary
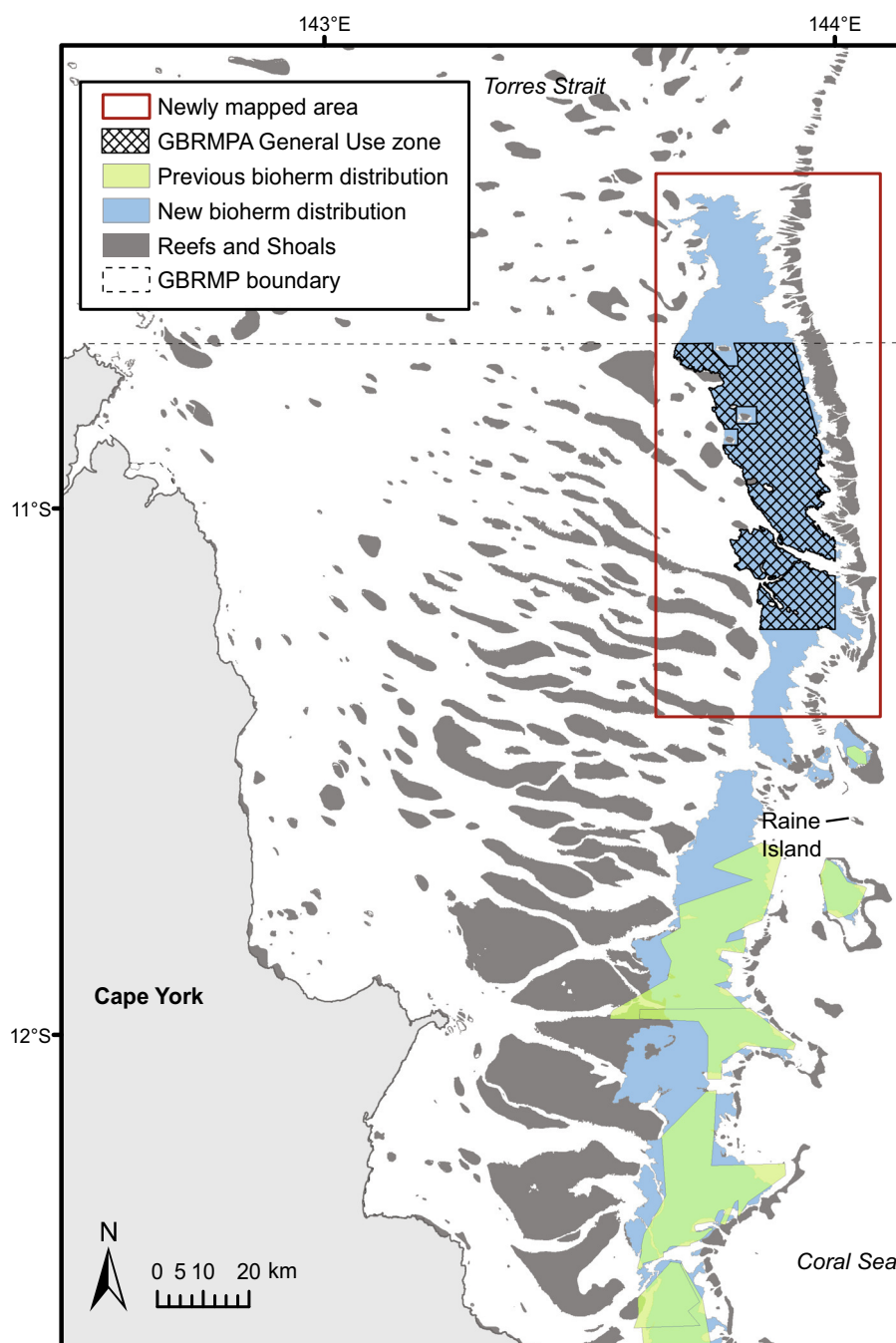
that we have defined and mapped a vast (1740 km^2) bioherm complex north of 11°30′S, extending into the Torres Strait and not previously mapped (Fig. 4).
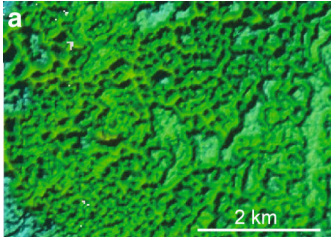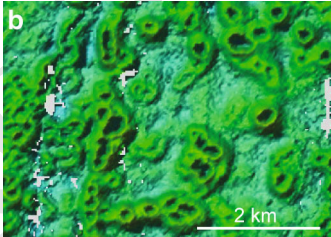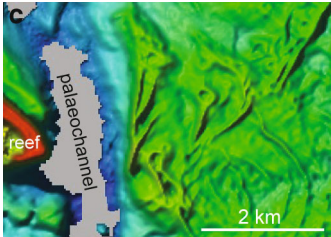
In the Cape York region, 6–25% (mean 15%) of the continental shelf area is covered by bioherms, decreasing in proportion southwards from 2 to 9% (mean 6%) of the shelf area covered in the Ribbon Reefs region (Table 3). Due to their considerable latitudinal and cross-shelf extent, the bioherms span a number of different Great Barrier Reef Marine Park Authority (GBRMPA) management zones and bioregions. In northern Cape York, the bioherms extend beyond the GBR Marine Park boundary into the Torres Strait, and 60% of the bioherms (1036 km^2) are overlapped by the GBRMPA General Use zone (Fig. 4), which permits trawling in benthic habitats.

