

Soft coral and sea fan (Octocorallia) biodiversity and distribution from a multi-taxon survey (2009–2014) of the shallow tropical Kimberley, Western Australia

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ABSTRACT – Any assessment of tropical reef ecosystems should extend beyond a hard coral inventory to include soft corals and other sessile benthic organisms. We assessed octocoral assemblages at 177 marine survey stations in the Kimberly region, Western Australia (<30 m depth), to establish species inventories and describe community structures. The 1,174 vouchered specimens yielded a total of 206 Linnean and morphospecies. The overall composition of this fauna was typical for tropical Indo-Pacific shallow water coral reefs. Octocoral communities demonstrated high species heterogeneity across habitats, with strong differences between inshore and offshore, and a latitudinal zonation along the Kimberley inshore. Of the recorded taxa, 45% were exclusively found offshore, 16% inshore and 39% occurred both inshore and offshore. The nearshore Bonaparte Peninsula, the midshelf region and the northern offshore regions were all ‘hotspots’ for soft coral diversity, while the southern offshore regions presented the most distinct species composition. These results have profound implications for conservation strategies relating to these remote benthic habitats.

KEYWORDS: Indian Ocean, Kimberley Marine Bioregion, Octocorals, Alcyonacea, Coelenterata, Cnidaria, ecological assessment, Woodside Collection Project

INTRODUCTION

The marine environments of the Kimberley, Western Australia (WA) are currently of significant interest as they are one of the last remaining large, unspoilt regions on Earth with high conservation values and a growing nature based economy (Department of Parks and Wildlife 2016). This conflicts with proposed industrial development associated with large oil and gas reserves (Department of Environment and Conservation 2009).

The importance of utilising natural history collections to provide baseline biodiversity information to inform conservation and environmental management decisions has long been recognised, but baseline data suitable for

‘characterising the assets’ in this region are scarce (Hooper and Ekins 2004; Blakeway and Radford 2004; Wood and Mills 2008; Pyke and Ehrlich 2010). In particular, soft corals and sea fans (Octocorallia; Order Alcyonacea) have received little collecting effort in WA waters, and even less in the Kimberly, resulting in a scarcity of publications and curated collections (Kükenthal 1910; Broch 1916; Marsh 1986, 1992, 1993; Griffith 1997; Keesing et al. 2011; Bryce and Sampey 2014). This study represents the first SCUBA collections from the Kimberley in recent times (2009 to 2014).

The Woodside Collection Project (Kimberley) was a multi-taxon marine biodiversity survey program. It completed 181 survey stations (Bryce et al. 2018) within a specified Project Area covering 476,000 km² (Sampey et al. 2014), which extended from the

Kimberley coast to the shelf edge. Here we report on the octocoral results for 181 survey stations, and over 1000 vouchered specimens. Furthermore, we discuss octocoral biodiversity, and implications for the marine habitat classification of the region.

Despite the diversity of organisms recognised as corals, benthic studies of tropical reefs are dominated by hard corals, thus a decline in coral cover is largely defined by declines of scleractinian corals (Przeslawski et al. 2008; Edmunds et al. 2014). The importance of hard corals in the formation of significant reef structures is well known, but future global warming trends point to a decline in their dominance (Blakeway and Radford 2004; Hoegh-Guldberg et al. 2007; Hughes et al. 2010; Edmunds et al. 2014). However, octocorals also play a large role in reef communities, and may become a dominant feature of future reef systems following a decline of hard corals (Przeslawski 2008; Smith et al. 2016; Baum et al. 2016). Transitions to octocoral dominance have been reported from the Indo-Pacific following environmental disturbances of coral reef systems, for example caused by bleaching events, blast fishing, coral predation by crown of thorns seastars, or decline in water quality (Benayahu and Loya 1981; Bradbury and Mundy 1989; Fabricius 1996, 1997, 1998; Fox et al. 2003; Ruzicka et al. 2013; Lenz et al. 2015; Smith et al. 2016; Baum et al. 2016).

Soft corals and sea fans occur worldwide in all reef habitats from the intertidal to abyssal depths. In the tropical Indo-Pacific they are represented by 90 genera and 23 families (Fabricius and Alderslade 2001). They are a major component of coral reef communities and marine benthos, and among the most important contributors to the total biomass of Indo-Pacific coral reef systems; they may cover up to 25% of the total reef substratum (Tursch and Tursch 1982; Fabricius and Alderslade 2001). Although most octocorals contribute little to the formation of limestone reef structure, members of the alcyoniid genus, *Sinularia*, are active reef builders depositing large amounts of structural calcareous sclerites into the rock layers (Jeng et al. 2011). Despite their ecological importance as filter feeders, the diversity of octocorals remains poorly known and new species, genera and families are still discovered and described on a regular basis (e.g. Breedy et al. 2012; McFadden and van Ofwegen, 2013; Bryce and Polisenio 2014; Bryce et al. 2015). Surveys into octocoral diversity are fundamental to assessing the biodiversity of ecosystems with respect to ecosystem function (food web dynamics and conductivity), assessing the long term changes in coral reef community structure and understanding and monitoring the

outcomes of habitat restoration activities (Williams 1992, Benayahu et al. 2003, Fabricius et al. 2007, Chanmethakul et al. 2010, Benayahu et al. 2012, Shackleton and Rees 2016).

AIMS

The aim of this study was to record the biodiversity of the shallow water (< 30 m) soft coral and gorgonian fauna in the Kimberley region of WA over a wide range of habitats and locations, and to comment on diversity trends, community composition and spatial patterns of this faunal group.

METHODS

STUDY AREA AND SITE DESCRIPTIONS

Octocoral vouchers were collected as part of a Western Australian Museum (WAM) series of biodiversity surveys in the Kimberley (2009–2014). Stations were within the Project Area defined by Sampey et al. (2014), in an area westward from the coast, including several midshelf sites (Browse Island, Eugene McDermott, Echuca, Heywood and Vulcan Shoals), to the continental edge atolls, from Rowley Shoals in the south to Ashmore and Hibernia Reefs in the north. Inshore stations covered reefs and islands near Cape Leveque in the south to Long Reef in the north (Figure 1). Bryce et al. (2018) provide a full explanation and description of the study area, including coordinates and general station data. Collections were made intertidally and by SCUBA, at depths ranging from 0–30 m. (Figures 1 and 2).

Distinct differences in environmental conditions and connectivity regimes have been recorded from the coast to the shelf edge (Wilson 2013, 2014). The Kimberley inshore (shoreline to 50 m bathymetry as defined by Bryce et al. 2018) is characterised by relatively turbid, macrotidal, nutrient rich conditions, with connectivity regimes controlled by local currents influenced by seasonal winds and tidal flows (Figure 2A, C). Within the midshelf (51–150 m bathymetry) are submerged shoals (Vulcan, Eugene McDermott, Heywood and Echuca Shoals) with a hard rock foundation and low coral cover and Browse Island (Heyward et al. 2012, Wilson 2014). The offshore area (>150 m bathymetry) includes Ashmore and Hibernia Reefs in the north and Rowley Shoals in the south, all situated on the edge of the continental shelf approximately 300 km off the coast (Figure 1). They are characterised by clear, nutrient poor, oceanic conditions, with direct pelagic connectivity to the highly biodiverse

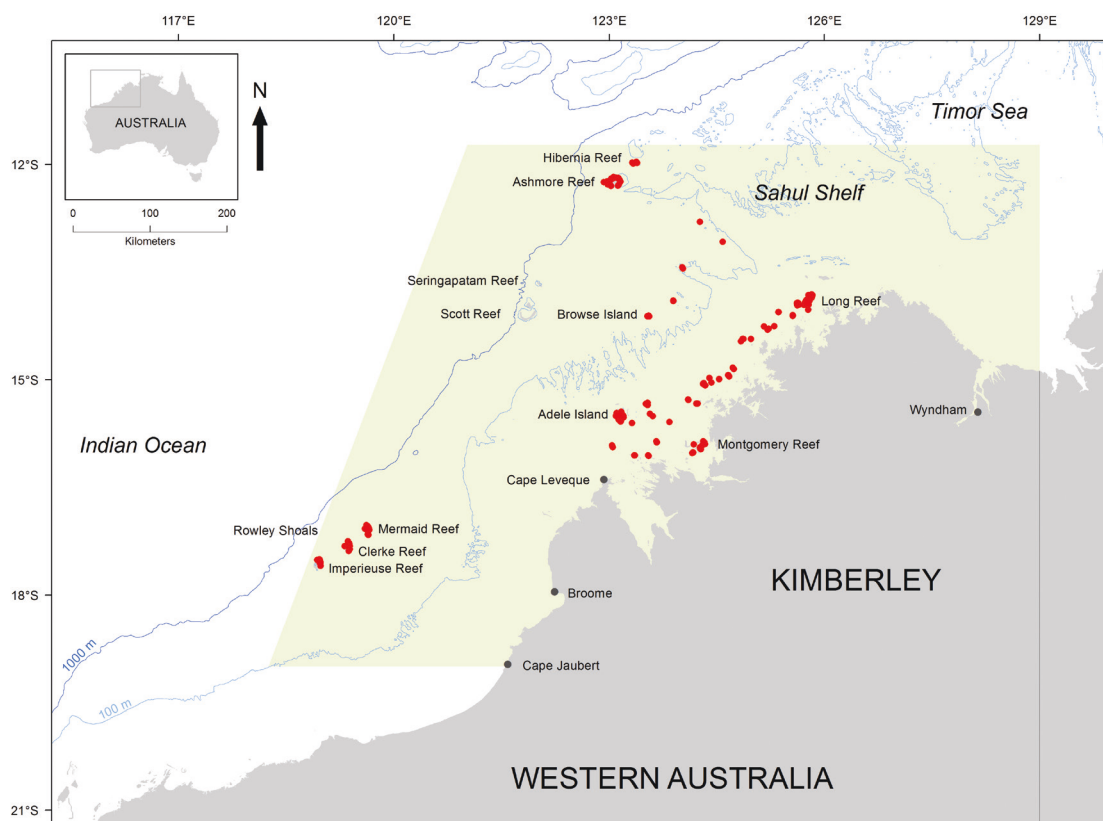


FIGURE 1 Location of octocoral survey stations (red dots) in the Project Area (shaded green; ~ 476,000 km²). The Project Area was divided into continental shelf zones, using the following bathymetric ranges: inshore (coastal shoreline to 50 m depth including all inshore islands and reefs), midshelf (51–150 m) and offshore (> 150 m).

region of Indonesia (Figure 2B, D). Ashmore Reef is the largest and most mature platform reef on the north-western side of the Sahul Shelf (150 km²), and consists of three low vegetated supratidal cays, two shallow lagoons open to the leeward northern side, and an extensive shoal area less than 50 m deep. The southern and windward reef edge has an unbroken margin backed by extensive sand flats and an outer reef slope dominated by strong surge channels, which develop into spur and groove formations (Wilson 2013). To the north-east of Ashmore Reef is an extensive and complex system of submerged reefs, with only Hibernia Reef being emergent. Hibernia Reef is a coral rich, intertidal platform with a shallow lagoon.

The Rowley Shoals are comprised of three distinct reefs, Imperieuse, Clerke and Mermaid Reefs, separated by deep water. Imperieuse and Clerke Reefs have unvegetated, supratidal sand cays, called Cunningham and Bedwell Islands respectively. The sand cay on Mermaid Reef is intertidal. The oval-shaped atolls have a north-south aspect and central lagoons. Each atoll has a narrow channel on the north-eastern side and steep drop offs on the western sides.

TAXONOMIC AND COLLECTION SCOPE

Percentage cover: Point intercept data collection was undertaken at 164 of 181 stations at both subtidal and intertidal sites. Of the midshelf sites, point intercept transects were only undertaken at Browse Island as all other midshelf stations were deep depths. The data was analysed for percent habitat cover for biotic (Octocorallia, Hexacorallia, Porifera, other invertebrates, seagrass, turf algae, macroalgae, crustose algae and coralline algae) and abiotic (sand, rubble and shell-grit, rock and silt) functional groups (See Richards et al. 2018 for a full explanation).

