Polychaetes (Annelida) of the Oceanic Shoals region, northern Australia: Considering small macrofauna in marine management

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Abstract

Northern Australia has been the focus of recent marine biodiversity research to support natural resource management for both industry and conservation, including the management of the Oceanic Shoals Australian Marine Park (AMP). Much of this research has targeted habitat-forming sessile invertebrates and charismatic megafauna, but smaller macrofauna and infauna may also be important due to their roles in ecosystem functions. In this study, we characterise the biodiversity of polychaetes collected from four marine surveys to the Oceanic Shoals AMP between 2009 and 2012 from which sediment samples were elutriated (500µm) to separate macrofauna. We also use this species-level inventory to examine several questions related to marine management: 1) Do polychaete assemblages vary among surveys? 2) Can environmental variables or geomorphology explain differences in community structure? 3) How do ecological patterns change according to taxonomic resolution (species, family) and functional group (feeding, habitat, mobility)? A total of 2561 individual polychaetes were collected from 266 samples, representing 368 species and 43 families, including new species and genera, as well as new family records for Australia (Iospilidae, Lacydoniidae). Polychaete species assemblages and functional groups showed variation among the surveys, but this was not observed at the family level. Species and family assemblages were weakly related to environmental factors, but functional groups showed stronger relationships. Plains and banks each supported distinct polychaete assemblages, although the latter showed temporal variation. Results provide baseline biodiversity and ecological data about polychaetes on the northern Australian shelf, and these are discussed in relation to marine management strategies. Notably, inter-survey and environmental patterns differ from those of larger sessile fauna (sponges) collected on the same surveys, highlighting the need to consider small macrofauna in monitoring programs of marine protected areas.

Introduction

Biodiversity studies serve a range of purposes, including developing species inventories, environmental impact assessments, and predictive modelling, all of which underpin appropriate marine environmental management (Katsanevakis et al. 2011). For all of these purposes, data is collected to establish environmental baselines and identify species and communities within a region. In addition, environmental data concurrently collected can reveal abiotic controls on biodiversity such as temperature, substrate type, topography and oxygen levels (e.g. Hillebrand et al. 2007). Since it is impractical to monitor all organisms or environmental conditions in a given area, biological and environmental surrogates may be used as proxies for overall biodiversity or habitat, although their effectiveness varies among environments, taxa, and surrogate types (Mellin et al. 2011, Sutcliffe et al. 2012), with likely differences among infauna and epifauna in suitable abiotic surrogates (McArthur et al. 2010).

Despite their recognised importance in ecosystem functioning, small macrofauna (including infauna) are not often included in biodiversity assessments related to marine management in Australia (Commonwealth_of_Australia 2005, van Keulen and Langdon 2011, Beckley and Lombard 2012, Kenchington and Hutchings 2018) (but see Stephenson et al. 1970). This is likely due to a combination of low public awareness and interest in infauna and perceived challenges of identification and sampling. In contrast, small macrofauna are often the focus of industry-associated environmental impact assessments (e.g. Dell'Anno et al. 2002) or deep-sea biodiversity studies (e.g. Galeron et al. 2001, Abdul Jaleel et al. 2014), possibly due to the increased likelihood that such activities will occur in soft sediment habitats where such taxa dominate. Similarly, coastal ecotoxicological studies frequently target polychaetes and other small macrofauna as bioindicators (Simpson et al. 2005).

Compared to large macrofauna and megafauna, smaller and less visible organisms may be equally, if not more, important regarding ecosystem services and sensitivity to environmental change. Infauna are integral in sediment irrigation and nutrient cycling (Snelgrove and Butman 1994, Przeslawski et al. 2009), and they have also been linked to habitat provision (Hutchings 1998), population regulation (Beukema et al. 2000), and contaminated sediment remediation (Mendez et al. 2001). Infauna and small macrofauna may also be an important indicator of community change due to natural (Forrest et al. 2007) and anthropogenic (Mangano et al. 2014) stressors. In many environments, particularly those in the deep sea, species richness and diversity are dominated by small macrofauna (Gray 2002).

Although they may not be consistently considered in marine management strategies, small macrofauna, including infauna, are the focus of several biodiversity studies along the Australian shelf (Currie et al. 2009, Wilson 2010, McCallum et al. 2013, Conlan et al. 2015, Poore et al. 2015). Some of these use operational taxonomic units (OTUs) due to lack of trained taxonomists able to identify to species-level (Long and Poiner 1994, Przeslawski et al. 2013), and this usually precludes comparisons across studies. Nevertheless, several studies have found that polychaete assemblages in tropical Australian shelf waters are related to sediment composition (mud and sand content) and depth (Long and Poiner 1994), although these may be very weak relationships (Przeslawski et al. 2013). Numerous studies focus on small macrofaunal biodiversity and ecology in Australian estuaries, coasts, or embayments (e.g. Stephenson et al. 1970, Alongi and Christoffersen 1992, Hutchings et al. 1993, Hutchings and Jacoby 1994, Chapman and Tolhurst 2007, Russell and Smit 2007), but there are far fewer studies that target small macrofauna in deeper Australian waters (>20 m). However, the increasing spatial and temporal coverage for which macrofaunal species data exists (e.g. global ophiuroid database in Woolley et al. 2016) means that their inclusion in marine management plans and monitoring programs is indeed feasible.

In Australia, a national network of marine protected areas (termed Australian Marine Parks; AMPs) was proclaimed in 2012, spanning tropical to temperate marine regions and shelf to the deep-sea (Cochrane 2016). Measuring the effectiveness of this network requires a national standard for marine monitoring that can report on ecosystem health and condition, identify responses to pressures (anthropogenic and natural) and define trends. This monitoring will include assessment of benthic and pelagic systems and make use of indicators that best characterise the biodiversity of the seabed and water column. Critical to this assessment are baselines that document the form and composition of habitats and provide a reference point for comparison over time.

The aim of the current study was to characterise polychaete (Annelida) and other small macrofaunal biodiversity and ecology of the outer continental shelf of northern Australia in an area overlapping the Oceanic Shoals AMP. For the purpose of this study, we define small macrofauna as 0.5–5 mm width which is the size range not often sampled by benthic sleds and trawls but readily captured by grabs and corers (Abdul Jaleel et al. 2014, Leduc et al. 2016). We then use this species-level inventory to examine several exploratory questions relevant to marine management and future research priorities: 1) Do polychaete assemblages vary among stations and surveys? 2) Can concurrently collected environmental data or geomorphology explain differences in community structure? 3) How do ecological patterns change according to taxonomic resolution (species, family) and functional group (feeding, habitat, mobility)? Since management decisions may be based on biological data collected from only one taxonomic group or habitat, we also relate these findings to previous work undertaken on megafauna (sponges) to assess the generality of ecological patterns among different groups. Results will show how baseline data on polychaete biodiversity can inform future management plans and monitoring programs for marine parks in the region. The current study complements (Przeslawski et al. 2014) and (Przeslawski et al. 2015), applying similar statistical methods and management implications to further contribute to our understanding of benthic biodiversity in northern Australia.