Morphology

The 25 m lidar data reveal a range of bioherm morphological variation, from complex net-like reticulate

Table 4 Morphological sub-type nomenclature, description, spatial distribution, and type example of (a) reticulate, (b) annulate and (c) undulate

Sub-type	Description	Spatial Distribution	Proportion (%)	Example
Reticulate	High-relief, irregular ridges with sharp sinuous crests, complex honeycomb rugosity, non-circular	Proximal to reef and shelf break to east, grading into annulate zone	16	
Annulate	Smooth, circular ring shapes, hollow centred with or without central pinnacle, often coalescing together with shared boundaries. Typically 200 to 250 m across from crest to crest, but can be up to 500 m across	More distal to reefs and shelf break, generally increasing in size westward	16	
Undulate	Sinuous and wave-like, smooth crests, with low relief above surrounding sediment	Between and around annulate and reticulate zones, grading into surrounding inter-reef sediment	68	

structures to circular ring-shaped end members, with smooth undulating zones between (Table 4). We define and describe three distinct morphological sub-types based on recurrent patterns of shape, texture, and size, termed as (1) reticulate, (2) annulate, and (3) undulate (Table 4).

Reticulate

The reticulate morphology is characterised by complex honeycomb or net-like irregular ridges, with high relief and sharp sinuous crests, which are non-circular (Fig. 5). The reticulate morphological sub-type comprises 16% of the total bioherm distribution and is dominant on the eastern half of the bioherms proximal to the shelf-edge barrier reefs.

Annulate

The annulate morphology is defined by smooth circular, hollow-centred ring shapes. Rings can be singular, but often coalesce together sharing boundaries (Fig. 5). A sharp high-relief pinnacle described in the literature as remnant Pleistocene karst antecedent topography (Phipps et al. 1985; Drew and Abel 1988) is clearly visible in the centre of some rings. Individual rings are commonly 200–250 m across, but can be up to 500 m across from crest to crest. This sub-type comprises 16% of the total bioherm distribution.

Undulate

Connecting the reticulate and annulate morphology types and grading out to the limit of bioherm boundaries, the remaining substrate is smooth, sinuous, and wave like, with low relief but still discernible from the surrounding seafloor (Fig. 5). The undulate sub-type comprises 68% of the total bioherm distribution.

