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Marine Ecology Progress Series

Accepted/In press: 30/09/2024

Peer reviewed version

Variation in coral rubble cryptofauna is scale-dependent and driven by small-scale habitat characteristics.

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ABSTRACT

Motile cryptofauna living in dead coral rubble represent some of the greatest biodiversity and basal energetic resources on tropical coral reefs. Yet, we know relatively little about how and why coral rubble cryptofauna communities change over space and time. As human impacts increase the degradation of living hard corals to dead coral rubble on many reefs worldwide, understanding the communities that will succeed in these degraded environments, and the factors paramount to their success, becomes increasingly central to coral reef ecology and conservation. Using a remote and uninhabited oceanic atoll in the Pacific Ocean, we quantified the natural spatial variability in motile cryptofauna diversity and community structure in coral rubble across scales (m to km) and tested whether variability at smaller scales could be explained by gradients in microhabitat. We show that coral rubble cryptofauna communities are most variable at intra-site scales (m) rather than inter-site scales (100s m) or between reef zones (km scales). We also show that a substantial amount of variation in cryptofauna density (55%) and phyla-level community structure (31%) is explained by small-scale habitat characteristics, specifically the substrate type below the rubble and the variability in macroalgal cover on individual rubble pieces. Our findings highlight the need to study small-scale processes that are relevant to motile cryptofauna and their community interactions if we are to elucidate the structuring forces of these diverse cryptic assemblages on coral reefs.

KEYWORDS:

Coral reef, community structure, degraded habitats, spatial variability, microhabitat

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1. INTRODUCTION

Living, growing structures formed by ecosystem engineers like trees and reef-building corals provide important habitat to a diverse range of organisms (Larsson & Danell 2001, Coker et al. 2014, Kristensen et al. 2015, Stella et al. 2022). After death, the structural artefacts left behind continue their legacy, sustaining and often enhancing biodiversity across the ecosystem by creating newly available habitat for generalist species, decomposers, and scavengers (Jonsson et al. 2005, Enochs & Manzello 2012, Andringa et al. 2019, Saldaña et al. 2023). Historically, research efforts have focused on the living structures of ecosystem engineers and their biological and ecological attributes, while their non-living forms have received much less attention (Barnhill et al. 2023). However, as climate change-induced impacts intensify on land and in the ocean, ecosystem engineers are suffering mass mortality, and their dead remains are becoming more prevalent (Anderegg et al. 2013, Hughes et al. 2017, Stavi et al. 2021). To fully understand how ecosystems are being and will continue to be affected by climate change requires that we incorporate the ecological role these dead materials play in overall ecosystem function (Barnhill et al. 2023, Saldaña et al. 2023). This, in part, requires an explicit understanding of the structure and function of biotic communities that inhabit dead materials left by ecosystem engineers, and how they contribute to ecosystem processes.

Tropical reef-building corals are suffering mass mortality at local and regional scales due to rising ocean temperatures, which can trigger coral bleaching and disease (Hughes et al. 2018, Burke et al. 2023). These global impacts are exacerbated by local human stressors like overfishing and coastal pollution that reduce reef resistance and resilience to ocean warming (Graham et al. 2015, Gove et al. 2023). After death, coral skeletons can rapidly degrade to form coral rubble (Morais et al. 2022). While coral rubble is a naturally occurring habitat across the seascape (Odum & Odum 1955, Rasser & Riegl 2002), human impacts are increasing the prevalence of coral rubble on many reefs and this is expected to increase in the coming decades

(Rogers et al. 2014, 2018, Morais et al. 2020, Tebbett et al. 2023). As a result, the role coral rubble plays in overall reef ecosystem structure and function has become a focus of research in recent years (Rasser & Riegl 2002, Biondi et al. 2020, Ceccarelli et al. 2020, Kenyon et al. 2020, Masucci et al. 2021, Wolfe et al. 2021).

Despite a seemingly barren and featureless appearance, coral rubble forms complex microhabitats that host a diversity of life including microbes and biofilms, sessile and encrusting taxa, and motile cryptobenthic fishes and invertebrates (Gischler & Ginsburg 1996, Enochs 2012, Kramer et al. 2014). Invertebrate motile cryptofauna (hereafter motile cryptofauna) like crabs, shrimps, molluscs, and polychaetes, comprise the highest density and diversity of animals directly associated with coral reef substrates (Plaisance et al. 2009). Their diversity and abundance enable them to perform a wide range of functional roles including scavenging, predation, cleaning fishes, sediment clearing, bioturbation and parasitism (Keable 1995, Becker & Grutter 2004, Stewart et al. 2006, Pollock et al. 2013). One of their more influential roles is arguably as a significant basal energetic resource to higher level consumers (Glynn 2011, Kramer et al. 2013a, 2014, 2017) and they are well represented among the gut contents of many reef fishes (Randall 1967, Kramer et al. 2015, Casey et al. 2019a).

Motile cryptofauna density, biomass and productivity are more than an order of magnitude greater in dead corals and coral rubble than within live coral colonies (Enochs & Manzello 2012, Fraser et al. 2021, Stella et al. 2022). Due to their disproportionate abundance in coral rubble and the increasing prevalence of coral rubble on reefs, motile cryptofauna will likely play an increasingly important role in coral reef food webs and ecosystem functioning (Fraser et al. 2021, Stella et al. 2022, Wolfe et al. 2023b). This is well supported by modelling projections that predict an initial increase in secondary productivity of benthic invertebrates on degraded reefs which may temporarily support reef trophodynamics (Rogers et al. 2014, 2018). However, despite their ubiquity, motile cryptofauna remain one of the most understudied

groups of organisms on coral reefs. Their small size, cryptic nature and the methodological difficulties involved with quantitative sampling, means they remain poorly described and underrepresented in ecological studies (Reaka-Kudla 1997, Small et al. 1998, Dennis & Aldhous 2004, Plaisance et al. 2011). This represents a substantial gap in our understanding of community organisation for some of the greatest metazoan biodiversity on coral reefs.

In many ecosystems, ecological communities are most variable at small spatial scales (cm to m) driven in part by gradients in microhabitat structure (Underwood & Chapman 1996, Coleman 2002, Anderson et al. 2005, Harris et al. 2015). For example in woodlands and rainforests, small-scale features like branch thickness, leaf density (Halaj et al. 2000) and leaf litter quality (Lassau et al. 2005) drive invertebrate abundance and community structure. Similarly, the high density, biomass and productivity of motile cryptofauna in coral rubble may be due to the increased complexity of interstitial spaces (Wolfe et al. 2023a) and the micro-structural complexity provided by encrusting taxa like macroalgae and turf algae living on the rubble (Kramer et al. 2013b, Roff et al. 2013, Lavender et al. 2017). However, motile cryptofauna in coral rubble have typically been described across broader spatial scales (10s m to km) that compare community structure between reef habitats and depths, and investigations into their driving forces focused on site-level gradients in wave exposure (Takada et al. 2012, Masucci et al. 2021) and water quality (Takada et al. 2008). While these studies show generalisable patterns at broader scales, it remains unclear at what scales motile crytopfauna are most variable and what role, if any, microhabitat structure plays in dictating these patterns.