Biodiversity surveys: Octocoral biodiversity surveys were conducted at 177 of 181 survey stations. Dives at four stations (16/K09, 70/K11, 71/K11 and 92/K12) were abandoned due to poor dive conditions. Transects were swum at 153 stations (nine stations had no species records and 15 had only biodiversity information). For these stations, soft corals were surveyed along two 50x2 m wide belt transects (T1, T2) utilising transect tape as a guide. Transect depth was between 12 and 15 m, independent of the tide due to the



FIGURE 2

Examples of habitats: A) Cassini Island (station 30/K10). Turbid conditions in the inshore subtidal. Sea fans indicate a periodic, strong current flow; B) Hibernia Reef (station 144/K113). Clear conditions on a fore-reef slope in the offshore subtidal. Large areas are covered by a variety of octocorals; C) White Island (station 66/K11). A massive *Lobophytum* specimen on an exposed intertidal mid-littoral platform in the inshore area; D) Ashmore Reef (station 138/K13). A large mid-littoral tide pool with soft corals (*Sarcophyton*) in the offshore; E) Montgomery Reef (station 51/K09). Inshore habitat with several fast flowing water channels bisecting the site on a falling tide indicating a high energy, intertidal zone.

prevailing macrotidal regime of the region (see Bryce et al. 2018). All octocorals encountered within the survey area were identified and abundance recorded. Species abundances for each transect (T1, T2) were counted to a maximum of 20 individuals. Station effort was standardised at 60 minutes and any post-transect survey time up to the 60 minute threshold was spent identifying, recording (presence/absence data only) and vouchering off-transect octocoral species. Octocoral voucher specimens were collected at each station for further taxonomic determinations to species level (either Linnean species or OTUs (Operational Taxonomic Units)). The concept of morphospecies assumes that each OTU represents a single species, which has not been identified within the Linnaean system; they have differences in morphological characters from published descriptions and/or are a preliminary identification. Subsequent research will determine if they represent an undescribed species or have been previously described in historic taxonomic literature. Matching OTU data within collections can create large datasets that can significantly enhance our understanding of biodiversity, ecology and distributional trends. This approach has proven useful for difficult sessile invertebrate determinations (Fromont et al. 2016). All specimens have been registered and deposited in the WAM, Perth.

MORPHOLOGICAL IDENTIFICATION

Specimens were photographed in situ and on deck, and then preserved in 75% ethanol with subsamples for DNA analysis preserved in absolute ethanol (100%). Sclerites were prepared for microscopy by cutting small pieces of the specimen from five different regions (polyps, surface of the polyp region, surface of the base, interior of the polyp region, interior of the base) and dissolving them in sodium hypochlorite (13% available chlorine). After the organic material had dissolved, the sclerites were rinsed with distilled water and dried on a glass microscope slide for further investigation. Durcupan ACM was used as a mounting medium for permanent slides (Fabricius and Alderslade 2001: 40).

SPATIAL INFORMATION, COLLECTION DETAILS AND MAPPING

Location and collecting details were checked and verified, and the location of the specimen records visualised using ESRI ArcGIS 10.4.1. Maps of species richness and sampling effort were

generated for each main location. The full list of locations, latitude and longitude and other relevant collection information for all taxa is in Bryce et al. (2018), Table 1.

STATISTICAL ANALYSES

Multivariate analyses of transect cover data were performed in the software package PRIMER v6 (Clarke and Warwick 2001; Clarke and Gorley 2006). Analyses were based on square root transformed habitat data per station using a Bray Curtis similarity coefficient and Non metric Multidimensional Scaling (MDS). ANOSIM was conducted on the factors, continental shelf zones (inshore/offshore) and tidal zones (subtidal/intertidal) to test for significant differences in benthic community structure.

Diversity was based on presence/absence data and calculated from the species inventory (number of species at site; R version 3.2.2. data analyses). Alpha diversity was completed for the 177 octocoral survey stations and separately for the 153 transect stations.

For species composition analyses a hierarchical cluster analysis (Ward's method) was conducted based on species presence/absence data for each transect site to group sites and define spatial patterns (De Cáceres and Legendre 2009; De Cáceres et al. 2010; Dufrêne and Legendre 1997). Original clusters were generated using a Bray Curtis dissimilarity analysis of a binary species presence/absence matrix for the 153 biodiversity transects examined. A matrix dendrogram was used to aggregate soft coral stations into groups based on composition similarity and groups were plotted onto a map to visualise spatial patterns. An indicator species analysis was conducted to determine which species typify each group using the package '*indicspecies*' and function *multipatt* in the statistical software R version 3.3.1.

RESULTS

COLLECTING EFFORT AND SPECIES COMPOSITION OF HIGHER OCTOCORAL TAXA

One hundred and seventy seven stations were surveyed for octocorals. Nine stations had no octocorals present (stations 8, 11 and 25/K09; 73, 82, 84 and 87/K11; 123 and 137/K13). One thousand, one hundred and seventy four (1174) specimen lots were collected from the 168 stations where octocorals were present. Transects were swum at 153 stations, while 15 stations had biodiversity only assessments

due to the absence of octocorals on the transects (stations 72, 89 and 90/K11; 91, 104 and 120/K12) or time limits at deeper depths (stations 107–109 and 121/K12; 146–148/K13; 176 and 181/K14).

Within the subclass Octocorallia, 206 species were from the order Alcyonacea, and one species, *Heliopora coerulea* (Pallas, 1766) from the order Helioporacea. Within the Alcyonacea all five informal suborders were present, representing 18 families and 59 genera (Bayer 1981) (Table 1). The five subordinal groups comprised 9 Stolonifera octocoral species, 116 Alcyoniina, 27 Scleraxonia, 42 Holaxonia, and 16 Calcaxonia (Figure 3A). Four taxa were identified to genus only. Species belonging to *Sinularia* (Alcyonacea), *Chromonephthya* and *Dendronephthya* (Nephtheidae) were identified to genus only due to high taxonomic uncertainty as a result of a high level of intracolony and intraspecies variability (McFadden et al. 2009). Nevertheless, the high variability in colony shape and colour, and also sclerite size and shape, suggests a high diversity within these genera. Species within *Xenia* were also identified to genus only due to identification problems (Janes and Mary 2012; McFadden et al. 2017). The following families had the highest number of identified taxa: Alcyoniidae (54), Nephtheidae (33), Plexauridae (33), Melithaeidae (20), Nidaliidae (15) and Ellisellidae (14) (Figure 3B). All other families were represented by only a few species (1–10).

OCTOCORAL COVER AND ZONATION PATTERNS

Transect point intercept analyses (ANOSIM) demonstrated strong clustering of communities at the functional group level associated with intertidal and subtidal habitats ($R = 0.276$, $p = 0.0001$), as well as offshore and inshore localities ($R = 0.415$, $p = 0.0001$) (Figure 4A, C). Mean octocoral cover varied between 0–30% (Figure 4B, D). Forty-six percent of stations had extremely low cover or no octocorals (<1%), while 48% had between 1–10% cover, and seven stations had >10% cover. In the intertidal, vectors demonstrated strong habitat affinities of soft corals with coralline algae in the inshore areas and with turf algae offshore, and an overall negative association with rock and silt. In the subtidal, vectors demonstrated strong affinities of soft corals with hard coral and sponge cover inshore and crustose and coralline algae cover offshore, and an overall negative association with macroalgae, turf algae and seagrass. Superimposing octocoral station cover over each station demonstrated low octocoral cover (0–7%) for intertidal areas (Figure 4B) and higher octocoral cover (up to 30%) at subtidal stations (Figure 4D). Octocoral cover was highest at the offshore subtidal sites of Ashmore and Hibernia Reefs, with the highest cover of 30% recorded from Hibernia Reef (station 144/K13). From the inshore subtidal stations, Cassini Island (station 34/K10) had the highest cover with 26%.

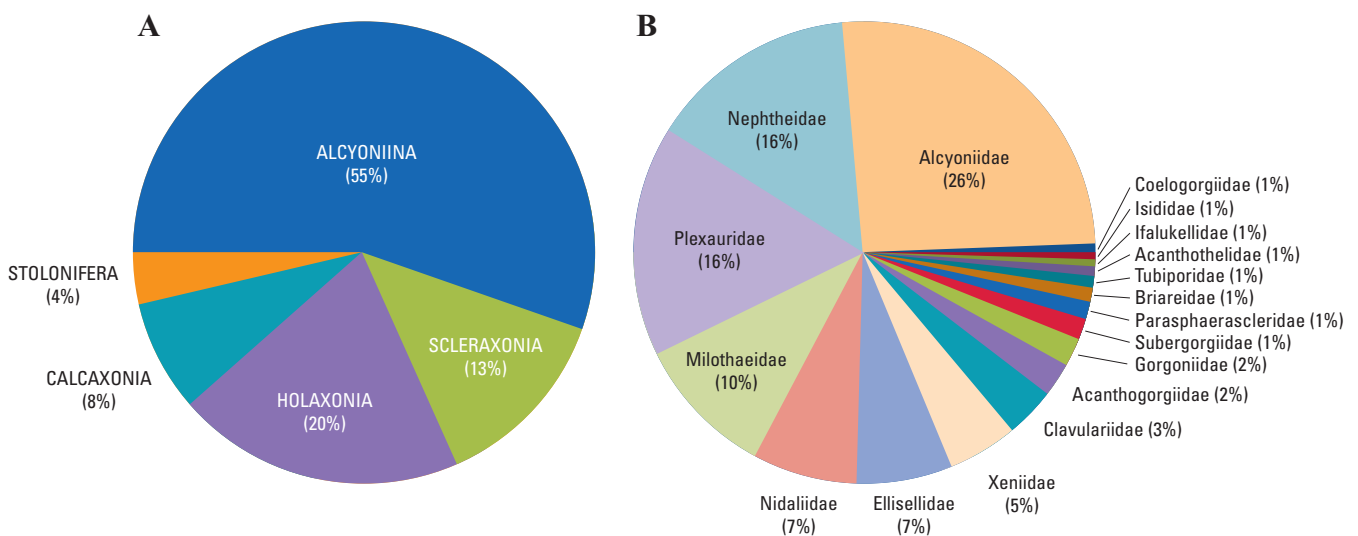


FIGURE 3 Percent composition of octocoral taxa comprising the 206 identified species in the surveys: A) octocoral subordinal groups; B) percentages of identified octocoral taxa within Alcyonacea families (rounded to the nearest percentage).

