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Exceptional biodiversity of the cryptofaunal decapods in the Chagos Archipelago, central Indian Ocean

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ABSTRACT

The Chagos Archipelago is geographically remote and isolated from most direct anthropogenic pressures. Here, we quantify the abundance and diversity of decapod crustaceans inhabiting dead coral colonies, representing a standardised microhabitat, across the Archipelago. Using morphological and molecular techniques we recorded 1868 decapods from 164 nominal species within 54 dead coral colonies, but total species estimates (Chao1 estimator) calculate at least 217 species. Galatheids were the most dominant taxa, though alpheids and hippolytids were also very abundant. 32% of species were rare, and 46% of species were found at only one atoll. This prevalence of rarer species has been reported in other cryptofauna studies, suggesting these assemblages maybe comprised of low-abundance species. This study provides the first estimate of diversity for reef cryptofauna in Chagos, which will serve as a useful baseline for global comparisons of coral reef biodiversity.

1. Introduction

There have been various predictions regarding the number of marine species on Earth, spanning several orders of magnitude (Grassel and Maciolek, 1992; May, 1994). One of the most recent estimates suggests that there are ~2.2 million eukaryotic marine species, with < 10% having been described (Mora et al., 2011a). Among marine systems, coral reefs account for < 0.2% of the ocean floor, yet are recognised as the most biologically diverse marine ecosystem (Sala and Knowlton, 2006), with global coral reef species richness estimates of 830,000 multi-cellular plants and animals (Fisher et al., 2015). Coral reef invertebrate species richness, described to date, is estimated at 168,000 species (Ruppert et al., 2004; Stella et al., 2011a), far surpassing the number of fish species (~5000 species; Bellwood et al., 2012) and reef-building corals (700 species; Veron, 2000). The majority of these reef invertebrates are small and cryptic, often referred to as the cryptofauna, and live within the reef framework itself (Reaka-Kudla, 1997; Plaisance et al., 2011). The cryptofauna contains many poorly-known groups and are hard to sample as a result of their small and cryptic nature (Plaisance et al., 2009). Hence this component of biodiversity is understudied and further research is needed to improve species diversity estimates for several specific groups (Reaka-Kudla, 1997; Small et al., 1998; Plaisance et al., 2009). However, in recent years there have been several large-scale initiatives undertaken, such as the Census of Marine Life (http://www.creefs.org) and the Moorea Biocode Project (http://bscit.berkeley.edu/biocode), which have emphasised the importance of documentation of small and understudied organisms such as invertebrate and microbial species.

Approximately 20% of reef invertebrates are crustaceans, making them one of the most speciose groups on coral reefs (Plaisance et al., 2011 and Stella et al., 2011). Crustacea play a major role in the trophic dynamics of detrital-based food webs on coral reefs and are an extremely important link between primary production and higher consumers, as well as contributing to microbial- and detrital-based food webs (Enochs and Manzello, 2012a; Kramer et al., 2014). Overall, energetic transfer by coral reef crustaceans is estimated to average 0.066 g

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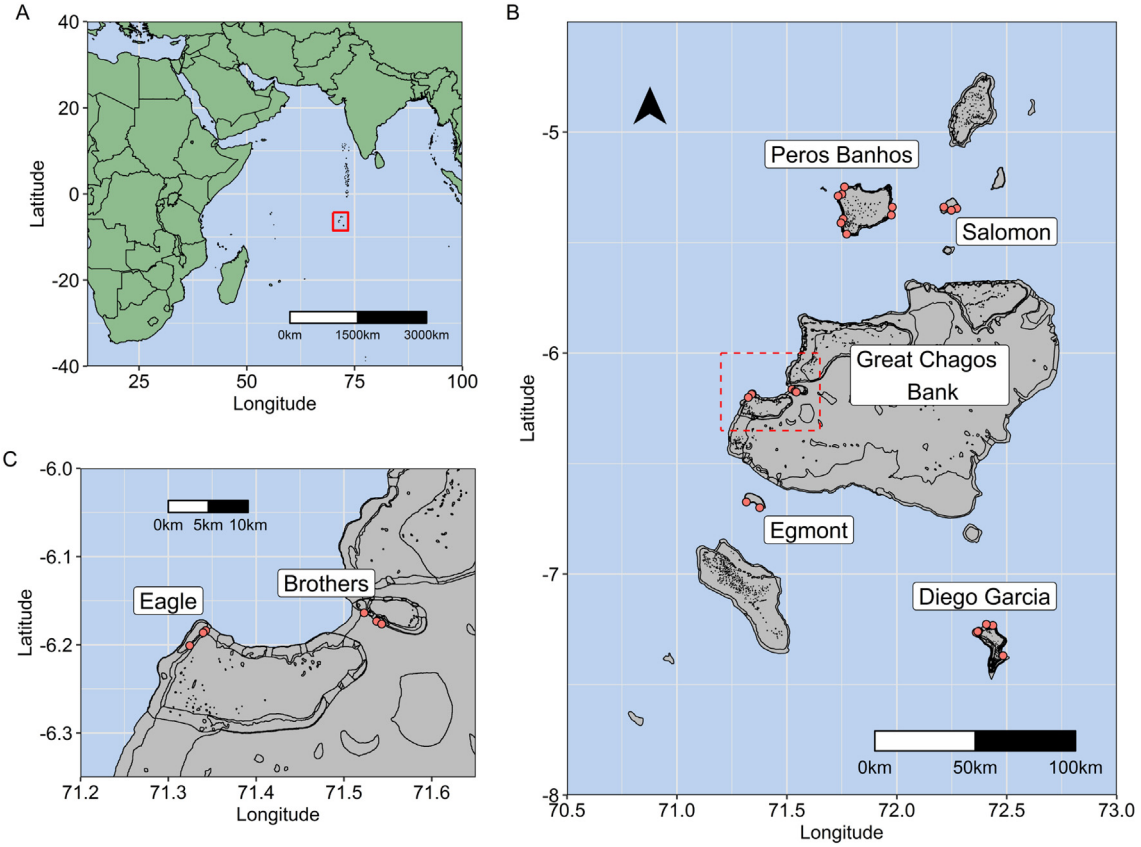

Fig. 1. The Chagos Archipelago; **(a)** illustrates the location of the Chagos Archipelago, **(b)** illustrates the atolls in the Archipelago with red circles representing the 25 sites where dead coral colonies were collected ($n = 54$) on the 2012 and 2013 expeditions. Two coral colonies were collected at each site except at the three sites at Salomon Atoll where three coral colonies were collected at two of the sites and four colonies at the remaining site, **(c)** a close up of Eagle and Brothers Islands (part of the Great Chagos Bank) shows the distribution of the six sites around these two islands. In **(b)** and **(c)** the grey areas depict the submerged and unsubmerged atolls and banks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

wet weight $m^{-2}d^{-1}$ (Kramer et al., 2014), comparable to productivity and transfer by fishes (0.20 g wet weight m − 2 d − 1; Depczynski et al., 2007). Crustacea are considered one of the most important dietary components of reef fish assemblages because 70% of reef fish are invertivores, and 60% of invertivores prey predominantly on benthic Crustacea (Williams and Hatcher, 1983; Randall et al., 1997; Froese and Pauly, 2014). In addition, decapods also have important functional roles in maintaining coral reef health with species cleaning fish of parasites, e.g. cleaner shrimp (Becker and Grutter, 2004), and some species defending coral colonies from predators and clearing excess sediment preventing smothering of coral polyps, e.g. *Trapezia* crabs (Pratchett, 2001; McKeon and Moore, 2014).