Methods

Study Area and Surveys

The study area is located in the outer Joseph Bonaparte Gulf and Timor Sea, where the continental shelf of northern Australia is characterised by shallow carbonate banks and terraces separated by valleys and plains (Fig 1). These banks and terraces cover a combined area of 72,400 km^2 and are recognised as Key Ecological Features (KEFs) in marine bioregional plans. A KEF is defined as an element of the marine environment considered to be of importance for biodiversity or ecosystem function at a regional scale (www.environment.gov.au) and is comparable to an ecologically or biologically significant marine area as identified by the Convention on Biological Diversity (Bax et al. 2016). The study area overlaps three KEFs: carbonate banks and terraces of the Sahul Shelf, carbonate banks and terraces of the Van Diemen Rise, and pinnacles of the Bonaparte Basin (Fig. 1). Seabed sediments are a mix of calcareous sand and gravel on the banks and terraces, and muddy sand in the deeper plains and valleys.

Biological and environmental data used in this study were collected on four seabed mapping surveys undertaken by Geoscience Australia and the Australian Institute of Marine Science on the *R.V. Solander* between 20 and 190 m depth: Surveys SOL4934 (27 Aug - 24 Sept 2009) and SOL5117 (30 July - 27 Aug 2010) sampled areas in the eastern Oceanic Shoals Marine Park (Heap et al. 2010, Anderson et al. 2011). Survey SOL5463 (18-31 May 2012) targeted the central Joseph Bonaparte Gulf (Carroll et al. 2012). Survey SOL5650 (12 Sept – 6 Oct 2012) sampled the western Oceanic Shoals Marine Park (Nichol et al. 2013) (Figure 1).

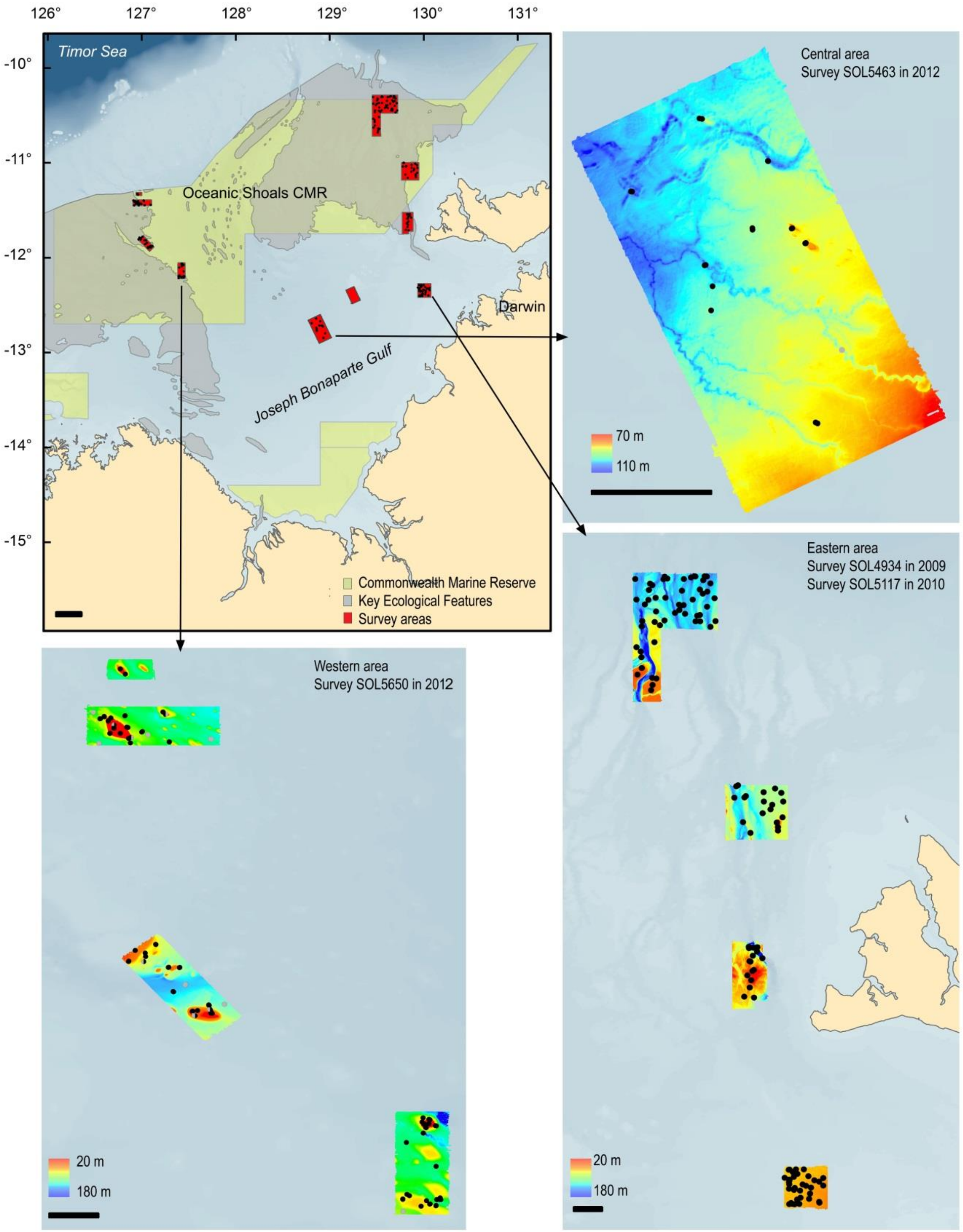

Figure 1 Map of study area with biological sampling locations overlaid on high-resolution bathymetry grids. Black dots indicate stations from which polychaetes were identified to species level, and grey dots indicate stations from which no polychaetes were identified. Some stations had multiple grabs or box cores deployed, and geographic coordinates of grabs can be at www.ga.gov.au/metadata-gateway/metadata/record/102241. A total of 56 samples were processed for fauna on SOL4934; 73 samples on SOL5117; 21 samples on SOL5463; and 116 samples on SOL5650. Scale bars are 10 km unless otherwise indicated.

Environmental and Biological Sample Collection

Ten grids were mapped using a multi-beam sonar system (Kongsberg EM3002D 300kHz) to provide data on depth and seabed reflectance which can indicate substrate hardness (e.g. rock, unconsolidated sediment, sand veneer) (McArthur et al. 2010, Siwabessy et al. 2013) (Fig. 1). At each station with soft substratum, sediment was collected using a Smith-McIntyre grab (~0.1 m^2) or boxcorer at stations within nine of these grids (Figure 1). There was no difference between assemblages collected from the grab and the box corer. We opted for the approach advocated by (van Son et al. 2016) in which sampling effort at each station (i.e. replicates) is reduced in favour of sampling an increased number of stations. Nonetheless, at some stations in the central and western areas, we assessed fine-scale (metres) biological variation by deploying the grab more than once; these are considered replicate samples within a given station as per (Aarnio et al. 2011). Stations were usually separated by kms, and grabs within a station were separated by metres. At each station, a small sediment sample (~ 50 ml) was retained from at least one primary grab for analysis of sediment (percentage mud, gravel, and carbonate), and a separate secondary grab was collected to characterise sediment geochemistry (total organic carbon, chlorophyll *a*, chl-*a :* pheophytin, sediment oxygen demand). Bathymetry and backscatter data were used to identify geomorphic features, but only the eastern area was analysed since it encompassed all types of identified features for the region (banks, terraces, ridges, plains, valleys). Further details on physical datasets used in the current study can be found in associated post-survey reports (Heap et al. 2010, Anderson et al. 2011, Carroll et al. 2012, Nichol et al. 2013).