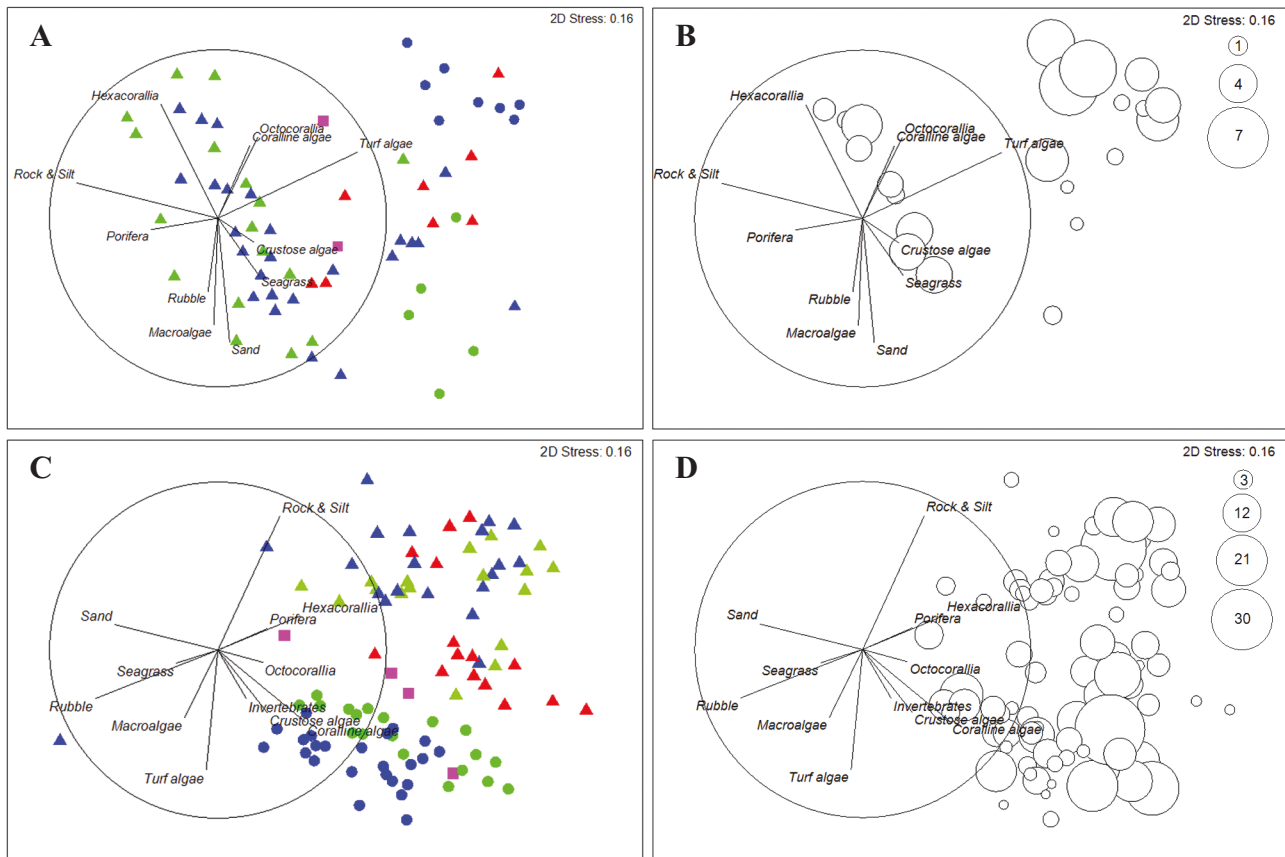


FIGURE 4 Non-metric multidimensional scaling ordination plots of transect point intercept data, based on Bray Curtis similarities: Blue triangle: Inshore South; Red triangle: Inshore Central; Green triangle: Inshore North; Pink square: Midshelf; Blue circle: Offshore South; Green circle: Offshore North. A) intertidal MDS plot of habitat cover based on functional groups; B) mean percentage intertidal octocoral cover superimposed over each station; C) subtidal MDS plot of habitat cover based on functional groups; D) mean percentage subtidal octocoral cover superimposed over each station. The vectors indicate the principle drivers of similarity between stations.

SPECIES ASSEMBLAGES

Octocoral species occurrence varied with locality, especially with respect to offshore versus inshore areas (Table 1). Forty-five percent of species were exclusive to offshore stations, including the midshelf, while 16% were associated with inshore. Thirty-nine percent occurred at both inshore and offshore areas. Of the specimens identified to genus level, *Sinularia*, *Dendronephthya* and *Xenia* were highly abundant at both inshore and offshore stations and *Chromonephthya* was only found inshore. Only a few species were relatively evenly distributed throughout the survey area (Table 1). Relative abundances were similar for both offshore and inshore areas (rating scale of 0–5: 0 = absent; 1 = ‘singletons’, one or few colonies (1–3); 2 = rare (4–10); 3 = uncommon (11–20); 4 = common (21–100); and 5 = very common (>101) (Fabricius and Déath 2001). Offshore, 40% of soft corals were represented by singletons, 17% were rare, 10% uncommon, 25%

common, and 8% very common. Similarly, inshore 40% of soft corals were represented by singletons, 14% were rare, 13% uncommon, 22% common and 11% very common (Table 1).

Within the subordinal group Stolonifera, *Coelogorgia palmosa* Milne-Edwards and Haime, 1857 (Coelogorgiidae) was a new Australian geographical record from this survey (Figure 5A) (Bryce and Poliseno 2014). *C. palmosa* was collected from six Ashmore Reef stations and four midshelf shoal stations, and absent from the remaining 18 Ashmore and Hibernia Reef stations on the outer shelf, and all inshore stations. While its abundance at some Ashmore Reef stations was remarkably high, with up to 100 colonies per dive, midshelf abundance was low.

The subordinal group Alcyoniina was very diverse with the families Alcyoniidae (7 genera), Nephtheidae (9), Parasphaerascleridae (1), Nidaliidae (3) and Xenidiidae (6) all represented. One

new species, *Parasphaerasclera kimberleyensis* Bryce et al. (2015) was found at Long Reef (station 44/K10). A second species from the newly erected genus *Parasphaerasclera*, *P. grayi* (Thomson and Dean, 1931), was collected inshore close to White Island (station 69/K11) and offshore at the Rowley Shoals (station 161/K14) respectively (Figure 5B). *P. grayi* has a wide Indo-Pacific distribution and represents a new record for Australia. These small digitate species were found in shallow water beneath overhangs. Another digitate species, *Paraminabea aldersladei*, Williams 1992 has also adapted to a cryptic lifestyle, preferring light limited overhangs and caves. It was also found in the inshore Kimberley, but was more numerous in the clear, offshore habitats of the Rowley Shoals, Ashmore and Hibernia Reefs.

The genera *Chironophthya* and *Siphonogorgia* (family Nidaliidae) are each represented by seven species (Figure 5C). These genera are typically distinguished by their calyx structure, polyp distribution on the colony, and colony shape. The history of these species is confused, but there is a high likelihood that the Kimberley material incorporates new species (Fabricius and Alderslade 2001; López-González et al. 2014). One specimen, *Nephthyigorgia kükenthali* Broch 1916, was collected from Rosella Shoals (station 91/K12), a depauperate, high energy sediment plain of coarse coral fragments and shell grit. This species was first described from Cape Jaubert, south of Broome and thought rare, but is now considered abundant in sandy environments of the Pilbara region (Keesing et al. 2011). This abundance is seen in recent survey material from the Pilbara, undertaken by the Commonwealth Scientific Research Organisation (CSIRO), and from the Kimberley by the Western Australian Marine Science Institute (WAMSI), with identifications by the senior author. These surveys are currently unpublished.

Species of the family Xenidiidae are more abundant inshore, but can be considered common from the coast to the outer shelf (Table 1). However, members of the genus *Heteroxenia* occur mainly on the outer shelf. A specimen (WAM Z67415) of *Asterospicularia randalli*, with star-like sclerites collected in Mermaid Reef lagoon represents a range extension for WA (Figure 5D). The genus was established in 1951 by Utinomi for a single Taiwan species, *A. laurae*, and later a second species, *A. randalli* was established by Gawel (1976) from Guam. Alderslade (2001) reported the latter in great abundance from the Great Barrier Reef and notes

that both species seem closely related or perhaps identical. To clarify the species, *A. randalli*, we undertook preliminary genetic work (*mtMuts*), which confirmed Alderslade's suspicions that *A. laurae* (from Genbank) and our specimen *A. randalli* are identical. Therefore we consider *A. randalli* as a synonym of *A. laurae*. The species seems to be restricted to shallow, clear-water habitats (Fabricius and Alderslade 2001).

Scleraxonian corals are highly abundant in inshore areas, with only some sea fans (*Melithaeidae*) being more abundant offshore. *Briareum stechei* (Kükenthal, 1910) is highly abundant inshore and offshore and represents a new geographic record for WA (Figure 6A). Two specimens of the rare *Subergorgia rubra* (Thomson, 1905) were collected from Rowley Shoals, and one each from Mermaid and Imperieuse Reefs. Previously, the only Australian record was from the Coral Sea (east coast of Australia and New Caledonia) (Figure 5E). In WA, only one record exists from a CSIRO benthic biodiversity survey (Cruise SS200705), in 2007 near the Montebello Islands in the offshore Pilbara region.

Within the subordinal groups Holoxonia and Calcaxonia, the most abundant and common species were the sea whips *Hicksonella princeps*, *Pinnigorgia flava*, *Rumphella aggregata* within the family Gorgoniidae; *Ctenocella pectinata*, *Dichotella gemmacea*, *Junceella fragilis*, and *J. juncea*, within the family Ellisellidae, and *Isis hippuris* within the family Isididae (Figure 6). Only one specimen of *Heliania spinescens* (Gray, 1859) (Ellisellidae) was collected from Mermaid Reef, Rowley Shoals (Figure 5F). Within WA waters, this species was previously only recorded approximately 900 km south at Exmouth, with two specimens having been dredged from depths over 100 m by CSIRO (Southern Surveyor voyage SS10/2005) during benthic biodiversity surveys of the deep continental shelf and slope.

The genus *Plumigorgia* is reported here for the first time in WA, formerly known only from Indonesia and from the Pacific Ocean (Great Barrier Reef, the Chesterfield and Marshall Islands, Micronesia and the South China Sea) (Alderslade 1986, Fabricius and Alderslade 2001, Grasshoff and Bargibant 2001, Bryce and Poliseno 2014). The genus is represented by *P. hydroides* found at a single Hibernia Reef station occupying a small 1 m² area (Figure 5H). The only other Indian Ocean record for this species is from Indonesia.

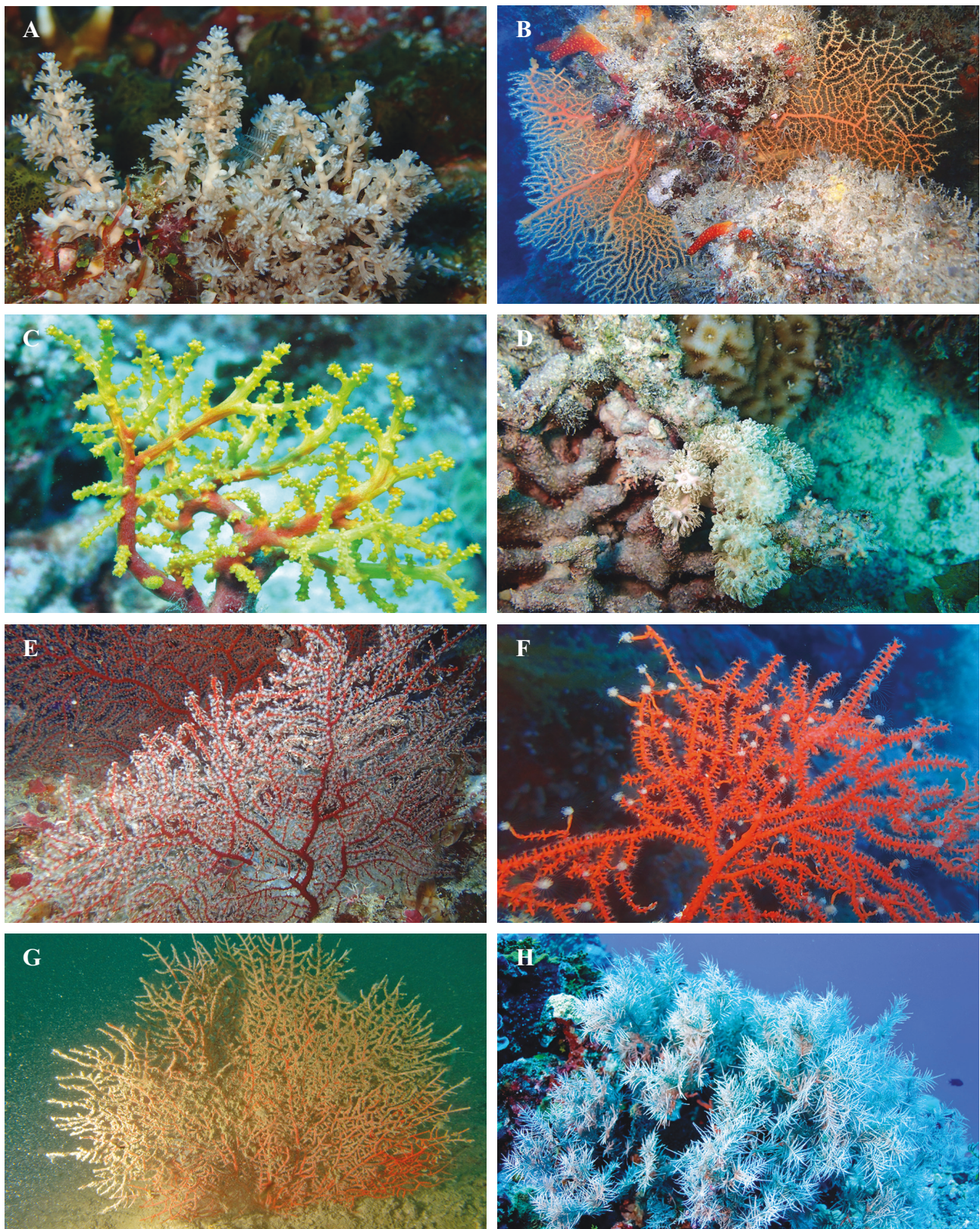


FIGURE 5 Uncommon species of Octocorallia from the Kimberley: A) *Coelogorgia palmosa* (Coelogorgiidae), new geographical record in Australia; B) Digitate colonies of *Parasphaerasclera grayi* (Parasphaerascleraeidae), new Australian record, attached to a rock together with the sea fan *Annella reticulata* (Subergorgiidae); C) A potentially new species of *Chironephthya* (Nidaliidae); D) *Asterospicularia randalii* (Xeniidae), new range extension for WA; E) The rare species *Subergorgia rubra* (Subergorgiidae); F) The rare species *Heliania spinescens* (Ellisellidae); G) The uncommon species *Verrucella granulata* (Ellisellidae); H) First record of *Plumigorgia hydroides* (Ifalukellidae) for Australia.