Crustaceans inhabit all reef microhabitats and are major components of invertebrate assemblages within live corals, dead corals, coral rubble, the epilithic algal matrix (Kramer et al., 2013), and sand (Kramer et al., 2014). Of these microhabitats, dead coral colonies have been identified as the most biodiverse habitats (Enochs, 2012; Kramer et al., 2014). This is probably because of the structural relief of the coral still remaining intact to provide habitat and shelter from predators, in comparison to the lower structural complexity of other microhabitats, such as sand and coral rubble. The heterogeneity of the benthic substrata increases on dead branching coral compared to live coral as sessile organisms, such as Porifera and Ascidiacea, colonise recently dead corals providing a variety of niches for motile cryptofauna (Enochs and Manzello, 2012b), resulting in higher biodiversity through complementarity and facilitative interactions (Hooper et al., 2005). In addition, the productivity of the complete faunal assemblage of dead coral colonies is estimated to be up to 149 g Ash-free Dry Weight (AFDW) $m^{-2}\,yr^{-1}$ (Kramer et al., 2014), suggesting this microhabitat is one of the most productive in the world, surpassed only by Californian macrophyte detritus and mussel beds in the Wadden Sea (Asmus, 1987; Taylor, 1998).

The greatest threat to natural biodiversity across all ecosystems is ongoing degradation and loss of critical habitats (e.g., Brooks et al., 2002; Waycott et al., 2009), which is being increasingly caused and compounded by global climate change (Mantyka-Pringle et al., 2012). This is especially acute for tropical coral reefs (Burke et al., 2011) which are impacted by multiple stressors including unsustainable and destructive fishing practices, sedimentation and pollution from coastal and maritime activities, and biological outbreaks of crown-of-thorns sea stars. These direct impacts are taking place against a background of increasing global climate change affects, such as mass coral bleaching events, eroding the resilience of reef ecosystems (e.g. Pandolfi et al., 2003; Harborne et al., 2017; Hughes et al., 2017). For instance, the Great Barrier Reef lost over 50% of it coral cover from 1985 to 2012 which has been further compounded by the 2015–2016 global mass bleaching event (D'eath et al., 2012; Hughes et al., 2018).

Despite the demonstrated importance of coral reef decapod assemblages there is little information on how decapod, or indeed cryptofauna communities, are affected by human-induced stressors (But see Coles, 1980, Tsuchiya, 1999, Idjadi and Edmunds, 2006, Leray et al., 2012). In other ecosystems, pollutants have been shown to impact abundance and diversity of decapods. For example, decapod communities on deep offshore banks suffered a dramatic decrease in both abundance and diversity following an oil spill, hypothesised to be a result of cascade effects from seaweed loss (Felder et al., 2014). Whilst, in a macrotidal estuarine environment an increase in species richness and abundance of mysid and caridean decapods over a 26-year study

period was only correlated with a decline in metal concentrations and increase in water quality (Plenty et al., 2018).

It is likely that biodiversity is being lost before we have even been able to effectively document the full range of species, especially invertebrate cryptofauna, that are reliant on coral reef environments. Our best strategy perhaps is to use the few remaining reefs approaching 'pristine' conditions, as a result of their remote locations away from direct human impacts, as baselines for measuring biodiversity and ecosystem processes (Knowlton and Jackson, 2008; Sandin et al., 2008). The Chagos Archipelago, or British Indian Ocean Territory (BIOT), located in the middle of the Indian Ocean, is isolated from most major direct anthropogenic pressures (Sheppard et al., 2012) and hence represents such a reference site for the Indian Ocean (Fig. 1).

The Chagos Archipelago has an important role in the biogeography and conservation of marine ecosystems, and especially, coral reefs, in the Indian Ocean (Sheppard et al., 2012). Chagos is a large no-take marine protected area (MPA), at approximately 640,000km^2, with fish biomass levels orders of magnitude higher than anywhere else in the Indian Ocean and likely some of the cleanest waters globally (Graham et al., 2013; Sheppard et al., 2012). These reefs are also biographically important as 'stepping stones' between the western Indian Ocean and Indonesian region which are connected through the east-west flow of the South Equatorial Current (SEC), which reverses for a few months a year (Obura, 2012). Chagos' reefs have also demonstrated high levels of resilience recovering within 10 years from severe mortality following the 1998 mass bleaching event, probably because of the reefs' high coral recruitment densities, high herbivorous fish biomass, and negligible levels of direct anthropogenic disturbance (Harris and Sheppard, 2008; Sheppard et al., 2012; Graham et al., 2013). This study investigates the abundance and diversity of decapods (Crustacea), inhabiting dead coral colonies, the most productive reef microhabitat (Enochs, 2012; Kramer et al., 2014), on coral reefs across the Chagos Archipelago. It provides the first inventory of reef cryptofauna from the Chagos Archipelago for any microhabitat, potentially providing an important baseline reference for biodiversity estimates for this microhabitat in an area away from the majority of direct anthropogenic impacts.

2. Methodology

2.1. Sampling design summary

Sampling of dead branching corals ($n = 54$) was undertaken during two separate expeditions from March to April 2012 and 2013 in the Chagos Archipelago. Sampling was conducted at 25 sites, all located on the outer reef and separated by at least 250 m across six atolls and islands; Diego Garcia Atoll, Peros Banhos Atoll, Salomon Atoll, Eagle and Brothers Islands of the Great Chagos Bank, and Egmont Atoll (Fig. 1). At each site, 2–4 dead *Acropora* or *Pocillopora* coral colonies of approximately 20 cm in diameter were sampled from 8 to 10 m depth, as detailed in Head et al. (2015). To quantify cryptofaunal diversity, all macro-organisms, > 1 mm in size, inhabiting each coral colony were removed and sorted first by immersing the coral colony in a bucket of freshwater for approximately 1 min, following Stella et al. (2011), and then passing the water through a 1-mm sieve. The seawater in which the coral colonies were stored and transported was also sieved. Finally, the coral colony was inspected and carefully broken up, using a hammer and chisel to collect any remaining hidden fauna. Coral colonies were defined as being dead if they had no observable live polyps, evidence of turf and crustose coralline algae, and sometimes erosion but a largely intact physical structure remained.

2.2. Species identification

Brachyura, Galatheidae, Hippolytidae and Palaemonoidea specimens were identified to species by taxonomic experts (Prof. P. Ng Kin Lee from Raffles Museum, Singapore, Dr. E. Macpherson from Centro de Estudios Avanzados de Blanes, and Dr. S. De Grave Oxford Natural History Museum respectively). Rare species were catalogued into the Raffles Museum, Singapore (Brachyura) and Oxford University Natural History Museum (Palaemonoidea, Hippolytidae and Galatheidae) collections. It was not possible to identify Brachyura and Galatheidae larval and megalopa forms morphologically to species level so to ensure there was no duplication in species counts and resulting over-estimation of species numbers, we chose to disregard the Brachyura and Galatheoidae larval and megalopa species counts, but their abundances were included.

For families Paguroidea, Porcellanidae and Alpheidae, morphological identifications could not be garnered from taxonomic experts so molecular methods were used to provide a set of putative species, known as molecular operational taxonomic units (MOTUs). MOTUs are now an established, useful exploratory tool in biodiversity assessments (Hebert et al., 2003; Puillandre et al., 2012). To determine MOTUs for Paguroidea, Porcellanidae and Alpheidae, genomic DNA was extracted from each specimen using the DNeasy Blood and Tissue kit (Qiagen) and partial fragments of the 16S ribosomal RNA gene (~520 bp) were amplified by polymerase chain reaction (PCR). PCR products were purified using ExoSap-IT (Affymetrix) and sequenced on an Applied Biosystem 3730xl DNA Analyzer. Forward and reverese sequences for each specimen were aligned in Geneious 6.1.5 (Biomatters Ltd., Auckland, New Zealand) using the Geneious alignment function with default settings and edited by eye to produce a consensus sequence. For a detailed molecular methodology see Supplementary materials. Following sequence alignment, three different species deliminitation methods were run for each family/superfamily; General Mixed Yule-Coalescent approach (GMYC) (Fujisawa and Barraclough, 2013), Poisson tree processes approach (PTP) (Zhang et al., 2013), automatic barcode gap discovery (ABGD) (Puillandre et al., 2012). GMYC and PTP are evolutionary-based species delimitation methods for single-locus datasets, which are based on neutral coalescent theory (Fujisawa and Barraclough, 2013; Zhang et al., 2013). In contrast, ABGD is more similar to the 'classical' DNA barcode gap analysis (Hebert et al., 2003), whereby an arbitrary distance threshold is applied to test whether two sequences are from two different groups, but ABGD differs by statistically inferring the barcoding gap from the data and partitions the dataset accordingly (Puillandre et al., 2012). ABGD and PTP species delimitation methods where chosen for their novelty and promise as improved species delimitation methods (Paz and Crawford, 2012; Zhang et al., 2013), and GMYC because it has been frequently used in empirical studies (e.g. Pons et al., 2006; Monaghan et al., 2009; Vuataz et al., 2011; Paz and Crawford, 2012). The results of each method for each taxon was compared (Table S2) and the performance evaluated (see Supplementary materials, Figs. S1–S4). The MOTUs estimate considered most accurate for each taxon was then used as a species richness estimate for that taxon.

