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Shallow reef associated echinoderm biodiversity and distribution on long-shore and cross-shelf surveys of the Kimberley, Western Australia

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ABSTRACT – This paper describes the echinoderm diversity and distribution arising from an extensive marine biological survey of the Kimberley region of Western Australia (the Kimberley Woodside Collection Project) which was a multi-taxon marine biodiversity survey program undertaken by the Western Australian Museum between 2009 and 2014. The study recorded a total of 203 species of echinoderms, plus a further 94 taxa with uncertain or no identification. The 203 species comprised 39 crinoids, 32 asteroids, 75 ophiuroids, 20 echinoids and 37 holothuroids. Forty-one of the species had not previously been recorded from among the 382 shallow water (<30 m) species known from the Kimberley. The 216 sites sampled were distributed among 5 sub regions; Inshore (110 sites), mid-shelf north (12), offshore south (48), offshore central (22) and offshore north (24). Diversity per site was lowest inshore (4.9 per site) and dominated by ophiuroids and crinoids reflecting the silt and rock habitats characteristic of the inshore subregion. In contrast the midshelf and offshore regions have predominantly coral reef/ atoll habitats. The offshore north subregion had the highest number of species per site (10.3) and had 12 times as many asteroid and echinoid species per station than the inshore subregion. Nine species contributed strongly to spatial patterns in species assemblage structure. Overall there was a significant difference in echinoderm assemblages between the inshore subregion and all other subregions. There was no difference between the northern midshelf and the northern offshore subregions which along with significant differences between all of the offshore subregions, suggests the north-south gradient is more influential than the gradient between midshelf and offshore.

KEYWORDS: Indian Ocean, Kimberley, Echinoderms, Continental Shelf, Biodiversity, Distribution, Woodside Collection Project

INTRODUCTION

The Kimberley region of north-western Australia is recognised as both a biodiversity hotspot and a largely undisturbed marine wilderness environment (Halpern et al. 2008). It is also vast, spanning seven degrees of latitude and the wide shallow continental shelf is dotted with islands and reefs up to 350 km offshore from the Australian mainland. Between 2013 and 2018, an extensive suite of coastal and offshore marine parks were established in the area (Department of Parks and Wildlife 2013, 2016; Director of

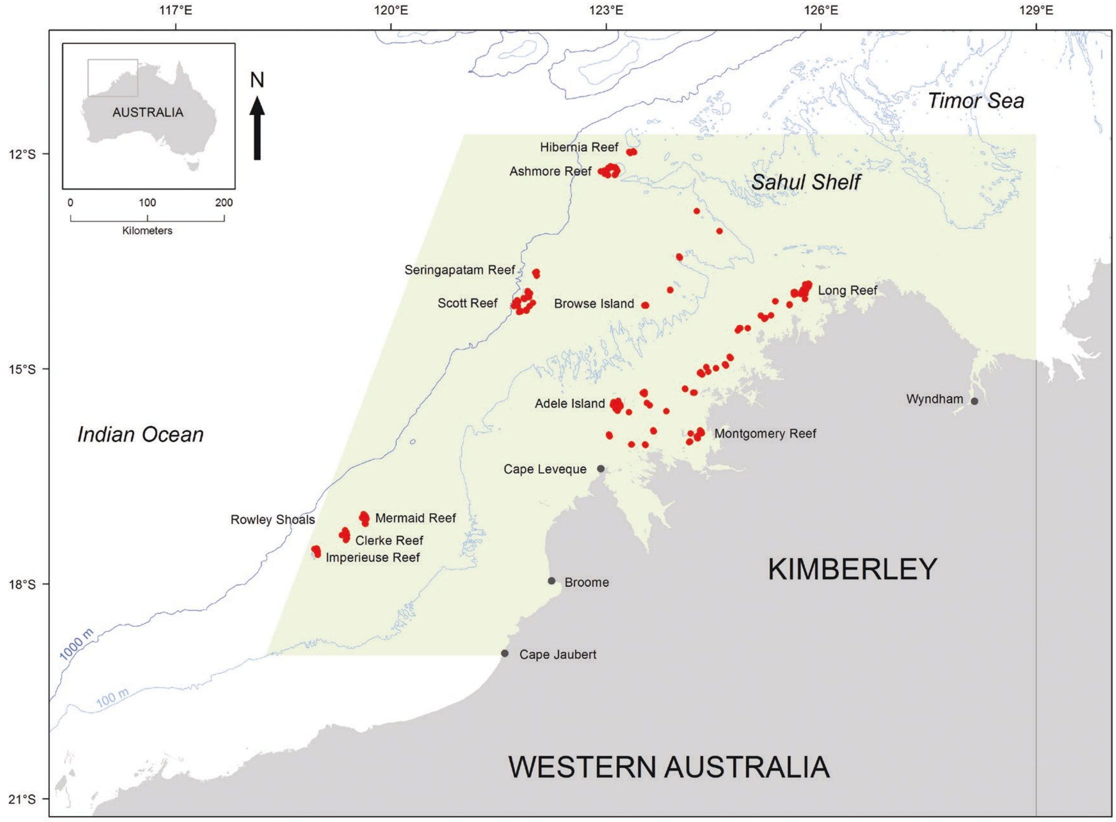

FIGURE 1 Stations surveyed between 2009 and 2014 and those surveyed in 2006 at Mermaid, Scott, and Seringapatam reefs (see Bryce and Marsh 2009). Project Area is delineated by the light green (~476,000 km^2). Map reproduced from Figure 1 of Bryce et al. (2018a). Subregions are the southern offshore reefs of the Rowley Shoals, central offshore are Scott and Seringapatam reefs, northern offshore are Ashmore and Hibernia reefs, the inshore subregion extends from just north of Cape Leveque northwards to Long Reef and the northern mid-shelf subregion includes the five reefs between Browse Island and Vulcan Shoal.

National Parks 2018) to help protect marine biodiversity and this has been accompanied by a large research effort to better document the habitats and biodiversity of the region (Keesing et al. 2011; Keesing 2014; Jones et al. 2017, Heyward et al. 2018; Bryce et al. 2018a, 2018b; Richards et al. 2018; Moore et al. 2020; Bearham et al. 2022) and the biophysical and ecological processes driving structure and function in the area (Waples et al. 2019). Echinoderms are a conspicuous, diverse and abundant part of invertebrate assemblages on intertidal and subtidal reef systems in the shallow waters of the tropical Indo-Pacific (Byrne and O'Hara 2017). They occupy most habitat types from high energy coral reef crests to deep subtidal soft sediment and their taxonomy is relatively well known. Thus, they present a useful candidate to examine broadscale patterns of distribution and abundance (e.g. O'Hara and Poore 2000). This study describes the results arising from the Kimberley Woodside Collection Project which was a multi-taxon marine biodiversity survey program undertaken by the WA Museum between 2009 and 2014 (Bryce et al. 2018). A species list is provided with diversity discussed in the context of previous reports of echinoderms in the region and an analysis of the long-shore and cross-shelf distribution patterns of echinoderm assemblages is made. The habitat features influencing echinoderm distribution are also examined.

MATERIALS AND METHODS

STUDY LOCATIONS

Echinoderms were sampled as part of a Western Australian Museum (WAM) series of biodiversity surveys undertaken in the Kimberley between 2009 and 2014 (Figure 1). The extent of the survey area is shown on the map in Bryce et al. (2018a). The offshore section extends from Rowley Shoals in the south to Ashmore and Hibernia reefs in the north, while inshore reefs were sampled from Irvine Island in the south and Long Reef in the north. Survey locations included midshelf reefs from

Browse Island northwards to Vulcan Shoal. Where comparable, data from Scott Reef on the outer shelf (Figure 1) collected in 2006 (Bryce and Marsh 2009) is also included. For the 2009 to 2014 surveys a full description of each of the 181 survey sites is given in Bryce et al. (2018a). Of these, 179 stations were successfully surveyed for echinoderms and quantitative habitat characteristics were collected at 164 stations. Site location coordinates and maps of sites on reefs are given in Bryce et al. (2018a) and Richards et al. (2018).