Here, our overarching aims were to quantify the variability in motile cryptofauna diversity and community structure (total density, biomass, and community composition at three taxonomic resolutions) in coral rubble across scales (m to km) and test whether variability at smaller scales could be explained by gradients in microhabitat. We partitioned community composition into three taxonomic levels (phyla, order and family) to determine how much variation could be

explained by microhabitat factors across these incremental increases in underlying ecological complexity. We did this at a remote, uninhabited coral reef atoll system that lacks the confounding effects of direct local human impacts on reef ecosystem structure and function. In doing so, we provide key insights into the natural variability of motile cryptofauna living in coral rubble across scales.

2. MATERIALS AND METHODS

2.1 Study site

Palmyra Atoll National Wildlife Refuge is the northernmost atoll in the Northern Line Islands, central Pacific. It consists of 12 km^2 of land area and 47.2 km^2 of subtidal reef (Williams et al. 2011). Palmyra has no permanent human population and is part of the Pacific Remote Islands Marine National Monument and is protected under United States federal law. Palmyra's remote location and its protected status provides the unique opportunity to study the natural variability of ecosystems with minimal direct human impacts.

2.2 Defining and surveying coral rubble habitats

Nine sites were surveyed around Palmyra in October to November 2022 (Fig. 1). Six of these sites were located on the wave sheltered backreef and three were on the wave exposed forereef (the reef slope facing the open ocean). Of the backreef sites, three were located on the open western terrace, and the remaining three were located on the closed eastern side of the atoll (Fig. 1). Overall, the nine sites were selected based on two factors: 1) their spatial breadth across the atoll which, given the concurrent gradients in other benthic communities like corals (Williams et al. 2011, 2013) should encompass a wide range of cryptofauna communities, and 2) that all these sites contained 'rubble patches', defined here as accumulations of dead coral rubble ≥ 1 m in length and width. During reconnaissance surveys on the backreef, we observed

two physically distinct rubble habitat types, likely formed by different physical mechanisms. Type 1, which we referred to as 'reef rubble', were rubble patches interspersed between other benthic habitats (e.g., live coral) on the coral-dominated reef (Fig. 1). Type 2, which we referred to as 'rubble beds', were featureless mass accumulations of coral rubble that spanned > 1 km in extent (Fig. 1), similar to rubble flats described at One Tree Reef in the southern Great Barrier Reef (Shannon et al. 2012). We hypothesised that the smaller 'reef rubble' patches were formed by the physical destruction of corals within close proximity, whereas the larger 'rubble beds' were the result of rubble accumulation over greater distances by strong hydrodynamic action. Once deposited, rubble within rubble beds may undergo further fragmentation through physical reworking (Shannon et al. 2012). We hypothesised that if reef rubble and rubble beds were indeed different rubble habitat types, then they may contain different cryptofauna communities. No rubble beds were located on the forereef, likely due its sloping geomorphology whereby rubble accumulates as a talus at the foot of the slope at great depths (Scoffin 1993), beyond the accessible survey limits of this study.

Within each rubble habitat type (n = 2 habitat types), a 0.5 m^2 quadrat was haphazardly placed over rubble and cryptofauna and rubble characteristic data were collected (described below). This was repeated twice within each rubble habitat type (n = 3 quadrats) of each reef zone (i.e. n = 6 quadrats per backreef site; n = 3 quadrats per forereef site).

2.3 Quantifying coral rubble cryptofauna communities

Within each 0.5 m^2 quadrat, approximately 1 L of coral rubble was scooped to an average depth of 5 – 10 cm directly from the rubble patch surface using a plastic beaker. Each scoop of rubble was immediately placed in double-bagged sealable plastic bags underwater and returned to the lab for processing. At the lab, each rubble scoop was emptied into a bucket and flushed with fresh water three times. After each flushing, the water was poured through a 1x1 mm mesh net

to retrieve cryptofauna individuals. This method was effective in capturing fauna >1 mm, but excluded fauna <1 mm, meaning the total density and diversity of organisms documented here is likely underestimated.

Using a dissecting microscope, each cryptofauna individual was identified to phylum, order and family and measured to the nearest 0.1 mm using standard linear measurements (carapace width for crab-like crustaceans, carapace length for shrimp-like crustaceans, longest distance of shell length for molluscs diameter for echinoderms with radial symmetry, and length for all types of worms. Individuals were blotted dry and weighed to the nearest whole mg on an analytical balance (± 0.0001mg). Total cryptofauna density (individuals L^{-1}), biomass, and community composition were determined for each rubble patch (n = 45 scoops in total).

2.3 Quantifying rubble habitat characteristics

Within each 0.5 m^2 quadrat, eight pieces of rubble were haphazardly collected (n = 24 – 48 pieces per site) and used to estimate the following rubble morphological parameters: (a) length (longest span in any direction), (b) mean width (n = 2 – 3 measurements per rubble piece), (c) number of branches (referred to here as 'branchiness'), and (d) mean branch length. The substrate type found immediately below the rubble layer (e.g. sand, dead *Halimeda* pellets, or more rubble) was recorded, and provided an additional rubble habitat characteristic.

Of the rubble pieces collected, the cover of sessile organisms growing on each individual piece of rubble was quantified. Sessile communities can differ between the top and underside of rubble pieces due largely to differences in light exposure, interstitial sediment, and water movement (Choi & Ginsburg 1983, Gischler & Ginsburg 1996, Kenyon 2021). We therefore photographed each rubble piece from both sides using a Olympus TG-6 camera and used these images to quantify the proportional cover of: encrusting algae (mainly crustose coralline algae (CCA), *Peysonnelia*), turf algae, macroalgae (including *Dictyota*, *Lobophora* and *Halimeda*),

sessile invertebrates (including live coral and sponges), and bare surface (if the surface appeared bare or covered in micro and endolithic algae). We did this using the guides function in Microsoft Powerpoint. A 66 x 38 grid (in which each grid cell = 0.5 cm) was placed over each image. The number of cells occupied by each sessile group on both sides of each rubble piece was counted.The proportion of each sessile group on a rubble piece was calculated by dividing the total number of grid cells occupied by the sessile group by the total number of grid cells occupied by the respective rubble piece.

2.5 Statistical analyses

2.5.1 Testing for differences in cryptofauna communities on the backreef

We tested for an effect of backreef habitat type (fixed factor, 2 levels: open western terrace and closed eastern; with site as a random factor nested within backreef habitat type) on cryptofauna total density, total biomass, richness (calculated using Margalef's index) (univariate responses), and community composition (multivariate response). We also separately tested for an effect of rubble habitat type (fixed factor, 2 levels: reef rubble and rubble bed; with site as a random factor nested within rubble habitat type) on the same community metrics.

We used a hierarchical nested permutational analysis of variance (PERMANOVA) (Anderson 2001a) using the PERMANOVA+ (Anderson et al. 2008) add-on for PRIMER-E (version 7.0) (Clarke & Gorley 2015). Analyses were based on square-root transformed data, a Euclidean (for total density, total biomass, Margalef's richness) and a Bray-Curtis (for community composition) similarity matrix, and 9999 permutations of the residuals under a reduced model (Anderson 2001b). Differences in dispersion amongst groups were tested using PERMDISP in PRIMER-E (version 7.0) (Clarke & Gorley 2015).