2.3. Data analysis

Species rarefaction curves, which plot the species richness as a function of the number of individuals sampled, were used to establish whether the sampling design reflected the 'true' species richness (Magurran and McGill, 2011). Non-parametric species estimators Chao1 and Abundance-based Coverage Estimator (ACE) were calculated to estimate the total species richness of the community from those observed from a sample, enabling estimates to be compared across samples. They use a mark-release-recapture like ratio to estimate richness by adding a correction factor to the observed number of species (Magurran and McGill, 2011). The Chao1 estimator is particularly useful for data sets skewed towards the low-abundance classes, as is likely to be the case for diverse communities such as decapods (Magurran and McGill, 2011). The ACE incorporates data from all species with fewer than ten individuals, rather than just singletons or

doubletons (Magurran and McGill, 2011). Mean species richness and abundance was calculated per coral colony because the number of coral colonies collected per atoll/island were uneven as a result of the limited expedition time. Generalised linear models (GLMs) were used to test for significance of the effect of geographical location (Atoll) on the response variables mean species richness and mean abundance per coral colony. Poisson models were fitted for the GLMs and all data were found to be under or over-dispersed so Quasi-Poisson models were fitted to introduce a dispersion parameter and obtain a quasi-likelihood estimate (Crawley, 2005).

A Venn diagram was used to visualise overlap in species occurrence between atolls. Non-metric multidimensional scaling (nMDS) based on Bray-Curtis similarity (Bray and Curtis, 1957) was used to visualise the ordination of the decapod community structure. A similarity profile (SIMPROF) was used to test whether the similarities observed in the data are smaller and/or larger than those expected by chance in combination with a cluster analysis (Clarke and Somerfield, 2008). Permutational analysis of variance (PERMANOVA), a multivariate analysis of variance, was used to test for significant differences between decapod communities in response to atoll location. It uses permutations to make the data distribution free, allowing it to handle non-normally distributed data and more complex unbalanced sampling designs. All analyses were undertaken in R (R-Development-Core-Team, 2008) using the Vegan package (Oksanen et al., 2015), or in PRIMER v.6 (Clarke, 1993).

3. Results

3.1. Total species richness and abundance

A total of 1868 individual decapods were recorded from 54 coral heads sampled across 25 sites at six atolls and islands in the Chagos Archipelago (Table 1). In all, at least 164 distinct species were recorded, and 32% of these species were rare (singletons) in the community. The Caridea were the most species rich and abundant component of the decapods and had the highest proportion of rare species (37%). At the family/superfamily level the Alpheidae were the most species rich at 51 species, and the Galatheidae were the most abundant at 343 individuals (Table 1). However, these species richness values are conservative as it was not possible to morphologically identify some of the Brachyura and Galatheidae larvae/megalopa forms, and some morphotypes failed to amplify when using molecular techniques (see Table S1). *Galathea* aff. *Spinosorostris* (n = 115) and *Saron neglectus* (n = 103), a galatheid and hippolytid species respectively, were the two most abundant species (Table 2). Only 38 species were represented by ten or more individuals across the Archipelago (Table S3).

Table 2
Abundances of the ten most common decapod species. It should be noted that Porcellanidae sp.4 and Paguroidea sp.4 are putative species defined by molecular methods.

Species	Abundance
Galathea aff *spinosorostris*	115
Saron neglectus	103
Galathea platycheles	92
Thorina maldivensis	92
Trapezia juveniles	82
Porcellanidea sp.4	76
Galathea eulimene	65
Jocaste luncina	63
Paguroidae sp.4	52
Tylocarcinus styx	50

The rarefaction curves were yet to plateau (Fig. 2) suggesting that the true species richness of the three infraorders and total decapod species richness is higher, and further sampling would be needed to capture the actual total species richness of this group. Only at Salomon and Egmont Atolls do the rarefaction curves indicate that the Anomura species richness may be beginning to plateau (Fig. 2b). The Chao1 and ACE richness estimators, whilst accounting for uneven sampling across the atolls, calculated the total decapod species richness for the Archipelago at 217 ± 19.53 (Chao1)/218.22 ± 7.58 (ACE) species (Table 3). This suggests that our sampling effort has captured approximately 75% of the decapod species richness inhabiting dead branching corals in the Chagos Archipelago. Diego Garcia Atoll and Peros Banhos Atoll are estimated to have the highest decapod species richness at 119.75 ± 13.26 (Chao1)/130.92 ± 6.15 (ACE) and 123.05 ± 12.68 (Chao1)/130.69 ± 5.90 (ACE) species respectively, and Eagle Island the lowest at 30.8 ± 2.86 (Chao1)/33.47 ± 2.29 (ACE) species (Fig. 3). Generally, the two species estimator results were closely aligned, though Chao1 tended to produce larger variation around the mean, suggesting less certainty in the Chao1 estimations (Fig. 3 and Table 3). Interestingly the species richness estimators suggested that there is little Anomura species richness still to be captured, with ACE estimating there are approximately eight more Anomura species to be discovered on this microhabitat (Table 3), despite the rarefaction curve not yet approaching a plateau. Instead the results indicate that most of the remaining species richness to be captured are Caridae species (Table 3).

Table 1
Biodiversity metrics for each decapod family/superfamily, with totals given for each infraorder and for decapods as a whole.

Infraorder	Superfamily/Family	Species delimitation method	Species richness	Abundance	Singletons	% Singletons
Caridea	Alpheidae	GMYC	51	222	20	
Caridea	Palaemonoidea	Morphology	20	170	7	
Caridea	Hippolytidae	Morphology	8	262	2	
Caridea	Total		79	654	29	37%
Anomura	Galatheidae	Morphology	8	343	3	
Anomura	Galatheidae (larvae)	–	–	34	–	–
Anomura	Paguroidea	PTP	13	163	1	
Anomura	Porcellanidae	PTP	7	98	4	
Anomura	Total		28	638	8	29%
Brachyura	Dromioidea	Morphology	3	11	0	
Brachyura	Eriphioidea	Morphology	2	9	1	
Brachyura	Grapsoidea	Morphology	2	4	1	
Brachyura	Majoidea	Morphology	7	98	2	
Brachyura	Pilumnoidea	Morphology	7	63	1	
Brachyura	Trapezioidea	Morphology	8	144	2	
Brachyura	Xanthoidea	Morphology	28	151	8	
Brachyura	Megalopa	–	–	96	–	–
Brachyura	Total		57	576	15	26%
Decapoda	Total		164	1868	52	32%