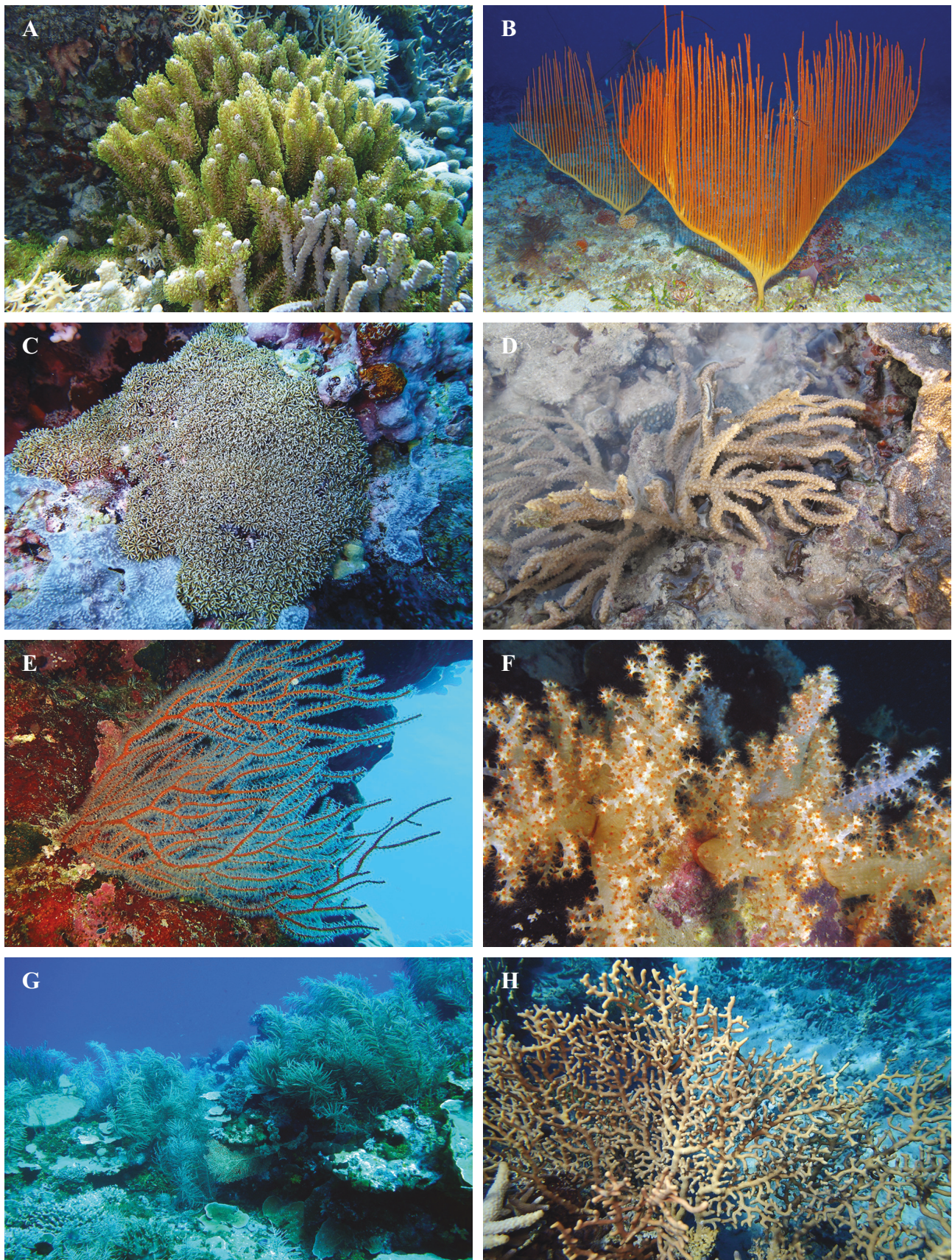


FIGURE 6 Abundant and common species of Octocorallia from the Kimberley survey area: A) *Briareum stechei* (Briareidae); B) *Ctenocella pectinata* (Ellisellidae); C) *Tubipora musica* (Tubiporiidae); D) *Hicksonella princeps* (Gorgoniidae); E) *Subergorgia suberosa* (Subergorgiidae); F) *Scleronephthya* sp. (OTU 5526); G) *Pinnigorgia flava* (Gorgoniidae); H) *Isis hippuris* (Isididae).

TABLE 1 Species of Octocorallia (Alcyonacea and Helioporacea) recorded from the Kimberley survey area with occurrence and relative abundances. (x = present). As abundances at each transect (T1, T2) were only recorded up to 20 individuals abundances were translated into relative abundances on a rating scale of 0–5: 0 = absent; 1 = 'singletons', one or few colonies (1–3); 2 = rare (4–10); 3 = uncommon (11–20); 4 = common (21–100); and 5 = very common (>101) (Fabricius and Déath 2001). Morphospecies numbers are indicted within the Taxa column after the species (e.g. *Carijoa* sp. 5548) and are represented in both the Queensland Museum and WAM databases for future comparability.

Taxa	Kimberley Inshore	Midshelf	Ashmore and Hibernia Reefs	Rowley Shoals
STOLONIFERA				
Family: Clavulariidae				
<i>Carijoa</i> sp. 5548	3	0	0	0
<i>Clavularia viridis</i> (Quoy & Gaimard, 1833)	1	0	0	3
<i>Clavularia</i> sp. 5363	2	0	0	0
<i>Clavularia</i> sp. 6067	0	0	1	5
<i>Clavularia</i> sp. 6068	0	0	3	0
<i>Clavularia</i> sp. 6069	0	4	4	0
<i>Clavularia</i> sp. 6070	4	0	0	0
Family: Coelogorgiidae				
<i>Coelogorgia palmosa</i> Milne-Edwards & Haime, 1857	0	2	5	0
Family: Tubiporidae				
<i>Tubipora musica</i> Linnaeus, 1758	5	2	4	0
ALCYONIINA				
Family: Alcyoniidae				
<i>Cladiella</i> sp. 5361	4	0	1	1
<i>Cladiella</i> sp. 5405	3	0	0	2
<i>Cladiella</i> sp. 6022	0	0	2	0
<i>Cladiella</i> sp. 6044	0	0	4	0
<i>Cladiella</i> sp. 6045	0	0	0	4
<i>Cladiella</i> sp. 6046	0	0	0	4
<i>Cladiella</i> sp. 6047	0	0	0	3
<i>Klyxum</i> sp. 5408	3	0	0	3
<i>Klyxum</i> sp. 6023	0	0	1	0
<i>Klyxum</i> sp. 6081	2	0	0	0
<i>Lobophytum batarum</i> Moser, 1919	0	0	2	0
<i>Lobophytum crassum</i> von Marenzeller, 1886	2	2	1	4
<i>Lobophytum sarcophytoides</i> Moser, 1919	1	0	0	0
<i>Lobophytum</i> sp. 5335	3	0	0	0
<i>Lobophytum</i> sp. 5506	3	0	0	0
<i>Lobophytum</i> sp. 5508	4	0	0	0
<i>Lobophytum</i> sp. 5787	4	0	0	0
<i>Lobophytum</i> sp. 5788	4	0	0	0
<i>Lobophytum</i> sp. 5789	4	0	0	0
<i>Lobophytum</i> sp. 6082	0	0	4	2
<i>Lobophytum</i> sp. 6083	0	1	4	2
<i>Lobophytum</i> sp. 6084	0	0	0	2
<i>Lobophytum</i> sp. 6085	0	0	0	4
<i>Lobophytum</i> sp. 6086	0	0	0	2
<i>Lobophytum</i> sp. 6087	0	0	0	5
<i>Lobophytum</i> sp. 6088	0	0	2	1
<i>Lobophytum</i> sp. 6089	1	1	0	0
<i>Paraminabea aldersladei</i> (Williams, 1992)	1	0	4	4

Taxa	Kimberley Inshore	Midshelf	Ashmore and Hibernia Reefs	Rowley Shoals
<i>Paraminabea</i> cf. <i>aldersladei</i> (6097)	0	0	0	1
<i>Sarcophyton glaucum</i> (Quoy & Gaimard, 1833)	4	4	4	5
<i>Sarcophyton trocheliophorum</i> von Marenzeller, 1886	0	1	0	0
<i>Sarcophyton</i> sp. 5395	4	0	0	0
<i>Sarcophyton</i> sp. 5396	2	0	0	0
<i>Sarcophyton</i> sp. 5397	1	0	0	0
<i>Sarcophyton</i> sp. 5398	1	0	0	0
<i>Sarcophyton</i> sp. 5399	1	0	0	0
<i>Sarcophyton</i> sp. 5400	1	0	0	0
<i>Sarcophyton</i> sp. 5409	2	0	0	0
<i>Sarcophyton</i> sp. 5412	1	0	0	0
<i>Sarcophyton</i> sp. 5786	4	0	0	0
<i>Sarcophyton</i> sp. 6102	0	0	0	2
<i>Sarcophyton</i> sp. 6103	0	0	0	1
<i>Sarcophyton</i> sp. 6104	0	0	0	2
<i>Sarcophyton</i> sp. 6105	0	0	0	1
<i>Sarcophyton</i> sp. 6106	0	0	1	0
<i>Sarcophyton</i> sp. 6107	0	0	4	0
<i>Sarcophyton</i> sp. 6108	0	0	4	0
<i>Sarcophyton</i> sp. 6109	0	0	4	0
<i>Sarcophyton</i> sp. 6110	0	1	4	0
<i>Sarcophyton</i> sp. 6111	0	0	4	0
<i>Sarcophyton</i> sp. 6050	1	1	0	0
<i>Sarcophyton</i> sp. 6051	1	0	0	0
<i>Sinularia brassica</i> May, 1898	5	0	4	3
<i>Sinularia (Dampia) pocilloporaeformis</i> Alderslade, 1983	2	0	1	1
<i>Sinularia</i> spp.	5	3	5	5
Family: Nephtheidae				
<i>Capnella garetti</i> Verseveldt, 1977	4	2	4	0
<i>Capnella imbricata</i> (Quoy & Gaimard, 1833)	1	0	5	0
<i>Capnella</i> sp. 5472	2	0	0	0
<i>Capnella</i> sp. 6061	0	0	2	0
<i>Chromonephthea</i> spp.	4	0	0	0
<i>Dendronephthya</i> spp.	5	2	4	5
<i>Lemnalia</i> sp. 5392	1	1	0	0
<i>Lemnalia</i> sp. 6125	0	0	4	0
<i>Lemnalia</i> sp. 6126	0	0	5	0
<i>Lemnalia</i> sp. 6127	0	1	4	3
<i>Lemnalia</i> sp. 6128	0	0	1	0
<i>Nephthea</i> sp. 6129	0	3	4	0
<i>Nephthea</i> sp. 5393	5	2	5	1
<i>Nephthea</i> sp. 5522	1	4	0	0
<i>Nephthea</i> sp. 5523	1	0	0	0
<i>Nephthea</i> sp. 6092	0	0	0	5
<i>Nephthea</i> sp. 6093	0	0	0	1
<i>Nephthea</i> sp. 6094	0	0	0	2
<i>Paralemnalia</i> sp. 5401	4	0	5	4
<i>Paralemnalia</i> sp. 5766	1	0	0	0
<i>Scleronephthya</i> sp. 5526	5	4	2	1

