

High prevalence of obligate coral-dwelling decapods on dead corals in the Chagos Archipelago, central Indian Ocean

Catherine E. I. Head^{1,2,5}  · Michael B. Bonsall^{1,4} · Heather Koldewey² · Morgan S. Pratchett³ · Martin Speight¹ · Alex D. Rogers¹

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Abstract Small and cryptic organisms that live within the interstices of reef habitats contribute greatly to coral reef biodiversity, but are poorly studied. Many species of cryptofauna have seemingly obligate associations with live coral and are therefore considered to be very vulnerable to coral mortality. Here we report the unanticipated prevalence of obligate coral-dwelling decapod crustaceans on dead colonies of branching corals in the Chagos Archipelago (British Indian Ocean Territory) in the central Indian Ocean. A total of 205 obligate coral-dwelling decapods, including *Trapezia* crabs, were recorded from 43 (out of 54) dead coral colonies of *Acropora* and *Pocillopora* collected across five different atolls. *Trapezia* individuals found on dead corals were mainly juveniles, and the few adults were almost exclusively male. Among the shrimps (Pontoniinae), however, it was predominantly adult females found on dead corals. Obligate coral-dwelling

species that typically occur only on live *Pocillopora* hosts (e.g., *Trapezia* spp.) were recorded on dead *Acropora*. These findings suggest that these obligate coral-dwelling decapods are not simply persisting on coral hosts that have died, but may be explicitly recruiting to or moving to dead coral hosts at certain stages in their life cycle. Variation in the abundance of live coral among sites had no effect on the presence or abundance of obligate coral-dwelling decapods on dead corals. This study shows that habitat associations of obligate coral-dwelling organisms, and their reliance on different habitat types, are complex and further work is required to establish their vulnerability to widespread habitat degradation on coral reefs.

Keywords Coral obligates · Dead coral · Chagos Archipelago

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✉ Catherine E. I. Head
catherine.head@zoo.ox.ac.uk

¹ Department of Zoology, University of Oxford, The Tinbergen Building, South Parks Road, Oxford OX1 3PS, UK

² Conservation Programmes, Zoological Society of London, Regents Park, London NW1 4RY, UK

³ ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

⁴ St Peter's College, New Inn Hall Street, Oxford OX1 2DL, UK

⁵ Linacre College, St Cross Road, Oxford OX1 3JA, UK

Introduction

Coral reefs exhibit extremely high levels of biodiversity with estimated species richness ranging from 172,000 to over nine million species worldwide (Reaka-Kudla 1997; Small et al. 1998; Ruppert et al. 2004). The contributions of conspicuous and well-studied taxa, such as scleractinian corals (Veron 2000) and reef fishes (Lieske and Myers 1994), to coral reef biodiversity are minimal. Rather, the vast majority of species living on coral reefs are small, cryptic invertebrate species that live within the interstices of coral reef habitats (Reaka-Kudla 1997). Many of these invertebrates have evolved to form close symbiotic associations with corals, particularly branching Scleractinia, which provide food (mostly, in the form of coral mucus and associated detritus), as well as a physical refuge from predators (Castro 1988; Stella et al. 2011a). In return,

corals often benefit from the presence of coral-dwelling invertebrates. For instance, obligate coral-dwelling crabs of the family Trapeziidae actively defend their coral hosts against corallivores, e.g., *Acanthaster planci* (Glynn 1982; Pratchett et al. 2000; Pratchett 2001; McKeon and Moore 2014), as well as removing excess sediment in turbid conditions which may otherwise smother the coral (Stewart et al. 2006, 2013).

Coral-dwelling invertebrates are generally divided into those that have obligate versus facultative associations with live coral hosts (Castro 1976; Stella et al. 2011a). Obligate coral-dwelling invertebrates are defined as those that are almost universally found on live coral colonies (Stella et al. 2011a), inferring that they have strong reliance on live corals for food, habitat, and/or recruitment. Most obligate coral-dwelling invertebrates also exhibit very specific host coral preferences and are generally associated with either *Acropora* or *Pocillopora* corals (e.g., Bruce 1998; Pratchett 2001; Stella et al. 2011a). Meanwhile, facultative coral-dwelling invertebrates opportunistically inhabit live coral colonies as one of the predominant structural microhabitats available within reef systems, but are not considered to be fundamentally dependent upon abundant live coral for their local persistence (Castro 1976; Stella et al. 2011a). Stella et al. (2011a) reported that 56 % of coral-dwelling invertebrates appeared to have an obligate reliance on live corals, largely because these species had not been recorded outside of live coral habitats. This suggests that these species, at least 487 species (collated by Stella et al. 2011a), would be extremely vulnerable to increasing coral loss (e.g., Burke et al. 2011), though few studies have explicitly tested their responses to localised coral loss, or explicitly tested occupation rates on recently dead (but intact) coral heads (But see Coles 1980; Tsuchiya 1999; Leray et al. 2012). Perhaps the best indication we have of the impact of reef condition on the live coral cryptofaunal communities is a study by Idjadi and Edmunds (2006) who showed positive significant relationships for reef topography with the diversity of live coral associates, but this was not the case for coral diversity and live coral cover.