SURVEY METHODS

Depending on the depth at each station, surveys were undertaken by reef walking, snorkelling or scuba diving. At each station, three 25 m transect tapes were aligned horizontally to the reef at a single depth (see Bryce et al. 2018 for depth of each station). Benthic composition and cover were determined at each site using either photographs along transects or in-situ point-intercept methods (see Richards et al. 2018 for full description of methods used to determine benthic cover). Echinoderms within 1 m of the tape were surveyed. All species of echinoderms larger than 1 cm were counted and recorded to morphospecies. Voucher specimens were collected for all species where:

1. that species was not represented from a location in any previous museum collections (based on list generated from the historical data),
2. the species was unable to be accurately identified in the field or,
3. the specimens were potentially new taxa or taxa known to require revision. Extra collections of echinoderms were made from three 0.25 m^2 quadrats in conjunction with collections made for polychaetes and crustaceans. The quadrats were randomly placed on the reef in the vicinity of the transects and all echinoderms within the quadrat were collected for later sorting.

The subtidal locations were sampled using SCUBA. Dive time was aimed to be ~1 hour, but sometimes this was not possible, due to conditions, air, or dive profile constraints. The time spent along transects was variable due to topography, echinoderm diversity, and dive conditions. Any remaining time post-transect, was spent undertaking ad hoc searching of suitable habitats (amongst sand and rubble, under rocks and crevices) for echinoderms to increase biodiversity presence / absence records. Generally, ~10 mins was spent at the beginning of the dive at the base of the reef (18–25 m), ~30 mins on transects (~12 m) and then the remaining time searching in shallow depths (5–12 m). When possible in situ photographs were taken to record live colouration.

The intertidal locations were sampled as reef walks, three transects and three 0.25 m^2 quadrats were sampled as for the subtidal locations. Extra time was spent searching for echinoderms on the reef flat and in rock pools and turning over rocks, which were frequently scarce.

Extra records of echinoderms were sourced from other researchers working on other taxa at the same stations, and photographs, or when small cryptic species were collected attached to other animals.

After returning to the vessel, the different classes of echinoderms were preserved in the following manner. Crinoids were retained in seawater in a cool place until ready to process. They were transferred into a shallow tray and flooded with ethanol (~75–96%) and pressed down gently with a container to flatten. Once the crinoid had ceased movement it was transferred to another container and layered between sheets of paper towel with a label included. Ophiuroids were transferred into a solution of $MgCl_2$ and seawater, small specimens usually stopped reacting immediately, the larger species, especially *Macrophiothix*, or the hard bodied *Ophiolepis* spp., required longer (overnight). Extra $MgCl_2$ was added as required. When the animals had ceased moving, they were transferred into ethanol, layered between sheets of paper towel and labelled.

Asteroids were kept in a bucket of seawater until they flattened and were then transferred to ethanol. Holothurians were placed into seawater until the tentacles had expanded and then $MgCl_2$ was added periodically until they ceased movement. They were then transferred into ethanol. Large specimens were injected to get sufficient ethanol into the body for preservation.

Any commensal animals (crustaceans and polychaetes) were removed, retained, labelled and passed on to the appropriate specialists.

SPECIES DIVERSITY

A full species list from the 2009 to 2014 surveys is provided, augmented with the 2006 survey records published by Bryce and Marsh (2009) (Table 1). Species diversity is defined here as the number of taxa identified to species and taxonomic diversity is defined as the number of unique taxa collected (i.e. some could only be identified to genus or family and these were added to the number for species diversity). Specimens that were only assigned to class are listed but not included in the analyses. Diversity is compared with the recent review undertaken of historical echinoderm records from the Kimberley published by Sampey and Marsh (2015).

STATISTICAL TREATMENTS

The echinoderm data analysed was presence/absence data from 179 sites surveyed between 2009 and 2014. Spatial patterns and the influence of habitat characteristics were possible for 164 of these sites for all 5 classes of echinoderms. Echinoderm records (excluding crinoids) for an additional 45 sites at Scott Reef and the Rowley Shoals documented by Bryce and Marsh (2009) were included to permit a broader spatial analysis of 4 classes of echinoderms. Habitat cover (percent) data were square root transformed to constrain variance. Analyses undertaken were similar to that for octocoral data collected on the same surveys (Bryce et al. 2018b) except that we found no basis to separate the inshore sites into southern, central and northern groups.

Our principal interest was in comparing spatial (subregional geographic) patterns. Sites in the Rowley Shoals (48, southern offshore), Scott and Seringapatam (22, central offshore), Ashmore and Hibernia (24, northern offshore) and 12 sites in the group of northern midshelf reefs and islands between Browse Island and Vulcan Shoals were all treated a priori as comprising separate geographic subregions. Agglomerative Hierarchical Clustering (AHC) (XLSTAT ver. 2018.1.1 by Addinsoft inc.) using Ward's agglomeration method and Euclidean distance dissimilarity was applied to presence/absence data for all unique echinoderm taxa at the 110 inshore and nearshore sites, distributed across 28 reefs and islands, sampled between 2009 and 2014, to determine how best to group these inshore sites geographically.

Multivariate analyses were made to determine the importance of habitat composition on echinoderm community assemblages using PRIMER v.6 (Clarke and Gorley 2005) with the PERMANOVA add-on (Anderson et al. 2008). The abundance data were converted using the Simple-matching similarity matrix to quantify the similarity among samples. Differences in echinoderm composition between subregions were visualised with a Nonmetric Multidimensional Scaling (nMDS) using subregions as a grouping factor. Echinoderms that most contributed to the differences in community composition between subregions (Spearman's correlation $R > 0.45$) were shown as vectors, as were habitat characteristics where $R > 0.30$. A permutation multivariate ANOVA or PERMANOVA based on the simple-matching similarity matrix was used to test for differences in echinoderm community composition between location (north, central south gradient) and shelf position (inshore/midshelf/offshore) as well as tidal zones (subtidal/intertidal nested within subregion). Permutation method used sums of squares type III, unrestricted permutation of the raw data, up to 999 permutations, and significance was accepted at $p < 0.05$. Pairwise comparisons were tested at Bonferroni levels of significance ($\alpha = 0.05/n$) to reduce the likelihood of a Type I error arising from a large number of comparisons.

RESULTS

DIVERSITY AND OCCURRENCE

Total echinoderm species diversity and taxonomic diversity (in parentheses) recorded was 203 (298) comprising 39 (66) crinoids, 32 (36) asteroids, 75 (110) ophiuroids, 20 (31) echinoids and 37 (51) holothuroids (Table 1). Two new asteroid species, i.e. *Aquilonastra alisonae* and *A. cassini* were described from the material collected (O'Loughlin and Bribiesca-Contreras 2015) and two other possibly new species were found, an ophiuroid belonging to the genus *Amphiura* and a crinoid belonging to the genus *Nemaster* (Table 1).

The most commonly occurring echinoderm was the ophiuroid *Ophiactis savignyi* at 72 sites or 33% of all sites. The most common echinoid was the burrowing *Echinometra mathaei* (23% of sites) and the most common crinoids were *Stephanometra indica* and *Lamprometra palmata* at 19% and 14% of sites that included searches for crinoids (i.e. excluding the offshore central region), respectively. The most common asteroids were *Linckia multifora* (20%), *Fromia monilis* (19%) and *Echinaster luzonicus* (15%). The most commonly occurring holothurian was *Holothuria edulis* (11%).

SPATIAL COMPARISONS

The echinoderm assemblages at 110 inshore sites at 28 reefs and islands grouped into three groups based on AHC with a Euclidean distance dissimilarity cut off of 25. However, sites at five of the islands and reefs were distributed across all three groups. These include island and reef groups in the south (e.g. Adele Island), central (e.g. Montgomery Reef) and north (e.g. Cassini Island and Long Reef). Sites at a further eight islands and reefs were distributed across two groups. There were only six islands or reefs with two or more sites where all sites were included in just one group. As there was no evidence that the three groups were based on geographic location, all inshore sites were regarded as one subregion for subsequent spatial analyses.