Macrofauna were processed as described by the grab and box corer protocols in *Field Manuals for Marine Sampling to Monitor Australian Waters* (Przeslawski and Foster 2018). Excess water from each primary grab sample was decanted through a 500 μm sieve, and the remaining sample was weighed and processed for infauna. Samples were elutriated for five minutes over a 500 μm sieve to collect animals lighter than the surrounding sediments. Material retained on the sieve was preserved in ethanol, with the exception of large polychaetes which were removed and fixed in formalin. To account for heavier animals such as molluscs which may not be collected during elutriation, the coarse fraction was sorted by hand and 25 ml of sieved sediment was preserved in ethanol for laboratory processing of microscopic animals.

Species Identification

Benthic animals were sorted according to phyla, and the polychaetes lodged at the Museum and Art Gallery of the Northern Territory (MAGNT), Darwin, where they were identified to species-level by taxonomic experts (Chris Glasby, Charlotte Watson) (See Supplementary Material A for species list and museum registration numbers). Polychaetes were first sorted to family and then to operational taxonomic units (OTUs) or species using Wilson et al. (2003). A reference specimen for each OTU/species is registered with the MAGNT, together with other well-preserved ethanol specimens, and all of the formalin preserved specimens.

For the purposes of this study, other annelids (oligochaetes, sipunculans, echiurans) that were represented in the collection in low numbers were not included in species-level identifications as suitable taxonomic literature was not available. Polychaete species are a paraphyletic group (Struck et al. 2011) and were classified according to their habitat (epifaunal, infaunal, both), mobility (motile, discretely motile, both and discretely mobile, sessile), and feeding guild (microphagous, macrophagous, omnivorous, both microphagous and omnivorous), the latter based on Jumars et al. (2015). This incorporates a previous recommendations that functional diversity be considered in studies of benthic macrofauna due to structural redundancy in which different components of benthic assemblages provide similar functions in different places (Chapman and Tolhurst 2007). Inclusion of functional diversity also allows us to test the stability of ecological patterns among various resolutions, from species to family to various functional levels.

For the eastern and central study areas (SOL4934, SOL5117, SOL5463), abundances of all other taxa were recorded. A non-taxonomist (R Przeslawski) identified crustaceans, sponges, chordates, cnidarians and bryozoans to operational taxonomic unit (OTU), and museum taxonomists identified molluscs (Richard Willan) and echinoderms (Tim O'Hara) to species level. These taxa were deposited at the Australian Museum and are included in the current study to identify the proportion of small benthic macrofauna comprised of polychaetes.

Statistical analyses

For biodiversity assessment (e.g. number of species and families, relationship to other taxa), all polychaetes collected from grabs and box cores that were able to be differentiated to species were included. For statistical analyses, only those polychaetes collected from grabs and box cores that successfully returned an appropriate sediment sample were included; this was defined as ≥50% full. A previous study revealed no effect of sediment volume from successful grabs on species richness or abundance (Przeslawski et al. 2013), likely because most animals live in the top first few centimetres of sediment (Blake 1994). Multivariate analyses were performed only on those samples that returned polychaetes able to be identified to species/OTU level, while univariate analyses of species richness and abundance included sediment samples from which no polychaetes were identified.

Univariate analyses were performed on species richness and abundance using 1-way ANOVAs and regressions in the statistical platform R (v 3.2.2), while multivariate analyses were performed in the PRIMER 6 and PERMANOVA+ on various assemblage matrices (species, family, habitat, mobility, feeding guild) using square-root transformations to reduce the influence of dominant groups (Clarke and Warwick 2001). Resemblance matrices were then calculated based on Bray-Curtis similarities. The effects of geomorphic features (banks/ shoals, ridges, terraces, plains, valleys) were analysed only for the eastern surveys (SOL4934, SOL5177) where all five geomorphic features were represented (Anderson et al. 2008). To investigate variation among surveys and geomorphic features, 2-way permutational analysis of variance (PERMANOVAs) were performed on multivariate data with year and geomorphic feature as factors, using unrestricted permutation of raw data and sequential sum of squares appropriate for single-factor designs (Anderson et al. 2008). To identify key environmental variables associated with polychaete biodiversity (as measured by species and family composition), the DISTLM routine was used, while regressions were used to investigate relationships between environmental variables and species richness. None of the environmental variables had a strong collinear relationship ($R^2 < 0.50$ in all pairings) so analyses included all of them: depth, substrate hardness, mud content, gravel content, carbonate content, total organic carbon, chlorophyll *a*, chl-*a :* pheophytin, and sediment oxygen demand. DISTLM is based on a distance-based redundancy analysis approach in which the value of the explained variation is examined for all possible combinations of environmental variables (Anderson et al. 2008). To quantify fine-scale spatial variation, 38 stations at which replicate grab or box corers had been deployed were analysed using a 1-way PERMANOVA with station as a factor.

Results

Polychaetes and other taxa

Crustaceans and polychaetes were the most dominant macrofaunal groups collected from grabs deployed in the eastern and central study area (Figure 2). Polychaetes represented 26% of individuals and 45% of species or OTUs collected, excluding samples from survey SOL5650 for which non-polychaete taxa were not identified (Figure 2). Polychaetes showed a significant but weak linear relationship to other taxa with respect to species richness ($R^2 = 0.0968$, $p= 0.0001$) but not abundance ($R^2 = 0.0139$, $p = 0.1212$).

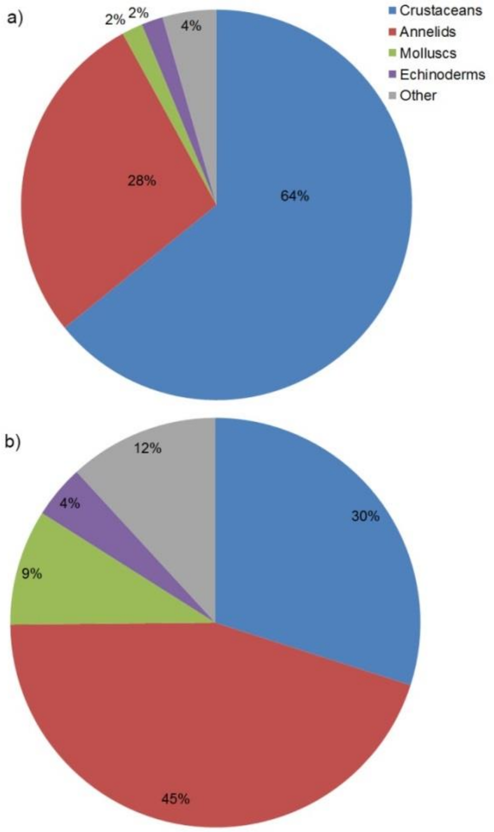

Figure 2: Proportion of (a) individuals (N=6766) and b) species or operational taxonomic units (OTU) (N = 668) of key taxa from the eastern (SOL4934, SOL5117) and central (SOL5463) study area. ‘Other’ includes bryozoans, sponges, cnidarians, chordates, chaetognaths, nemerteans, nematodes, sipunculans, and echiurans, although the latter five groups are not included in (b) as they were not differentiated to OTU.