There was no effect of backreef habitat type on cryptofauna total density, total biomass, richness or community composition at each of three taxonomic levels (phylum, order and

family) (Table S1, Supplemental Material). Similarly, there was also no effect of rubble habitat type on any of the measured community metrics. (Table S2, Supplemental Material). Furthermore, there was no significant dispersal effects amongst groups (Table S3, Supplemental Material). As a result, data collected on the backreef across both habitat types and both rubble habitat types were pooled for further analyses.

2.5.2 Determining scales of variation in cryptofauna communities

The cryptofauna data were assigned to three hierarchical levels of spatial organisation: ‘reef zone’ (forereef, backreef) which spanned kilometres, ‘site’ (n = 9) spaced 100s of metres apart, and ‘quadrat’ spaced metres apart at each site (n = 3 - 6 per site, n = 45 across all sites). To determine which of these scales (reef zone, inter-site, intra-site) captured the most underlying variation in total cryptofauna density, total biomass, and richness (univariate responses) and community composition at three taxonomic resolutions (phylum, order, family) (multivariate responses), we used variance components analyses. In hierarchical designs such as ours, larger spatial scales necessarily have fewer degrees of freedom than smaller spatial scales. Therefore, when estimating individual components of variation, estimates obtained for larger scales subsequently have lower precision than estimates obtained for smaller scales. Nevertheless, comparisons of the relative importance of the factors based on estimates of variance components are rigorous as both analysis of variance (ANOVA) estimators and multivariate analogues of ANOVA estimators are unbiased, so their accuracy is not affected by sample size (Searle et al., 1992).

For the three univariate responses, we used a hierarchical nested analysis of variance (ANOVA), with ‘site’ nested in ‘reef zone’. All factors were treated as random. By treating the factors as random, we tested the significance of variation between levels within each factor. Assumptions of normality and homogeneity of variance for each metric was tested using a

Shapiro-Wilk test and Levene's test, respectively. To accommodate the unbalanced design and to force non-negative variance components, a restricted maximum likelihood estimation model (REML) was used to calculate the variance components. Variance for each metric is presented as both absolute variance and as a percent of total variation (termed the 'magnitude of effect' (Graham & Edwards 2001). This allows for both quantification of total variability attributed to each spatial scale and the proportion of total variability that occurs between specific scales to be determined. Levene's test was performed using the *leveneTest* function (car package) and the Shapiro-Wilk test was performed using the in-built *shapiro.test* function in R 4.2.3. Hierarchical ANOVAs were performed using *lmer* function (lme4 package) in R 4.2.3 (R Core Team, 2023 .

For the multivariate responses, we again used PERMANOVA, with 'site' nested within 'reef zone', with both factors treated as random. Measures of variability at the three spatial scales, reef zone (km), inter-site (100s m), and intra-site (quadrat, m), were calculated from the mean squares of the PERMANOVA, using the multivariate analogue of the ANOVA variance component estimators and statistical significance tested using 9999 permutations of the raw data under a reduced model. PERMANOVA variance components are presented as absolute variance (i.e. the square root of estimates of the variance components) (Anderson et al., 2008) and as a proportion of total variability within each response variable (Underwood & Chapman, 1996).

Given the unbalanced sampling design, where we had a greater number of backreef sites (n = 6) than forereef sites (n = 3), and an uneven number of quadrats at the lowest spatial scale (n = 6 per site on backreef; n = 3 per site on forereef), we conducted a sensitivity analysis using a constrained jackknife approach to determine if our estimates of variation were influenced by our sampling effort. We randomly subset the data with a smaller number of replicates at the lowest spatial scale (but ensuring the full complement of levels was retained at the higher

scales) to see whether/how this changed the estimates of variance components. We conducted a traditional leave-one-out jackknife analysis (i.e. dropping only one sample from each resampled dataset). We also conducted an analysis where we dropped 18 random backreef samples from each resampled dataset. By dropping these 18 samples, we created datasets where the sampling effort on the backreef and forereef were equal, i.e. n = 3 quadrats per site. We performed resampling 10 times, and the analyses were conducted on all community metrics – density, biomass, richness, and community composition at all three taxonomic levels.

2.5.3 Visualising rubble habitat characteristics

To simultaneously visualise the correlation across all rubble habitat characteristics (rubble morphometrics (rubble length, width, branchiness, branch length), cover of sessile organisms, and the substrate types below the rubble patches), we used Principal Component Analysis (PCA). To visualise variability of rubble morphometrics at the site and quadrat scales, we calculated the coefficient of variation (CoV), a unitless measure calculated as the ratio of the standard deviation to the mean.

2.5.4 Testing for correlations between cryptofauna communities and rubble habitat characteristics

To test whether variations in rubble habitat characteristics explained variation in cryptofauna community composition, we used a permutational distance-based multivariate multiple regression model (DISTLM) (McArdle & Anderson 2001). DISTLM is used for modelling the relationship between a resemblance matrix and a single (multivariate regression) or set of predictor variables (multivariate multiple regression). The technique makes no prior assumptions about the distribution of the response variable , and therefore normality does not have to be satisfied (Anderson et al. 2008).

Models were constructed for three univariate responses using a Euclidean similarity matrix (cryptofauna total density and total biomass, and Margalef's richness), and three multivariate responses using a Bray-Curtis similarity matrix (community composition at the phylum, order, and family taxonomic resolution). Additionally, we constructed univariate models for the four most abundant taxa (*Gammarida*, *Amphinomidae*, *Eunicidae* and *Anthuridae*) and two others (*Xanthidae* and *Gnathiidae*) chosen due to their ecological significance to coral reef trophodynamics (Kramer et al. 2015, Artim et al. 2017, Casey et al. 2019b, Nicholson et al. 2020).

Prior to model fitting, the predictor variables were investigated for co-linearity using draftsman plots and Pearson's (r) pairwise correlations. For the rubble morphometrics and sessile organism cover, each variable's mean value correlated with its respective standard deviation ($r > 0.7$). We chose to retain the standard deviation for each predictor rather than the mean, with two exceptions: the mean number of branches was retained (we deemed this more reflective of each individual rubble piece's structural complexity) and mean bare surface cover since its standard deviation also correlated with the standard deviation of encrusting algae. The remaining eleven predictors (Table A1, Appendix) were included in the model-fitting process. Each predictor was log-transformed, normalised (to account for the differences in units and ranges among the predictors) and fitted conditionally in a step-wise manner to the cryptofauna community resemblance matrix. Tests were based on 9999 permutations of the residuals under the reduced model (Anderson 2001a). Model selection was based on Akaike's Information Criterion (Akaike 1998) with a second-order bias correction applied (AICc) (Hurvich & Tsai 1989) to account for the relatively high number of predictor variables relative to the response variable replication. Once the optimal model was selected, we further investigated the underlying relationships between the response and top contributing predictor variables using

distance-based redundancy analysis (dbRDA) (McArdle & Anderson 2001) (for the multivariate models) and boxplots and scatter plots (for the univariate models).

3. RESULTS

3.1 Cryptofauna communities in coral rubble (density, biomass, richness, community composition)

Across our samples, we identified 2603 individual motile cryptofauna from 6 phyla, 28 orders, and 57 families (Fig. 2; Table S4 in Supplemental Material)). Mean (± 1 standard error) density of cryptofauna across all quadrats (n = 45) was 58 ± 5.3 individuals L^{-1} (range = 17 – 194 individuals L^{-1}), mean biomass was 1.4 ± 0.21 mg (range = 0.03 – 5.01 mg), mean number of families was 13 ± 0.5 (range 6 – 21), and mean richness was 3.2 ± 5.3 (range 1.3 – 5.1).