TABLE 1 Species list of echinoderms sampled as part of the 2009–2014 Woodside Collection. The list is grouped by subregion and includes species documented by Bryce and Marsh (2009) at Mermaid, Scott, and Seringapatam reefs in 2006. The numbers in the columns indicate the number of sites where the species occurred. Notes: 'd' indicates dead collected echinoid specimen(s); * indicates species not recorded in Sampey and Marsh (2015); 'NS' indicates where crinoids were not sampled; 'z##### 'indicates Western Australian Museum registration number of the specimen.

	INSHORE	MIDSHELF	OFFSHORE		
	(110 Sites)	North (12 Sites)	South (48 Sites)	Central (22 Sites)	North (24 Sites)
ASTEROIDEA					
Family: Astropectinidae					
Astropecten granulatus Müller & Troschel, 1842	1	0	0	0	0
Family: Echinasteridae					
Echinaster callosus Marenzeller, 1895	0	0	1	0	0
Echinaster luzonicus (Gray, 1840)	0	5	14	10	3
Echinaster varicolor H.L. Clark, 1938	0	1	0	0	0
Family: Asterinidae					
Aquilonastra alisonae O'Loughlin & Bribiesca-Contreras, 2015	2	0	0	0	0
Aquilonastra anomala (H.L. Clark, 1921)	0	0	1	0	0
Aquilonastra cassini O'Loughlin & Bribiesca-Contreras, 2015	2	0	0	0	0
Aquilonastra cepheus (Müller & Troschel, 1842)	0	0	2	0	2
Aquilonastra sp. (z83585, z83613, z83614, z83627, z83703, z83704, z83705, z83833)	0	0	4	0	0
cf. *Aquilonastra* sp. (z83516, z83563, z83625, z83626)	0	0	3	0	0
Disasterina abnormalis Perrier, 1875	0	0	0	2	0
Indianastra sarasini (deLoriol, 1897)	0	0	1	0	0
Family: Asteropseidae					
Asteropsis carinifera (Lamarck, 1816)	1	0	0	0	0
Family: Goniasteridae					
Fromia eusticha Fisher, 1913	0	1	0	0	0
Fromia hemiopla Fisher, 1913	0	0	0	0	1
Fromia indica (Perrier, 1869)	0	3	0	3	3

	INSHORE	MIDSHELF	OFFSHORE		
		North	South	Central	North
	(110 Sites)	(12 Sites)	(48 Sites)	(22 Sites)	(24 Sites)
Fromia milleporella (Lamarck, 1816)	0	1	3	0	2
Fromia monilis (Perrier, 1869)	1	4	21	9	6
Fromia cf. *monilis* (Perrier, 1869) (z68431)	0	0	0	0	1
Fromia pacifica H.L. Clark, 1921	0	1	0	0	1
Fromia sp. (z68246)	0	0	0	1	1
Iconaster longimanus (Möbius, 1859)	1	0	0	0	0
Neoferdina cumingi (Gray, 1840)	0	0	7	1	3
Family: Ophidiasteridae					
Cistina columbiae Gray, 1840	0	0	3	1	1
Dactylosaster cylindricus (Lamarck, 1816)	0	0	1	0	0
**Gomophia watsoni* (Livingstone, 1936)	1	0	1	0	1
Linckia guildingi Gray, 1840	0	3	1	1	0
Linckia laevigata (Linnaeus, 1758)	0	3	13	11	0
Linckia multifora (Lamarck, 1816)	1	2	20	14	7
Nardoa tuberculata Gray, 1840	1	0	0	2	2
Ophidiaster cribrarius Lütken, 1871	0	0	1	0	0
Ophidiaster granifer Lütken, 1871	0	0	1	1	0
Ophidiaster hemprichi Müller & Troschel, 1842	0	1	4	0	0
Family: Oreasteridae					
**Anthenea tuberculosa* Gray, 1847	1	0	0	0	0
Choriaster granulatus Lütken, 1869	0	0	4	5	0
Culcita novaeguineae Müller & Troschel, 1842	0	1	7	9	1
CRINOIDEA					
Family: Antedonidae					
Dorometra nana (Hartlaub, 1890)	2	0	0	NS	0
cf. *Dorometra* sp. (z83892)	0	0	1	NS	0

	INSHORE	MIDSHELF	OFFSHORE		
		North	South	Central	North
	(110 Sites)	(12 Sites)	(48 Sites)	(22 Sites)	(24 Sites)
**Euantedon* cf. *exquisita* (A.H. Clark, 1909) (z67874)	1	0	0	NS	0
**Toxometra* cf. *lepta* (H.L. Clark, 1938) (z83819)	0	0	1	NS	0
Family: Colobometridae					
Cenometra bella (Hartlaub, 1890)	4	0	0	NS	1
Cenometra cf. *bella* (Hartlaub, 1890) (z26347)	1	0	0	NS	0
cf. *Cenometra* sp. (z23177)	1	0	0	NS	0
Colobometra perspinosa (Carpenter, 1881)	2	0	0	NS	0
**Cyllometra manca* (Carpenter, 1888)	1	0	0	NS	0
**Decametra* cf. *informis* (Carpenter, 1881) (z53804)	1	0	0	NS	0
**Decametra minima* (A.H. Clark, 1912)	1	0	0	NS	0
Decametra parva (A.H. Clark, 1912)	2	0	0	NS	0
Iconometra anisa (H.L. Clark, 1915)	1	0	0	NS	0
**Oligometra carpenteri* (Bell, 1884)	4	0	0	NS	0
Oligometra serripinna (Carpenter, 1881)	6	1	4	NS	1
Petasometra clarae (Hartlaub, 1890)	5	0	1	NS	4
Petasometra helianthoides A.H. Clark, 1912	5	0	0	NS	0
Family: Comatulidae					
**Alloeocomatella polycladia* Messing, 1995	0	0	3	NS	0
**Alloeocomatella* cf. *polycladia* Messing, 1995 (z26362)	1	0	0	NS	0
**Anneissia bennetti* (Müller, 1841)	0	1	7	NS	2
Capillaster multiradiatus (Linnaeus, 1758)	0	4	0	NS	3
Capillaster sentosus (Carpenter, 1888)	0	0	0	NS	3
cf. *Clarkcomanthus* sp. (z26368, z83712)	1	0	1	NS	0
**Clarkcomanthus albinotus* Rowe, Hoggett, Birtles & Vail, 1986	6	0	0	NS	0
**Clarkcomanthus alternans* (Carpenter, 1881)	0	3	0	NS	3
**Clarkcomanthus comanthipinna* (Gislén, 1922)	0	3	1	NS	5

	INSHORE	MIDSHELF	OFFSHORE		
		North	South	Central	North
	(110 Sites)	(12 Sites)	(48 Sites)	(22 Sites)	(24 Sites)
Clarkcomanthus littoralis (Carpenter, 1888)	3	2	3	NS	4
Clarkcomanthus cf. *littoralis* (Carpenter, 1888) (z83689, z83690, z83720, z83802, z83823, z83858, z83859, z83860)	0	0	5	NS	0
Clarkcomanthus luteofuscum (H.L. Clark, 1915)	0	0	7	NS	2
Clarkcomanthus cf. *luteofuscum* (H.L. Clark, 1915) (z83616, z83617, z83893)	0	0	2	NS	0
Clarkcomanthus mirabilis (Rowe, Hoggett, Birtles & Vail, (1986)	0	1	0	NS	0
**Clarkcomanthus mirus* (Rowe, Hoggett, Birtles & Vail, 1986)	0	2	0	NS	2
Comanthus cf. *briareus* (Bell, 1882) (z68275)	0	0	0	NS	1
Comanthus gisleni Rowe, Hoggett, Birtles & Vail, 1986	5	1	8	NS	2
Comanthus parvicirrus (Müller, 1841)	9	4	0	NS	10
Comanthus cf. *parvicirrus* (Müller, 1841) (z26348)	1	0	0	NS	0
Comanthus suavia Rowe, Hoggett, Birtles & Vail, 1986	4	1	0	NS	4
Comanthus wahlbergii (Müller, 1843)	1	0	0	NS	2
Comanthus cf. *wahlbergii* (Müller, 1843) (z65100)	1	0	0	NS	0
cf. *Comanthus* sp. (z26369)	1	0	0	NS	0
Comaster audax Rowe, Hoggett, Birtles & Vail, 1986	0	4	0	NS	3
Comaster multifidus (Müller, 1841)	14	0	0	NS	0
**Comaster nobilis* (Carpenter, 1884)	0	1	0	NS	1
**Comatella nigra* (Carpenter, 1888)	6	1	0	NS	0
Comatella sp. (z26349)	1	0	0	NS	0
Comatella stelligera (Carpenter, 1888)	11	1	0	NS	1
Comatula pectinata (Linnaeus, 1758)	0	0	0	NS	1
cf. *Comatula* sp. (z26358, z26359, z26360)	3	0	0	NS	0
cf. *Nemaster* sp. nov.? (z67662)	0	1	0	NS	0
**Palaeocomatella difficilis* (Carpenter, 1888)	1	0	0	NS	0
**Palaeocomatella* cf. *difficilis* (Carpenter, 1888) (z53742)	1	0	0	NS	0
**Phanogenia gracilis* (Hartlaub, 1893)	8	0	2	NS	7
Phanogenia sp. (z26350)	1	0	0	NS	0