Taxa	Kimberley Inshore	Midshelf	Ashmore and Hibernia Reefs	Rowley Shoals
<i>Scleronephthya</i> sp. 6112	0	0	0	2
<i>Scleronephthya</i> sp. 6113	0	0	0	1
<i>Scleronephthya</i> sp. 6114	1	0	0	0
<i>Stereonephthya</i> sp. 5438	1	0	0	0
<i>Stereonephthya</i> sp. 5767	4	0	0	0
<i>Stereonephthya</i> sp. 6035	0	1	2	0
<i>Stereonephthya</i> sp. 6036	0	0	4	0
<i>Stereonephthya</i> sp. 6037	0	1	4	0
<i>Stereonephthya</i> sp. 6038	0	0	4	0
<i>Stereonephthya</i> sp. 6121	0	0	0	4
<i>Stereonephthya</i> sp. 6122	0	0	0	4
<i>Stereonephthya</i> sp. 6123	0	4	0	0
Family: Parasphaerascleridae				
<i>Parasphaerasclera grayi</i> (Thomson & Dean, 1931)	2	0	0	2
<i>Parasphaerasclera kimberleyensis</i> Bryce et. al., 2015	1	0	0	0
Family: Nidaliidae				
<i>Chironephthya</i> sp. 6032	0	0	1	0
<i>Chironephthya</i> sp. 6033	0	0	2	0
<i>Chironephthya</i> sp. 6062	0	0	0	1
<i>Chironephthya</i> sp. 6063	0	0	0	1
<i>Chironephthya</i> sp. 6064	0	0	0	1
<i>Chironephthya</i> sp. 6065	0	0	0	1
<i>Chironephthya</i> sp. 6066	1	0	0	0
<i>Nephthyigorgia kükenthali</i> Broch, 1916	1	0	0	0
<i>Siphonogorgia</i> sp. 6034	0	0	4	0
<i>Siphonogorgia</i> sp. 6115	0	0	0	3
<i>Siphonogorgia</i> sp. 6116	0	0	0	1
<i>Siphonogorgia</i> sp. 6117	0	0	0	2
<i>Siphonogorgia</i> sp. 6118	0	0	0	1
<i>Siphonogorgia</i> sp. 6119	0	0	0	1
<i>Siphonogorgia</i> sp. 6120	0	0	0	1
Family: Xeniidae				
<i>Anthelia</i> sp. 5490	1	0	0	0
<i>Anthelia</i> sp. 6054	0	0	2	0
<i>Asterospicularia randalli</i> Gawel, 1976	0	0	0	1
<i>Heteroxenia</i> sp. 5769	1	0	0	0
<i>Heteroxenia</i> sp. 6080	1	0	4	3
<i>Sansibia</i> sp. 5365	1	0	0	0
<i>Sansibia</i> sp. 5367	4	0	0	0
<i>Sansibia</i> sp. 6100	0	0	2	0
<i>Sansibia</i> sp. 6101	1	0	0	0
<i>Sympodium</i> sp. 6 124	0	1	0	0
<i>Xenia</i> spp.	5	4	5	3
SCLERAXONIA				
Family: Briareidae				
<i>Briareum stechei</i> (Kükenthal, 1908)	5	0	4	4
<i>Briareum violaceum</i> (Quoy & Gaimard, 1833)	5	0	4	0

Taxa	Kimberley Inshore	Midshelf	Ashmore and Hibernia Reefs	Rowley Shoals
Family: Anthothelidae				
<i>Alertigorgia mjobergi</i> Broch, 1916	4	0	0	0
<i>Iciligorgia brunnea</i> (Nutting, 1911)	3	0	1	0
Family: Subergorgiidae				
<i>Annella reticulata</i> (Ellis & Solander, 1786)	3	0	1	2
<i>Subergorgia rubra</i> (Thomson, 1905)	0	0	0	1
<i>Subergorgia suberosa</i> (Pallas, 1766)	5	1	4	1
Family: Melithaeidae				
<i>Melithaea</i> sp. 5337	1	1	0	2
<i>Melithaea</i> sp. 5338	0	0	4	2
<i>Melithaea</i> sp. 5339	1	1	4	3
<i>Melithaea</i> sp. 5362	2	0	0	0
<i>Melithaea</i> sp. 5425	4	1	4	4
<i>Melithaea</i> sp. 5426	3	1	4	0
<i>Melithaea</i> sp. 5427	4	0	4	0
<i>Melithaea</i> sp. 5470	1	0	0	0
<i>Melithaea</i> sp. 5410	1	0	0	0
<i>Melithaea</i> sp. 5511	1	0	0	0
<i>Melithaea</i> sp. 5600	4	4	0	0
<i>Melithaea</i> sp. 5773	1	0	0	0
<i>Melithaea</i> sp. 5774	2	0	0	0
<i>Melithaea</i> sp. 5475	2	0	0	0
<i>Melithaea</i> sp. 5776	4	0	0	0
<i>Melithaea</i> sp. 5777	2	0	0	0
<i>Melithaea</i> sp. 6039	0	0	3	0
<i>Melithaea</i> sp. 6040	0	1	4	0
<i>Melithaea</i> sp. 6041	0	0	4	0
<i>Melithaea</i> sp. 6043	0	1	0	0
HOLOXONIA				
Family: Acanthogorgiidae				
<i>Acanthogorgia</i> sp. 5403	1	0	2	4
<i>Acanthogorgia</i> sp. 6025	0	0	1	1
<i>Acanthogorgia</i> sp. 6052	1	0	0	0
<i>Acanthogorgia</i> sp. 6053	1	0	0	0
<i>Anthogorgia</i> sp. 5488	2	0	0	0
Family: Plexauridae				
<i>Astrogorgia</i> sp. 5487	4	0	1	0
<i>Astrogorgia</i> sp. 6026	0	0	1	0
<i>Astrogorgia</i> sp. 6031	0	1	0	1
<i>Astrogorgia</i> sp. 6055	0	0	0	1
<i>Astrogorgia</i> sp. 6056	0	0	0	2
<i>Astrogorgia</i> sp. 6057	0	0	0	1
<i>Astrogorgia</i> sp. 6058	0	0	0	1
<i>Astrogorgia</i> sp. 6059	0	0	0	4
<i>Bebryce</i> sp. 5491	2	0	0	0
<i>Bebryce</i> sp. 6024	0	0	1	0
<i>Echinogorgia</i> sp. 5495	1	0	0	0
<i>Echinogorgia</i> sp. 5772	3	0	0	0
<i>Echinogorgia</i> sp. 6071	0	0	0	1

Taxa	Kimberley Inshore	Midshef	Ashmore and Hibernia Reefs	Rowley Shoals
<i>Echinogorgia</i> sp. 6072	1	0	0	0
<i>Echinogorgia</i> sp. 6073	1	0	0	0
<i>Echinomuricea</i> sp. 6074	1	0	0	0
<i>Euplexaura</i> sp. 5441	3	0	1	0
<i>Euplexaura</i> sp. 5500	4	0	0	0
<i>Euplexaura</i> sp. 6078	0	0	0	1
<i>Menella</i> sp. 5507	4	0	0	0
<i>Menella</i> sp. 5771	2	0	0	0
<i>Menella</i> sp. 6090	0	0	0	1
<i>Menella</i> sp. 6091	1	0	0	0
<i>Paracis</i> sp. 6095	0	0	0	1
<i>Paracis</i> sp. 6096	0	0	0	1
<i>Paraplexaura</i> sp. 5494	2	2	0	0
<i>Paraplexaura</i> sp. 5496	1	0	0	0
<i>Paraplexaura</i> sp. 5497	1	0	0	0
<i>Paraplexaura</i> sp. 5498	1	0	0	0
<i>Paraplexaura</i> sp. 6030	0	0	4	0
<i>Paraplexaura</i> sp. 6098	0	0	0	2
<i>Paraplexaura</i> sp. 6099	1	0	0	0
<i>Villogorgia</i> sp. 6027	0	0	4	1
Family: Gorgoniidae				
<i>Hicksonella princeps</i> Nutting, 1910	2	2	5	1
<i>Pinnigorgia flava</i> (Nutting, 1910)	0	0	4	0
<i>Pseudopterogorgia australiensis</i> (Ridley, 1884)	3	0	0	0
<i>Rumphella aggregata</i> (Nutting, 1910)	5	2	1	3
CALCAXONIA				
Family: Ellisellidae				
<i>Ctenocella pectinata</i> (Pallas, 1766)	4	0	0	0
<i>Dichotella gemmacea</i> (Milne Edwards & Haime, 1857)	4	0	0	0
<i>Dichotella</i> sp. 5779	1	0	0	0
<i>Dichotella</i> sp. 5780	4	0	0	0
<i>Dichotella</i> sp. 5781	2	0	0	0
<i>Ellisella ceratophyta</i> (Linnaeus, 1758)	4	0	1	0
<i>Ellisella</i> sp. 6028	0	0	1	0
<i>Ellisella</i> sp. 6076	0	0	0	3
<i>Ellisella</i> sp. 6077	0	0	0	1
<i>Heliania spinescens</i> (Gray, 1859)	0	0	0	1
<i>Junceella fragilis</i> (Ridley, 1884)	5	3	5	3
<i>Junceella juncea</i> (Pallas, 1766)	5	0	0	1
<i>Verrucella granulata</i> (Esper, 1788)	1	0	0	0
<i>Viminella</i> sp. 6029	3	0	3	0
Family: Ifalukellidae				
<i>Plumigorgia hydroides</i> Nutting, 1910	0	0	1	0
Family: Isididae				
<i>Isis hippuris</i> Linnaeus, 1758	3	0	5	0
HELIOPORACEA				
Family: Helioporidae				
<i>Heliopora coerulea</i> (Pallas, 1766)	x	x	x	x

DESCRIPTION OF SOFT CORAL ALPHA BIODIVERSITY AND MAJOR SPATIAL PATTERNS

Alpha diversity was investigated for the 177 octocoral stations surveyed (Figure 7) and separately for the 153 survey stations where transects were conducted (Figure 8). The former included species information beyond the transects and stations where biodiversity only collections were conducted to 30 m depth (Figure 7). The latter represented species richness along a 100 m transect set at approximately 12 m depth (Figure 8). Alpha diversity analyses demonstrated strong inshore/offshore patterns and a latitudinal zonation along the inshore Kimberley. Soft coral species richness varied between stations and localities, but was clearly higher at deeper stations and at northern offshore stations when compared to inshore locations (Table 1). Species richness across all stations ranged from 0–31 species per survey station, and 0–28 species per transect (Figures 7 and 8 respectively). Intertidal stations were consistently depauperate, while reef front stations had relatively high species richness. The highest alpha diversity (>23) in the survey area was found offshore at Ashmore and Hibernia Reefs and inshore at Jamieson and Heritage Reefs and Patricia Island (Figure 7). High species richness (16–22) was recorded from Ashmore and Hibernia Reefs (offshore north), from the deeper stations at the Rowley Shoals (offshore south), from Heywood Shoals (midshelf), Cassini, Maret, Montalivet and Condillac Islands and Jamieson Reef (inshore north), and from De Freycinet and White Islands and Black Rock (middle inshore) (Figure 7). Offshore, the highest transect species richness with 31 species was found on a steep fore reef slope on the north side of Ashmore Reef (station 130K/13). Generally, biodiversity increased with decreasing longitude and latitude. The offshore biodiversity ‘hotspots’ of Ashmore and Hibernia Reefs were linked to the coastal Bonaparte Archipelago ‘hotspots’ via the diverse midshelf region. Inshore, transect species richness peaked at the northern extremity of the Bonaparte Archipelago with 27 species from a fore reef slope at Jamieson Reef (station 110/K12).

A comparison of soft coral diversity data between all transects and stations (to a depth of 30 m) provided a more complete picture of trends and ‘hotspots’, than transect data alone. This was due to the inclusion of ‘biodiversity stations’ and sampling at greater depths (Figures 7 and 8). The biodiversity stations highlighted the importance of the midshelf habitats as biotic links between offshore and inshore habitats. The importance

of collecting at greater depths, which was especially apparent at the Rowley Shoals, cannot be understated (Figure 8). Overall biodiversity was always higher than ‘transect biodiversity’, with some stations having a distinct low species richness or no soft corals at all on the transects, while overall richness could be relatively high. For example, at Robroy Reef (118/K12) only three species and at Brue Reef (85/K11) only two species were recorded on the transects, yet station species richness was 15 and 13 respectively.