The Arthropoda (primarily crustaceans) and Annelida (polychaetes) were the most abundant phyla, representing 47% and 36% of all individuals, respectively (Fig. 2). The most abundant orders were Amphipoda, Isopoda, Amphinomida and Eunicida, which also contained the most abundant families *Gammarida, Anthuridae, Amphinomidae* and *Eunicidae*. The phylum Mollusca dominated, representing 71% of the total cryptofauna biomass, with the family *Cypraeidae* (cowries) and order Neogastropoda contributing 48% and 18% to total biomass, respectively. The second top contributing phylum Echinodermata represented 11% of total biomass, with the family Holothuriidae (sea cucumbers) representing 9% of total biomass. The phyla Arthropoda and Annelida encompassed the greatest number of families identified, with 21 and 20 families, respectively.

3.2 Scales of variation in cryptofauna density, biomass, and richness (univariate)

Across the intra-site (m), inter-site (100s m) and reef zone (km) scales we examined, cryptofauna density, biomass and richness were always greatest at the smallest intra-site scale (Fig. 3, Table S5 in Supplemental Material). Variation in total cryptofauna density was greatest at intra-site and inter-site scales, representing 51% and 49% of the total variation, respectively (Fig. 3A). Variability in total cryptofauna biomass was greatest at the intra-site and reef zone scales, representing 55% and 35% of the total variation, respectively. Variability in total richness was greatest at the intra- and inter-site scale, representing 64% and 36% of the total variation, respectively.

There was significant variation in total cryptofauna density at the inter-site (100s m) scale (ANOVA; $F_{7,44} = 7.07$, $p < 0.001$) but not at the reef zone (km) scale (ANOVA; $F_{1,44} = 0.52$, $p = 0.480$). Similarly, there was significant variation in cryptofauna richness at the inter-site (100s m) scale (ANOVA; $F_{7,44} = 2.84$, $p = 0.018$) but not at the reef zone (km) scale (ANOVA; $F_{1,44} = 0.26$, $p = 0.613$). In contrast, there was significant variation in total cryptofauna biomass at the reef zone (km) scale (ANOVA; $F_{1,44} = 6.70$, $p = 0.014$) but not at the inter-site (100s m) scale (ANOVA; $F_{7,44} = 1.04$, $p = 0.420$).

3.3 Scales of variation in cryptofauna community composition (multivariate)

At all three taxonomic resolutions, cryptofauna community variability decreased as scale increased. Variability was greatest at the intra-site scale (quadrat, m), and then decreased at the inter-site scale (100s m), and then again at the reef zone scale (km) (Fig. 3B). Variability at the intra-site scale also increased as taxonomic resolution increased (from phylum, to order to family), while the proportion of variability at the inter-site and reef zone scale was unaffected by taxonomic resolution (Fig. 3B). There was significant variation in community composition

at both the reef zone and inter-site scale at all three taxonomic resolutions (Table S6 in Supplemental Material).

Patterns of univariate and multivariate variation across the three spatial scales remained the same following our jackknife analyses, reinforcing that the largest portion of variation was always found at the smallest spatial scale despite our unbalanced sampling design. As expected, the largest spatial scale (reef zone, km) had the least precision for estimating variance components (Table S7, Supplemental Material). While in this study it was logistically necessary to have only two levels at the largest spatial scale (km), future studies could aim to increase this (reducing the number of lower-level replicates, if necessary) to improve the precision of variance components estimates across spatial scales ranging kilometres.

3.4 Summary of rubble habitat characteristics

Across our samples, mean (± 1 standard error) rubble length was 7.1 ± 3.4 cm, and mean rubble thickness was 2.3 ± 1.4 cm. The mean number of branches was 1.0 ± 1.2, and mean branch length was 0.9 ± 1.4 cm (Fig. 4). Encrusting algae was the most dominant sessile organism living on rubble, with a mean cover of 52.7 ± 30.8 %, followed by bare surface (39.2 ± 30.9 %). Three substrate types were recorded below the sampled rubble. The most common was more rubble (found under 62% of quadrats), followed by sand at three out of the six backreef sites (27% of quadrats), and *Halimeda* sediment was found predominantly at forereef sites (11% of quadrats) (Fig. 4).

There were correlations among the rubble habitat characteristics (Fig. 4). Sandy substrates strongly correlated with bare surface cover on rubble, whilst rubble substrates strongly correlated with encrusting algae on rubble. Rubble morphological characteristics were uncorrelated or had weak correlations with substrate type and algal cover. Some sites had low intra-site variability in rubble morphological characteristics, whereas others were much more

variable. For example, the southwest backreef (site: PS, Fig. 1) was consistently characterised by sandy substrates and rubble pieces with a higher percentage of bare surface cover (Fig. 4, note the low overall dispersion among replicates). In contrast some sites, like the northwest backreef (site: TG, Fig. 1), showed high intra-site variability in rubble habitat characteristics, and were characterised by rubble substrates and rubble pieces with a higher percentage of encrusting algae (Fig. 4).

3.5 Correlations between cryptofauna communities and rubble habitat characteristics

Substrate type below the rubble, variability in macroalgae and turf algae cover, variability in rubble thickness, and the average number of rubble branches together explained 54.8 % of the total variation in cryptofauna density (Table 1). Of these five predictors, substrate type and variability in macroalgae cover were the top performing predictors, explaining 21.7% and 17.6% of the total variation in cryptofauna density, respectively. Cryptofauna density was greatest over sandy substrates (compared to rubble or *Halimeda* sediment substrates) and showed a positive trend with variability in macroalgal cover (Fig. 5A, B). In contrast, rubble habitat characteristics did not explain as much of the variation in cryptofauna biomass (9.3 % variation explained) or cryptofauna richness (17.4 % variation explained) (Table 1).

Substrate type, variability in rubble length and variability in turf algae cover best explained variations in cryptofauna community composition (Fig. 5B). At the phylum level, these three predictors explained 31.4% of the total variation in cryptofauna community composition, with substrate type explaining the most variation (22.3%) (Table 1). As taxonomic resolution increased model performance decreased, with rubble habitat characteristics explaining just 12.7% and 5.4% of the cryptofauna community composition at the order and family level, respectively (Table 1).

Variations in rubble habitat characteristics correlated with variations in the density of the four most abundant cryptofauna organisms in our samples (Table 1). Variability in rubble length and substrate type explained 22% of the total variation in *Gammarida* (Arthropoda) density, while substrate type and variability in macroalgae cover explained 33% of the total variation in *Anthuridae* (Arthropoda) density. Similarly, substrate type, variability in macroalgae cover and variability in rubble length explained 36% of the total variation in *Amphinomidae* (Annelida) density (Table 1). Both *Anthuridae* and *Amphinomidae* were best predicted by substrate type (20.8 and 23%, respectively), with the density of both groups greatest over sandy substrates (Fig. 5C, D). Variability in turf algae cover and various rubble morphometrics including variability rubble thickness, mean number of branches and variability in length, explained 30% of the total variation in *Eunicidae* (Annelida) density. However, no single predictor explained more than 12% of the total variation and two explained less than 5% (Table 1). As such, these relationships were not explored further. Variations in *Xanthidae* (crab) density were best explained by the cover of bare substrate on rubble, variability in turf algae cover, encrusting algae cover and macroalgae cover, together explaining 47% of the total variation in *Xanthidae* density (Table 1). The cover of bare substrate on rubble alone explained 23.9%; *Xanthidae* density decreased as the cover of bare substrate on the rubble increased (Fig. 5E). Finally, rubble habitat characteristics did not explain any appreciable variation in *Gnathiidae* density (Table 1).