	INSHORE	MIDSHELF	OFFSHORE		
		North	South	Central	North
	(110 Sites)	(12 Sites)	(48 Sites)	(22 Sites)	(24 Sites)
cf. *Phanogenia* sp. (z26351, z26352, z26353, z26354, z26355, z26356, z26361)	4	0	0	NS	0
Comatulidae sp. (z26364, z26365, z26366)	3	0	0	NS	0
Family: Himerometridae					
Amphimetra tessellata (Müller, 1841)	0	1	0	NS	0
Amphimetra cf. *tessellata* (Müller, 1841) (z26338, z26346)	2	0	0	NS	0
Himerometra robustipinna (Carpenter, 1881)	1	1	0	NS	0
Himerometra cf. *robustipinna* (Carpenter, 1881) (z67901, z67984)	2	0	0	NS	0
Himerometra sp. (z68483)	0	1	0	NS	0
Himerometridae sp. (z26184)	1	0	0	NS	0
Family: Mariametridae					
Lamprometra palmata (Müller, 1841)	18	1	4	NS	4
Lamprometra cf. *palmata* (Müller, 1841) (z83771, z83822)	0	0	2	NS	0
Stephanometra indica (Smith, 1876)	26	0	7	NS	3
Mariametridae sp. (juv) (z83580, z83984)	0	0	2	NS	0
Family: Zygometridae					
Zygometra punctata A.H. Clark, 1912	1	0	0	NS	0
Crinoidea sp. (z67762, z67762, z68006, z69071, z68266, z69992, z88765)	3	1	0	NS	3
ECHINOIDEA					
Family: Echinometridae					
Echinometra mathaei (Blainville, 1825)	0	4	24	18	3
Echinostrephus molaris (Blainville, 1825)	0	1	8	13	1
Heterocentrotus mamillatus (Linnaeus, 1758)	0	0	10	5	0
Family: Parasaleniidae					
Parasalenia gratiosa A. Agassiz, 1863	0	0	5	2	1
Parasalenia poehlii Pfeffer, 1887	0	0	8	0	2

	INSHORE	MIDSHELF	OFFSHORE		
		North	South	Central	North
	(110 Sites)	(12 Sites)	(48 Sites)	(22 Sites)	(24 Sites)
Family: Temnopleuridae					
Mespilia globulus (Linnaeus, 1758)	3	0	0	0	0
Temnotrema elegans Mortensen, 1918	0	0	0	2	0
Temnotrema sp. (z67876, z26090)	2	0	0	0	0
Temnopleuridae sp. (z83518, z83552)	0	0	2	0	0
Family: Toxopneustidae					
cf. *Nudechinus* sp. (z50867)	0	0	0	1	0
Pseudoboletia cf. *maculata* Troschel, 1869 (z68423, z83642)	0	0	1	0	1
Tripneustes gratilla (Linnaeus, 1758)	2	0	1	0	2
cf. Toxopneustidae sp. (z83517)	0	0	1	0	0
Family: Cidaridae					
Eucidaris metularia (Lamarck, 1816)	0	0	4	10	7
Phyllacanthus imperialis (Lamarck, 1816)					d
**Phyllacanthus* cf. *irregularis* Mortensen, 1928 (z67595)	1	0	0	0	0
**Phyllacanthus longispinus* Mortensen, 1918	3	0	0	0	0
Cidaridae sp. (z83519)	0	0	1	0	0
Family: Echinocyamidae					
**Echinocyamus* cf. *crispus* Mazzetti, 1893 (z84489)	0	1	0	0	0
Family: Fibulariidae					
**Fibulariella acuta* (Yoshiwara, 1898)	0	0	0	0	1
Family: Clypeasteridae					
Clypeaster reticulatus (Linnaeus, 1758)	0	0	0	0	1
Family: Diadematidae					
Diadema savignyi (Audouin, 1829)	0	1	2	4	4
Diadema setosum (Leske, 1778)	1	0	0	0	0

	INSHORE	MIDSHELF	OFFSHORE		
		North	South	Central	North
	(110 Sites)	(12 Sites)	(48 Sites)	(22 Sites)	(24 Sites)
cf. *Diadema* sp. (z84495)	0	0	1	0	0
Echinothrix calamaris (Pallas, 1774)	0	1	0	7	1
Echinothrix diadema (Linnaeus, 1758)	0	1	5	5	3
Family: Echinoneidae					
Echinoneus cyclostomus Leske, 1778	0	2	2	0	0
Family: Echinolampadidae					
Echinolampas ovata (Leske, 1778)					d
Family: Brissidae					
**Brissus agassizii* Döderlein, 1885			d		
Metalia spatagus (Linnaeus, 1758)	0	0	1	0	1
Metalia cf. spatagus (Linnaeus, 1758) (z26089)	1	0	0	0	0
Family: Loveniidae					
Breynia desorii Gray, 1851	1	0	0	0	0
Lovenia sp. (z68322)	0	0	0	0	1
Family: Maretiidae					
**Nacospatangus interruptus* (Studer, 1880)	0	0	1	0	0
Echinoidea sp. (z67815, z83533, z83901, z84490, z84494, z68435)	1	1	2	0	2
HOLOTHUROIDEA					
Family: Synaptidae					
Euapta godeffroyi (Semper, 1868)	0	0	2	1	1
Polyplectana kefersteinii (Selenka, 1867)	0	0	1	0	0
Synaptula macra (H.L. Clark, 1938)	6	0	0	3	0
Synaptula recta (Semper, 1867)	8	0	0	0	0
Synaptula sp. (z67634, z67966, z53787, z53788)	3	0	0	0	0

	INSHORE	MIDSHELF	OFFSHORE		
		North	South	Central	North
	(110 Sites)	(12 Sites)	(48 Sites)	(22 Sites)	(24 Sites)
Family: Cucumariidae					
Leptopentacta grisea Clark, 1938	1	0	0	0	0
Plesiocolochirus australis (Ludwig, 1875)	3	0	0	0	0
Plesiocolochirus cf. *dispar* (Lampert, 1889) (z37788)	0	0	0	1	0
Plesiocolochirus sp. (z26229, z26230, z26231, z26235, z26233, z26234)	5	0	0	0	0
Staurothyone cf. *rosacea* (Semper, 1869) (z26162)	1	0	0	0	0
Family: Phyllophoridae					
Hemithyone semperi (Bell, 1884)	1	0	0	0	0
Stolus buccalis (Stimpson, 1855)	3	0	0	0	0
Stolus cf. *buccalis* (Stimpson, 1855) (z26221)	1	0	0	0	0
Thyone micra Clark, 1938	4	0	0	0	0
Thyone cf. *papuensis* Théel, 1886 (z26220)	1	0	0	0	0
Thyone sp. (z26227, z26218)	2	0	0	0	0
Family: Psolidae					
**Psolidium spinuliferum* (Clark, 1938)	1	0	0	0	0
Family: Sclerodactylidae					
Afrocucumis africana (Semper, 1867)	1	0	0	0	0
Cladolabes schmeltzii (Ludwig, 1875)	2	0	0	0	0
Family: Holothuriidae					
Actinopyga echinites (Jaeger, 1833)	3	0	1	0	0
Actinopyga lecanora (Jaeger, 1833)	1	0	0	0	0
Actinopyga cf. *lecanora* (Jaeger, 1833) (z26147, z26148)	2	0	0	0	0
Actinopyga mauritiana (Quoy & Gaimard, 1834)	0	0	2	2	0
Actinopyga cf. *mauritiana* (Quoy & Gaimard, 1834) (z26149)	1	0	0	0	0
Actinopyga miliaris (Quoy & Gaimard, 1834)	0	0	5	0	1