The morphological variation generally follows an east–west cross-shelf gradient, with the complex reticulate morphology dominating proximal to the eastern margin of the bioherms adjacent to the shelf-edge barrier reefs (Fig. 5b). The annulate sub-type generally occurs west of the reticulate zone, becoming less complex but with individual rings increasing in size to westward. The undulate morphology sub-type is most prevalent, connecting the reticulate and annulate zones out to the limit of the bioherm boundaries, where it grades into the deeper surrounding seafloor. These patterns of size, shape, texture, and cross-shelf gradation are generally consistent latitudinally.
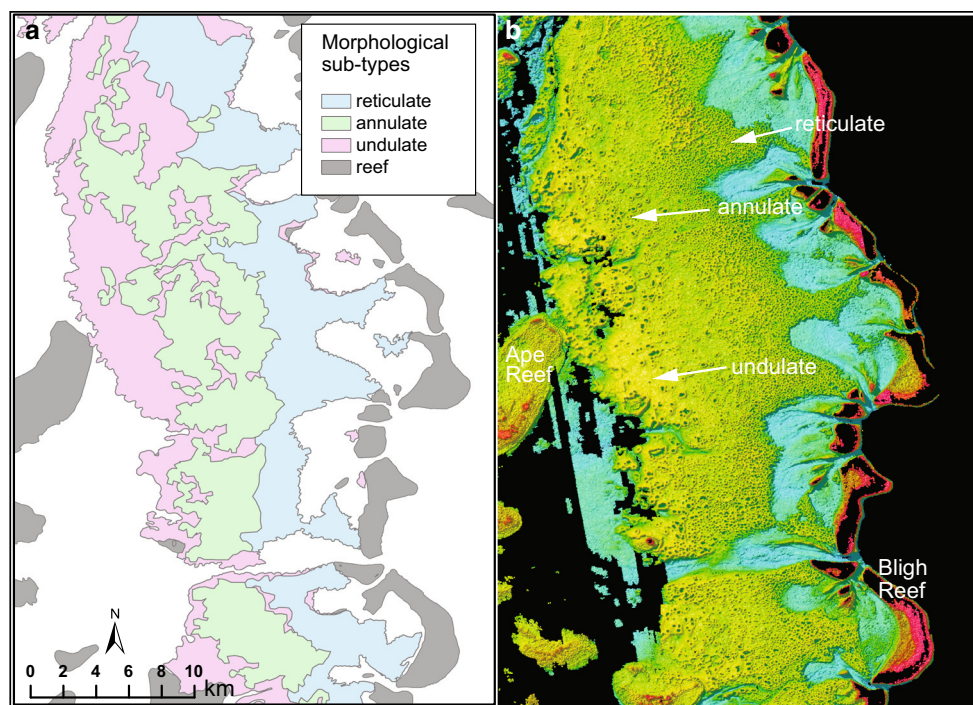
Fig. 5 **a** Distribution of cross-shelf variation in morphological sub-types on a large bioherm area in the Cape York region, and **b** 25 m lidar data for the same area. The complex reticulate morphology dominates proximal to reefs, grading into the annulate zone, where morphology becomes less complex and size of rings increases westward. The smooth, low-relief undulate morphology connects and surrounds the reticulate and annulate sub-types. See Fig. 1 for location

Discussion

Spatial distribution

Few attempts at quantifying the spatial extent of the GBR bioherms have been published (Table 1), with just one estimate of the GBR bioherms covering an area of approximately 2000 km² (Drew 1993). When the original maps were digitised, we found them to actually cover an area of 3474 km². The new bioherm map presented here covers an area of 6167 km², three times the original 2000 km² estimate. Reported *Halimeda*-rich gravel deposits north of Raine Island (Maxwell 1973) were not found by a subsequent later survey (Drew and Abel 1988); however, our investigation found evidence of extensive *Halimeda* bioherms north of Raine Island extending into the Torres Strait, covering an extra 1° of latitude and an area greater than the Ribbon Reefs bioherms area combined. This newly mapped area represents an additional 1740 km² of bioherm inter-reef habitat not previously recorded (Fig. 4). This far northern Cape York region is remote and poorly studied; therefore, no seismic or vibra-coring data from this area were available to the present study. However, previous temperature and current modelling shows upwelling of cool nutrient-rich water from below the Coral Sea thermocline occurs at Raine Island Entrance (Thomson and Wolanski 1984), which is known to influence bioherm formation (Wolanski et al. 1988). A new geophysical and coring survey of the far northern bioherms would reveal their thickness, internal structures, relationship to antecedent topography, age, and accretionary history since the start of the Holocene marine transgression.

The oligotrophic waters of the GBR lagoon lack the volume of essential nutrients (nitrogen and phosphorous) required to produce sufficient living *Halimeda* biomass, to accumulate calcium carbonate bioherms (Drew and Abel 1985, 1988; Wolanski et al. 1988; Drew 2001). Substantial quantities of cool, nutrient-rich waters upwelling from below the thermocline in the Coral Sea have been shown to pump through the narrow passages between outer-shelf reefs via tidal jets (Thomson and Wolanski 1984; Wolanski et al. 1988; Drew 2001), delivering the required volume of nutrients. Outer-shelf geometry (Marshall and Davies 1988) and bathymetry of the inter-reef passages (Thomson and Wolanski 1984; Wolanski et al. 1988) interacting with surface wind stress, residual currents, and topographically induced mixing (Andrews and Furnas 1986) have been proposed as contributing factors to whether upwelled nutrients will reach the GBR lagoon in sufficient concentrations to accumulate bioherms. Oddly, there are no obvious bioherms on the outer-shelf adjacent to Princess Charlotte Bay, despite its well-developed chain of barrier reefs with narrow inter-reef passages comparable to the