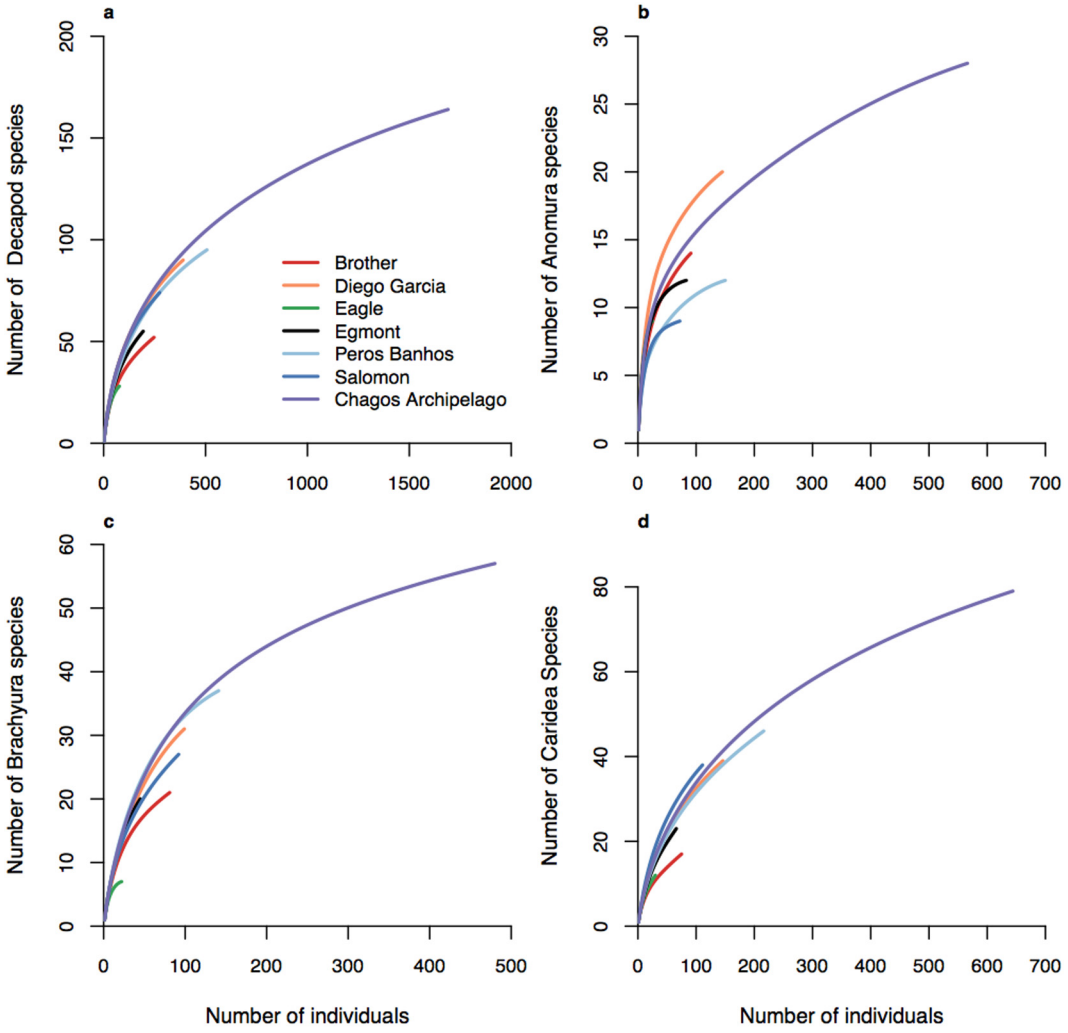

Fig. 2. Rarefraction curves for **(a)** the decapods; and divided into the decapod's three infraorders **(b)** Anomura, **(c)** Brachyura, **(d)** Caridea.

Table 3
Total species richness estimators Chao1 and ACE compared to the observed species richness from 54 sampled dead coral colonies, for each infraorder and for the decapods as a whole.

	Observed species richness	Chao1	Standard error	ACE	Standard error
Anomura	28	31.5	± 3.44	36.41	± 3.21
Brachyura	57	72	± 10.33	68.71	± 3.91
Caridea	79	112.83	± 16.87	112.61	± 5.72
Decapods	164	217	± 19.53	218.22	± 7.58

3.2. Species richness per coral colony

The mean decapod species richness per coral colony (Fig. 4a) was 15 ± 1.14 species across the Chagos Archipelago. Egmont Atoll having the highest mean species richness at 22.5 ± 5.39 (Fig. 4.a). The effect of site, as a factor, on species richness was significant (GLM, $F = 2.53$, $p = 0.04$) and GLM ANOVA co-efficients suggest this significance may lie between Eagle Island (ANOVA, $t = -2.17$, $p = 0.04$) and the other atolls and islands, which had a significantly lower species richness at 7.17 ± 2.44 species (Fig. 4a). All data were over-dispersed (Table 4) suggesting there is variation in species richness controlled by other factors, in addition to geographical location, such as coral colony structure, food availability and species interactions.

When decapod species richness is divided into the three major infraorders, the Anomuras comprise the lowest fraction of 3.7 ± 0.31 mean species across the Archipelago, whilst Brachyura mean species richness was 4.86 ± 0.53, and the Caridea mean species richness 6.38 ± 0.64 (Fig. 4). The effect of site, as a factor, on the Anomura mean species richness was significant (GLM, $f = 3.32$, $p = 0.001$) but was not significant for the Brachyura or Caridea (Table 4). Diego Garcia Atoll had the highest mean Anomura species richness alongside Egmont Atoll at 6 ± 0.65 and 6 ± 1.08 mean species respectively.

3.3. Abundance per coral colony

The trends across the atolls and islands in mean decapod species abundance per coral colony were similar to the trends in mean species richness, but unlike the species richness they were not significant (Table 4). The mean decapod abundance per coral colony across the Chagos Archipelago was 31.98 ± 3.26. Egmont Atoll had the highest mean at 48.5 ± 13.67 individuals, and Eagle Island had the lowest mean at 12.8 ± 5.95 individuals (Fig. 5a). The data were over-dispersed (Table 4), suggesting high variability in species abundances influenced by other factors. A lack of significance in the trends across the atolls maybe partly a result of relatively large variation around the mean abundances, particularly at Egmont Atoll and Brothers Islands (see error bars on Fig. 5a).

Major trends in the abundance of decapods across the atolls (Fig. 5) were generally similar to patterns of variation in species richness (Fig. 4). One notable exception was that decapod abundance at Brothers