Polychaete biodiversity

A total of 2561 polychaetes were collected from 203 grabs and 63 box cores deployed in the Oceanic Shoals region. The collection included 50 families and 368 species, with at least ten confirmed new species and three possible new genera. The records of the families Iospilidae and Lacydoniidae are the first published for mainland Australian waters; neither they nor another family and Longosomatidae are currently listed in the Australian Fauna Directory (http://www.environment.gov.au/biodiversity/abrs/online-resources/fauna), although Wilson (2010) found a single longosomatid in the Arafura Sea. New taxa of Pilargidae have been previously described (Glasby and Hocknull 2010, Glasby and Marks 2013), and descriptions of other new taxa including Chrysopetalidae (C. Watson), *Ceratocephale* (CJ Glasby & R Wilson) and *Litocorsa* (CJ Glasby & S Salazar Vallejo) are in preparation. Almost half of the collection included singletons (32%, 118 species) or doubletons (15%, 53 species) (i.e. occurred once or twice in the entire collection). Species accumulation curves revealed that further sampling in the study area is likely to yield over 400 species (Figure **3**). A full species list and museum registration numbers are available in Supplementary Material A and via the MAGNT collection on the Atlas of Living Australia (http://collections.ala.org.au/), and associated data and station metadata can be downloaded at www.ga.gov.au/metadata-gateway/metadata/record/102241.

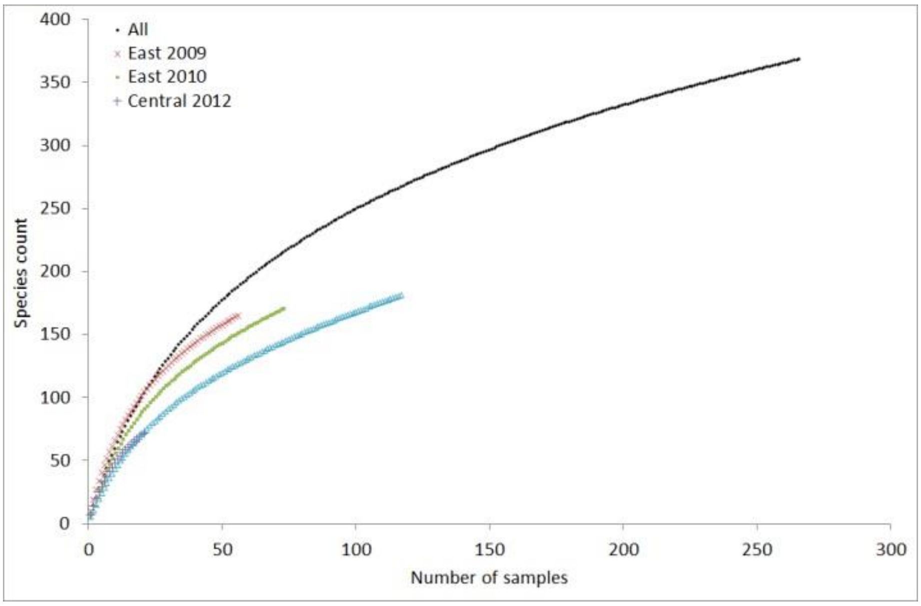

Figure 3 Species accumulation curves of polychaetes from grab and box core samples taken at Oceanic Shoals region, northern Australia.

The most diverse family was Spionidae (30 species) followed by Pilargidae and Syllidae (22 species each) (Figure **4**). The most abundant and widespread species was the spionid *Prionospio cf queenslandica/australensis* (118 individuals from 60 sites). The species with the largest population recorded at a single site was Syllidae sp. 16, with over 84 individuals collected from a bank in the eastern Oceanic Shoals region (Grab 60GR45 from survey SOL5650).

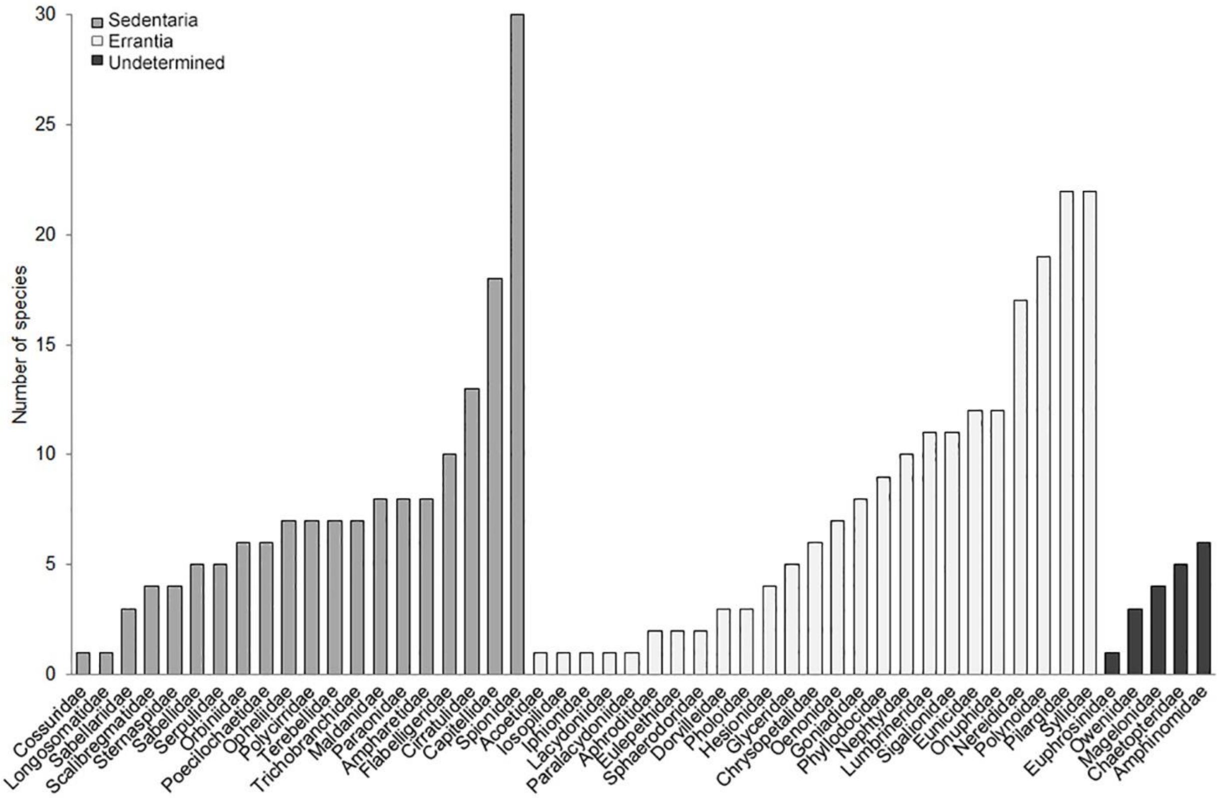

Figure 4 The number of species identified within each family (x-axis labels) and super/infraorder (bar shading) of polychaetes collected in this study. Sedentaria, Errantia and Undetermined were defined as polychaete groupings based on Weigert et al. (2014).