	INSHORE	MIDSHELF	OFFSHORE		
		North	South	Central	North
	(110 Sites)	(12 Sites)	(48 Sites)	(22 Sites)	(24 Sites)
Bohadschia argus Jaeger, 1833	0	0	11	6	0
Bohadschia marmorata Jaeger, 1833	0	0	5	3	1
Holothuria cf. *arenicola* Semper, 1868 (z68018, z68138, z68358)	0	0	0	0	3
Holothuria atra Jaeger, 1833	3	1	9	5	0
Holothuria cf. *atra* Jaeger, 1833 (z67892, z83998)	1	0	1	0	0
Holothuria edulis Lesson, 1830	2	0	10	11	1
Holothuria cf. *hilla* Lesson, 1830 (z68089)	0	0	0	0	1
Holothuria fuscogilva Cherbonnier, 1980	0	0	0	1	1
Holothuria fuscopunctata Jaeger, 1833	0	0	0	0	1
Holothuria inhabilis Selenka, 1867	0	0	1	0	0
Holothuria impatiens (Forsskål, 1775)	8	0	2	1	2
Holothuria leucospilota (Brandt, 1835)	2	0	0	2	0
Holothuria scabra Jaeger, 1833	1	0	0	0	1
Holothuria whitmaei Bell, 1887	0	0	5	0	0
Holothuria sp. (z68054, z68207, z69994)	1	0	0	0	2
Labidodemas pertinax Ludwig, 1875	0	1	0	0	0
Labidodemas semperianum Selenka, 1867	0	1	0	1	2
Pearsonothuria graeffei (Semper, 1868)	0	0	11	5	1
Family: Stichopodidae					
Stichopus chloronotus Brandt, 1835	3	2	0	0	4
Stichopus herrmanni Semper, 1868	0	0	2	0	0
Stichopus horrens Selenka, 1867	0	0	2	2	2
Stichopus sp. (z26211, z53762)	2	0	0	0	0
Thelenota ananas (Jaeger, 1833)	0	1	7	0	0
Thelenota anax Clark, 1921	0	0	1	1	1
Holothuroidea sp. (z26232, z68133, z68257, z69991, z69993)	3	0	0	0	2

	INSHORE	MIDSHELF	OFFSHORE		
		North	South	Central	North
	(110 Sites)	(12 Sites)	(48 Sites)	(22 Sites)	(24 Sites)
OPHIUROIDEA					
Family: Amphiuridae					
**Amphioplus didymus* Clark, 1938	4	0	0	0	0
Amphioplus hastatus (Ljungman, 1867)	1	0	0	0	0
Amphioplus sp. (z53706)	1	0	0	0	0
Amphipholis squamata (Delle Chiaje, 1828)	15	1	0	0	0
Amphiura abbreviata Koehler, 1905	1	0	0	0	0
Amphiura bidentata Clark, 1938	1	0	0	0	0
Amphiura constricta Lyman, 1879	7	0	0	0	1
**Amphiura diacritica* Clark, 1938	1	0	0	0	0
**Amphiura duncani* Lyman, 1882	0	0	0	0	4
**Amphiura* cf. *duncani* Lyman, 1882 (z69898)	0	0	1	0	0
Amphiura leucaspis H.L. Clark, 1938	1	0	0	0	0
Amphiura velox Koehler, 1910	11	0	0	0	0
Amphiura sp. (z53772, z67764, z67833, z67837, z67838, z67879, z67920, z68084, z68163, z69903, z69911, z69921, z83609, z83839, z83842, z83888)	4	3	3	0	2
Amphiura sp. nov.? (z26331)	1	0	0	0	0
cf. *Amphiodia* sp. (z26144)	1	0	0	0	0
**Dougaloplus echinatus* (Ljungman, 1867)	5	0	2	0	0
Dougaloplus sp. (z50856)	0	0	0	1	0
Ophiocentrus dilatata (Koehler, 1905)	6	0	0	0	1
Ophiocentrus verticillatus (Döderlein, 1896)	0	0	0	0	1
Ophiocentrus sp. (z69910, z83891)	1	0	1	0	0
Amphiuridae sp. (z83557, z83558, z83561, z26333, z26334, z27895, z67593, z67605, z67827, z67832, z67835, z67890, z67993, z69908, z69912, z68165, z84474)	9	1	1	0	1
Family: Hemieuryalidae					
Ophioplocus imbricatus (Müller & Troschel, 1842)	19	0	0	0	0

	INSHORE	MIDSHELF	OFFSHORE		
		North	South	Central	North
	(110 Sites)	(12 Sites)	(48 Sites)	(22 Sites)	(24 Sites)
Family: Ophiactidae					
Ophiactis fuscolineata H.L. Clark, 1938	3	0	0	0	1
Ophiactis luteomaculata H.L. Clark, 1915	1	0	0	0	0
Ophiactis macrolepidota Marktanner-Turneretscher, 1887	8	0	0	0	0
Ophiactis cf. *macrolepidota* Marktanner-Turneretscher, 1887 (z84483)	1	0	0	0	0
Ophiactis modesta Brock, 1888	4	0	0	0	0
Ophiactis cf. *modesta* Brock, 1888 (z26116)	1	0	0	0	0
Ophiactis savignyi (Müller & Troschel, 1842)	48	4	10	2	8
Ophiactis cf. *savignyi* (Müller & Troschel, 1842) (z67886, z67926, z83608)	2	0	1	0	0
Ophiactis sp. (z67579, z69909, z83647, z83658, z84029, z84477, z84480)	3	1	3	0	0
Family: Ophiolepididae					
Ophiolepis aff. *cincta* Müller & Troschel, 1842 (z68077)	0	0	0	0	1
Ophiolepis cincta Müller & Troschel, 1842	1	0	1	0	1
Ophiolepis rugosa Koehler, 1898	0	0	0	0	1
Ophiolepis superba H.L. Clark, 1915	2	0	0	0	0
Ophiolepis unicolor H.L. Clark, 1938	4	0	0	0	0
Family: Ophiotrichidae					
Macrophiothrix caenosa Hoggett, 2006	16	0	1	0	0
Macrophiothrix callizona H.L. Clark, 1938	2	0	0	0	1
Macrophiothrix demessa (Lyman, 1861)	0	0	0	1	3
Macrophiothrix koehleri A.M. Clark, 1968	3	0	0	0	0
Macrophiothrix lineocaerulea (H.L. Clark, 1928)	1	0	0	0	0
Macrophiothrix longipeda (Lamarck, 1816)	1	0	0	0	0
Macrophiothrix lorioli A.M. Clark, 1968	0	0	0	0	6