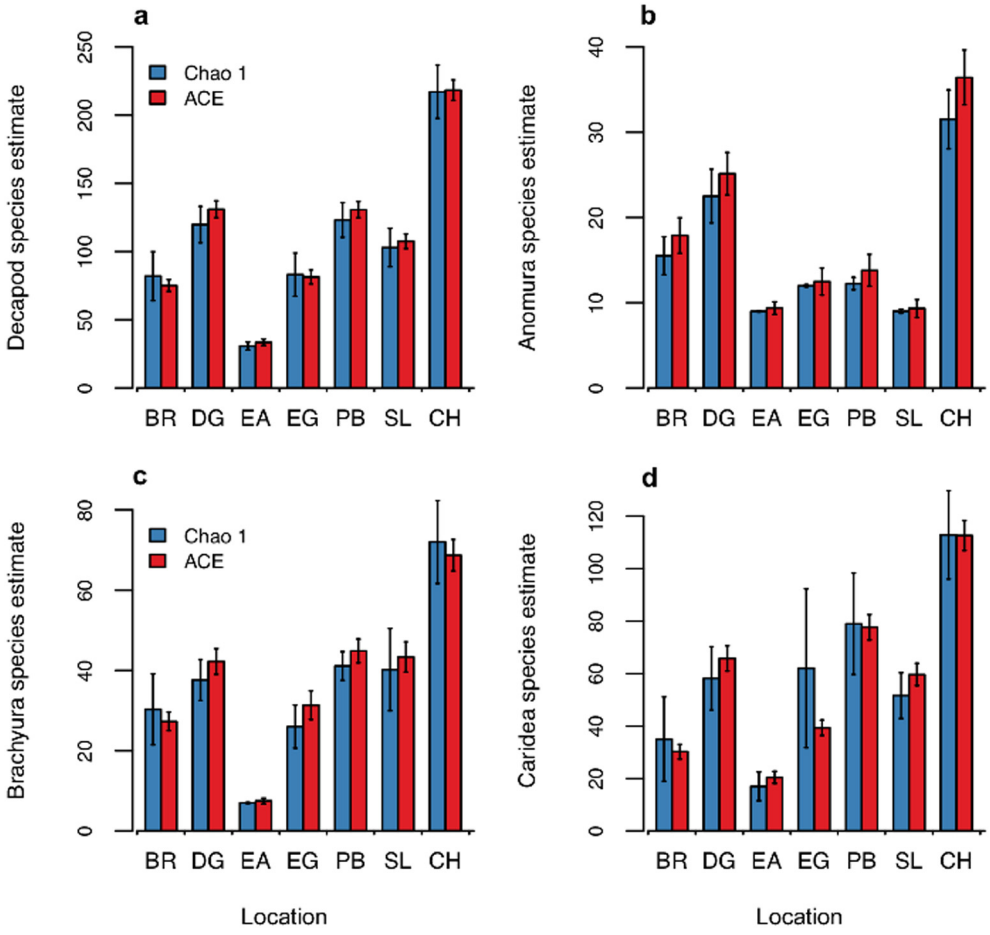

Fig. 3. Bargraphs illustrating species richness estimates calculated from two estimators: Chao1 and ACE across each atoll/island and, as a point of reference only, for the archipelago in total, for the **(a)** decapods, and divided into the decapod's three infraorders; **(b)** Anomura, **(c)** Brachyura, and **(d)** Caridea. Atoll/island abbreviations: BR = Brothers Islands, DG = Diego Garcia, EA = Eagle Island, EG = Egmont, PB = Peros Banhos, SL = Salomon, and CH = Chagos Archipelago.

Islands was higher than recorded at Diego Garcia Atoll, despite having lower species richness. The effect of site, as a factor, on the Anomura abundance was significant (GLM, $f = 3.32$, $p = 0.01$), but this was not the case for the Brachyura and Caridae (Table 4). The ANOVA coefficients from the GLM suggests that Anomura mean abundance was significantly lower at both Eagle Island (ANOVA, $t = -2.14$, $p = 0.04$) and Salomon Atoll (ANOVA, $t = -2.05$, $p = 0.05$) than at all other atolls.

3.4. Community structure

PERMANOVA test showed no significant effect of site, as a factor, on decapod community structure, nor on any of the three infraorders that comprise the decapods (Table 5). Eagle Island and Brothers Island are geographically at least 20 km apart but are also both part of a large atoll, called the Great Chagos Bank (GCB), so the PERMANOVA test was run twice to consider these islands together as the GCB and separately as islands. Separately the effect of atoll accounted for 23% of the variation in decapod community structure, and when pooled together the effect of atoll explained 17%, giving validation to the separation of these islands in the analysis (See R^2 in Table 5). The nMDS plot (Fig. 6a) illustrates this lack of significant structure in the community between atolls, and demonstrates that only one site on the southern tip of the Eagle Island was significantly dissimilar in its community structure (*sample stat* $= 0.007$, $p = 0.05$) at a 20% similarity level. The nMDS plot also shows some clustering of sites at a 40% similarity level, however, only the 20% similarity level is supported by the SIMPROF test, as demonstrated by the cluster plot (Fig. 6b). Despite the lack of community structure between atolls and islands, the Venn diagram (Fig. 7) illustrates that only 14 of 164 species were shared between all atolls and islands, and each atoll and island had many unique species (except Eagle Island which only had one species unique to this island), for instance Diego Garcia Atoll had the highest number of unique species at 26 species. The ranking of unique species per atoll in the Venn diagram broadly reflects the ranking of species richness per atoll (Fig. 3), suggesting that rare species could be one of the main drivers of these differences in species richness between atolls. Therefore, the nMDS was repeated with transformed data ($^2\sqrt{}$ transformed) to account for the low abundance of some species but the lack of community structure remained the same. The Bray-Curtis dissimilarity indices (Table 6) demonstrate that Peros Banhos Atoll and Eagle Island are the least similar in community structure and Peros Banhos Atoll and Diego Garcia Atoll are the most similar.

4. Discussion

At least 164 species of decapod crustaceans were recorded from dead coral colonies *(n = 54 colonies)* in the Chagos Archipelago. However, rarefaction curves did not plateau, suggesting that further sampling would reveal even more distinct species. Based on projections of species-abundance curves, we conservatively estimate that the total species richness of decapod crustaceans within the specific microhabitat type sampled in this study would be at least 217 species (Chao1). A high proportion of species (32%) were rare (singletons). High levels of rare species are a common pattern in reef cryptofaunal populations, such as molluscs (Bouchet et al., 2002) and isopods (Kensley, 1998), implying that much of reef cryptofauna is comprised of low-abundance species. For instance, a study of crustacean communities on dead coral colonies in Moorea and the Northern Line Islands, in the Pacific Ocean, found 44% to be singletons and a further 33% represented by several

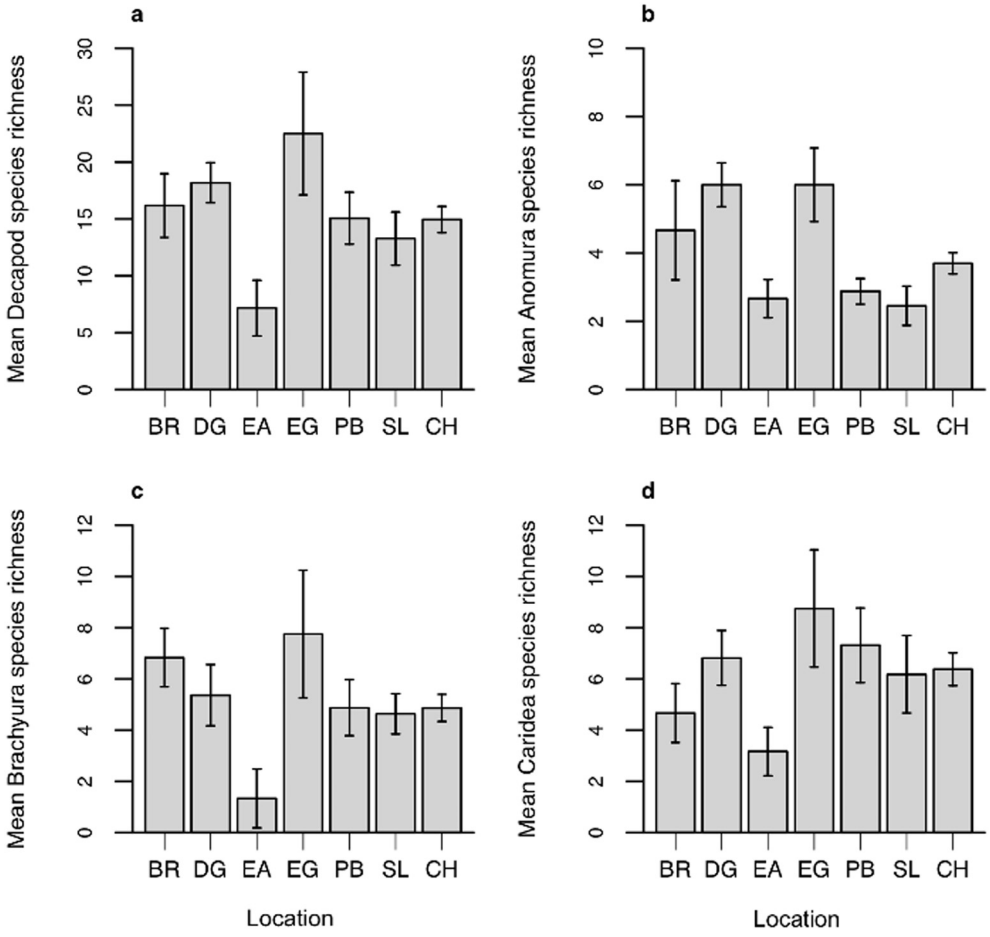

Fig. 4. Bargraphs illustrating the mean species richness per coral colony for each atoll/island and, as a point of reference only, also for the archipelago as a whole for the **(a)** decapods, and divided into the decapod's three infraorders; **(b)** Anomura, **(c)** Brachyura, and **(d)** Caridea. Atoll/island abbreviations: BR = Brothers Islands, DG = Diego Garcia, EA = Eagle Island, EG = Egmont, PB = Peros Banhos, SL = Salomon, and CH = Chagos Archipelago.