Variation among surveys and stations

Multivariate analyses revealed significant differences in polychaete species assemblages among all surveys, including those from the same area in the eastern Oceanic Shoals regions (2009 and 2010 survey) (Pseudo F = 5.7556, p = 0.001) (Figure 5a); however, these differences were not observed at the family level (Pseudo F = 2.0076, p = 0.0900) (Figure 5b). Functional groups showed differences among only some surveys. For both habitat and mobility groups, there were significant differences between the two eastern surveys (2009, 2010), as well as between the western survey (2013) and both eastern surveys (2009, 2010) (Pseudo F = 4.9292, p = 0.001; Pseudo F = 4.5398, p = 0.001; respectively). Among feeding groups, there were significant differences between all surveys except 2012 and 2013 (Pseudo F = 6.5967, p = 0.001).

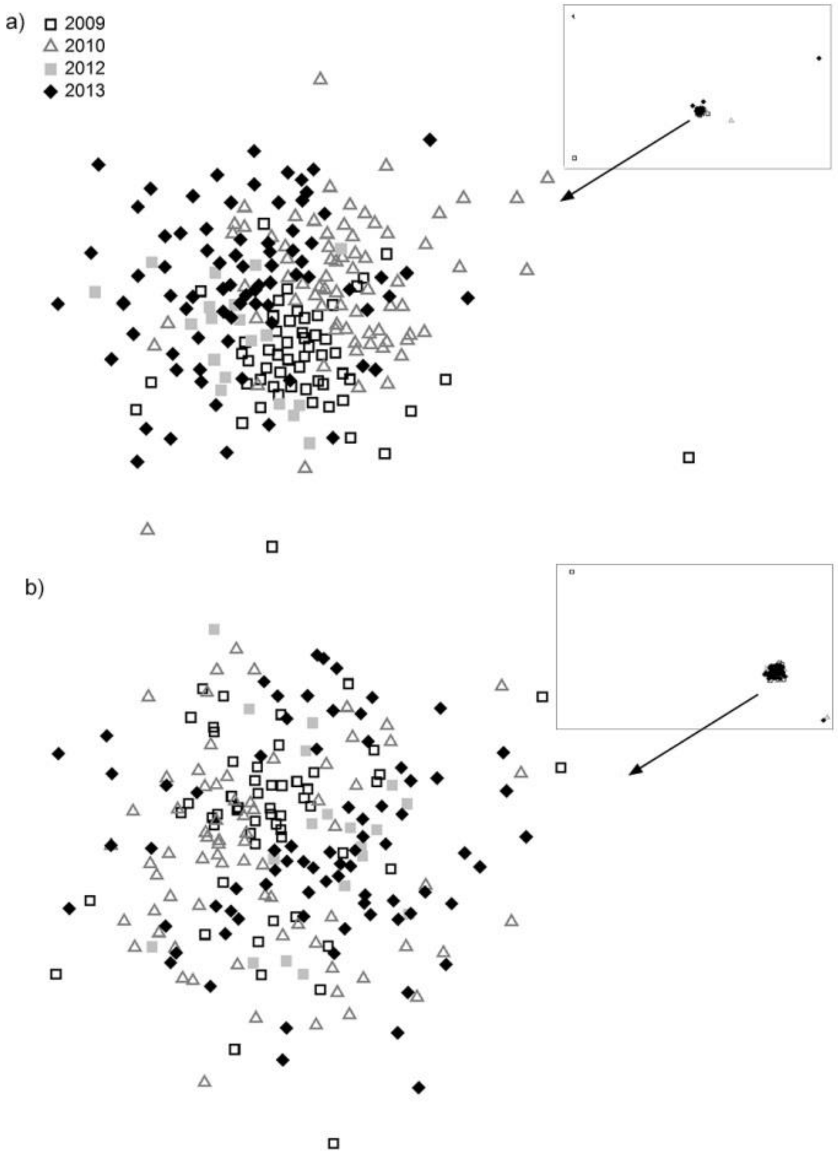

Figure 5 Variation among surveys in (a) species and b) family polychaete assemblages as shown by a n-MDS in which each point represents an assemblage from a given grab, and the distance between points represents similarity between assemblages. Inset images indicate whole n-MDS plot before zooming in. Stress = 0.09 for species assemblages and 0.21 for family assemblages.

Species richness showed variation among surveys (F = 8.916, $p < 0.0001$), with significantly higher species richness in the east than the west, and higher species richness between the 2009 eastern survey than the central survey as confirmed by Tukeys HSD tests (Figure **6**). Total abundance also showed significant variation among surveys (F = 4.5923, p = 0.0037), with higher abundance from the 2009 eastern survey than central and western surveys (Figure **6**).

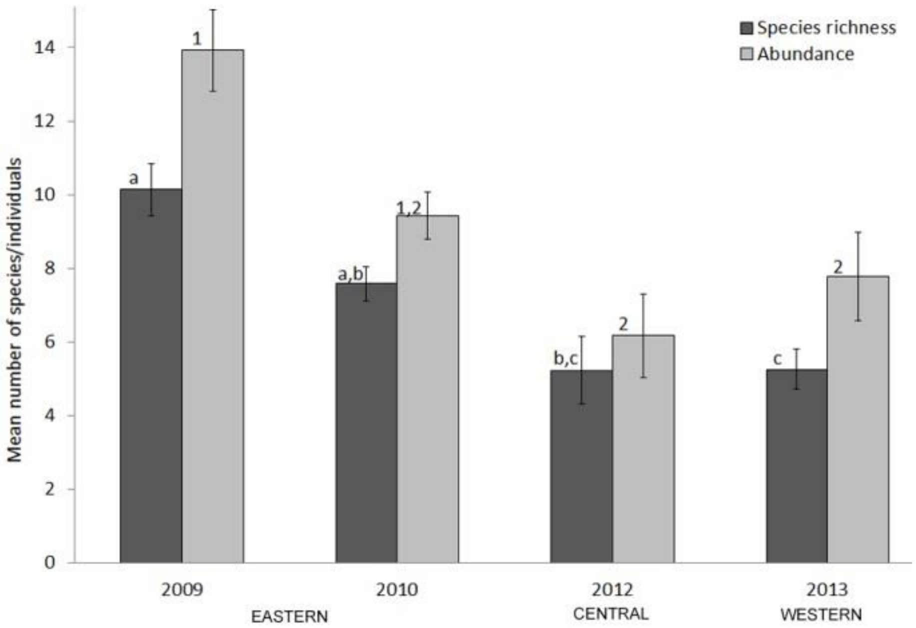

Figure 6 Inter-survey variation in polychaete species and abundance. Different letters or numbers represent significant differences as determined by Tukeys HSD multiple comparisons. Error bars are SEMs.

To test whether samples within stations are more similar than those among stations, 38 stations across all three study areas were analysed from which replicates were taken at each station (two stations from SOL4934, nine from SOL5463, 27 from SOL5650). Overall, polychaete assemblages were more similar within a station than among them, (df = 37, Pseudo F = 1.246, p = 0.001). However, this trend did not apply to all stations, and variation was frequently higher within stations than among them.