	INSHORE	MIDSHELF	OFFSHORE		
		North	South	Central	North
	(110 Sites)	(12 Sites)	(48 Sites)	(22 Sites)	(24 Sites)
**Macrophiothrix martensi* (Lyman, 1874)	5	0	0	0	0
Macrophiothrix megapoma H.L. Clark, 1938	6	0	0	0	0
Macrophiothrix microplax (Bell, 1884)	1	0	0	0	0
**Macrophiothrix nereidina* (Lamarck, 1816)	7	1	0	1	2
Macrophiothrix paucispina Hoggett, 1991	6	0	0	0	0
Macrophiothrix propinqua (Lyman, 1861)	0	2	6	0	9
Macrophiothrix cf. *propinqua* (z68317, z83735, z83953)	0	0	2	0	1
Macrophiothrix cf. *rhabdota* (H.L. Clark, 1915) (z67761)	0	1	0	0	0
**Macrophiothrix smaragdina* (Studer, 1882)	3	0	0	0	0
**Macrophiothrix variabilis* (Duncan, 1887)	3	0	2	0	1
**Macrophiothrix* cf. *variabilis* (Duncan, 1887) (z67674)	0	1	0	0	0
Macrophiothrix sp. (z67576, z67581, z67807, z68337, z83513, z83664, z83684, z84018, z26258, z26135, z26136)	5	1	3	0	1
Ophiogymna cf. *pellicula* (Duncan, 1887) (z50855)	0	0	0	1	0
Ophiomaza cacaotica Lyman, 1871	1	0	0	0	0
Ophiothela danae Verrill, 1869	6	0	2	0	2
Ophiothrix armata Koehler, 1905	0	0	2	2	0
Ophiothrix ciliaris (Lamarck, 1816)	19	0	0	0	0
Ophiothrix exigua Lyman, 1874	2	0	0	1	0
**Ophiothrix foveolata* Marktanner-Turneretscher, 1887	0	0	0	0	1
Ophiothrix plana Lyman, 1874	4	1	1	0	1
Ophiothrix purpurea von Martens, 1867	0	1	5	3	4
Ophiothrix trilineata Lütken, 1869	0	0	20	0	1
Ophiothrix sp. (z26335, z27899, z53777, z53819, z67556, z67557, z67563, z67566, z67625, z67636, z67671, z67736, z67768, z67860, z67861, z67867, z67871, z67887, z67913, z67963, z69895, z69917, z69919, z69920, z69979, z83523, z83562, z83602, z83610, z83784, z83870, z83923, z84400, z83883, z84016, z84019)	9	4	8	0	2
Ophiotrichidae sp. (z67766)	0	1	0	0	0

	INSHORE	MIDSHELF	OFFSHORE		
		North	South	Central	North
	(110 Sites)	(12 Sites)	(48 Sites)	(22 Sites)	(24 Sites)
Family: Euryalidae					
Astrobrachion adhaerens (Studer, 1884)	2	0	0	0	0
Family: Ophiacanthidae					
Ophiacantha sp. (z50852)	0	0	1	0	0
Family: Ophiocomidae					
Breviturma brevipes (Peters, 1851)	0	2	1	0	3
Breviturma dentata (Müller & Troschel, 1842)	0	0	2	1	2
Breviturma doederleini (de Loriol, 1899)	0	2	0	1	4
Breviturma pica (Müller & Troschel, 1842)	0	0	7	0	1
Breviturma cf. *pica* (Müller & Troschel, 1842) (z69896, z83843, z83844, z83845, z83882)	0	0	3	0	0
Breviturma pusilla (Brock, 1888)	0	1	1	0	4
Breviturma cf. *pusilla* (Brock, 1888) (z50805)	0	0	1	2	0
Ophiocoma anaglyptica Ely, 1944	0	2	0	0	2
Ophiocoma cf. *anaglyptica* (z68353)	0	0	0	0	1
Ophiocoma erinaceus Müller & Troschel, 1842	0	3	15	0	7
Ophiocoma cf. *erinaceus* Müller & Troschel, 1842 (z68252)	0	0	0	0	1
Ophiocoma schoenleinii Müller & Troschel, 1842	0	0	1	1	3
Ophiocoma sp. (z67685, z67687, z83650, z83669, z68299)	0	1	2	0	1
cf. *Ophiocoma* sp. (z68241, z83982, z83992)	0	0	2	0	1
Ophiocomella sexradia (Duncan, 1887)	6	0	3	0	0
Ophiomastix annulosa (Lamarck, 1816)	0	0	4	1	3
Ophiomastix caryophyllata Lütken, 1869	2	0	0	0	0
Ophiomastix elegans (Peters, 1851)	19	0	0	0	2
Ophiomastix cf. *elegans* (Peters, 1851) (juv) (z26119)	1	0	0	0	0
Ophiomastix mixta Lütken, 1869	8	0	0	0	0

	INSHORE	MIDSHELF	OFFSHORE		
		North	South	Central	North
	(110 Sites)	(12 Sites)	(48 Sites)	(22 Sites)	(24 Sites)
Ophiomastix pictum (Müller & Troschel, 1842)	0	0	1	1	0
Ophiomastix variabilis Koehler, 1905	3	0	2	0	0
cf. Ophiocomidae sp. (z83815)	0	0	1	0	0
Family: Ophiodermatidae					
Ophiarachnella gorgonia (Müller & Troschel, 1842)	8	0	0	0	2
Ophiarachnella infernalis (Müller & Troschel, 1842)	20	0	0	0	0
Ophiarachnella septemspinosa (Müller & Troschel, 1842)	4	0	1	1	0
**Ophiarachnella similis* (Koehler, 1905)	0	0	1	0	0
Ophiarachnella sphenisci (Bell, 1894)	6	0	0	0	0
Ophiodermatidae sp. (z83991)	0	0	1	0	0
Family: Ophiomyxidae					
Ophiarachna delicata (H.L. Clark, 1932)	0	0	1	0	0
Ophiarachna incrassata (Lamarck, 1816)	0	0	0	1	3
Ophioconis cinta Brock, 1888	4	2	4	0	3
Ophioconis sp. (z83560)	0	0	1	0	0
Family: Ophiopezidae					
**Ophiochaeta hirsuta* Lütken, 1869	1	1	1	0	2
**Ophiochaeta* cf. *hirsuta* Lütken, 1869 (z26069, z26070)	2	0	0	0	0
**Ophiopeza spinosa* (Ljungman, 1867)	0	0	2	0	0
Family: Ophiuridae					
Ophiuridae sp. (z83846)	0	0	1	0	0
OPHIUROIDEA					
Identified to class only	9	8	12	0	13

The most diverse subregion was the inshore subregion with 110 species but with an average of just 4.9 species per site (Table 2). The northern offshore subregion had the highest number of species per site, with 10.3 species per site (Table 2). For asteroids and echinoids the northern offshore subregion had 12 times as many species per station on average than the inshore subregion. There were no asteroids or echinoids in the top 50 occurring species in the inshore subregion, the top 14 occurring were ophiuroids (8) or crinoids (6) (derived from Table 1). Ophiuroids and crinoids were the only classes that had individual species present at > 15% of sites in any of the inshore subregions (Figure 3). Holothurians, asteroids and echinoids had at least one species common to > 15% of sites in all offshore subregions and the central midshelf subregion (Figure 2).

TABLE 2 Species diversity and taxonomic diversity (latter in brackets) in each subregion of the study area. 'NS' indicates not sampled

	INSHORE	MIDSHELF		OFFSHORE	
		North	South	Central	North
	(110 Sites)	(12 Sites)	(48 Sites)	(22 Sites)	(24 Sites)
Crinoidea	26 (44)	18 (20)	11 (18)	NS	22 (23)
Echinoidea	5 (8)	6 (7)	13 (18)	9 (10)	14 (16)
Holothuroidea	19 (30)	5 (5)	19 (20)	15 (16)	15 (18)
Ophiuroidea	50 (64)	15 (24)	28 (47)	13 (16)	35 (45)
Total	**110 (156)**	**56 (68)**	**91 (124)**	**50 (56)**	**99 (117)**
Mean per site	4.94 (5.79)	8.42 (9.83)	8.58 (9.92)	8.95 (9.27)	10.33 (11.25)