Dead coral microhabitats have a different community structure of purely facultative species that tend to be smaller in body size (Coles 1980; Leray et al. 2012), though the occasional observations of obligate species on dead corals have been reported (Preston and Doherty 1990; Stella et al. 2011b). Motile cryptofaunal species diversity estimates have been shown to be much higher on dead coral than on live coral microhabitats across a range of geographical regions (Patton 1994; Plaisance et al. 2009; Enochs and Manzello 2012). Dead corals are also thought to be the most important microhabitats for crustacean abundance, biomass, and productivity (Kramer et al. 2014). Pronounced differences in crustacean community structure

patterns have been shown on similar microhabitats between different parts of the reef, e.g., lagoonal, reef slope, and reef flat (Peyrot-Clausade 1989; Plaisance et al. 2011), as well as across the reef shelf (Klumpp et al. 1988; Preston and Doherty 1990). Coral colony size, complexity, and surface area of dead and live coral microhabitats have consistently been positively correlated with species richness and abundance of their decapod communities (Abele and Patton 1976; Coles 1980; Leray et al. 2012).

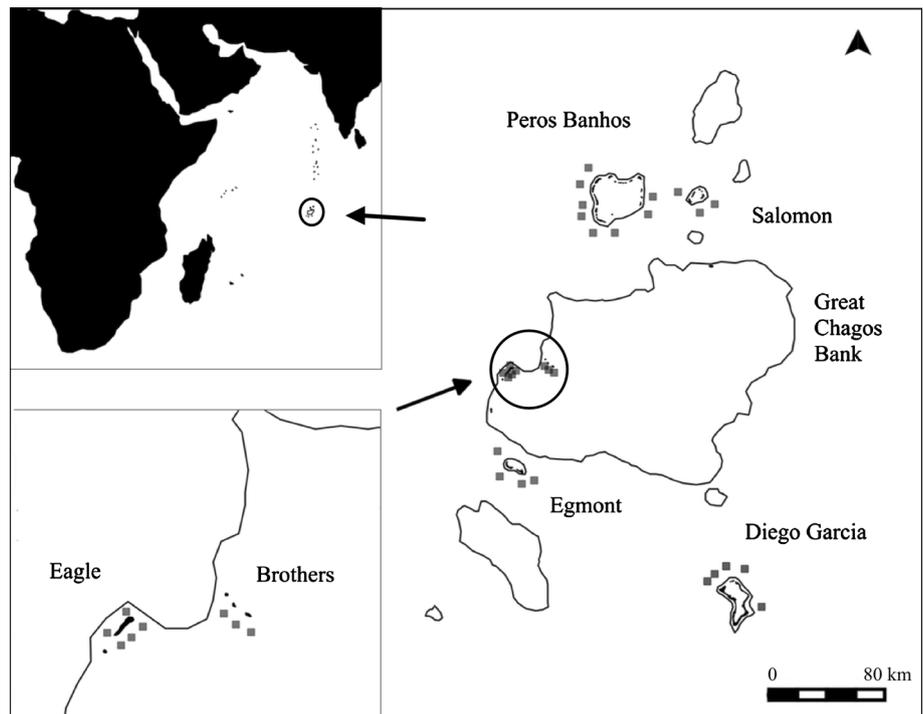
In this study, we report on the unanticipated abundance of obligate coral-dwelling decapod species on dead colonies of *Acropora* and *Pocillopora* in the Chagos Archipelago. Dead coral colonies (e.g., Electronic Supplementary Materials, ESM, Fig. S1a, b) were collected from five different atolls in the Chagos Archipelago in order to explore patterns of biodiversity within this habitat type (e.g., Plaisance et al. 2009). We did not, however, expect to find large numbers of decapod crustaceans that have been widely reported to occur only on live coral hosts (Castro 1976; Stella et al. 2011a). We refer to the live coral obligates reported here as ‘obligate coral-dwelling’ decapods as we found these individuals on dead coral, and hence it is unclear whether these organisms are completely dependent on live coral throughout their life cycle. This study investigates the abundance, habitat associations, size, life-history stage, and gender of *Trapezia* crabs and shrimps from the sub-family Pontoninae, the only live obligate taxa found on the dead corals. One possibility is that these obligate coral-dwelling species are simply persisting for a period of time on established coral hosts following host coral mortality, in which case, we would expect to find relatively large, mature individuals continuing to live on preferred coral hosts. Alternatively, dead corals may represent marginal habitats that are only used in the absence of suitable live coral hosts, in which case the occupation of dead corals would be highest in areas with low abundance of suitable live coral hosts. Testing these hypotheses is potentially very important to understand the biological reasons for this spillover to dead coral microhabitats and whether these microhabitats may have a poorly known functional role in the life cycles of these species.

Materials and methods

Study site

Data were collected from the Chagos Archipelago during the 2012 Chagos Scientific Expedition (Fig. 1). The Chagos Archipelago (British Indian Ocean Territory) is isolated from major anthropogenic disturbances (e.g., sedimentation and pollution) affecting most reefs throughout the world (Burke et al. 2011; Sheppard et al.

Fig. 1 Chagos Archipelago; grey squares represent the 28 sites where dead coral colonies were collected. A close-up of Eagle and Brothers Islands (part of the Great Chagos Bank) in the bottom left corner shows the distribution of the eight sites at these two islands



2012) and are a biographically important ‘stepping-stone’ connecting reefs in the Western Indian Ocean to the highly diverse coral triangle (Sheppard et al. 2012; Fig. 1).