4. DISCUSSION

Coral rubble cryptofauna represent an abundant basal energetic resource that support higher trophic level consumers and overall coral reef biodiversity (Kramer et al. 2016, Wolfe et al. 2021, Stella et al. 2022). Yet, we know relatively little about how and why coral rubble cryptofauna communities change over space and time. Here we show that coral rubble

cryptofauna communities are most variable at intra-site scales (m) rather than inter-site scales (100s m) or between reef zones (km scales). We also show that a substantial amount of variation in cryptofauna density and phyla-level community composition is explained by small-scale habitat characteristics, including the substrate type below the rubble and the variability in macroalgal cover on individual rubble pieces. Our findings highlight the need to study small-scale processes that are relevant to individual cryptofauna organisms and their community interactions if we are to elucidate the structuring forces of these diverse cryptic assemblages on coral reefs.

4.1 Scales of variation in cryptofauna communities in coral rubble

Across the intra-site (m), inter-site (100s m) and between reef zone (km) scales we examined, all cryptofauna community parameters measured were most variable at the smallest intra-site scale. This is congruent with benthic invertebrate assemblages in other ecological systems. For example, in temperate systems, benthic invertebrates inhabiting kelp holdfasts are most variable at metre scales, from holdfast to holdfast (Anderson et al. 2005), while in the deep sea, infaunal communities change substantially more with differences in sediment depth layers than with differences associated to larger geographical or bathymetrical scales (Ingels & Vanreusel 2013). Similarly, invertebrate assemblages on temperate rocky shores are most variable at centimetre to metre scales (Underwood & Chapman 1996, Benedetti-Cecchi 2001, Fraschetti et al. 2005). On tropical coral reefs, other benthic groups also tend to show the greatest variability at smaller spatial scales. For example, algal turf assemblages are most variable at centimetre scales rather than at metre or kilometre scales (Harris et al. 2015). Understanding the primary spatial scales at which organisms interact with one another and their environment is an essential basis to identifying the processes that dictate community structure (Underwood & Chapman 1996). These commonalities across trophic levels and ecological systems suggest

that small-scale processes contribute a substantial amount to driving benthic community organisation in the marine environment (Coleman 2002, Fraschetti et al. 2005).

Beyond the intra-site scale, the univariate responses of cryptofauna communities (overall density, biomass, and richness) showed different patterns of variation across spatial scales. Variation in cryptofauna density and richness were both significant at the inter-site scale (100s m) but not at the reef zone scale (km). However, variance components for cryptofauna density were almost equivalent at the intra-site (m) and inter-site scales. This suggests that quantifying processes acting at metres to 100s of metres should capture a large proportion of variation in cryptofauna density in coral rubble. In contrast though, variance components for cryptofauna richness at the intra-site scale was almost double that at the inter-site scale, suggesting that processes acting at the metre scale or smaller influence the diversity of cryptofauna organisms. Variation in cryptofauna biomass was significant at the reef zone scale (km) and at the intra-site scale (m), but not significant at the inter-site scale (100s m). Further, the majority of variance components were divided between the reef zone scale (km) and intra-site scale (m). This suggests that broad-scale (km scale) processes may have direct influences on small-scale processes that in turn structure cryptofauna biomass in coral rubble.

In contrast to univariate responses (cryptofauna density, biomass and richness), the multivariate community responses showed consistent patterns of variation across spatial scales. Cryptofauna community composition was significantly different across inter-site and reef zone scales, suggesting that small-scale (m) to larger-scale (km) processes dictate community structure. Variance components at the intra-site scale increased with increasing taxonomic resolution, a similar finding observed for benthic invertebrates in temperate kelp holdfasts (Anderson et al. 2005) and temperate soft sediments (Vanderklift et al. 1996, Olsgard et al. 1998), and reflects the increased ecological information gained via lower-level taxonomic resolution. At the inter-site scale, differences in variance components across taxonomic resolutions were marginal.

Similarly at the reef zone scale, phylum-level community composition had the greatest variance components, with marginal differences between order- and family-level variance components. This suggests that processes acting at kilometres and 100s of metres structure cryptofauna communities at a broad taxonomic level (phylum in this case) with not much change in community variance with increasing taxonomic resolution.

While these findings are novel for cryptofauna communities inhabiting rubble on tropical coral reefs, the diversity of the sampled assemblages in this study (57 families from six phyla) is comparably much lower than studies from Australia where greater than 122 families occur at individual study sites (Stella et al. 2022, Wolfe et al. 2023b). Due to its remoteness and size, island biogeography theory may explain the lower species richness found at Palmyra Atoll compared to Australia (Maragos & Williams, 2011), however there are methodological limitations within this study that may have influenced this as well. While we identified most organisms to family, some individuals were grouped at the phylum level (e.g. Ribbon worms: Nemertea), while others were grouped at the order level (e.g. the gastropod Mollusca: Neogastropoda, Littorinimorpha). Furthermore, the density and biomass of coral rubble cryptofauna can be dominated by Harpacticoid copepods that are <1 mm in size (Fraser et al. 2021, Wolfe et al. 2023a) and that would have been missed by our sampling approach. Therefore, it is likely the abundance and biodiversity of motile cryptofauna we describe here is underestimated. Despite this, the diversity of cryptofauna (57 families) is impressive considering that of the two most frequently studied marine organisms at Palmyra Atoll – hard corals and non-cryptic reef-associated fish – there are only 26 families and 31 families recorded respectively (Williams et al. 2008, Caselle & Carlsen unpubl. data). This finding underscores the significance of cryptofauna as a source of biodiversity on Palmyra's coral reefs, and the need for further study into their functional importance.

4.2 Association of cryptofauna with rubble habitat characteristics

The substrate type below the sampled rubble best explained variation in cryptofauna density, including variation in the two most abundant organisms - annelids *Amphinomidae* and arthropods *Anthuridae*. In particular, we found sandy substrates below coral rubble supported increased cryptofauna density compared to either more rubble substrate or *Halimeda* sediment (the calcium carbonate pellets left by the calcifying macroalga *Halimeda*). While sandy habitats on coral reefs have comparably low rates of community production (Brock & Smith 1983, Johnstone et al. 1990, Kramer et al. 2014), here we demonstrate that sandy substrates covered by coral rubble can support diverse cryptofauna communities.