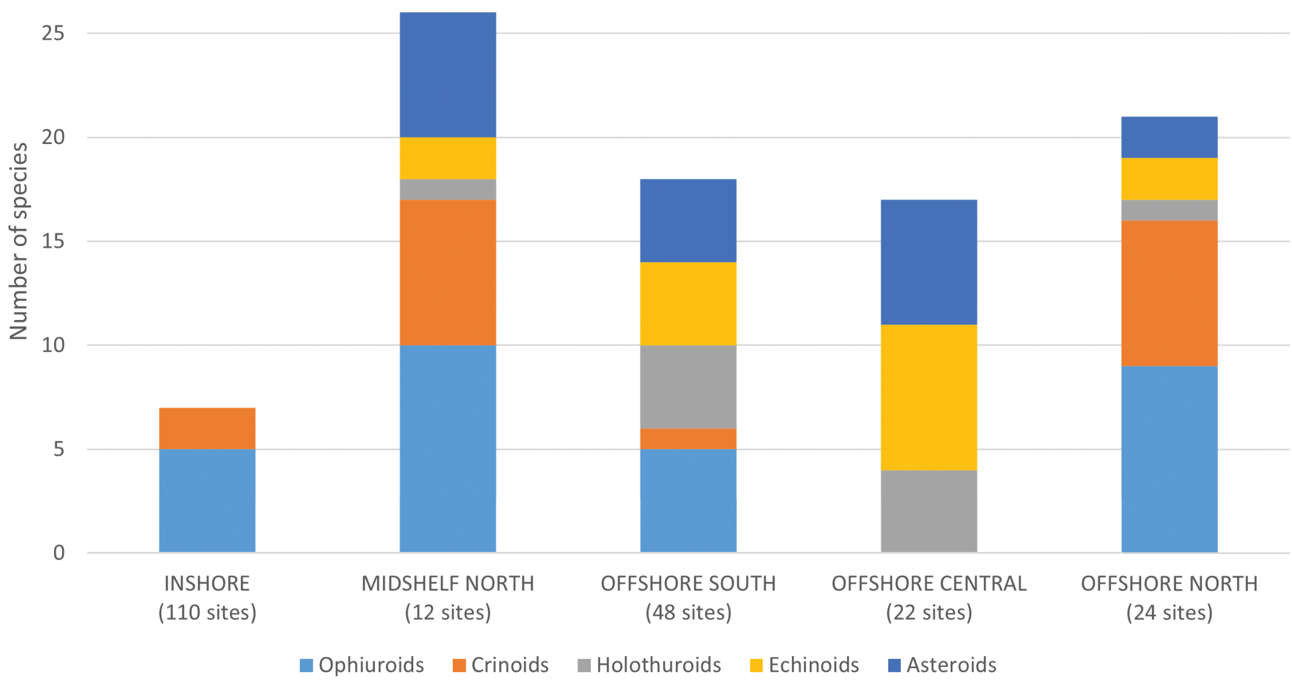

FIGURE 2 Number of species occurring at greater than 15% of sites in each subregion for each class of echinoderms. Note that crinoids were not sampled at the offshore central subregion sites.

There were significant differences in echinoderm assemblages across the five sub-regions (PERMANOVA, p=0.001, Table 3; Figure 3. Ten planned pairwise comparisons (alpha = 0.05/10 = 0.005) were conducted between north, central and south sections (within shelf location) and between shelf locations (within the three latitudinal sections). All subregions differed from each other (p=0.001) except the northern midshelf and northern offshore sites (p=0.295) and the northern midshelf and southern offshore sites (p= 0.006). Seven species; the asteroids *L. multifora*, *F. monilis*, the ophiuroids *Ophiothrix trilineata* and *Ophiocoma erinaceus*, the holothurians *H. edulis*, *Bohadschia argus* and echinoid *E. mathaei* contributed strongly to spatial patterns in species assemblage structure, in particular defining the offshore assemblages. *Linckia multifora* (64% and 42% of sites respectively), *F. monilis* (43%, 44%), *H. edulis* (50%, 21%), *B. argus* (27%, 23%) and *E. mathaei* (82%, 50%) typified both the central (e.g. Scott Reef) and southern offshore (e.g. Rowley Shoals) sites, while the ophiuroids *O. trilineata* (42% of sites) and *O. erinaceus* (31%) were prominent among southern offshore sites (Figure 3). The crinoid *Comanthus parvicirrus* contributed strongly to the northern offshore subregion (42% of sites) while the ophiuroid *O. savignyi* contributed strongly to the inshore subregion (44% of sites) (Figure 3).

There were significant differences between echinoderm assemblages in subtidal and intertidal sites (PERMANOVA, p=0.001, Table 3) except in the northern midshelf subregion (p=0.285) with all other planned comparisons of subtidal/intertidal within subregions significant at alpha = 0.05/5 = 0.01. (e.g. all p between 0.001 and 0.003).

INFLUENCE OF HABITAT

There were significant differences in habitat cover across the four sub-regions where habitat cover data were collected (PERMANOVA, p=0.001, Table 4; Figure 4. Six planned pairwise comparisons (alpha = 0.05/6 = 0.008) were conducted between northern and southern sections (within shelf location) and between shelf locations. All subregions differed from each other (p=0.001) except the northern midshelf and inshore sites (p=0.033).

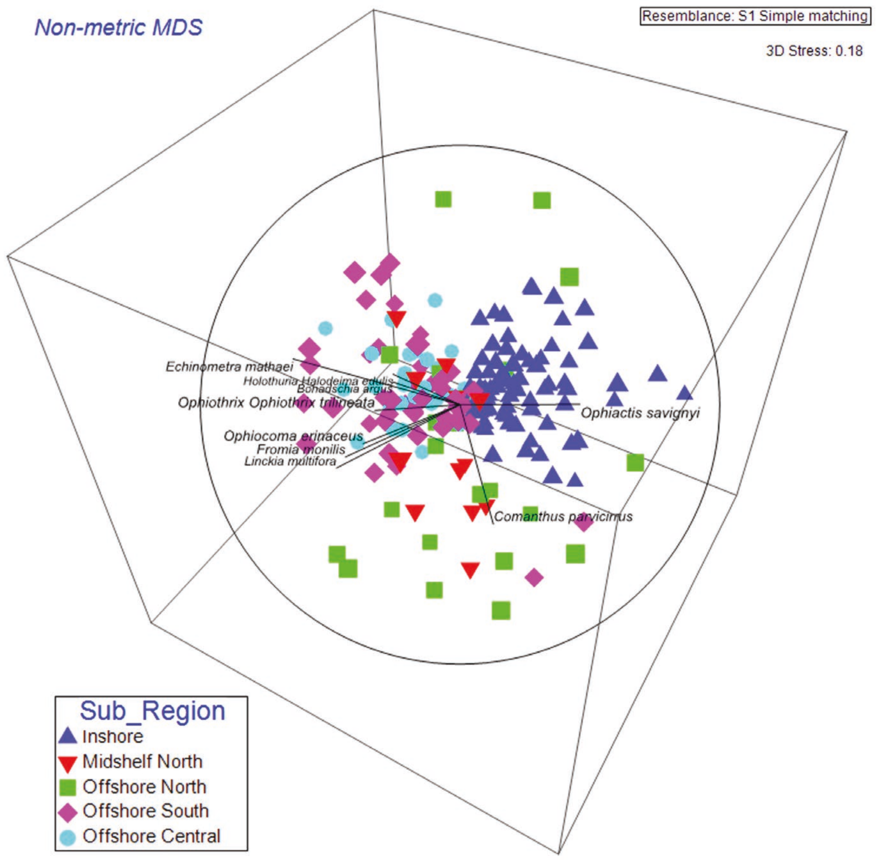

FIGURE 3 Non-metric multidimensional scaling plot of echinoderm species (except crinoids) assemblages for sites in each of the five subregions. Crinoids were excluded because they were not sampled from the central offshore subregion. Species names shown are for those species for which there was a Pearson's R value of 0.45 or greater.

TABLE 3 PERMANOVA summary table for comparison of echinoderm species (except crinoids) assemblages between the five subregions. Subtidal and intertidal sites are nested within subregion.

	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Subregion	4	348.86	87.22	7.7797	0.001	996
Tidal zone (subregion)	5	240.17	48.04	4.2847	0.001	998
Residuals	214	2399.10	11.21			
Total	**223**	**3048.90**				

TABLE 4 PERMANOVA summary table for comparison of habitat cover type between four of the five subregions. Subtidal and intertidal sites are nested within subregion.