Sampling design

Dead branching coral colonies of approximately 20 cm in diameter were collected from 28 sites across the Chagos Archipelago at Diego Garcia Atoll, Peros Banhos Atoll, Salomon Atoll, Eagle and Brothers Islands of the Great Chagos Bank, and Egmont Atoll (Fig. 1). Sites were separated by at least 250 m and located on the outer reef. At each site, 2–4 individual dead *Acropora* or *Pocillopora* coral colonies were collected from between 8 and 12 m depths. Coral colonies were defined as being dead if they had no observable polyps, evidence of turf and crustose coralline algae, and sometimes erosion (e.g., ESM Fig. S1a, b). Benthic transects were undertaken in a cross-formation, 10 m × 10 m, with the dead coral colony located at the centre, to enable percentage coral cover estimates within a 5-m radius of the dead coral colony. Photographs (using a Olympus Xz-1 digital camera) were taken every 0.5 m along the transect using a fixed camera frame to keep the camera a standard 1 m above the reef.

Sample collection

Prior to collection, coral colonies were enclosed within a water-tight (250 Micron gauge) polythene bag to contain

all motile fauna. Colonies were then chiselled and/or prised from the reef substrate ensuring minimal disruption to their physical integrity; colonies that did break apart or crumble during the collection process were abandoned. Care was taken to ensure that there were no living corals or other large sessile fauna (e.g., sponges) attached to the coral head. Once detached from the reef, colonies were completely enclosed in the bag for transport. Colonies were enclosed in individual bags for up to 2 h prior to processing.

All cryptofauna were removed and sorted first by immersing the coral colony in a bucket of freshwater for approximately 1 min, following Stella et al. (2010), and then passing the water through a 1-mm sieve. The seawater in which the coral colonies were stored and transported was also sieved. All specimens were recorded and preserved in 90 % ethanol for transport. Selected fauna for which colour patterns are known to be useful in identification, such as the Alpheidae, were photographed before preservation in ethanol. The coral colony was also placed in a full bucket of seawater, and the displaced seawater was measured to calculate volume as a proxy for coral colony size. Finally, the coral colony was inspected and carefully broken up, using a hammer and chisel to collect any remaining hidden fauna.

Of the cryptofauna collected, we chose to focus on the crustaceans, as these were the most abundant taxa, alongside the molluscs, inhabiting the dead coral microhabitats. These taxa were further sorted into morphotypes and then identified to the lowest taxonomic level possible using

standard morphological characteristics. Within the crustacean taxa, all live coral obligates observed were within the Trapeziidae family and Pontoniinae sub-family (Bruce 1969, 1998, 2004; Castro et al. 2004). Special care was then taken to identify these live coral obligates to the lowest taxonomic level possible (Castro et al. 2004; S. de Grave pers comm). In most cases, it was possible to identify these obligates to species, but for a few individuals only genus level identification was possible (see “Results”). For each of these individuals, body size, life stage, and gender were also recorded. Carapace width for *Trapezia* crabs and carapace length for the Pontoniinae were used as standardised proxies for body size (Anger and Moreira 1998). Pontoniinae carapace length was measured under a graduated microscope lens as the linear length of the carapace from the posterior of the orbital cavity to the most posterior tip of the carapace (Anger and Moreira 1998), and for *Trapezia* crabs the linear maximum carapace width was measured. The life-history stage of an individual was classified as adult or juvenile by determining whether or not the individual had fully developed sex organs. If the individual had fully developed sex organs, its gender was recorded.

Data analysis

Rank abundance models were fitted to explore patterns of abundance for obligate coral-dwelling species within the Archipelago. Comparisons of rank abundance models were made using Chi-squared goodness-of-fit tests (χ^2). Rarefied species richness was calculated to compare species richness with uneven sample sizes (number of dead coral colonies collected) between atolls. Rarefaction corrects for bias in species number resulting from unequal sample sizes by standardisation to the number of species expected in a sample if it had the same total size as the smallest sample (Magurran and McGill 2011). Shannon–Weaver Diversity Index, Simpson Diversity Index, and Pielou’s Evenness Coefficient were all calculated for the Archipelago and individually for all six atolls and islands. Species diversity indices were analysed in Species Diversity and Richness IV (Seaby and Henderson 2006). Benthic photo-transects were analysed using Coral Point Count (CPC) software (Kohler and Gill 2006). Ten points were randomly assigned to each photograph, and the benthic cover beneath that point was recorded. From this dataset, live branching *Acropora* and *Pocillopora* species counts were combined and percentage cover calculated for use in this analysis. All other analyses were undertaken in R (R Development Core Team 2008). A binomial test was used to test the hypothesis that the probability of coral obligates present on dead coral colonies was significantly greater than the absence. Sign tests were used to investigate the probability of each decapod

obligate species being present on dead *Acropora* versus dead *Pocillopora* colonies. Chi-squared goodness-of-fit tests (χ^2) were used to determine whether a certain life-history stage and/or gender predominated in the obligate coral-dwelling assemblages.

Generalised linear models (GLMs) were used to describe presence and absence, abundance, body size, life-history stage, and gender of the obligate coral-dwellers, and to relate these indices and traits to at least two of the following environmental predictor variables: percentage local live branching coral cover (data were first arc-sine transformed), genera of the dead coral colony, biogeography (atoll location), and niche structure of the coral colony habitat using volume of the coral colony as a proxy (coral colony size). It should be noted that coral colonies of approximately 20 cm diameter were collected, but inevitably there was still some variation in coral colony size, and therefore, this was included as an environmental variable in the statistical analysis. Because of the binomial nature of the dependent variables of presence/absence, life-history stage, and gender of obligate coral-dwellers, the logit-link function and binomial family function were used in these models. For the dependent variable of obligate coral-dweller abundance, the log-link function and Poisson family function were used. Finally, for the mean body size model, the Gaussian family function and identity-link function were used. A series of GLMs were fitted for each dependent variable to the appropriate predictor variables and their interactions and then simplified. Model significance was assessed using *F*-values or χ^2 values depending on the nature of the dependent variable. All models that demonstrated over- or under-dispersion (residual deviance higher/lower than degrees of freedom) were fitted with the quasi-family function to introduce a dispersion parameter and obtain a quasi-likelihood estimate (Crawley 2005).