DESCRIPTION OF MAJOR PATTERNS OF SOFT CORAL COMMUNITY COMPOSITION, INCLUDING SPATIAL PATTERNS

A matrix dendrogram was used to aggregate the 153 transects into groups based on similarity of octocoral composition and resulted in five clusters (C1–C5; Figure 9).

The octocoral assemblages were spatially associated and displayed a clear pattern of benthic community structure within the survey area. To further visualise and define these spatial patterns the clusters were depicted on the Project Area map (Figure 10). The five clusters (C1–C5) were strongly related to environmental conditions and characterised by spatial patterns of habitat occurrences (Table 2). Cluster 1 (green) consists of 83% of inshore stations from Montgomery Reef, Adele Island and Champagny Islands in the southern end of the inshore area. This group consisted of 61% intertidal sites and was dominated by the soft coral genera *Sarcophyton* and *Clavularia*. Cluster 2 (purple) is represented by 81% of inshore subtidal stations along the entire length of the inshore, as well as four midshelf subtidal stations from Browse Island and two offshore subtidal lagoonal stations. It was comprised of a suite of octocoral species, with indicator species including a diverse assemblage of sea whips (*Junceella fragilis*, *Junceella juncea*, *Dichotella gemmacea*, *Ctenocella pectinata*, *Pseudopterogorgia australiensis*, *Rumphella aggregata*, *Subergorgia suberosa*) and soft coral families, such as Nephtheidae (*Dendronephthya*, *Chromonephthya*, *Scleronephthya*), Plexauridae (*Euplexaura*, *Menella*, *Astrogorgia*) and Briareidae. Cluster 3 (brown) includes offshore Rowley Shoals sites as well as two inshore sites (Fraser Island and Woodward Island). Cluster 4 (blue) is composed of 95% of the inshore intertidal stations, with a high clustering of stations at the northern inshore. Interestingly, there appears to be a soft coral connection to the offshore area with the remaining 5% of stations

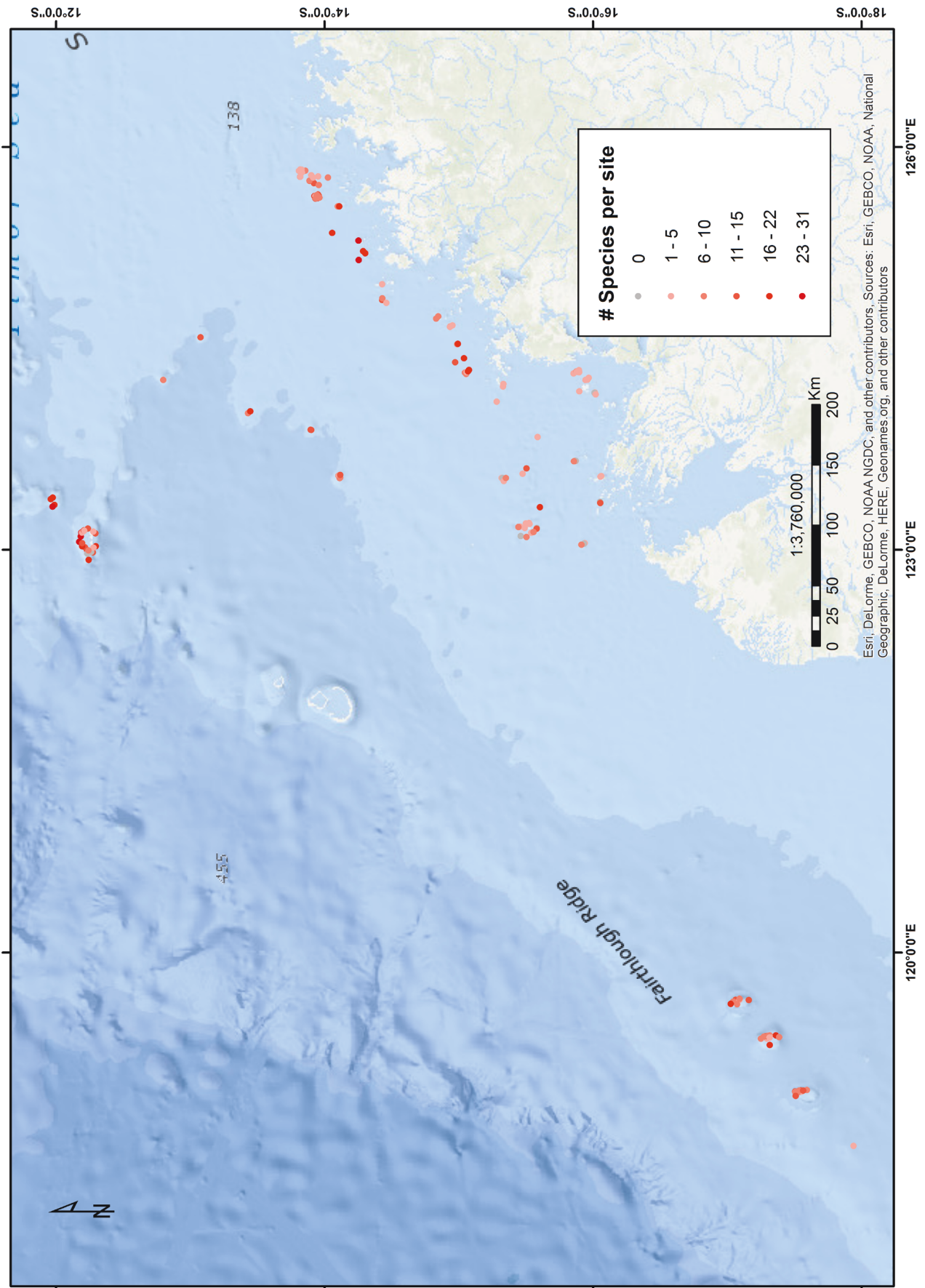


FIGURE 7 Alpha-diversity of all octocoral sampling stations.

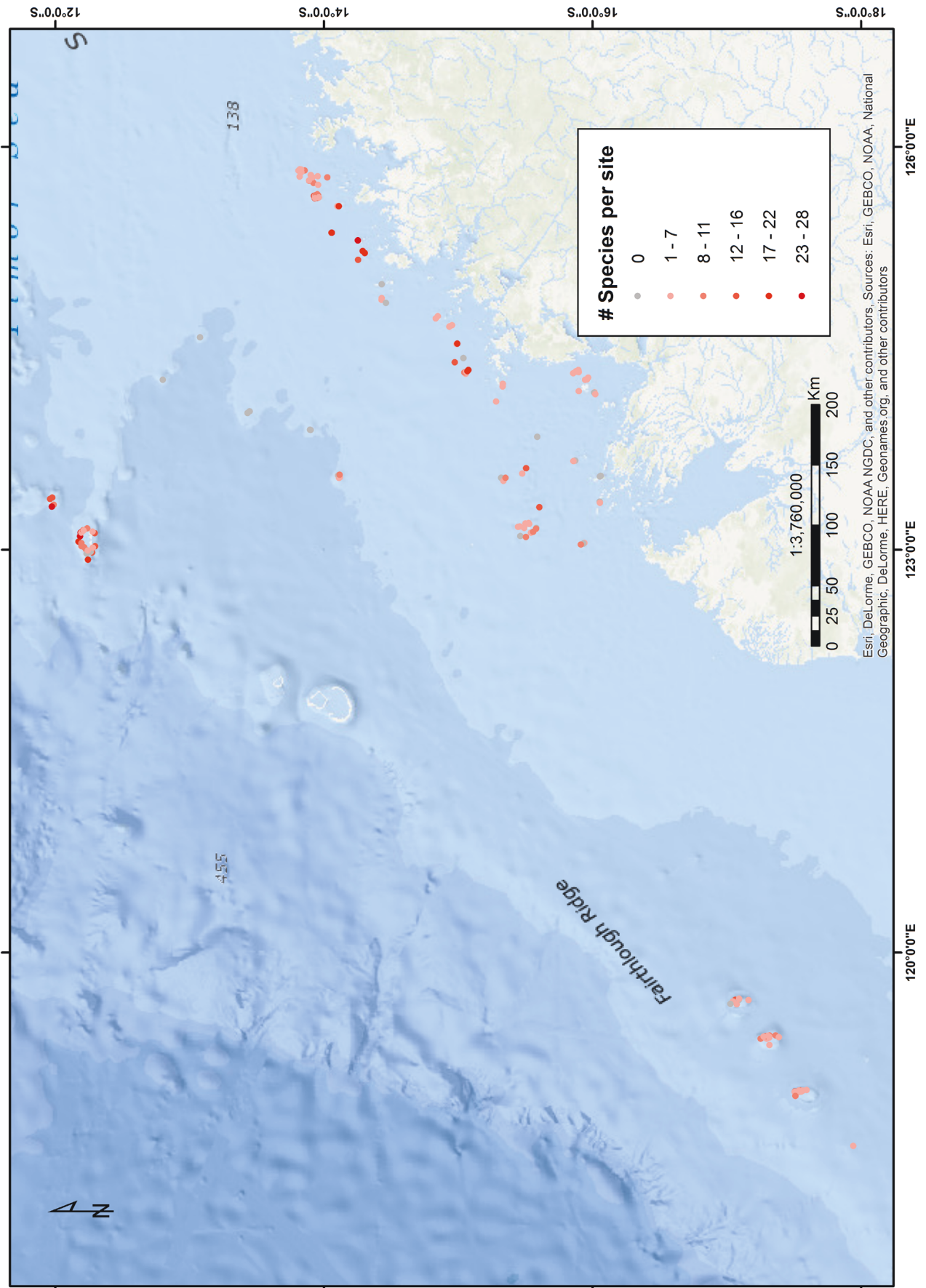


FIGURE 8 Alpha-diversity for species associated with the octocoral transect stations.

being composed of a midshelf station (Browse Island), four intertidal and one lagoonal station at Ashmore Reef in the far north of the survey area. This group was dominated by the soft coral genera *Tubipora*, *Lobophytum* and *Capnella*. Offshore, Ashmore and Hibernia Reefs appeared distinct (Cluster 5 – pink) and were distinguished from the other groups by a complex and diverse suite of soft corals, sea whips and sea fans.

DISCUSSION

CORAL SPECIES AND ASSEMBLAGES

The large Project Area surveyed in this study, approximately 476,000 km², provided considerable latitudinal and longitudinal gradients, and spanned shallow inshore waters (<30 m) across a wide continental shelf to the continental edge (>200 m depth). The complex environmental differences and drivers occurring in the area, such as the origin of seabed sediments, nutrient levels and turbidity,

tidal regimes and currents, as well as differences in levels of connectivity, account for distinctive offshore and inshore reefal communities, and this was clearly reflected in octocoral species community composition and distribution (Wilson 2014; Bryce et al. 2018). Main vectors driving the cross shelf distribution of benthic organisms in the Project Area were the high cover of rock, silt and hard corals at the inshore locations, and the high cover of turf algae, coralline algae, sand, rubble, and soft corals in the offshore regions. Habitat separation of benthic organisms in the intertidal was driven by rock and silt, turf algae and macro-algae in the intertidal areas and high cover of coralline algae, hard and soft corals in the subtidal areas (Richards et al. 2018). When sites were compared using proportional composition of octocoral taxa, clear associations between octocoral assemblages and habitats were apparent. Associations between octocoral species communities and localities were apparent with strong inshore versus offshore patterns and a latitudinal zonation along the Kimberley inshore.