	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Subregion	3	44956	14985	20.454	0.001	998
Tidal zone (subregion)	4	35378	8844	12.072	0.001	999
Residuals	156	1144290	733			
Total	**163**	**201170**				

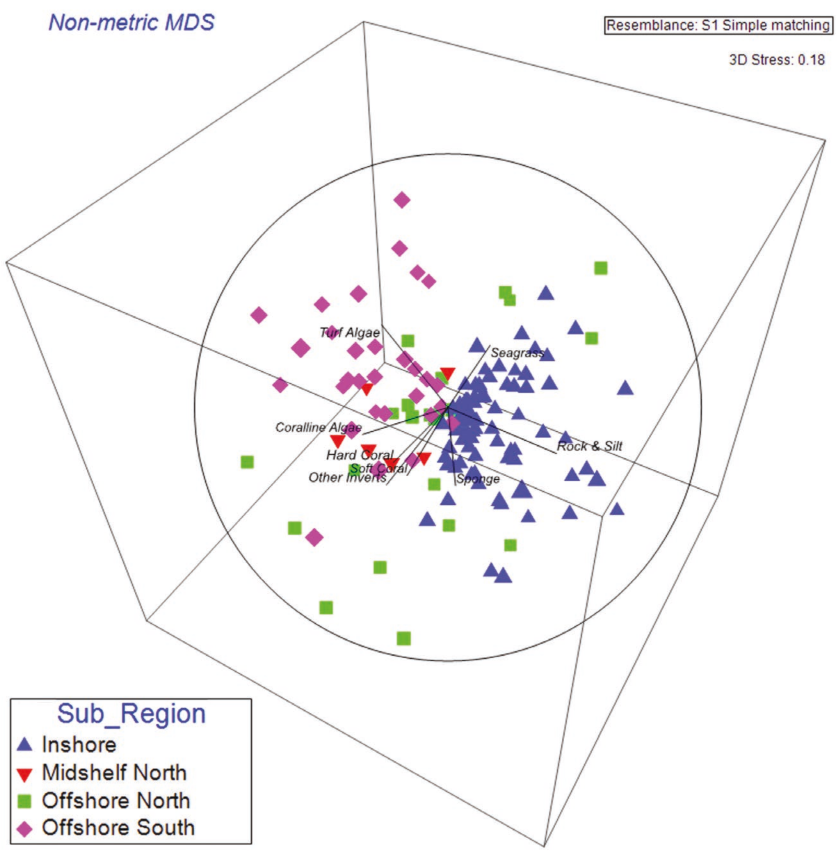

FIGURE 4 Non-metric multidimensional scaling plot of echinoderm species (including crinoids) assemblages for sites in four of the five subregions. The central offshore subregion is excluded as habitat cover data were not available for those sites. Habitat types shown for those for which there was a Pearson's R value of 0.3 or greater.

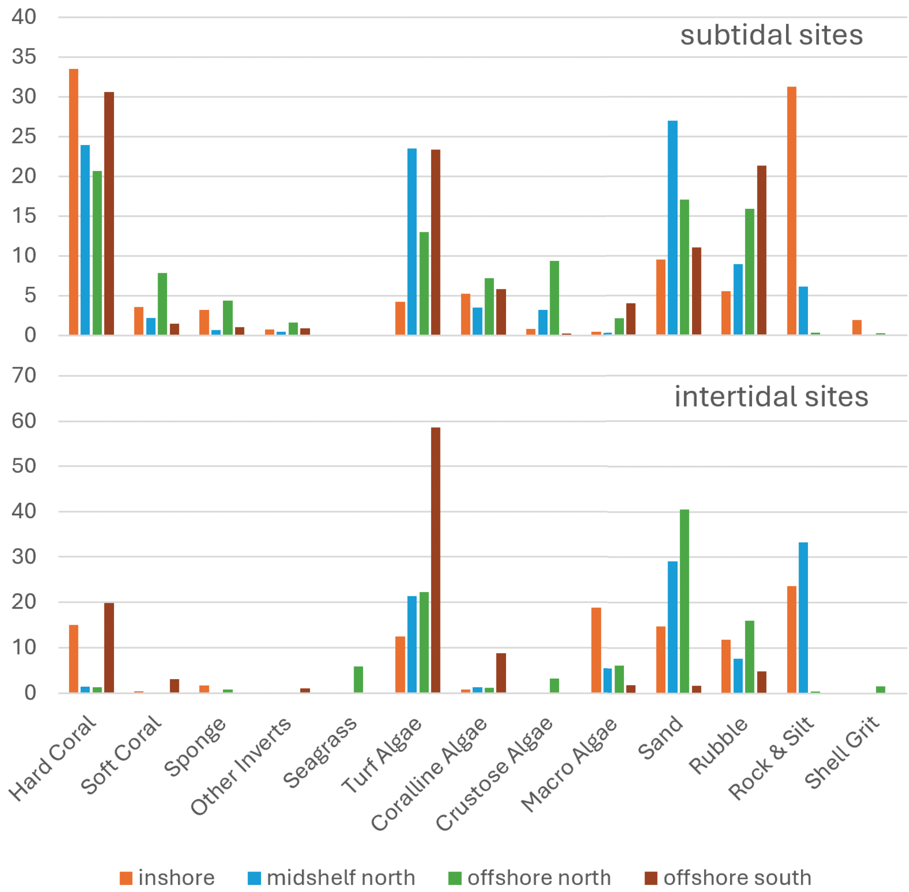

FIGURE 5 Comparison of mean cover (percentage) of different habitat types at each of the four subregions where habitat data were collected. Upper panel shows subtidal sites, lower panel shows intertidal sites.

All subregions had moderate to high coral cover (20–34%, Figure 5). Macroalgae and silt and rock habitats were more prevalent at the inshore sites than at offshore sites (Figure 5). The southern offshore sites had more turf algae habitats (Figure 5) while the northern offshore sites did not show any clear grouping associated with particular habitat types (Figures 4). The offshore reef locations were less likely to have heavily silted habitats present (Figure 5).

There were significant differences in habitat cover between subtidal and intertidal sites (PERMANOVA, p=0.001, Table 4). Coral cover was lower at intertidal sites but they had more rubble and macroalgae present (Figure 5).

DISCUSSION

DIVERSITY

Sampey and Marsh (2015) reviewed the echinoderm fauna historically reported from the Kimberley region and found a total of 382 shallow water (< 30 m) species had been recorded to that time. This study has added a further 41 species or more than 10% (five asteroids, 16 crinoids, six echinoids, one holothurian and 13 ophiuroids; see Table 1) to the known shallow water echinoderm diversity of the region. Two new species of asteroids *Aquilonastra alisonae* and *A. cassini* were described from the collections made in this study (O'Loughlin and Bribiesca-Contreras 2015).

REGIONAL PATTERNS

There was a significant difference in echinoderm assemblages between the inshore subregion sites and all other subregions (northern midshelf and all offshore subregions). There was no difference between the northern midshelf and the northern offshore subregions which, along with significant differences between all of the offshore subregions, suggests the north-south gradient is more influential than the gradient between midshelf and offshore. Bryce et al. (2018b) examined the patterns in octocoral assemblages for the same sites and regions and made similar findings, i.e. strong gradients between inshore and offshore and latitudinally, indicating that this might be common to a range of invertebrate groups.

Habitat type was associated with differences in echinoderm distribution with inshore habitats having heavily silted habitats present and a much higher occurrence of filter and deposit feeding crinoids and ophiuroids. In contrast asteroid, echinoid and holothuroid diversity were much higher on the midshelf and offshore reef habitats in the other regions with five to 17 species of these three classes combined occurring at > 15% of sites in the three offshore and one midshelf subregions (Figure 2). The five species from these three classes *L. multifora*, *F. monilis*, *E. mathaei*, *H. edulis*, *B. argus* were important in defining the offshore assemblages are common coral reef species inhabiting reef flat and shallow subtidal habitats typical of the offshore reefs surveyed. Echinoderm assemblages also differed between intertidal and subtidal sites in both the inshore and offshore regions.

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