Results

Prevalence and diversity of obligate coral-dwellers

Obligate coral-dwelling decapods were present on 43 of the 54 dead coral colonies collected from across the Archipelago. There was a significant probability (0.80) of an obligate coral-dweller occurring on a dead coral colony (95 % CI 0.66–0.89, $p < 0.01$). The Pontoniinae shrimp and *Trapezia* crabs were found on 59 % (32 of the 54) and 62 % (34 of the 54) dead coral colonies, respectively.

Two-hundred and five obligate coral-dwelling decapod individuals from seven identified species were recorded across 43 of the 54 dead coral colonies sampled during this study, including two species of *Trapezia* and five species of shrimps from the sub-family Pontoniinae (Fig. 2). In

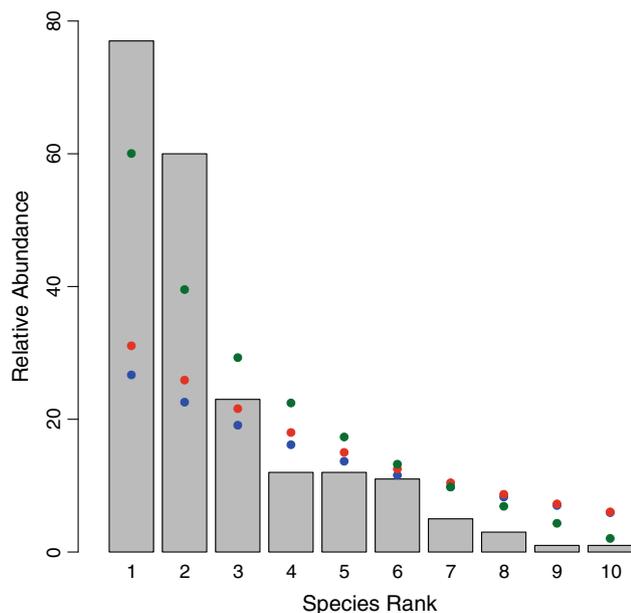


Fig. 2 Fits of broken stick (green points), geometric (blue points), and exponential (red points) to the relative abundance of ten species groups across the Chagos Archipelago. Species ranks are: (1) *Trapezia* spp. (juveniles), (2) *Jocaste lucina*, (3) *Harpiliopsis spinigera*, (4, 5) *Harpiliopsis* spp. and *Jocaste japonica*, (6) *Trapezia tigrina*, (7) *Harpilius* spp., (8) *Harpiliopsis depressa*, and (9, 10) *Coralliocaris graminea* and *Trapezia bidentata*

addition, there was a high abundance of *Trapezia* juveniles (*Trapezia* spp.) that could not be identified to species and some Pontoninae shrimp from the *Harpiliopsis* and *Harpilius* genera (*Harpiliopsis* spp. and *Harpilius* spp.) that could not be identified to species, as the individuals were juveniles or because of damage to the samples. Therefore, for all following analyses, the obligate coral-dwellers observed were categorised into ten taxa (seven identified to species level, plus three taxa identified to genus: *Trapezia* spp., *Harpiliopsis* spp., and *Harpilius* spp.). *Trapezia* spp. (juveniles) and a shrimp species, *Jocaste lucina*, were the dominant taxa accounting for 77 and 60 individuals, respectively (Fig. 2). Many of the taxa occurred rarely in the samples, with *Coralliocaris graminea* and *Trapezia bidentata* each found only once (Fig. 2). These eight obligate coral-dwelling decapod taxa (seven species and *Harpilius* spp., as no *Harpilius* species were otherwise identified) comprised 6.5 % of the decapod species identified on the 54 dead coral colonies, and they comprised approximately 11 % of all decapod individuals present.

All models fitted to the rank abundance data (Fig. 2) were statistically different from the data (broken stick model $\chi^2 = 31.27$ with 9df, $p < 0.001$; geometric model $\chi^2 = 173.95$ with 9df, $p < 0.001$; exponential model $\chi^2 = 131.79$ with 9df, $p < 0.001$), which demonstrates the

high heterogeneity within the coral-dwelling obligate assemblage on dead corals.

Habitat associations and specialisation

The prevalence and abundance of obligate coral-dwellers on dead *Acropora* versus dead *Pocillopora* colonies differed for each taxa. There was a significantly higher probability (0.86) of finding *Trapezia* spp. (juveniles), which are considered live *Pocillopora* obligates (Castro 1976; Castro et al. 2004), on dead *Acropora* rather than dead *Pocillopora* colonies (95 % CI 0.76–0.93, $p < 0.01$). Other live *Pocillopora* specialists found on dead *Acropora* were *Trapezia tigrina*, *Harpilius* spp., *Harpiliopsis spinigera*, and *Harpiliopsis* spp., whilst *Harpiliopsis depressa* and *T. bidentata* were found exclusively on dead *Pocillopora* colonies. Of the three live *Acropora* obligates, two species, *Jocaste japonica* and *C. graminea*, were found exclusively on dead *Acropora* colonies, whilst there was a significantly higher probability (0.80) of finding *J. lucina* on dead *Acropora* than on dead *Pocillopora* (95 % CI 0.68–0.89, $p < 0.01$).