Table 4
The GLM results demonstrating the effect of site on the mean species richness and abundance per coral colony. * indicates significant *p* values.

	Mean species richness per coral colony			Mean abundance per coral colony		
	p value	F statistic	Dispersion parameter	*p* value	F statistic	Dispersion parameter
Anomura	0.001*	5.27	1.12	0.01*	3.32	7.12
Brachyura	0.08	2.09	3.08	0.39	1.06	7.33
Caridea	0.28	1.29	3.19	0.44	0.99	9.62
Decapods	0.04*	2.53	4.2	0.085	2.07	15.95

specimens found only at one locality (Plaisance et al., 2009). In Chagos, many species were also unique to only one atoll (46%) suggesting perhaps that a low level of connectivity exists between atolls in the Archipelago and/or the species have relatively short larvae dispersal ability. Alternatively, both rarity patterns may be reflective of low sampling efforts given the extraordinary biodiversity within such groups.

4.1. Rare species

The high proportion of rare species in this decapod community raises the question of the role of rare species in ecosystem function. Rare species are intuitively much more susceptible to extirpation and extinction, but the ecological consequences of losing rare species are frequently overlooked (Lyons et al., 2005; Mouillot et al., 2013). Until recently, it was often assumed that highly diverse assemblages possess high levels of functional redundancy, whereby the loss of some species would not necessarily impact on ecosystem function (Loreau et al., 2001; Hooper et al., 2005). However, Mouillot et al. (2013) demonstrated that in three diverse ecosystems rare species (of reef fishes, alpine plants, and tropical trees) supported the most distinct combination of traits, and moreover species that have low functional redundancy and are likely to support the most vulnerable functions are rarer than expected by chance. Accordingly, some rare species have a critical contribution to ecosystem function (Zavaleta and Hulvey, 2004; Bracken and Low, 2012). Recent studies have also shown non-saturating patterns between biodiversity and functioning in marine ecosystems, suggesting that loss of species may have a substantially larger effect on the functioning of ecosystems than anticipated (Danovaro et al., 2008; Loreau, 2008; Mora et al., 2011a; Mora et al., 2014), and if a high proportion of these species are rare there is a greater risk of biodiversity loss. This positive relationship between biodiversity and functioning is likely a result of interspecific facilitation and complementarity (Cardinale et al., 2002; Hooper et al., 2005; Danovaro et al., 2008).

4.2. Comparisons with other crustacean studies

Whilst relatively few studies have investigated the cryptofauna biodiversity of dead coral microhabitats (but see Coles, 1980; Preston and Doherty, 1990; Plaisance et al., 2009; Enochs, 2011), this study has revealed that decapod species richness in Chagos is higher than at any other location for this size-class (> 1 mm). Plaisance et al. (2009) found total Crustacea species richness estimates of 90 Operational Taxonomic Units (OTUs) for Moorea and 150 OTUs for the Northern Line Islands, both remote atolls in the Pacific. Off the coast of Panama, total estimated cryptofauna species richness was 261–370 OTUs (Enochs and

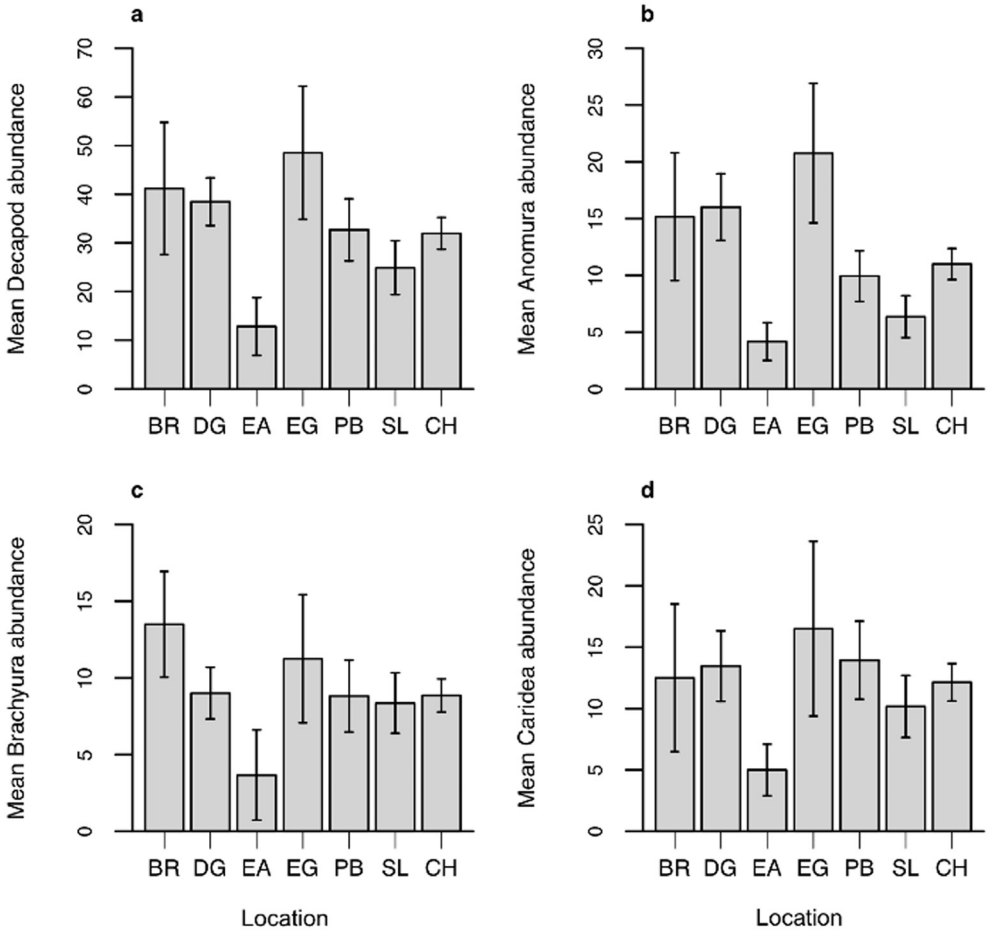

Fig. 5. Bargraphs illustrating the mean species abundance per coral colony for each atoll/island and, as a point of reference only, for the archipelago as a whole, for the **(a)** decapods, and divided into the decapod's three infraorders; **(b)** Anomura, **(c)** Brachyura, and **(d)** Caridea. Atoll/island abbreviations: BR = Brothers Islands, DG = Diego Garcia, EA = Eagle Island, EG = Egmont, PB = Peros Banhos, SL = Salomon, and CH = Chagos Archipelago.

Table 5
PERMANOVA statistics evaluating the significant difference in community structure with atoll/island location. R^2 shows the proportion of variance explained by atoll/island. GCB is an abbreviation for the Great Chagos Bank.

	p value	Pseudo-F statistic	R^2
Anomura	0.09	1.32	0.26
Brachyura	0.08	1.26	0.25
Caridea	0.38	1.03	0.22
Decapods	0.11	1.15	0.23
Decapods (Brothers & Eagle Islands combined as GCB)	0.37	1.04	0.17

Manzello, 2012a), however, the arthropods accounted for approximately 27% of the observed richness, putting a maximum arthropod species richness estimate at approximately 100 OTUs. On Hawaiian reefs, Coles (1980) reported 115 observed decapod species on 18 dead corals, however sizes of the corals varied and no total species estimates are available so direct comparisons cannot be made. Preston and Doherty (1990) sampled 1080 corals from the Great Barrier Reef (GBR) and yielded 28 species of agile shrimp (families: Hippolytidae, Pandalidae, Palaemonoidae and Processidae) from 25,324 individuals. In Chagos we had a much smaller sample size but also found 28 species from just the Hippolytidae (twenty species) and Palaemonoidae (eight species) (none from Pandalidae and Processidae), and there was an overlap of at least four species with the GBR study. This is surprising as we would except a higher species richness on the GBR in comparison to the Chagos Archipelago, because the GBR is much closer to the Coral Triangle, the epicentre of coral reef biodiversity (Bellwood et al., 2012). However, it should be noted that taxonomic knowledge has very likely improved in the intervening years and sampling methods differed somewhat (Preston and Doherty, 1990) to our own, which is a consideration with many of the qualitative comparisons made here.