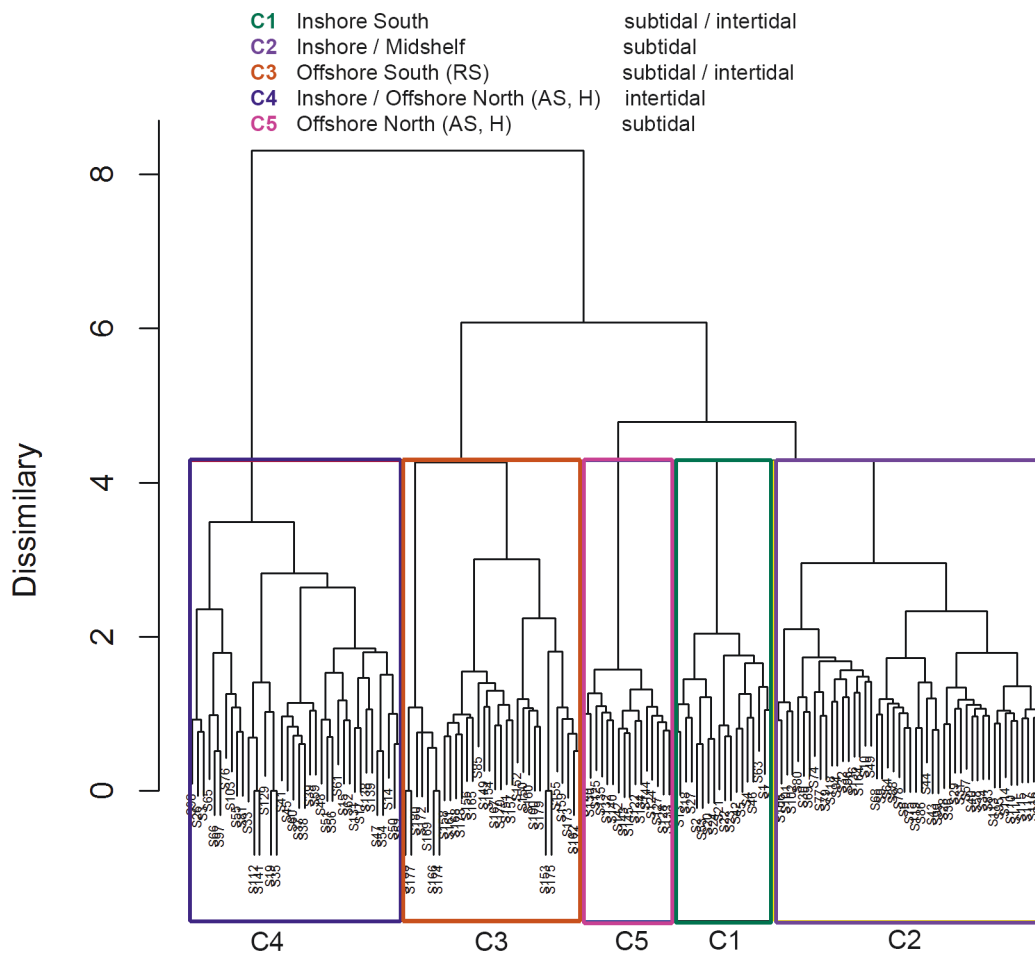


FIGURE 9 Dendrogram depicting transects grouped according to their similarity in octocoral species composition. Dendrogram based on a hierarchical cluster analysis resulted in 5 clusters (C1–C5). RS = Rowley Shoals, AS = Ashmore Reef and H= Hibernia Reef.

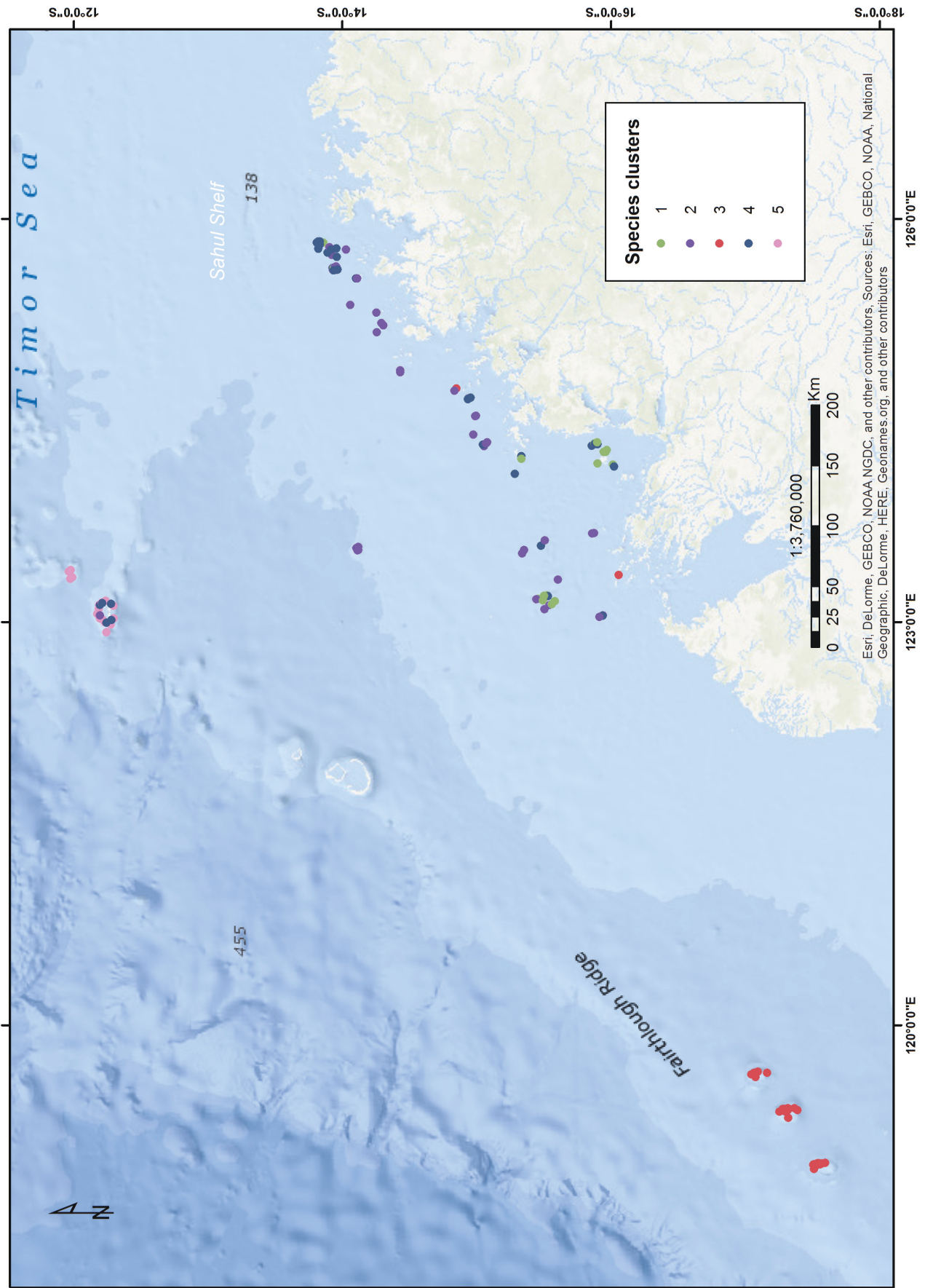


FIGURE 10 Cluster species composition for each octocoral transect. The five clusters from the dendrogram C1–C5 in Figure 9 were plotted on the map to visualise spatial patterns.

Octocoral species assemblages can be grouped into 5 regions: 1) Inshore stations in the southern end of the survey area (C1); 2) inshore subtidal stations along the central inshore section including the midshelf subtidal sites (C2); 3) inshore and offshore intertidal stations within the northern end of the survey area (C4); the Rowley Shoals (C3) and 5) Ashmore and Hibernia Reefs (C5) (see Figure 10). Species patterns revealed a clear connection between the northern inshore and offshore areas, as well as strong associations between the middle inshore area and the midshelf stations. Surprisingly, lagoonal sites within atolls did not present as a particular habitat type. The three atolls of the Rowley Shoals in the offshore south exhibited a homogeneous and distinct community, which is in agreement with a previous octocoral biodiversity survey (Fabricius 2008).

Octocoral richness also varied across stations. Thirty-nine percent of octocoral species in the survey area were found over the entire inshore and offshore range of habitats, while the remaining species were either restricted to turbid inshore reefs or the clear waters of the shelf edge atolls. Nearly half of all octocoral species (45%) were exclusively present at clear offshore and midshelf sites, while only a few species (16%) were restricted to turbid inshore areas. Nevertheless, the latter were all singletons and may be globally rare and highly restricted in their distribution, but further collecting is required. This pattern could be attributed to the direct pelagic connectivity of these shelf edge reefs with the species rich bioregions of eastern Indonesia, while inshore, reef connectivity is controlled by local currents driven by seasonal wind and tidal flow (Wilson 2014).

Different genera of octocorals demonstrate different habitat preferences, with growth strongly contrasting between locations. Intertidal stations were less diverse than subtidal stations and were characterised to a large extent by the genera *Tubipora*, *Clavularia*, *Sarcophyton*, *Lobophytum*, *Sinularia*, *Capnella*, and *Xenia*. For soft corals, intertidal environments are stressful, subject to strong wave and tidal action and desiccation during long exposure times at low tides. Soft coral body plans for these harsh sites were predominantly encrusting, short lobed or massive, to flat species. Inshore subtidal stations were comprised of a diverse assemblage of sea whips (*Junceella fragilis*, *Junceella juncea*, *Dichotella gemmacea*, *Ctenocella pectinata*, *Pseudopterogorgia australiensis*, *Rumphella aggregata*, *Subergorgia suberosa*) and soft coral families (Alcyoniidae, Nephtheidae, Plexauridae and Briareidae). Northern offshore localities were

more species rich than the south and this can be attributed to the flow of tropical water from the Western Pacific arriving at suitable habitats during recruitment (Wilson 2014). Relative abundances were similar offshore and inshore, with 40% of the octocorals represented by one or a few colonies, 14–17% rare, 10–13% uncommon, 22–25% common and 8–11% very common (Table 1).

All major groups and genera of Indo-Pacific octocorals were represented (Fabricius and Alderslade 2001). This comprehensive survey revealed many new geographic records, range extensions and new, and potentially new, species. This can be attributed to the large survey area with a diverse array of habitats incorporating less accessible areas, such as reef overhangs and exposed sites, which may not have been sampled in the past. A similar trend has been observed in sampling programs of other areas poorly sampled for octocorals, such as the Pilbara and King George River estuary in north-western Australia (Keesing et al. 2004, Pitcher et al. 2016).

Offshore biodiversity ‘hotspots’, such as Ashmore and Hibernia Reefs, were linked to the inshore Bonaparte Archipelago ‘hotspots’ (Robroy Reefs, Jamieson and Heritage Reef, Maret, and Montalivet Islands and Condillac and Patricia Islands) via the diverse midshelf region (Browse Island and the several visited shoals).

Alcyoniidae is a dominant family in the Kimberley region consistent with patterns of global and regional Australian soft coral diversity. The family has been reported from other Indo-Pacific locations, such as Palau eastward to the Great Barrier Reef and the east coast of Africa (Benayahu 1985; Fabricius and Déath 2001, Benayahu et al. 2003, Fabricius et al. 2007, Chanmethakul et al. 2010, Benayahu et al. 2012). Alcyoniidae are widely distributed in all habitat types from the intertidal to greater depths, and can cover large areas. They are able to survive harsh conditions, such as heavy sediment loads and extended exposure, which is an important advantage for surviving extreme Kimberley conditions.

Dominant families were Nephtheidae, Plexauridae, and Melithaeidae, and speciose families included Nidaliidae and Ellisellidae (Figure 3B). Melithaeidae, Plexauridae, Nidaliidae, Ellisellidae, and several genera among the family Nephtheidae are heterotrophic suspension feeders that depend on currents to transport food particles towards their polyps. All other families in this study are represented by only a few species and

are generally species limited taxa, but they do incorporate new species and range extensions, and are therefore important contributors to the overall knowledge of regional biodiversity.