Local live branching coral cover

The obligate coral-dweller prevalence model showed no significant affect of live branching coral cover (from within a 5-m radius of the dead coral colony) on obligate presence across any of the atolls. The total obligate coral-dweller assemblage showed over-dispersion (*dispersion parameters* = 1.14), suggesting that other ecological processes are driving the obligate coral-dwellers presence on dead coral colonies. Similarly, local live branching coral abundance had no affect and showed over-dispersion (*dispersion parameters* = 4.59).

Dead coral colony size

There was a significant positive effect of coral colony size on total obligate coral-dweller abundance ($F = 4.09$, $p = 0.048$). However, coral colony size only explained 9.3 % of the variation, and large over-dispersion in the model (*dispersion parameter* = 4.16) also suggested variation in obligate coral-dweller abundance that was not explained by coral colony size or biogeography. Brothers had the highest abundance, at six obligates coral-dwellers per coral colony, and Eagle had the lowest, at 2.2 per coral colony (Table 1). However, the total obligate coral-dweller abundance model showed no significant difference in abundance between any of the atolls or islands. Brothers and Eagle are geographically the closest but still at least 20 km apart (Fig. 1). Both islands are part of a large atoll called the Great Chagos Bank (Fig. 1), so Eagle and

Table 1 Biodiversity indices for the Chagos Archipelago overall and for the six surveyed atolls and islands

Location	Total <i>N</i>	Mean <i>N</i> ± se	Rarefied <i>d</i> ± se	<i>H'</i>	<i>l</i> − <i>λ</i>	<i>J'</i>
Brothers	36	6.00 ± 9.17	5.56 ± 0.88	0.62	0.49	0.45
Diego Garcia	51	4.64 ± 4.64	4.85 ± 1.04	0.54	0.41	0.49
Eagle	13	2.17 ± 2.32	4.83 ± 0.39	0.42	0.59	0.45
Egmont	15	3.75 ± 4.11	5.72 ± 0.49	0.71	0.62	0.48
Peros Banhos	57	3.56 ± 2.99	3.85 ± 0.90	0.46	0.54	0.51
Salomon	33	3.00 ± 3.00	4.55 ± 0.89	0.43	0.36	0.43
Chagos Archipelago	205	3.80 ± 4.80	4.97 ± 1.15	0.50	0.50	0.72

Indices include: total abundance of obligates (Total *N*), mean abundance of obligates with standard error (Mean *N* ± se), rarefied species richness with standard error (Rarefied *d* ± se), Shannon–Weaver diversity index (*H'*), Simpson's diversity index (*l* − *λ*), and Pielou's species evenness coefficient (*J'*). All indices are measures per dead coral colony, except Total *N* that measures the species abundance per atoll

Brothers were first considered separately and then combined in a second model to reflect the Great Chagos Bank. This showed no change in the non-significance of atoll effect on obligate abundance.

Pontoniinae shrimp obligate abundance also had a significant positive relationship with coral colony size ($F = 4.85$, $p = 0.03$), which explained 9.68 % of the variation in abundance. *Trapezia* obligate abundance increased with coral colony size, but this relationship was not significant, suggesting that the Pontoniinae obligate assemblage drives the overall affect of coral colony size on total obligate abundance. Large over-dispersion in the *Trapezia* (dispersion parameter = 2.44) and Pontoniinae (dispersion parameter = 3.50) obligate abundance models suggest that there was variation in both assemblages not explained by either environmental parameters tested.

Body size

The majority of obligate coral-dwellers had a carapace length of between 1 mm and 4 mm (Fig. 3a, b). Carapace length was used as a standardised measure of body size (see “Materials and methods” section). The mean obligate coral-dwellers body size was highest at Brothers and smallest at Eagle (Fig. 3a). However, there was no significant relationship between obligates' mean body size and reef location, or coral colony size (see ESM and Fig. S2 for further analysis). The data were over-dispersed (dispersion parameter = 2.66), indicating that variation in body size is controlled by other environmental factors (e.g., food source availability).

Life-history stage and gender

Chi-squared goodness-of-fit tests demonstrated that there were significantly more adults than juveniles in the obligate coral-dwellers assemblage (Table 2). This trend was clearly driven by the larger Pontoniinae shrimp obligate

assemblage, which had significantly more adults than juveniles (Table 2). In contrast, the *Trapezia* obligate assemblage had significantly more juveniles than adults (Table 2; ESM and Fig. S3). The largest difference in the proportion of total obligate adults and juveniles occurred at Eagle with the lowest difference at Diego Garcia (Fig. 3c). Coral colony size had no significant affect on the proportions of the two life stages (Fig. 3d).

It is only possible to accurately sex adult decapods; therefore, only the adults were included in the gender analysis. Chi-squared goodness-of-fit test showed that there were significantly more female than male decapods; this was driven by the larger assemblage of Pontoniinae shrimp obligates which also had a significantly higher female to male ratio (Table 2). In contrast, the *Trapezia* assemblage had a significantly higher male-to-female ratio (Table 2), but were dominated by juveniles so the adult assemblage for which gender could be determined was very small and comprised of only two species, *T. tigrina* and *T. bidentata* (Fig. 2).