The rubble pieces are likely providing structurally complex, habitable substrate and algal and other organic matter food resources (Klumpp et al. 1988, Enochs & Manzello 2012, Takada et al. 2012, 2014). Also sand, while not a structurally complex habitat, does retain algal and detrital resources (Johnstone et al. 1990, Kramer et al. 2014). A high proportion of the organisms found within dead coral substrates are deposit feeders and omnivores (Enochs 2012, Kramer et al. 2017). Across the three substrate types we recorded, sand may act as the best sink for organic matter from the overlaying rubble. This may explain the increased densities of *Amphinomidae* and *Anthuridae* we observed living in rubble that overlaid a sandy substrate. *Amphinomidae* are an omnivorous group of polychaetes with a preference for colonising environments with accumulations of decaying organic matter (Fauchald & Jumars 1979, Cosentino & Giacobbe 2011, Schulze et al. 2017). *Anthuridae* are anecdotally suggested to be detritivores, carnivores, browsers or filter feeders (Poore & Bruce 2012), and so too may benefit from the increased food resources likely found in sandy substrates. Whilst dead *Halimeda* sediments could potentially perform the same trapping function of organic matter as sand, at Palmyra Atoll this substrate type is typically characteristic of the forereef zone. Strong surge may frequently stir up and redeposit this sediment (Williams et al. 2011), thus reducing its ability to retain organic content. The arrangement of rubble overlaying sand may represent a

'sweet spot' to rubble cryptofauna. It marries the habitat-provisioning of rubble and its relatively extensive surface area colonised by a variety of algal and encrusting taxa that promotes detrital resources, with the retainment ability of sand, providing a food-rich environment to fauna inhabiting rubble.

Variation in motile crytofauna community composition at the phylum level was also best explained by the substrate type below the sampled rubble. Increasing taxonomic resolution (from phyla to family) resulted in a substantial reduction in the explanatory power of rubble habitat characteristics. This is not surprising given that the strength of community-environment relationships often differ depending on the taxonomic resolution of the community data (Lu et al. 2016). For example at a course taxonomic resolution, variations in benthic invertebrate communities in temperate fjords closely reflect gradients in anthropogenic pollution, whereas the same communities viewed at the species-level correlate more with small-scale habitat characteristics like sediment grain size (Warwick 1988a b). From the perspective of these tiny organisms, the rubble characteristics measured here may represent broad-scale habitat features that allow phyla-level taxa with similar traits to occupy the same niche space. However, perhaps to understand community organisation of coral rubble motile cryptofauna at a finer taxonomic resolution requires an appreciation of other small-scale processes, like organism dispersal capabilities, competition, predation or finer-scale habitat characteristics like the availability and quality of organic matter (Pacala & Levin 1997, Harris et al. 2015, Lu et al. 2016).

Variability in macroalgal cover was the second-best predictor of cryptofauna density in coral rubble at Palmyra. This is consistent with coral rubble cryptofauna in Australia, where macroalgal cover on rubble had a direct positive influence on total cryptofauna density (Wolfe et al. 2023b). The physical structure of macroalgae enhances occupiable space available to small benthic fauna through an increase in micro-habitat complexity that provides refuge from fish predationand may enhance nutritional resource availability to herbivorous cryptofauna

(Stoner 1985, Roff et al. 2013, Ape et al. 2018). Furthermore, macroalgae may reduce water flow, increasing the deposition of sediment (Gibbons & Griffiths 1986) rich in detritus and other particulate organic matter that act as a food source to cryptofauna (Takada et al. 2012). In contrast, variability in rubble thickness and the average number of branches accounted for little variation in cryptofauna density. These findings imply that micro-complexity gained from sessile organisms growing on rubble is more beneficial to cryptofauna than the structural complexity of the rubble itself. However, rubble structural complexity may indirectly affect crytofauna density because branchier rubble pieces tend to have higher macroalgal overgrowth (Wolfe et al. 2021). While we found that the variation in rubble crab, *Xanthidae*, density was not well explained by variations in algal cover on rubble, their density was negatively associated with increasing bare surface cover on rubble. *Xanthidae* are omnivores with a preference for algae, ranging from crustose coralline algae to turf algae (Knudsen 1960, Skilleter & Anderson 1986, Kyomo 1999), suggesting their densities may be regulated in some way by the abundance of sessile organisms growing on rubble.

With the ever-increasing degradation of living hard corals to dead coral rubble on many reefs (Williams & Graham 2019), understanding the communities that will succeed in these environments, and the factors paramount to their success, becomes increasingly central to coral reef ecology and conservation. Motile cryptic fauna represent a significant source of coral reef biodiversity and basal energetic resources to higher lever consumers, and therefore understanding their role in future coral reef functioning and reef trophodynamics deserves attention. The overall findings here suggest that cryptofauna communities are primarily structured by small-scale processes. Habitat characteristics like the substrate type below rubble and sessile organisms growing on rubble may explain broad community metrics, like density and phyla-level community composition, suggesting a link with habitat complexity and food availability. Future research is needed to explicitly quantify these parameters and their effects

in structuring motile cryptofauna communities, and how ever-changing environmental conditions on contemporary reefs may impact the structure and function of these diverse cryptic assemblages.

ACKNOWLEDGEMENTS

We thank the U.S. Fish and Wildlife Service (USFWS) for granting access to Palmyra Atoll refuge and The Nature Conservancy (TNC) for logistical support. We also thank the crew and volunteers at the Palmyra Atoll Research Station for assistance in the field, and Dr Joe Pollock of TNC and Dr Amanda Pollock of USFWS for supporting and facilitating project development. This work was supported by a Natural Environment Research Council (NERC) of the UK ENVISION Doctoral Training Partnership grant awarded to LSG [grant reference number NE/S007423/1]. Additional funds were provided by The Nature Conservancy (Hawai'i and Palmyra Program). Fieldwork was conducted under the special use permit 12533-22018 granted by the U.S. Fish and Wildlife Service.

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TABLES

Table 1. Summary results of a distance-based permutational multivariate multiple regression model (DISTLM) for associations of cryptofauna community composition and rubble habitat characteristics at Palmyra Atoll, central Pacific. The optimal predictors of variation in community composition, along with the proportion of variability they explained (% variability) are shown.

Predictor	AICc	Pseudo-F	P value	% Variability	% Total
Total density					
Substrate type	307.48	5.836	0.008	21.7	
Standard deviation macroalgal cover	298.56	11.857	0.002	17.6	
Standard deviation rubble thickness	295.15	5.651	0.022	7.5	
Average number of branches	293.76	3.691	0.060	4.6	54.8
Total biomass					
Standard deviation encrusting algae cover	29.398	4.424	0.040	9.3	9.3
Richness					
Standard deviation rubble thickness	-32.16	9.045	0.004	17.4	17.4
Community composition (Phylum)					
Substrate type	272.57	3.933	$p < 0.001$	22.3	
Standard deviation rubble length	272.22	2.654	0.038	4.8	
Standard deviation turf algal cover	272.17	2.430	0.061	4.3	31.4
Community composition (Order)					
Standard deviation turf algal cover	318.22	3.218	0.002	7.0	
Standard deviation rubble length	317.65	2.757	0.005	5.7	12.7
Community composition (Family)					
Standard deviation turf algal cover	340.4	2.457	0.004	5.4	5.4
***Gammarida* density**					
Standard deviation rubble length	40.03	6.768	0.013	13.6	