Ecological relationships

Polychaete species assemblages were significantly related to all environmental factors except chlorophyll-*a* (Supplementary Material 1a), while family assemblages were only significantly related to gravel and hardness (Supplementary Material 1b). These relationships, however, were very weak with the best representative model using mud content, gravel content, and substrate hardness explaining only 4.2% of the variation in species assemblage (Supplementary Material 1a). In contrast, functional groups yielded stronger relationships with best models explaining 13–18% of the variation in functional assemblages (Supplementary Material 1c-d). From these models, sediment (mud and gravel content) and geochemical characteristics (chl-*a*:pheophytin and sediment oxygen demand) were consistently identified as the strongest environmental predictors (Supplementary Material 1c-e).

Species richness and abundance showed significant but weak linear relationships to all environmental factors except gravel content, chlorophyll-*a*, and chl-*a :* pheophytin (Table 1). There were more species and individuals with increasing carbonate content, substrate hardness and sediment oxygen demand; and there were less species and individuals with increasing depth, mud content, and total organic carbon.

Table 1 Regression results of the relationships between environmental variables and polychaete species richness or abundance. Environmental variables were square-root transformed to reduce skewness and heteroscedasticity. Bold text indicates a significant relationship.

		Species richness		Abundance	
Factor	Range	Adjusted R^2	p	R^2	P
Depth	**20 to190 m**	**0.0355 -**	**0.0016**	**0.0301**	**0.0034**
Mud content	**0.1 to 99%**	**0.1973 -**	**<0.0001**	**0.1813**	**<0.0001**

Gravel content	0 to 77%	0.0105	0.0579	0.0094	0.0682
Carbonate content	**3.5 to 94%**	**0.0703 +**	**<0.0001**	**0.0596**	**<0.0001**
Substrate hardness	**-50 to -11**	**0.1630 +**	**<0.0001**	**0.1277**	**<0.0001**
Chlorophyll-*a*	0.01 to 3.94 ug/g-dwt	0.0007	0.2812	0.0023	0.2181
Chl-*a* : Pheophytin	0.0015 to 1.1633	0.0074	0.1010	0.0032	0.1889
Sediment oxygen demand	**0 to 8.04 %O_2/g-dwt/d**	**0.0241 +**	**0.0110**	**0.0154**	**0.0345**
Total organic carbon	**0.02 to 1.52%**	**0.0538 -**	**0.0002**	**0.0426**	**0.0010**

Among the eastern samples, geomorphology and year significantly interacted to affect polychaete species assemblages (df = 4, Pseudo F = 1.6394, p = 0.001). Pairwise tests showed that assemblages from plains were significantly different than those from all other geomorphic features, and this relationship held across both the 2009 and 2010 surveys. In contrast, assemblages from banks were significantly different than those from all other features in 2010, but not from any other features except plains in 2009. Similar results were noted for family assemblages (df = 4, Pseudo F = 1.8616, p = 0.001). Geomorphological patterns were different among all functional groupings: For habitat groups, samples from plains were significantly different than all other features except terraces, and samples between banks and valleys were also different (Pseudo F = 3.3341, p = 0.001). For mobility groups, there were no differences among geomorphic features (Pseudo F = 1.8219, p = 0.056). For feeding groups, there was a significant interaction between year and geomorphology (Pseudo F = 1.9728, p = 0.035), with no differences among geomorphic features in samples from 2010 but differences between plains and all features except valleys, as well as differences between terraces and valleys in 2009 samples.

Geomorphic features in the eastern study area were also associated with significantly different levels of species richness (df = 4, F = 59.264, p = 0.0203) and abundance (df = 4, F = 113.51, p = 0.0380). Pairwise comparisons revealed that plains had significantly more species and individuals than banks (Figure 7**)**.

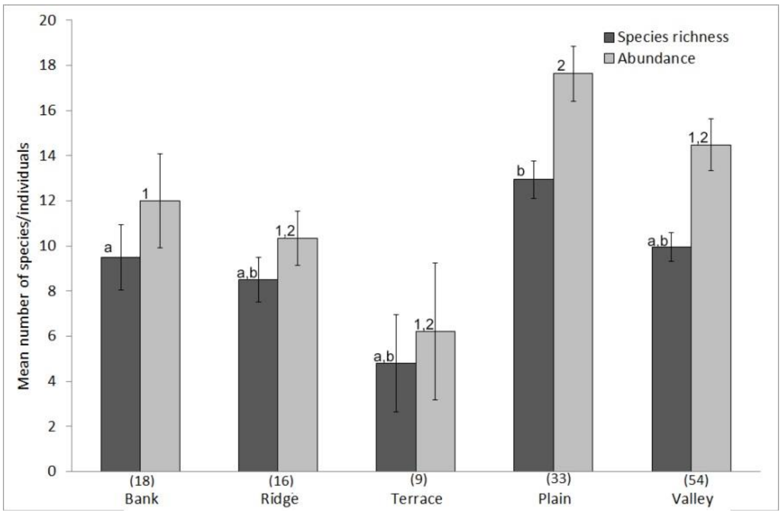

Figure 7: Polychaete richness and abundance among geomorphic features from the eastern study area (surveys SOL4934, SOL5117). Different letters or numbers represent significant differences as determined by Tukeys HSD multiple comparisons. Parentheses indicate number of grabs deployed at each geomorphic feature. Error bars are SEMs.

Discussion

Polychaete biodiversity in the current study showed that the Oceanic Shoals Marine Park and its surrounding region may be a hotspot for biodiversity of this group, with 368 species and 50 families collected from 266 sampling locations. This reflects higher species richness than any other study on Australian polychaetes in the open ocean, although due to different sampling methods such as sieve size and sub-sampling, only general comparisons can be made between studies (Table 2).

Alternatively, the comparatively high species richness in the Oceanic Shoals Marine Park may instead reflect high-resolution taxonomic identifications that were not used in some of the other studies (Long and Poiner 1994, Przeslawski et al. 2013).

Table 2 Summary of biodiversity studies of Australian polychaetes in the open ocean (>20 m depth)

Region	Depth range	No samples	No species	No families	Sieve size (µm)	Ref
Tropical shelf (Oceanic Shoals)	20-190	266	368	50	500	Current study
Tropical shelf (Arafura Sea)	70-230	107	275 [a]	42 [a]	300	(Wilson 2010)
Tropical shelf (Gulf of Carpentaria)	~20-70	315	196 [b]	Na	1000	(Long and Poiner 1994)
Tropical shelf (Ningaloo)	20-200	145	76 [b]	37	500[c]	(Przeslawski et al. 2013)
Tropical shelf (Kimberley)	< 50 m	69[d]	260[d]	43[d]	various	(Hutchings et al. 2014)
Continental slope (western)	100-1000	57	57	12	300	(Poore et al. 2015)
Temperate shelf (Great Australian Bight)	~50-200	65	93	Na	1000	(Currie et al. 2009)
Canyons (southern Australia)	100-1500	27	173	43	1000	(Conlan et al. 2015)
Canyons (New Zealand)		28	169	36	420	(Probert et al. 2009)

[a] Includes specimens pooled from epibenthic sled, dredge, and grab, with latter sub-sampled.
[b] Species richness determined by operational taxonomic unit (OTU)
[c] Sub-sampled
[d] Pooled historical datasets and museum collections, does not include locations from which no polychaetes were collected

The large number of taxa that could not be assigned to an existing species name is suggestive of a unique polychaete fauna being present in the AMP. However, this hypothesis is tentative because it likely also reflects the poor current taxonomic knowledge of tropical shelf and deep water polychaetes in general. Taxa that could be assigned a species name in the current study are typically endemic to northern Australia, or have a wider distribution across the Indo-Malay-Philippines Archipelago. Fewer species have a widespread Indo-west Pacific distribution.