Across Chagos, neither coral colony size nor biogeography was a driver of the proportion of females to males in the total obligate assemblage (Fig. 3e, f). However, at the local assemblage level, Eagle did have a significantly higher proportion of females to males compared to other locations ($t = 2.05$, $p = 0.04$). Diego Garcia and Peros Banhos also had a much higher proportion of females to males, but this was not significant (Fig. 3e; also see ESM and Fig. S4 for further analysis).

Discussion

This study revealed an unanticipated prevalence of obligate coral-dwelling decapods on dead coral colonies within the Chagos Archipelago. All ten decapod taxa considered in this study are widely regarded as ‘live coral-dwelling obligate species’ with strong host specificity for either *Pocillopora* or *Acropora* corals; *T. bidentata* (Castro et al.

Fig. 3 Mean body sizes (mm) of the total coral obligates assemblage **a** at each atoll or island regardless of coral colony size and **b** on coral colonies of varying sizes separated by atoll or island location. Abundance of juveniles versus adults in the total coral obligate assemblage **c** at each atoll or island location and **d** on coral colonies of varying sizes. Abundance of males versus females in the total coral obligate assemblage **e** at each atoll or island location and **f** on coral colonies of varying sizes. Atoll legend: *BR* Brothers, *DG* Diego Garcia, *EA* Eagle, *EG* Egmont, *PB* Peros Banhos, *SL* Salomon

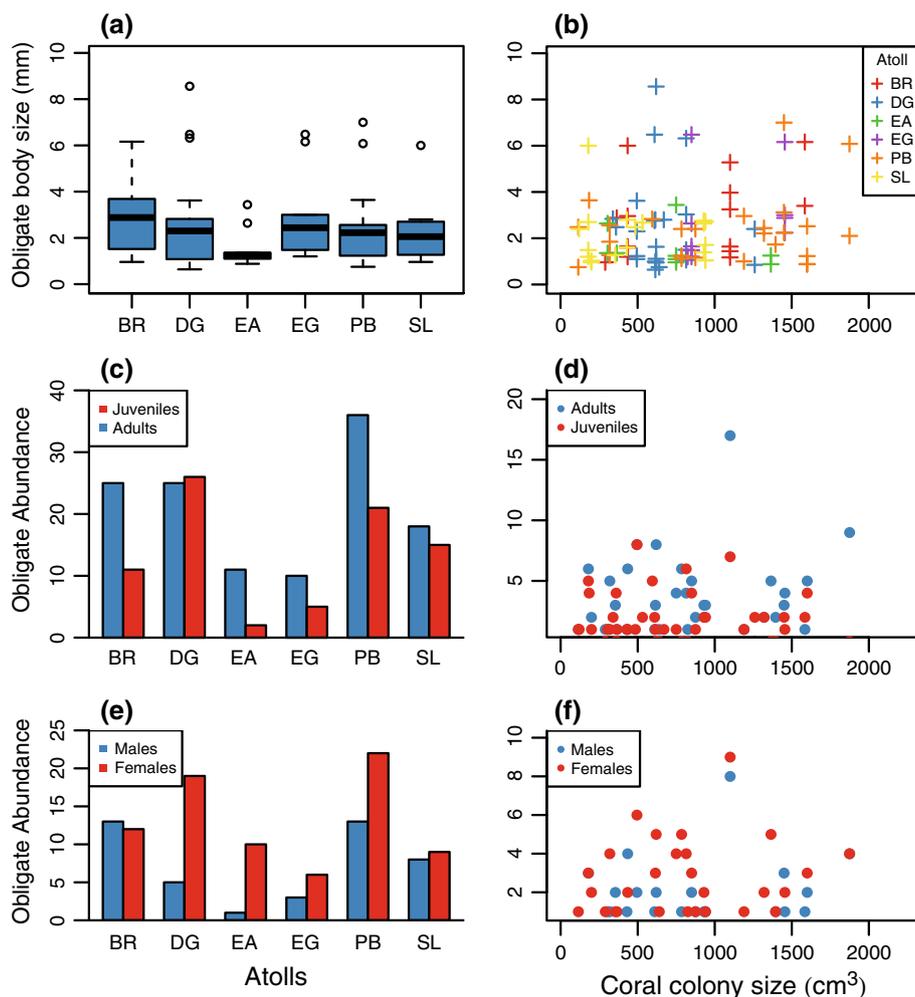


Table 2 Chi-squared goodness-of-fit values (χ^2) and abundance of (a) adults and juveniles in: the total coral obligate assemblage, the *Trapezia* obligate assemblage, and the Pontoniinae shrimp obligate assemblage, (b) the abundance of males and females (adults only) in: the total coral obligate assemblage, the *Trapezia* obligate assemblage, and the Pontoniinae shrimp obligate assemblage (gender could not be identified for four shrimp species)

	Abundance		χ^2	p value
(a) Life stage	Adults	Juveniles		
Coral obligates	125	80	9.88	0.001
<i>Trapezia</i> obligates	12	77	47.47	5.58e ⁻¹²
Shrimp obligates	113	3	9.88	0.001
(b) Gender	Males	Females		
Coral obligates	43	78	10.12	0.001
<i>Trapezia</i> obligates	10	2	5.33	0.02
Shrimp obligates	33	76	16.96	3.81e ⁻⁰⁵

2004), *T. trigrina* (Castro et al. 2004), *Trapezia* spp. (juveniles) (Castro et al. 2004), *H. depressa* (Bruce 1998), *Harpilius* spp. (Bruce 2004), *C. graminea* (Bruce 1998;