Substrate type	39.705	2.429	0.104	9.2	22.8
***Amphinomidae* density**					
Substrate type	49.842	5.508	0.008	20.8	
Standard deviation macroalgal cover	45.021	7.152	0.018	11.8	
Standard deviation rubble length	44.361	2.947	0.097	4.6	37.2
***Anthuridae* density**					
Substrate type	26.558	6.263	0.006	23.0	
Standard deviation macroalgal cover	21.76	7.127	0.010	11.4	34.4
***Eunicidae* density**					
Standard deviation turf algal cover	39.421	5.068	0.024	10.5	
Standard deviation rubble thickness	35.268	6.477	0.016	12.0	
Average number of branches	35.112	2.410	0.138	4.3	
Standard deviation rubble length	34.558	2.846	0.099	4.9	31.7
***Xanthidae* density**					
Average bare surface cover	-30.694	13.483	$p < 0.001$	23.9	
Standard deviation turf algal cover	-34.812	6.438	0.015	10.1	
Standard deviation encrusting algae cover	-38.731	6.196	0.018	8.7	
Standard deviation macroalgal cover	-40.439	3.958	0.052	5.2	47.9
***Gnathiidae* density**					
Standard deviation rubble thickness	-19.063	2.217	0.143	4.9	4.9

FIGURES

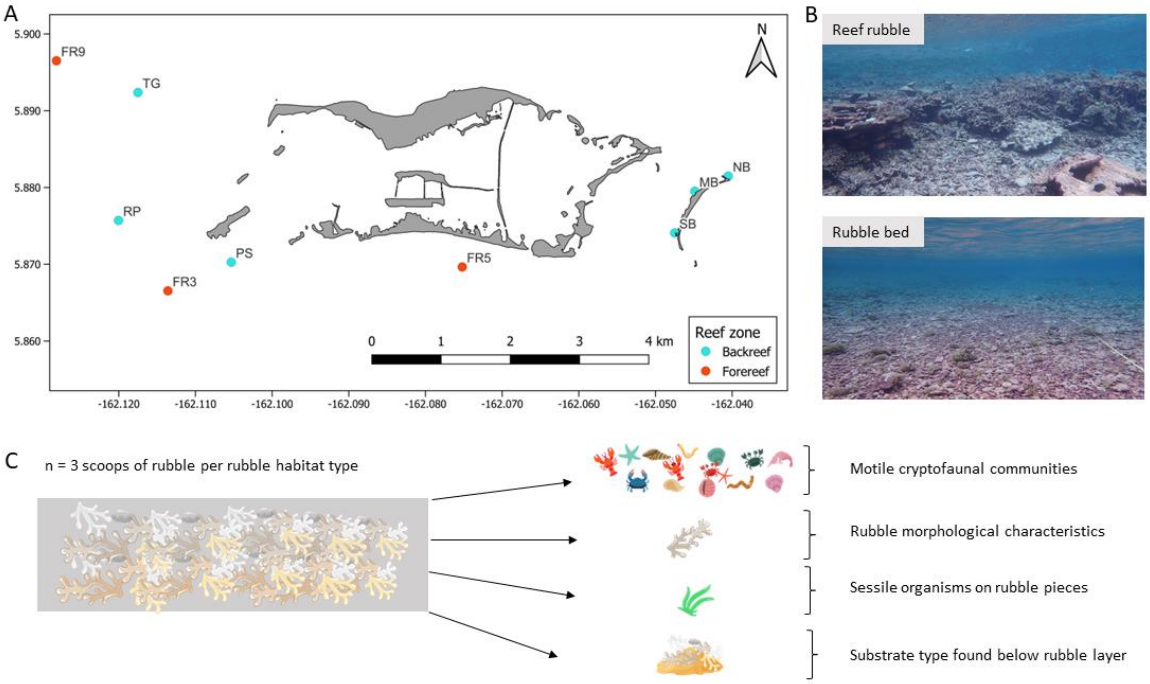

Figure 1. A) Location of survey sites (n = 9) around Palmyra Atoll, central Pacific. B) Two distinct rubble habitats were identified within reef zones (n = 2 for backreef; n = 1 for forereef). C) Coral rubble collected within quadrats (n = 3) from each rubble habitat per site to characterise rubble cryptofauna communities and rubble habitat features.

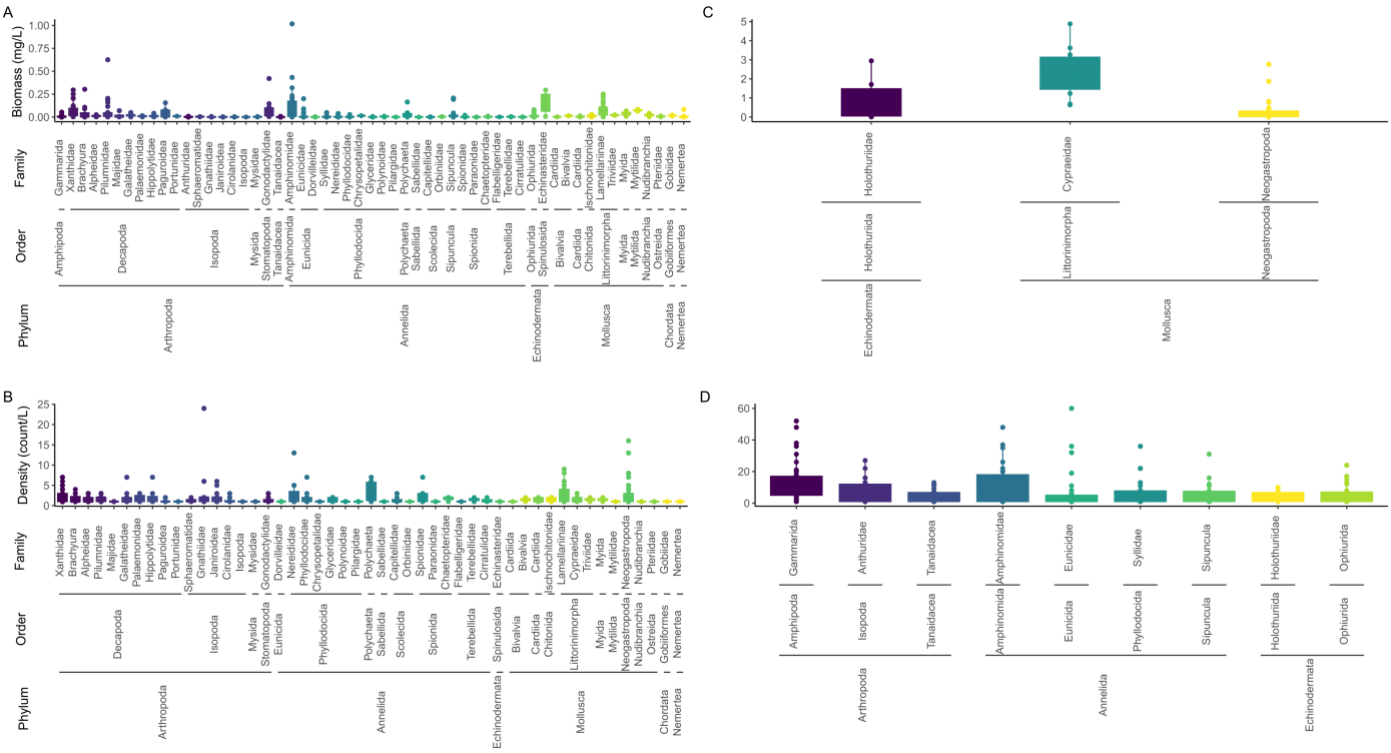

Figure 2. Biomass (A) and density (B) of motile cryptofauna living in coral rubble (n = 45 quadrats, n = 9 sites, n = 2 reef zones) at Palmyra Atoll, central Pacific. Those groups showing the highest values for both biomass and density are shown in C andD, respectively to better highlight the within-family variability.