Environmental patterns

Polychaete species assemblages and functional groups showed clear differences among surveys, with a possible temporal difference occurring between the 2009 and 2010 eastern surveys. Recruitment of small macrofauna is often seasonal (Riddle et al. 1990) and dependent on long-term climatic and oceanographic patterns (Williams et al. 2001) which may supersede local spatial differences (but see Hutchings and Jacoby 1994). In contrast, potential spatio-temporal differences were not observed in family assemblages, suggesting that a coarser resolution may be more appropriate when investigating spatial patterns.

Polychaete assemblages from Oceanic Shoals AMP region showed a high level of variation that was not necessarily related to broad-scale spatiotemporal patterns, with assemblages separated by tens of metres sometimes more different than those separated by 100s of metres. Similar observations were made on infaunal assemblages from the Carnarvon Shelf in north-western Australia (Przeslawski et al. 2013). These observations indicate that replicate samples should be collected at a given location to accurately quantify variation on multiple scales, and if variability is high, intensive replicate sampling may be required to detect trends (Rogers et al. 2008). The weak or lacking ecological relationships detected in the current study may thus reflect the high fine-scale variation and limited replication.

We found no strong environmental drivers for polychaete species or family assemblages, but this may be due to the limited replication and high variation mentioned above. In contrast, a study on south Australian canyons found that benthic environmental variables explained a large percentage (up to 49.3%) of the variation in macrofaunal communities (Conlan et al. 2015), but these results may have reflected the much larger depth range sampled (100-1500 m) compared to the current study (20-190 m) and associated larger range of environmental conditions. Compared to taxonomic groupings, functional groups were more strongly associated with environmental variables (mud, gravel, chl-a:pheophytin, sediment oxygen demand), likely due to the regulation by sediments on polychaete feeding, habitat and mobility (McArthur et al. 2010).

Comparison with sponges

To assess the generality of ecological patterns across taxonomic groups, we compared results from the current study on polychaetes with companion studies on sponges, also in the same study area and with similar species accumulation curves (Przeslawski et al. 2014, Przeslawski et al. 2015). In all of these studies, substrate hardness and depth were related to biodiversity, but these relationships were generally weak (Table 3). The current study also supports previous findings that banks support distinct benthic assemblages but shows that this may change over time for some taxa (Table 3).

Other environmental patterns were quite different between sponges and polychaetes (Table 3). Firstly, polychaete assemblages showed potential spatiotemporal variation, while sponge assemblages were similar among surveys. Secondly, sponges were dominated by rare taxa, many observed only once, while polychaetes had fewer singletons and doubletons. In addition, although both polychaetes and sponges were significantly related to the other taxonomic groups, the relationship between polychaetes and other small macrofauna was very weak, suggesting sponges may be a better proxy for overall benthic biodiversity than polychaetes in this region. Finally, the importance of geomorphic features varied according to taxonomic group, with plains showing distinct assemblages and higher species richness for polychaetes, and banks showing higher species richness for sponges (Table 3). These differences suggest that patterns identified in biodiversity assessments or monitoring from megafauna may not apply to smaller macrofauna. Further research is needed to test this hypothesis, using more replication or alternative models to account for high spatial variation (e.g. Dunstan et al. 2011).

Table 3: Comparison of results from the current study on polychaetes with results from previous studies on sponges in the Oceanic Shoals Marine Park. Only comparable results are shown (i.e. only environmental factors common among all studies).

	Polychaetes (current study)	Sponges (Przeslawski et al. 2014)	Sponges (Przeslawski et al. 2015)
Study area	eastern, central, western	Eastern	eastern, western
Data inclusions	all sites	all sites	all sites (biodiversity), raised geomorphic features only (spatiotemporal, environmental)
Biodiversity patterns	2558 specimens from 271 grabs/box cores	n/a[1]	~750 specimens from 106 sleds
	368 species from 50 families	n/a[1]	348 species from 55 families
	36% singletons, 15% doubletons[2]	64% singletons	60% singletons, 12% doubletons[3]
	richness significantly but weakly related to other taxa ($R^2 = 0.0968$)	n/a[1]	richness significantly related to other taxa ($R^2 = 0.5160$)
Spatiotemporal patterns[4]	assemblages differed among all surveys	no differences in assemblages between surveys	no differences in assemblages between surveys
	richness was higher in the east than west	n/a	no difference in richness between east and west
Environmental patterns	assemblages weakly related to substrate hardness and depth	assemblages weakly related to substrate hardness and depth	assemblages weakly related to substrate hardness and depth

	richness weakly related to depth and moderately to substrate hardness	richness not related to depth, weakly related to substrate hardness	richness not related to any factor
	assemblages from plains different from all other geomorphic features	no differences in assemblages between plains and other features	n/a
	assemblages from banks different from all other features in 2010, but not in 2009	assemblages from banks different from all other features	n/a
	plains had significantly higher richness than banks	banks had significantly higher richness than plains	n/a

[1] Results superseded by Przeslawski et al. 2015

[2] To standardise with sponges for which abundance was not recorded, the values presented here include species collected only from one or two grabs, not only one or two individuals as defined in the text.

[3] Includes 22 additional species in an opportunistic study area ~400 km to the east

[4] Refers to potential spatiotemporal patterns as indicated by differences between surveys. To test for spatiotemporal variation, appropriate spatial and temporal replication would need to be undertaken.

Relevance to marine management

We used baseline biodiversity data to address several exploratory questions of potential interest to marine managers and researchers. First of all, we found that small macrofaunal assemblages vary among surveys. This information will guide future surveys to ensure an appropriate sampling design that accounts for potential spatiotemporal variation. As such, any patterns or trends can then be correctly interpreted (e.g. spatial differences will not be inferred due to surveys being conducted in different times and locations). Second, we showed that environmental factors related to depth, substrate hardness, and sediment and geochemical characteristics were only weakly related to polychaete assemblages, whereas assemblages and richness varied among geomorphic features. This information is a foundation for understanding ecosystem processes in the region and identify potential environmental indicators (or lack thereof) for future monitoring programs. Finally, we compare ecological patterns among various levels of taxonomic resolution (species, family, various functional groups) and show that species-level data varies among all surveys, but this does not apply to coarser resolutions. This contradicts findings from other studies in which family-level assemblages showed similar patterns to species-level assemblages (Thompson et al. 2003, Lampadariou et al. 2005), although both of these studies included non-polychaete fauna and were focussed on detecting impacts rather than broad spatial patterns. This suggests that optimal taxonomic resolution for a given study may depend upon the target taxa and hypotheses to be tested. Conversely, functional groups in the current study had stronger relationships with environmental variables than species or family assemblages. These results help inform the effort needed to identify biological specimens for a given purpose; for example, species level may not be required if the main aim is to identify environmental surrogates for future monitoring.