Vytopil and Willis 2001), *J. lucina* (Bruce 1969; Patton 1994), *J. japonica* (Bruce 1969; Patton 1994), *Harpiliopsis* spp. (Bruce 1998), and *H. spinigera* (Abele and Patton 1976; Bruce 1998). *C. graminea*, *J. lucina*, and *J. japonica* are all considered to be live *Acropora* obligates (Bruce 1969, 1998; Vytopil and Willis 2001). The other five species are regarded as live *Pocillopora* obligates (Bruce 2004; Castro et al. 2004), though both *H. spinigera* and *H. depressa* have also been observed on live *Stylophora* (Edwards and Emberton 1980; Stella et al. 2011a). To the best of our knowledge, there have been only two other recorded observations of obligate coral-dwelling decapods on dead coral hosts, specifically *Trapezia cymodoce* (Stella et al. 2011b) and *H. depressa* (Preston and Doherty 1990), both on *Pocillopora* on the Great Barrier Reef (GBR). The observations of *H. depressa* were relatively rare comprising less than 1 % of the agile shrimp population (Preston and Doherty 1990). In the case of *T. cymodoce*, the observation was made in the weeks immediately following a major coral mortality event, and of the 20 bleached colonies, 14 retained both individuals of their *T. cymodoce*

pairs (Stella et al. 2011b). Chagos has been subject to major bleaching events leading to substantial coral mortality in the past, most notably in 1998 (Sheppard 1999; Sheppard et al. 2002), but no mass coral mortality events have been recorded since (Sheppard et al. 2012).

This study observed a mean species richness of 4.97 obligate coral-dweller species ($se \pm 1.15$) per dead coral colony (with a mean volume of 764 cm^3 , and a mean abundance of 3.8 individuals but with large variation between coral colonies ($se \pm 4.80$; Table 1). Patton (1994) reported a mean of 4.5 obligate coral-dweller species and abundances of 9.1 on live *Acropora* colonies on the GBR, with a larger mean volume of 4900 cm^3 in comparison with this study, whilst Abele and Patton (1976) reported nine species (cumulative species number) on live *Pocillopora* colonies of approximately 1500 cm^3 size in the Gulf of Panama. However, it is not possible to make direct comparisons of obligate coral-dweller diversity found here with the above records from live coral colonies due to differences in geographical location, coral colony sizes, host colony genera and species, and coral complexity, which are all known to affect the associated species inhabiting live coral and their diversity (e.g., Abele and Patton 1976; Vytopil and Willis 2001).

The high prevalence of obligate coral-dwelling decapods on dead but intact corals in Chagos is hard to explain, especially given limited knowledge about the life history and ecology of these organisms. It seems plausible that at least some of these individuals and species have persisted since these coral colonies actually died. However, based on extensive growth of both turf and crustose coralline algae (CCA) on all colonies (ESM Fig. S1), it appears likely that the corals surveyed in this study had been dead for at least several months (if not years) and there have been no reports of coral infauna persisting this long following host coral mortality. Stella et al. (2011b) found that some *Trapezia* remained with original host colonies for at least 5 weeks following bleaching, although their fitness was adversely affected as fecundity levels were reduced. Our results also show that the host specificity of these coral-dwelling obligates for *Acropora* or *Pocillopora* does not always hold on the dead coral colonies and depends on the species. Most notably, *Trapezia* spp., which are normally found exclusively on *Pocillopora* colonies (Castro 1976; Castro et al. 2004), were significantly more prevalent on dead *Acropora* versus dead *Pocillopora* colonies. This may be because of the small size of the *Trapezia* juveniles making them more vulnerable to predation, so the generally more complex branching structure of dead *Acropora* colonies likely affords them higher protection (Vytopil and Willis 2001). This was also the case for *Harpilius* spp., *Harpiliopsis* spp., and *H. spinigera*. These observations suggest that these organisms are not simply persisting on host corals with

which they established strong affinities before they died. Rather, it appears that many of the coral-dwelling species recorded in this study had actively recruited to dead coral hosts. Many of the dead coral colonies in our study were in very close proximity to live branching coral (ESM Fig. S1c); hence, it is possible that the adult obligate coral-dwellers were moving between live versus dead coral hosts. *Trapezia* spp., for example, are fiercely territorial (Stewart et al. 2013), but have been known to move among coral colonies at night possibly to secure a larger, healthier colony or secure a mate (Castro 1978; Stella et al. 2011b). Where live coral colonies are fully saturated with these cryptofaunal species, there may be temporary or recurrent spillover to nearby dead corals. However, further research will need to be conducted to test for movement between live and dead coral microhabitats, as well as testing for differences in individual fitness of organisms occupying these different habitats.

The occurrence of significant sex bias in the Pontoninae shrimps and in the *Trapezia* suggests that subordinate individuals may be forced to occupy sub-optimal habitats over the course of their life cycle. If so, this would emphasise the importance of the mosaic of habitats on healthy reef ecosystems. Juveniles were significantly more abundant than adults in the *Trapezia* assemblage, suggesting that dead coral colonies may be acting as an essential or preferred habitat for *Trapezia* juveniles, potentially as a refuge from the highly territorial adults. In live coral colonies, *Trapezia* juveniles have predominantly been found inhabiting the dead base of the colony (Abele and Patton 1976; Castro 1976) possibly for better protection from predators, or as the result of competition by the larger adult pairs that prefer the live tissue.