348 Cape York and Ribbon Reefs regions (Fig. 1). This absence
349 has been attributed to the input of fluvial mud from the
350 Normanby River catchment, reducing light levels and
351 smothering vegetation (Drew and Abel 1988). However, the
352 Princess Charlotte Bay shelf-edge barrier reefs and inter-reef
353 passages are some 70 to 80 km distant from the coast, and
354 unlikely to be regularly influenced by coastal sediment dis-
355 charge which is generally restricted to within 10–20 km
356 from the coast (Furnas 2003; Devlin and Brodie 2005), and
357 inshore of the 20 m-depth contour (Furnas 2003). Other
358 contributing mechanisms are considered here to possibly
359 explain the absence of bioherms in this shelf interval.

360 The North Queensland coastline and shelf-edge lies
361 generally north–south, and a strong longshore current runs
362 northerly to north-westerly in response to the dominant
363 south-easterly trade winds (Wolanski and Ruddick 1981;
364 Devlin and Brodie 2005). At Princess Charlotte Bay, the
365 coastline and shelf edge change direction from north–south
366 to east–west, disrupting the predominant northerly long-
367 shore current. This abrupt change in shelf-edge geometry
368 and subsequent disruption to prevailing currents may
369 impact nutrient upwelling and delivery into the GBR
370 lagoon through the reefs, thereby precluding bioherm for-
371 mation. The geomorphology of the adjacent continental
372 slope submarine canyons should also be considered due to
373 their close relationship to the shelf-edge barrier reefs and
374 inter-reef passages. For example, the southern limit of the
375 Ribbon Reefs bioherms (latitude 16°7′S) coincides with the
376 location where the numerous canyons indenting the shelf-
377 edge changes to being less abundant and slope-confined
378 (see Puga-Bernabéu et al. 2011, 2013 for descriptions of
379 canyon morphology). Therefore, more detailed hydrologi-
380 cal and seabed survey data are required to help explain the
381 absence of bioherms in the Princess Charlotte Bay region.

382 The new calculations of *Halimeda* bioherm spatial extent
383 and therefore volume of Holocene calcium carbonate clearly
384 exceed that of the modern shelf-edge barrier reefs of the
385 northern GBR; however, this volume is challenging to
386 quantify in detail (Rees et al. 2007). The current GBRMPA-
387 gazetted "reef" area includes both shallow coral reefs and
388 relatively deeper shoals and banks, which our analysis
389 reveals are in some cases *Halimeda* bioherms, thereby
390 making quantitative comparisons between modern reefs and
391 bioherms difficult. Future research will aim to more accu-
392 rately quantify their volume and role as carbonate sinks and
393 shelf carbon budgets in comparison to coral reefs.

394 **Morphology**

395 The bathymetry analysis reveals that bioherm shapes and
396 patterns are not consistent with the previous parallel ridges

397 and troughs representation which permeates the literature
398 (Fig. 2). The previous description has been compared to
399 the lenticular morphology of phylloidal algal mounds from
400 the late Palaeozoic (Wray 1977; Drew and Abel 1988) and
401 *Halimeda* deposits from the upper Miocene reefs of the
402 Sorbas basin, southeastern Spain (Braga et al. 1996; Martín
403 et al. 1997), which are considered to be analogous to their
404 Holocene counterparts in the GBR. However, the northern
405 GBR *Halimeda* bioherms appear to exhibit much more
406 complex and variable morphologies over very large spatial
407 scales. We have identified and described three new mor-
408 phological sub-types, the boundaries of which grade into
409 each other (Table 4; Fig. 5). These reticulate/annulate
410 patterns are reminiscent of coral patch reef morphology
411 observed in shallow lagoons, which are interpreted to be
412 controlled by antecedent topography (e.g. Purdy 1974;
413 Purdy and Winterer 2006) coupled with hydrodynamic
414 influences. However, recent studies of Holocene reticulate
415 reef patterns have revealed that these morphologies also
416 form on flat erosional surfaces lacking in karstified
417 topography (Blakeway and Hamblin 2015; Schlager and
418 Purkis 2015). These authors propose that at small to
419 intermediate scales (m to km), reticulate patterns can be
420 biologically controlled rather than substrate controlled,
421 with access to nutrients and protection from predation and
422 erosion cited as possible drivers of "biotic self-organisa-
423 tion" (Schlager and Purkis 2015). For example, modelling
424 by Blakeway and Hamblin (2015) showed that organisms
425 which tend to collapse, such as branching *Acropora*, pro-
426 duce "cellular" (i.e. reticulate) reefs similar to the reticu-
427 late and annulate bioherm morphology described here.
428 However, the relationship between *Halimeda* bioherm
429 origin, accumulation, morphological variation, and the
430 underlying antecedent topography is currently poorly
431 understood due to the lack of detailed and dense geo-
432 physical survey and sediment core data across the full
433 extent of bioherm distribution. Bioherms are accreting
434 above a prominent seismic reflector (Fig. 3b) interpreted to
435 be the Pleistocene erosional unconformity ("Reflector A";
436 Orme et al. 1978; Davies and Marshall 1985; Marshall and
437 Davies 1988), but the available data are insufficient to
438 elucidate any unambiguous relationship with antecedent
439 topographical highs or pinnacles, or to test the Blakeway
440 and Hamblin (2015) self-organisational model against liv-
441 ing *Halimeda* growth and collapse. Regardless of the pro-
442 cesses controlling the origin of these morphological sub-
443 types, the question remains as to whether these patterns are
444 unique to the GBR; however, high-resolution bathymetry
445 data from elsewhere in the modern (e.g. Kalukalukuang
446 Bank, Indonesia; Nicaraguan Rise; Big Bank Shoals, Timor
447 Sea) is required.