Decapod community structure also varies between these studies. In Chagos, galatheids were the most dominant, and alpheids and hippolytids were also very abundant (Table 1), with the four most dominant species belonging to the galatheids and hippolytids (Table 2). The high abundance of palaemonoids and *Trapezia* crabs was unexpected as most of these species are considered obligate live coral dwellers and populations have not been reported on dead coral colonies elsewhere as far as we are aware (Discussed in Head et al., 2015). In comparison decapod communities on dead corals in Hawaii were dominated by xanthids, pagurids and alpheids (Coles, 1980). Whilst in Moorea and Northern Line Islands Brachyura dominated the communities (Plaisance et al., 2009). The Chagos community was comparatively more even across the infraorders but the Caridea were the most abundant over all.

4.3. Factors affecting cryptofauna diversity

Our knowledge of the factors affecting cryptofauna diversity on any microhabitat are very limited, but some studies have been undertaken (e.g. Idjadi and Edmunds, 2006). Enochs et al. (2011) found that low-porosity (gaps in rubble structure) and slow-flow environments supported a higher abundance and biomass of motile cryptofauna on dead coral and coral rubble microhabitats. The size of the coral colonies, their structural complexity and surface area have also been demonstrated to be positively correlated with the abundance and species richness of decapod communities on both live and dead coral colonies, with more complex corals thought to provide better refuge from predators and better niche separation (Abele and Patton, 1976; Coles,

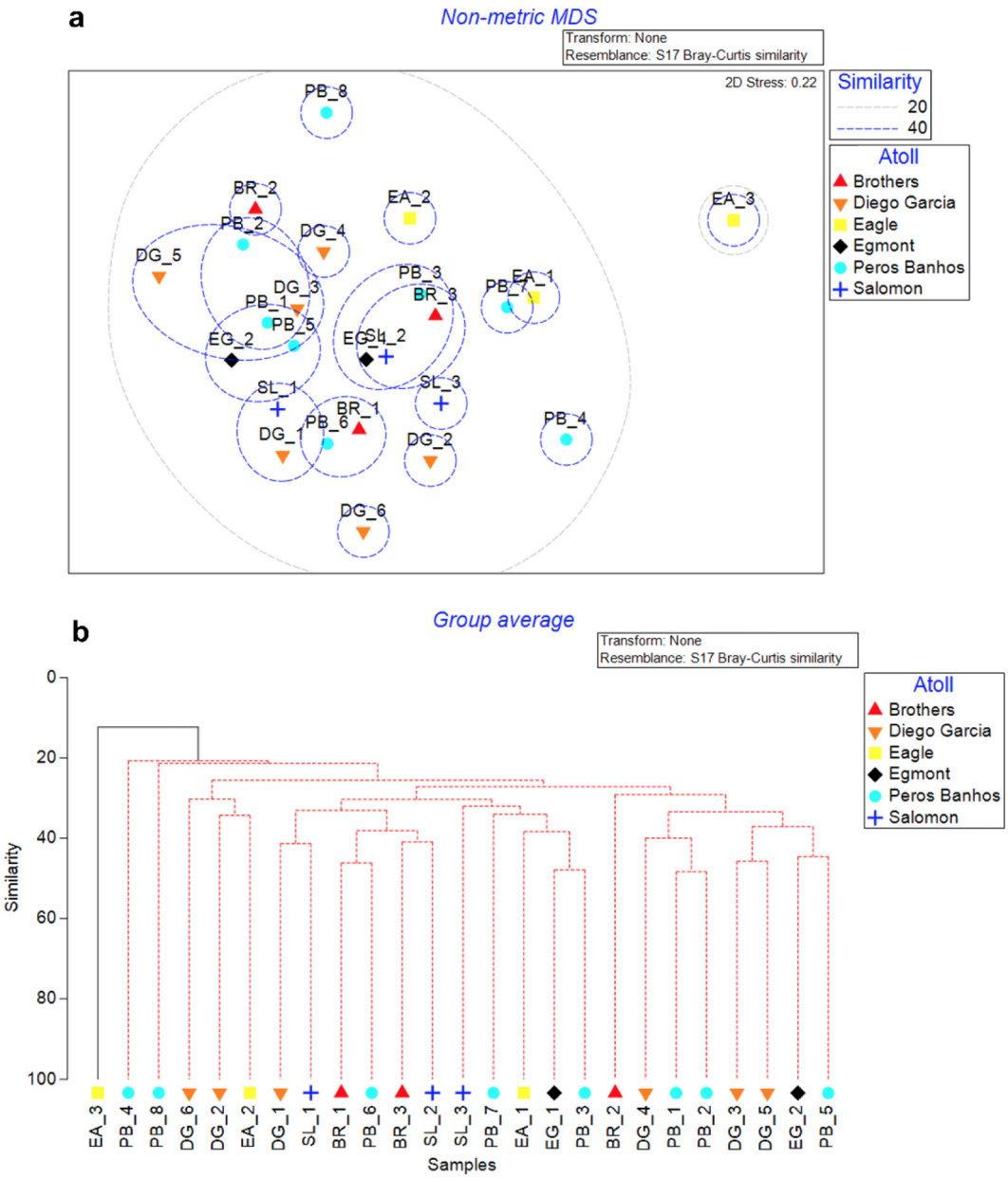

Fig. 6. (a) nMDS plot using Bray Curtis similarity illustrates the lack of community structure between the atolls/islands at a 20% similarity level. **(b)** The cluster diagram illustrates that only one site at Eagle Island was significantly dissimilar at a 20% similarity level supported by a SIM prof test.

1980; Vytopil and Willis, 2001; Leray et al., 2012). In this study the size of the coral colony was controlled to a certain extent by selecting colonies of approximately 20 cm in diameter, however, even small variations in coral colony size can affect cryptofauna abundances (Head et al., 2015), so this may have accounted for some variation in decapod abundances. It is also likely that decapod diversity is affected by the abundance and composition of the wider cryptofauna community on the dead coral colonies, e.g. molluscs, through predation, competition and other interspecific interactions. With crustaceans found in the diet of > 50% of reef fish, predation by invertivore fish species will also likely impact cryptofauna abundance. Quantitative dietary information, though essential to understanding reef trophic dynamics, is only just emerging for invertivore fish. Most notably a study by Kramer et al. (2015) found that wrasse (Labridae), a speciose and abundant reef fish family, over > 90 mm in length had a predominantly 'macro-crustacean' (i.e. Brachyura, Anomura, Caridea, Stomatopoda) diet consuming mostly Brachyura (40%).

In this study, Eagle Island had significantly lower mean species richness per coral colony then the other atolls and islands, and the island's mean abundance per coral colony and total estimated richness was also the lowest across the Archipelago. One site on the southern tip of Eagle Island also stands out in its community structure, because of the particularly low decapod richness and abundance on coral colonies at this site compared to all others. At the time of surveying the reefs around Eagle Island were suffering from a crown-of-thorns (COTs), *Acanthaster planci,* outbreak (Roche et al., 2015). Whilst only coral colonies that had been dead for months, if not years, were sampled (see sampling design) and therefore their mortality would not have been as a result of the current COTs outbreak, it is possible that such outbreaks have indirect effects on the local ecosystem potentially resulting in this low decapod diversity. There are reports of reduced diversity of live coral associates following COTs outbreaks (Leray et al., 2012), but the effect of COTs outbreaks on other cryptofauna communities is unknown.