Marine filter feeding communities are dominated by soft corals, sea fans, sponges and ascidians and can form extensive garden-like habitats characterised by high biomass and diversity. These benthic organisms are vital components of nearshore and offshore tropical ecosystems through their contribution to carbon cycling and productivity, provision of habitat for an array of associated biodiversity, and play a vital role as nursery areas. Octocoral transect cover peaked at 30% at only a few stations. Generally, octocoral cover was low, attributable to an artefact of sampling where the majority of transects were placed on coral reef sites and at a depth comparable with other coral studies. An example is a mid-littoral reef platform at Long Reef (station 56/K10) with zero octocoral cover on the transect, but the reef platform bordering the transect had the octocoral *Tubipora* as the dominant benthic organism with 28% cover (Richards et al. 2013). Benthic studies of tropical reefs are dominated by hard corals, and a focus on coral cover is largely defined by scleractinian cover (Przeslawski et al. 2008; Edmunds et al. 2014). However, a more balanced approach needs to also include the examination of other benthic taxa including octocorals, which not only play a dominant role in extant benthic community structure, but may well populate and dominate future reefs (Blakeway and Radford 2004; Hoegh-Guldberg et al. 2007; Hughes et al. 2010; Edmunds et al. 2014; Baum et al. 2016). Numerous studies over the last several decades have documented declines in the abundance of reef building corals after disturbance events and a phase shift to dominance by fleshy, non-calcifying invertebrates (Benayahu and Loya 1981; Bradbury and Mundy 1989; Fabricius 1996, 1997, 1998; Fox et al. 2003; Przeslawski 2008; Ruzicka et al. 2013; Lenz et al. 2015; Smith et al. 2016). The faunistic importance of octocorals as key contributors to ecosystem services in the Kimberley illustrates the need for further soft coral surveys that will encompass the full spectrum of reef types and habitats, especially inter-reefal and understudied environments, such as soft sediment and sandy areas.

MANAGEMENT IMPLICATIONS

To date, this study is the most comprehensive study for soft corals undertaken within the Kimberley. This synthesis of soft coral data

will facilitate future surveys in the region and will help fill remaining knowledge gaps. Comprehensive surveys in remote areas, such as the Kimberley marine environments, are important to provide a clearer understanding of soft coral taxonomy, systematics and distributional patterns in tropical Indo-Pacific marine environments. These data provide valuable insight into the regions biodiversity and habitats, with important implications for marine area protection, but future consideration should be given to environmental parameters, sampling effort and methodology, and geomorphic zones in order to gain a more comprehensive understanding (Fabricius 2008; Keesing et al. 2011; Pitcher et al. 2016; Fromont et al. 2016). This work underpins the hypothesis that the west coast of Australia is a unique ecosystem supporting a rich and diverse octocoral fauna (Marsh 1993; Bryce 2009; Masini et al. 2009; Wilson 2013; Richards et al. 2013), and further investigations will enhance our understanding of these environments. Meaningful ecological management areas, for potential estimates of habitat loss and to assess long term changes in community structures, can be defined by providing better ecological information and by locating appropriate reference sites within similar community types (EPA 2004; Pitcher et al. 2016; Moore et al. 2016). Long term monitoring of environmental conditions and impacting pressures is also essential to evaluate management effectiveness and to inform future research and decision making (Department of Wildlife 2016). These survey results on octocoral assemblages within the Kimberley will provide useful data for future monitoring and environmental management of marine areas, in particular where impact monitoring is proposed.

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TABLE 2 Survey stations per cluster ordered to match Figures 9 and 10 in this paper and Figure 2 in Bryce et al. 2018.

Station #	Locations	Bryce et al. 2018 (Figure 2)
C1: Offshore intertidal walking		
1	Adele Island	Inshore subtidal
2	Adele Island	Inshore subtidal
4	Adele Island	Inshore subtidal
5	Adele Island	Inshore subtidal
7	Adele Island	Inshore intertidal walking
12	Adele Island	Inshore subtidal
13	Adele Island	Inshore subtidal
18	Montgomery Reef	Inshore intertidal walking
20	Montgomery Reef	Inshore intertidal walking
21	Montgomery Reef	Inshore intertidal walking
22	Montgomery Reef	Inshore intertidal walking
23	Montgomery Reef	Inshore intertidal walking
24	Montgomery Reef	Inshore intertidal walking
27	Montgomery Reef	Inshore intertidal walking
42	Cassini Island	Inshore intertidal dive/snorkel
46	Long Reef	Inshore intertidal dive/snorkel
53	Long Reef	Inshore subtidal
63	Champagne Islands	Inshore intertidal walking
C2: Midshelf intertidal walking		
6	Adele Island	Inshore subtidal
9	Adele Island	Inshore subtidal
10	Adele Island	Inshore intertidal dive/snorkel
28	Cassini Island	Inshore subtidal
29	Cassini Island	Inshore subtidal
30	Cassini Island	Inshore subtidal
31	Cassini Island	Inshore subtidal
32	Cassini Island	Inshore intertidal walking
34	Cassini Island	Inshore subtidal
36	Cassini Island	Inshore subtidal
40	Cassini Island	Inshore subtidal
43	Long Reef	Inshore subtidal
44	Long Reef	Inshore subtidal
49	Long Reef	Inshore intertidal dive/snorkel
57	Long Reef	Inshore subtidal
58	Cassini Island	Inshore subtidal
64	White Island	Inshore subtidal

Station #	Locations	Bryce et al. 2018 (Figure 2)
68	White Island	Inshore subtidal
69	Outcrop NW Black Rocks	Inshore subtidal
74	Beagle Reef	Inshore subtidal
75	Beagle Reef	Inshore subtidal
77	Mavis Reef	Inshore subtidal
78	Mavis Reef	Inshore subtidal
79	Albert Reef	Inshore subtidal
80	Brue Reef	Inshore subtidal
83	Brue Reef	Inshore subtidal
86	King and Conway Islands	Inshore subtidal
88	King and Conway Islands	Inshore subtidal
93	White Island	Inshore subtidal
94	De Freycinet Island	Inshore subtidal
95	De Freycinet Island	Inshore subtidal
96	Hedley Island	Inshore subtidal
99	Outcrop North of Colbert Island	Inshore subtidal
101	Browse Island	Midshelf subtidal
102	Browse Island	Midshelf subtidal
105	Browse Island	Midshelf subtidal
106	Browse Island	Midshelf subtidal
110	Jamieson Reef	Inshore subtidal
111	Jamieson Reef	Inshore subtidal
113	Condillac Island	Inshore subtidal
114	Patricia Island	Inshore subtidal
115	Heritage Reef	Inshore subtidal
116	West Montalivet Island	Inshore subtidal
117	West Montalivet Island	Inshore subtidal
118	Robroy Reefs	Inshore subtidal
119	Robroy Reefs	Inshore subtidal
136	Ashmore Reef	Offshore subtidal lagoonal
164	Imperieuse Reef (Rowley Shoals)	Offshore subtidal lagoonal
C3: Inshore intertidal walking		
85	Fraser Island	Inshore subtidal
100	Woodward Island	Inshore intertidal walking
149	Mermaid Reef (Rowley Shoals)	Offshore subtidal fore-reef slopes
150	Mermaid Reef (Rowley Shoals)	Offshore subtidal lagoonal
151	Clerke Reef (Rowley Shoals)	Offshore subtidal fore-reef slopes
152	Clerke Reef (Rowley Shoals)	Offshore subtidal fore-reef slopes
153	Clerke Reef (Rowley Shoals)	Offshore subtidal lagoonal
154	Clerke Reef (Rowley Shoals)	Offshore subtidal fore-reef slopes

Station #	Locations	Bryce et al. 2018 (Figure 2)
155	Clerke Reef (Rowley Shoals)	Offshore subtidal lagoonal
156	Clerke Reef (Rowley Shoals)	Offshore subtidal fore-reef slopes
157	Imperieuse Reef (Rowley Shoals)	Offshore subtidal fore-reef slopes
158	Imperieuse Reef (Rowley Shoals)	Offshore subtidal fore-reef slopes
159	Imperieuse Reef (Rowley Shoals)	Offshore subtidal lagoonal
160	Imperieuse Reef (Rowley Shoals)	Offshore intertidal walking
161	Imperieuse Reef (Rowley Shoals)	Offshore subtidal fore-reef slopes
162	Imperieuse Reef (Rowley Shoals)	Offshore subtidal lagoonal
163	Imperieuse Reef (Rowley Shoals)	Offshore intertidal walking
165	Imperieuse Reef (Rowley Shoals)	Offshore subtidal fore-reef slopes
166	Imperieuse Reef (Rowley Shoals)	Offshore intertidal walking
167	Imperieuse Reef (Rowley Shoals)	Offshore subtidal fore-reef slopes
168	Imperieuse Reef (Rowley Shoals)	Offshore subtidal fore-reef slopes
169	Clerke Reef (Rowley Shoals)	Offshore intertidal walking
170	Clerke Reef (Rowley Shoals)	Offshore subtidal fore-reef slopes
171	Clerke Reef (Rowley Shoals)	Offshore subtidal lagoonal
172	Clerke Reef (Rowley Shoals)	Offshore intertidal walking
173	Clerke Reef (Rowley Shoals)	Offshore subtidal fore-reef slopes
174	Clerke Reef (Rowley Shoals)	Offshore intertidal walking
175	Clerke Reef (Rowley Shoals)	Offshore subtidal lagoonal
177	Mermaid Reef (Rowley Shoals)	Offshore intertidal walking
178	Mermaid Reef (Rowley Shoals)	Offshore subtidal fore-reef slopes
179	Mermaid Reef (Rowley Shoals)	Offshore subtidal lagoonal
180	Mermaid Reef (Rowley Shoals)	Offshore intertidal walking

C4: Offshore intertidal dive/snorkel

3	Adele Island	Inshore intertidal walking
14	Montgomery Reef	Inshore intertidal walking
15	Montgomery Reef	Inshore intertidal walking
17	Montgomery Reef	Inshore intertidal walking
19	Montgomery Reef	Inshore intertidal walking
26	Montgomery Reef	Inshore intertidal walking
33	Cassini Island	Inshore intertidal dive/snorkel
35	Cassini Island	Inshore intertidal dive/snorkel
37	Cassini Island	Inshore intertidal dive/snorkel
38	Cassini Island	Inshore intertidal dive/snorkel
39	Cassini Island	Inshore subtidal
41	Cassini Island	Inshore intertidal dive/snorkel
45	Long Reef	Inshore intertidal walking
47	Long Reef	Inshore subtidal
48	Long Reef	Inshore intertidal walking

Station #	Locations	Bryce et al. 2018 (Figure 2)
50	Long Reef	Inshore intertidal dive/snorkel
51	Long Reef	Inshore intertidal walking
52	Long Reef	Inshore intertidal walking
54	Long Reef	Inshore intertidal dive/snorkel
55	Long Reef	Inshore intertidal walking
56	Long Reef	Inshore intertidal walking
59	Cassini Island	Inshore intertidal walking
60	Cassini Island	Inshore intertidal walking
61	Wildcat Rocks	Inshore intertidal walking
62	Champagne Islands	Inshore intertidal walking
65	White Island	Inshore intertidal walking
66	White Island	Inshore intertidal walking
76	Mavis Reef	Inshore subtidal
81	Brue Reef	Inshore intertidal walking
97	Hedley Island	Inshore intertidal walking
98	Hedley Island	Inshore intertidal walking
103	Browse Island	Midshelf intertidal walking
112	Condillac Island	Inshore intertidal walking
129	Ashmore Reef	Offshore intertidal dive/snorkel
131	Ashmore Reef	Offshore intertidal dive/snorkel
138	Ashmore Reef	Offshore intertidal dive/snorkel
139	Ashmore Reef	Offshore subtidal lagoonal
141	Ashmore Reef	Offshore intertidal dive/snorkel
C5: Inshore intertidal dive/snorkel		
122	Ashmore Reef	Offshore subtidal lagoonal
124	Ashmore Reef	Offshore subtidal lagoonal
125	Ashmore Reef	Offshore subtidal fore-reef slopes
126	Ashmore Reef	Offshore subtidal fore-reef slopes
127	Ashmore Reef	Offshore subtidal fore-reef slopes
128	Ashmore Reef	Offshore subtidal fore-reef slopes
130	Ashmore Reef	Offshore subtidal fore-reef slopes
132	Ashmore Reef	Offshore subtidal fore-reef slopes
133	Ashmore Reef	Offshore subtidal fore-reef slopes
134	Ashmore Reef	Offshore subtidal fore-reef slopes
135	Ashmore Reef	Offshore subtidal fore-reef slopes
140	Ashmore Reef	Offshore subtidal fore-reef slopes
142	Hibernia Reef	Offshore subtidal fore-reef slopes
143	Hibernia Reef	Offshore subtidal fore-reef slopes
144	Hibernia Reef	Offshore subtidal fore-reef slopes
145	Hibernia Reef	Offshore subtidal fore-reef slopes

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