Implications for conservation and management

The vast expanse of living *Halimeda* veneer on top of the bioherms, and the relief and topography of the bioherms themselves, create a significant and structurally complex inter-reef habitat. Ecosystems with this type of structural complexity are recognised as having higher species richness, fish density, and biomass (Alvarez-Filip et al. 2009; Graham and Nash 2013). This habitat complexity is extended to the local scale within each individual bioherm and annulate ring having diverse physical and biological characteristics between the flatter mound tops in shallow water, their outer and inner sloping surfaces, and within the deeper hollows and any central pinnacles. Their ecosystem value in terms of biodiversity and nursery refugia (e.g. Adams et al. 2006; Mumby 2006) and role in larval dispersal and patch reef connectivity (e.g. Almany et al. 2009; Munday et al. 2009) may be comparable to that of seagrass meadows and mangrove habitats.

The sheer size of the northern GBR bioherms, the most extensive, actively accumulating *Halimeda* deposits in the world, contributes to their Outstanding Universal Value from a geological and geomorphological perspective (Whiteway et al. 2013). The suggestion that the *Halimeda* bioherms may contain a more complete record of Holocene calcium carbonate history than the adjacent coral reefs (Drew 1983; Drew and Abel 1985; Phipps et al. 1985) has global implications for Holocene reef carbonate budgets due to their contribution as a geological carbon sink within the carbon budget. Additionally, these bioherms are linked to upwelling, so their up to 20 m-thick sediments may also preserve high-resolution records of palaeoclimate and palaeoceanography.

The spatial distribution of the bioherms extends across a number of different GBRMPA management zones and bioregions. Large portions of the new bioherm map lie within the Marine National Park and Habitat Protection zones. However, some regions fall within the General Use Zone (Fig. 4), where benthic trawling is permitted, potentially impacting the living *Halimeda* habitat and underlying structural complexity. There are inconsistencies in the GBRMPA-assigned bioregions across the *Halimeda* bioherms. For example, bioherm areas overlap both the Reef and the Non-Reef bioregion maps (GBRMPA 2009), and the bioregion designated as *Halimeda* banks does not represent the actual *Halimeda* bioherm distribution; therefore, their classification remains unclear. Undoubtedly, coral reefs and *Halimeda* bioherms are very different habitats and need to be classified unambiguously to ensure appropriate management and conservation. The boundaries of protected areas may need to be reconsidered if these important carbon sinks and inter-reef habitats are to be conserved and maintained, ensuring resilience and population connectivity in adjacent reef ecosystems experiencing unprecedented pressures from a changing climate, ocean acidification, and human impacts from coastal development.

This study significantly advances our understanding of the vast spatial extent of the northern GBR *Halimeda* bioherms, their morphology, and structural complexity, and provides a crucial new geomorphic context for future studies. Their vast size and volume perhaps elevate their importance to rival that of the northern GBR coral reefs as calcium carbonate sinks and structures of geological significance. This new bioherm map will facilitate managers in clarifying the northern GBR *Halimeda* bioherms bioregion classification and contribute to the appropriate management and conservation of these important benthic habitats.

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