Egmont Atoll consistently had the highest species richness and abundance per coral colony across the infraorders, except in Brachyura

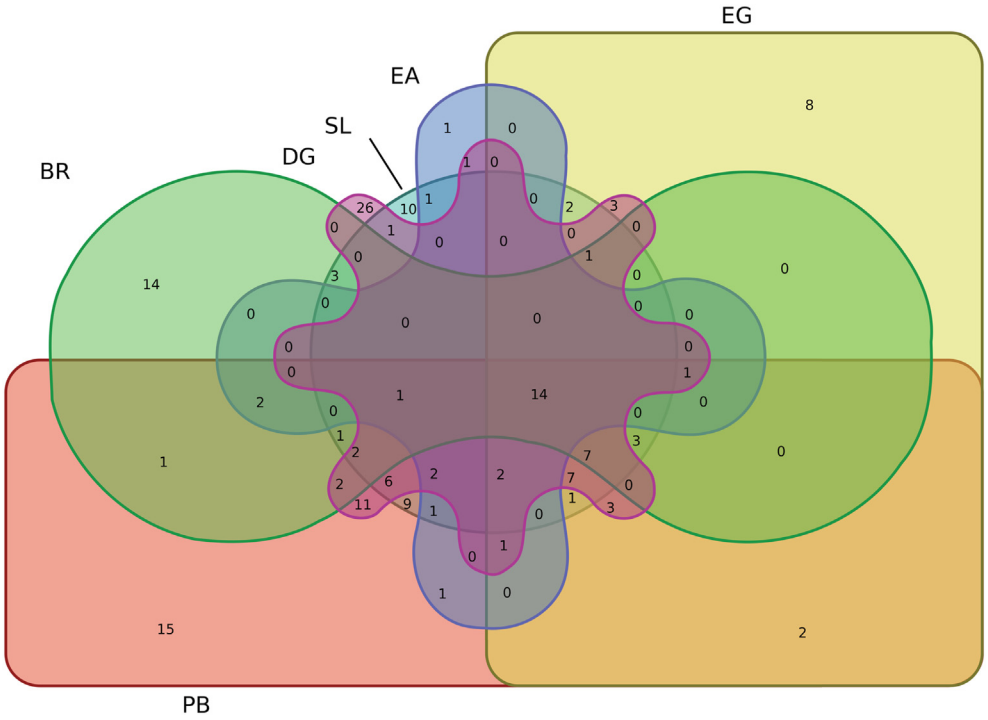

Fig. 7. Venn diagram illustrating the species overlap between atolls/islands in the Chagos Archipelago ($n = 54$). Atoll abbreviations: DG = Diego Garcia, EG = Egmont, PB = Peros Banhos, SL = Salomon, EA = Eagle Island, and BR = Brothers Islands.

Table 6
Bray-Curtis dissimilarity indices for each atoll/island across the Chagos Archipelago.

	Brothers Islands	Diego Garcia	Eagle Island	Egmont	Peros Banhos
Diego Garcia	0.60				
Eagle Island	0.65	0.73			
Egmont	0.61	0.46	0.6		
Peros Banhos	0.54	0.41	0.77	0.59	0.44
Salomon	0.52	0.49	0.69	0.56	0.53

abundance, though none were significant. Whilst, Peros Banhos Atoll and Diego Garcia Atoll had the highest total decapod species richness estimates of at least 119.75 ± 13.26 and 123.05 ± 12.68 (Chao1) species respectively. This is possibly because Peros Banhos Atoll and Diego Garcia Atoll are the largest atolls (not including the Great Chagos Bank) and therefore may have a higher habitat availability and diversity of niches promoting diversity. Diego Garcia Atoll also had the highest number of species (26 species) unique to a particular atoll across the Archipelago (Fig. 7). Diego Garcia Atoll is geographically the most isolated atoll, in terms of distance, within the archipelago (Fig. 1), which could result in higher levels of endemism. Very little is known about the ocean current patterns around the Archipelago, which would partially control dispersal of larvae and hence connectivity, except that the prevailing SEC current runs east to west and changes direction half way through the year (Obura, 2012). On live coral microhabitats, reef structural complexity has been found to be significantly positively correlated with crypotfauna diversity, whereas surrounding live coral cover, nor coral diversity were not (Idjadi and Edmunds, 2006). Reef structural complexity in Peros Banhos Atoll is the highest of all Chagos atolls, and it is significantly greater than on Diego Garcia Atoll's reefs, whilst structural complexity in Diego Garcia Atoll is lower than all other atolls (Graham et al., 2013). Therefore, structural complexity could account for Peros Banhos Atoll's high species richness but not Diego Garcia Atoll's. Structural complexity potentially needs to be investigated at a smaller spatial-scales surrounding the coral colonies sampled.

4.4. Comparisons with other reef fauna

Molluscs made up a large proportion of the remaining cryptofauna inhabiting the dead coral colonies in Chagos. The molluscs numbered 976 individuals, most of which were gastropods (820 individuals), with a species richness of 72 observed species (Head, 2015) compared to the 164 observed species of decapods and 1868 individuals. Therefore, decapods comprised more than double the species richness and abundance across the Archipelago than the gastropods. Panama's reefs demonstrated an opposing trend, with molluscs having a higher species richness than arthropods, at 132 to 77 OTUs respectively (Enochs and Manzello, 2012a).

The estimated fish species richness in Chagos is at least 784 species (Graham et al., 2013), this compares to at least 217 estimated decapod species from just one microhabitat, but the total decapod species richness across all microhabitats is likely much higher (Kramer et al., 2014). If decapod mean abundance per coral colony (20 cm diameter) of 32 individuals is scaled up to an estimate per m^2, and mean fish abundance per 500 m^2 (774 individuals per 500 m^2; Graham et al., 2013) is scaled down to per m^2, then a comparison can be made between mean decapod abundance and mean fish abundance (160 and 1.5 individuals per m^2, respectively) in Chagos. This demonstrates that the abundance of decapods on dead coral colonies is approximately two orders of magnitude greater than that of fishes. This difference in abundance is less than that estimated at Lizard Island, GBR, where Crustacea, pooled from all microhabitats, were found to be four orders of magnitude greater than that of fishes (Kramer et al., 2014). However, this measured all crustaceans and perhaps more importantly it included smaller size-classes of organisms than our study (we included organisms > 1 mm), and was therefore dominated by small crustacean taxa such as harpacticoid copepods, substantially increasing the abundance estimates, which likely explains the greater difference in crustacean and fish abundance estimates compared to Chagos. These crustacean/decapod biodiversity estimates demonstrate how important these

organisms are for coral reef ecosystems, yet they are rarely studied, especially compared to other components of the reef fauna such as fish.

Coral reefs worldwide are under immense anthropogenic pressures, which can alter reef biodiversity and structure, and often create more depauperate ecosystems (Hughes et al., 2010; Burke et al., 2011). The effects of anthropogenic stressors on the reef fish and coral assemblages are relatively well known (e.g. Mora et al., 2011b; McClanahan et al., 2014), especially in comparison to the effects on the cryptofaunal component. The Chagos reef ecosystem is one of the most resilient reefs globally, based on the ecosystem's recovery from the 1998 mass bleaching event (Sheppard et al., 2012), and one of the most removed from direct human impacts, including pollution, representing a reference site for biodiversity (Burke et al., 2011; Sheppard et al., 2012). Here we have shown greater decapod diversity, on one microhabitat in Chagos, than reported anywhere else to date. This biodiversity assessment can be used as a baseline against which to compare this component of biodiversity in other areas experiencing higher levels of anthropogenic stressors, at least in the Indian Ocean. However, biogeographical gradients in species richness across the Indian Ocean would also need to be taken into account when making such comparisons. This study also highlights the prominence of dead coral colonies as microhabitats for decapod diversity and the importance of corals in supporting diverse invertebrate fauna even after their death.

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Author contributions

CH, AR and HK conceived the ideas and designed methodology; CH, HK and MP collected the data; CH and TJ undertook specimen molecular processing; CH, TJ, MT and MB analysed the data; CH led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2018.07.063.

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