Stomach content analysis of *Trapezia* collected from live coral hosts has revealed that they feed predominantly on coral mucus and some coral tissue, as well as various detrital particles (Knudsen 1967; Preston 1973; Patton 1974; Castro 1976; Rotjan and Lewis 2008) presumed to be ingested within coral mucus (Gerlach 1960; Castro 1976). Strong dependence on corals for food has been the central basis of the tenet that *Trapezia* will be extremely vulnerable to coral loss (e.g., Stella et al. 2011a). However, it is known that *Trapezia*, as well as *Coralliocaris* and *Jocaste* species at least, can utilise additional food sources as they have been observed consuming zooplankton (Patton 1994), and all of these species have appendages well developed for suspension feeding (Bruce 1976). Nonetheless, the lack of preferred food resources on dead coral microhabitats may cause these obligates to become nutritionally starved in the longer term, thereby affecting their individual fitness (e.g., Stella et al. 2011b).

The abundance of live *Pocillopora* colonies has been reported to be the major limiting factor for populations of

Trapezia at most reef locations (Castro 1978; Stella et al. 2011b) with high levels of occupation across suitable coral hosts and strong competition among individuals and species for preferred corals. For example, Stewart et al. (2006) observed 95 % of live *Pocillopora* colonies to be occupied by *Trapezia*. Competition for space is likely to increase further as coral cover declines (Glynn 1976), potentially forcing obligate coral-dwelling organisms to utilise dead or marginal coral microhabitats, though there may be increasing competition from cryptofaunal species that specifically utilise recently dead coral habitats (Coles 1980; Plaisance et al. 2009; Enochs 2012). However, we do not know how inhabiting sub-optimal dead coral microhabitats affects the fitness of obligate coral-dwelling organisms, and hence how long they can actually persist on dead coral hosts.

Coral assemblage dynamics differ dramatically on a local scale, and the small size of these obligates means that the local abundance of live coral hosts could be a driver of their presence on dead coral colonies. The abundance of these obligate coral-dwellers was highest at Brothers and lowest at Eagle, two of the geographically closest locations, which were the two locations surveyed that form part of the Great Chagos Bank. These two islands also had the highest and lowest mean local live branching coral cover at 14 and 5 %, respectively. At Eagle, low cover of branching corals was directly attributable to localised outbreaks of crown-of-thorns starfish (pers. obs.). However, we found no correlation between the presence or abundance of obligate coral-dwellers on dead corals and the local abundance of live branching corals between or within the atolls. Similarly Enochs et al. (2011) found that live coral cover had no significant affect on the motile cryptofauna occupying dead corals, but rather dead coral porosity (gaps in rubble structure) and water flow had a greater affect, with low-porosity, slow-flow environments supporting a higher abundance and biomass of motile cryptofauna. Idjadi and Edmunds (2006) also observed no significant correlation with live coral cover or diversity and cryptofauna diversity, but there was a significant positive correlation between reef structural complexity and cryptofauna diversity.

The abundance of Pontoniinae shrimp obligates was found to be driven at least partly by the dead coral colony size, as shown previously for live coral colonies (Abele 1976; Abele and Patton 1976; Coles 1980; Enochs 2012). However, colony size only explained approximately 10 % of the variation in abundance and so many other factors, including inter- and intra-species interactions, proximity to live coral colonies, dispersal characteristics, predation pressure, and habitat heterogeneity, are likely to be important (Abele and Patton 1976). We attempted to control for coral colony size by collecting dead corals of approximately 20 cm in diameter. As even small variations in

coral colony size showed a significant correlation with Pontoniinae abundance, it is likely that coral colony size is an important driver of Pontoniinae obligate abundance. The complexity of the coral colonies has also been shown to affect the abundance and species richness of coral associates, as well as the host coral genera preferred by different coral associates, with more complex habitats thought to provide better refuge from predation and probably better niche separation (Castro 1988; Patton 1994; Vytopil and Willis 2001; Stella et al. 2010). It is also likely that the abundance of individual species is strongly affected by the abundance, diversity, and composition of cryptofaunal assemblages within each coral colony.

For *Trapezia* spp., colony size did not influence abundance, but this is perhaps not unexpected. In live coral hosts, *Trapezia* spp. are highly territorial, and each coral colony supports just one breeding pair, regardless of colony size (Preston 1973; Patton 1974), and often territory size is thought to exceed their nutritional requirements (Huber and Coles 1986). However, of the 13 *Trapezia* adults found on the dead coral colonies, only two adults occurred on the same coral colony, and both of these were male. The lack of adult mating pairs on the dead coral colonies suggests that these species could not persist in the absence of live coral habitats. Furthermore, *Trapezia* body size was not significantly affected by coral colony size. This is in contrast to live coral colony size that has been shown to correlate with body size of *Trapezia ferruginea* (Abele and Patton 1976).

This study has revealed high prevalence of at least seven obligate coral-dwelling species on dead coral colonies, predominated by *Trapezia* juveniles and female Pontoniinae shrimp, indicating that dead coral colonies may play an important role in the life cycle of some coral-dependent organisms. Dead coral colonies may also act as sub-optimal habitat for these obligate coral-dwelling taxa, allowing them to survive a period of time when there is an insufficient live coral habitat, or when they are searching for new territories. However, dead branching corals are temporary habitats that erode over time (Sheppard et al. 2002; Perry et al. 2012); therefore, even availability of this sub-optimal habitat for these taxa will be dependent on long-term coral loss. Results from this study add further complexity to our limited knowledge of the relationships between corals and the high diversity of motile invertebrates that inhabit live and dead colonies. These relationships are, however, fundamental to understanding the consequences of coral loss on species persistence and biodiversity.

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