The logistics of including small macrofauna in datasets used to monitor the performance and effectiveness of marine protected areas needs to be considered in the context of marine management goals (see Table 4 in Cochrane et al. 2016). This particularly applies to areas which may return high numbers of new or undescribed species which need to be deposited in an appropriate national repository (e.g. museum) to facilitate taxonomic studies and inventory regional biodiversity. For example, Poore et al. (2015) identified over 805 provisional species in one of the most comprehensive inventories of small benthic macrofauna in deep waters offshore western Australia. This result included only crustaceans and polychaetes partially identified, but even this incomplete effort required a large team of taxonomic experts. A comparison of sampling strategies for meiofauna, macroinfauna, and megafauna confirmed that macroinfauna sampling was the most resource-intensive, taking 12-22 hours from gear deployment to complete identification (Rogers et al. 2008). Management decisions may therefore be based on information about fish, sessile epibenthic invertebrates (e.g. sponges) or environmental proxies such as sediment and depth because macrofaunal sampling is deemed too expensive and time-consuming. However, patterns from fish and sessile epibenthic invertebrates may not be applicable to macrofaunal communities with very high rates of turnover (Kenchington and Hutchings 2018).

Despite these challenges, small macrofauna have been successfully targeted in select national and global biodiversity classifications (e.g. ophiuroids in Stöhr et al. 2012) and used to infer driving ecosystem processes (Woolley et al. 2016). They remain a key component for baseline and monitoring studies, particularly in nutrient-limited environments where small animals dominate (Leduc et al. 2016). In addition, future studies can use small macrofaunal biodiversity data to further investigate potential ecological patterns, including the identification of species archetypes based on responses to environmental gradients (Dunstan et al. 2011). This approach has successfully been employed by using biodiversity data (O'Hara et al. 2011, McCallum et al. 2013) to predict species archetypes from small macrofauna along the western Australian margin (Woolley et al. 2013). Polychaetes may be a particularly good choice for such an approach due to their diverse feeding guilds, habitats, and life cycles even within a given family.

Although the current study is focussed on small macrofauna > 500µm, we would be remiss not to consider meiofauna and microbes in the context of marine environmental management. These groups are increasingly being recognised as good indicators of environmental quality (Danovaro and Pusceddu 2007, Ingels et al. 2014) due to their small size and high abundance (shared with small macrofauna), as well as their rapid generation times and lack of planktonic phase (not always shared with small macrofauna) (Alves et al. 2013). As with small macrofauna, the inclusion of meiofauna and microbes in a sampling regime should be informed by hypotheses or monitoring objectives, as well as the local environment and available equipment and taxonomic or genetic expertise, with the latter arguably the reason meiofauna and microbes are often excluded from marine biodiversity and monitoring studies (but see Rees et al. 2014 for recent applications of eDNA).

The choice of biological metrics and associated sampling gear will depend on the aims and hypotheses of a particular study as they relate to quantifying biodiversity (Williams et al. 2015). The effort spent collecting small macrofauna is relatively low compared to larger macrofauna and megafauna because far more animals can usually be acquired in a much smaller spatial area. However, the time spent sorting these animals from the sediments or associated elutriate can be great, and the effort needed to identify them is comparable to other faunal groups. For example, a study focussing solely on habitat-forming epifauna may not need to sample small animals or infauna, while a study focused on broad biodiversity patterns across multiple habitats should target as many taxa and environments as possible. Environmental characteristics and resource constraints may mean that standard physical sampling methods may not be the most appropriate. For example, deep-sea habitats are often costly to appropriately sample due to time and cost deploying gear as well as the need for large sample numbers due to low abundance; an alternative may be to use imagery to quantify traces left by animals rather than the animals themselves (Widdicombe et al. 2003, Przeslawski et al. 2012).

The current study has provided baseline biodiversity and ecological data about the polychaetes and other small macrofauna of the Oceanic Shoals Marine Park which can be applied to marine management strategies in the following ways:

- Prior to any marine survey or monitoring activity, target measures of biodiversity need to be decided, appropriate gear identified, and qualified taxonomists engaged, including consideration of the trade-off between taxonomic resolution and spatial coverage (Chapman 1998). This follows from previous recommendations ‘to have clear management objectives with benefits and costs that can be measured’ (Kool et al. 2015).

- Sampling of small macrofauna and meiofauna becomes particularly important in nutrient-limited or deep-sea environments (Leduc et al. 2016), the latter of which now comprise a large proportion of Australia’s marine network (Devillers et al. 2015). These animals may also be appropriate monitoring targets in areas at risk of nutrient loading or pollution (Liz and Michael 2003).
- Macrofaunal and infaunal sampling must be informed by known ecological patterns and processes. Notably, the high spatial heterogeneity of these communities (Leduc et al. 2012) requires replicates at a scale of metres to appropriately quantify variation or long-term change at the larger scales of marine reserves (Blanchard and Feder 2014). The number of replicates needed will vary among regions and scientific objectives (Rogers et al. 2008).
- For the Oceanic Shoals AMP region, monitoring of small macrofauna may be best focused on polychaetes, as these are the most diverse and second-most abundant group in the current study. In addition, the current study provides a species inventory which can be used as a baseline to expedite future taxonomic identifications in the region.
- The carbonate banks and terraces of the Sahul Shelf and Van Diemen Rise (incorporating the Oceanic Shoals Marine Park) support distinct assemblages of polychaetes (current study) and sponges (Przeslawski et al. 2014), reinforcing their listing as Key Ecological Features. However, the current study also identifies plains as a geomorphic feature of interest due to their association with high polychaete species richness, as well as distinct taxonomic, feeding and habitat assemblages.
- Functional groups should be used to investigate environmental drivers, particularly in groups as functionally diverse as polychaetes. The current study found stronger relationships with sediment and geochemical variables using functional groups (feeding, habitat, mobility) rather than taxonomic groups. Classification of functional groups requires knowledge of both taxonomy and life history, and so appropriate experts should be engaged prior to the collection of samples.
- If general biodiversity or baseline patterns are to be investigated over unspecified habitats or taxonomic groups, sampling for marine benthic surveys should be carried out using multiple gear types to target a range of biota, including grabs or box cores to target small macrofauna. An ideal scenario is the use of one gear type from each of the major groups specified in (Flannery and Przeslawski 2015), i.e. sled, grab and image system to provide the best indication of benthic biodiversity over an unsampled area.
- If baseline biodiversity information such as that acquired here is to be used as a foundation for marine monitoring activities, temporal variability must be accounted for. Identification of a suitable monitoring surrogate may thus depend on whether larger magnitude changes are targeted (suiting large sessile macrofauna and megafauna such as sponges) or more subtle or short-term changes are targeted (suiting small macrofauna such as polychaetes). If the reasons underpinning temporal variation are known, they may then be controlled for in the experimental design (e.g. seasonal effects can be omitted by sampling in the same season each year).

This study has characterised biodiversity of polychaetes and other small macrofauna in the Oceanic Shoals Marine Park and surrounding region. Results from the current study can provide a baseline for future monitoring programs, as well as inform the inclusion of small macrofauna in such programs. Ultimately, there is a trade-off between multiple sampling methods, taxonomic resolution, spatial coverage and replication. Information about the ideal combination of sampling methods at a given spatial scale, habitat, or region to detect biodiversity patterns will help maximise the number and range of specimens collected, as well as the spatial coverage of the collection.

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