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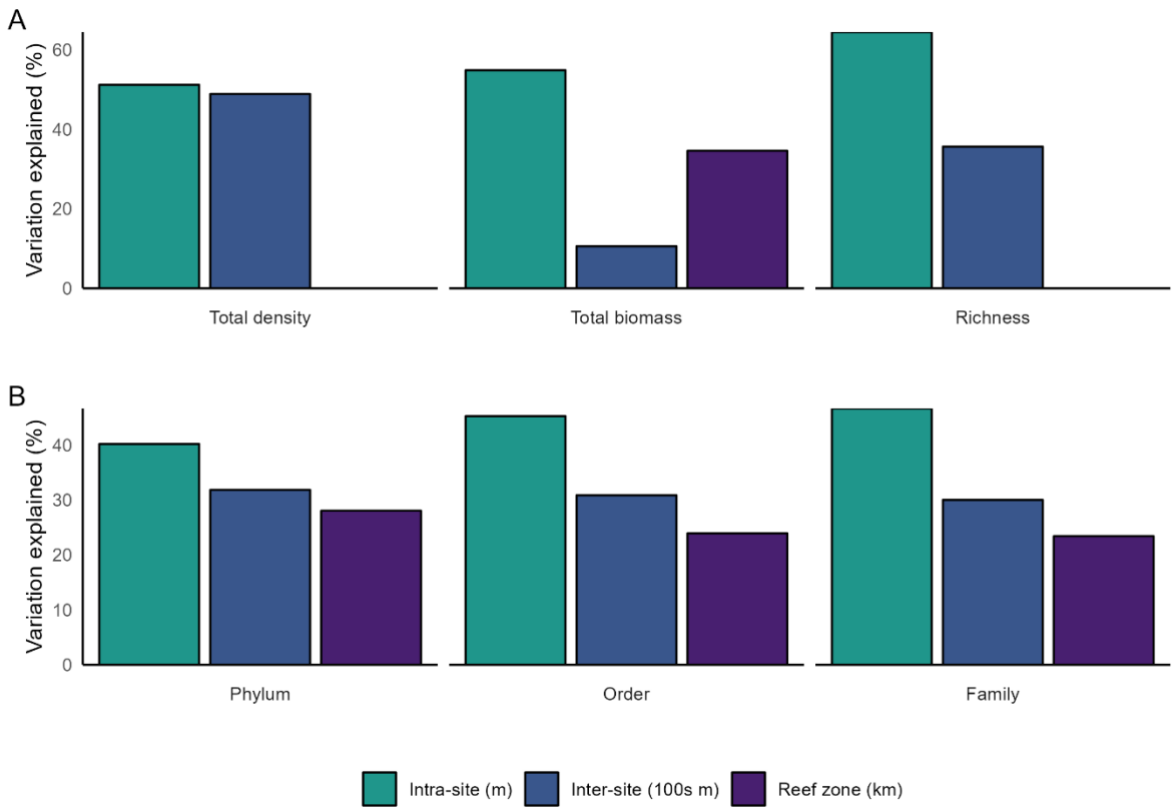

Figure 3. A) Percentage of total variation in cryptofauna total density, total biomass, and richness (univariate responses) explained by each spatial scale. B) Percentage of total variation in cryptofauna community composition (multivariate response) at three taxonomic resolutions explained by each spatial scale. Variance components in A are derived from nested ANOVA, and variance components in B are derived from PERMANOVA.

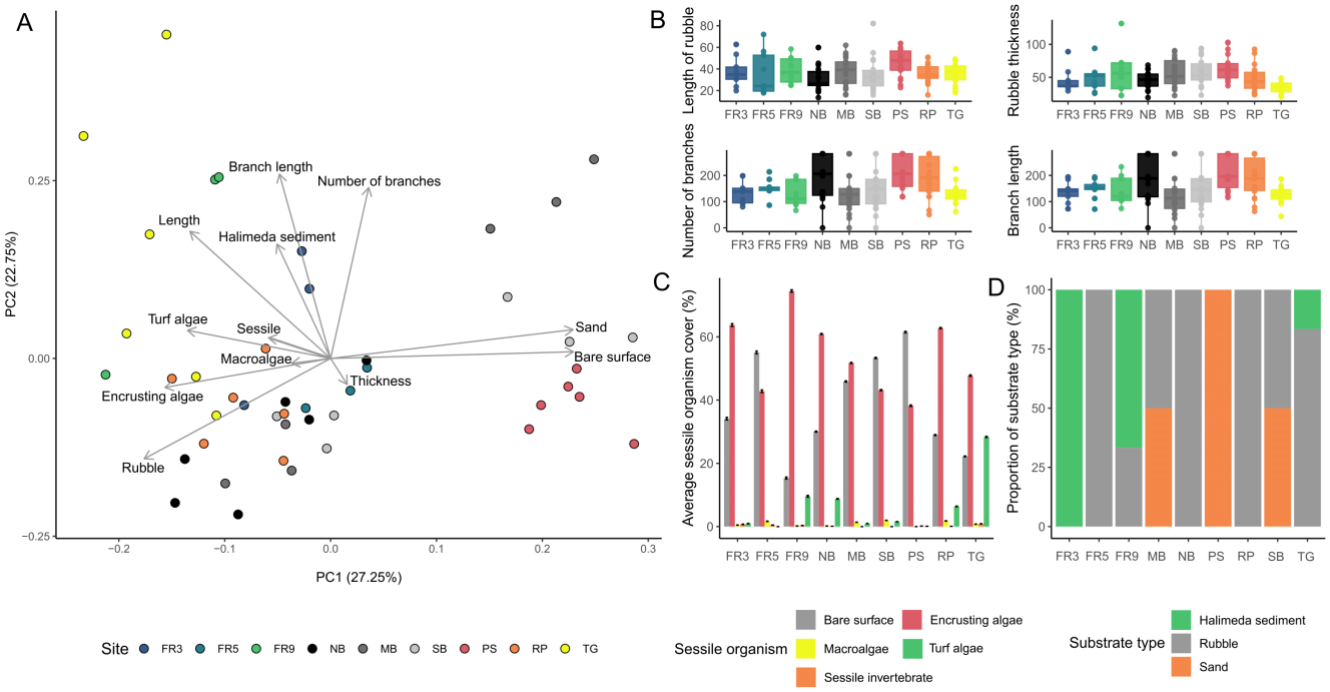

Figure 4. A) Principal components analysis (PCA) of rubble characteristics sampled from nine sites across Palmyra Atoll, central Pacific. B) Box (median and 50% quantile) and whisker (95% quantile) plots of the coefficient of variation (CoV) of rubble morphometrics across sites. Each point represents the mean from each quadrat (n = 8 rubble pieces per quadrat, n = 360 rubble pieces for all sites). C) Mean percentage cover of sessile organisms on rubble across sites. D) Substrate type found below each scooped rubble sample, expressed as a proportion of the total quadrats scooped at each site (n = 3 - 6 quadrats per site, n = 45 quadrats for all sites). For location of sites around Palmyra see Fig. 1.

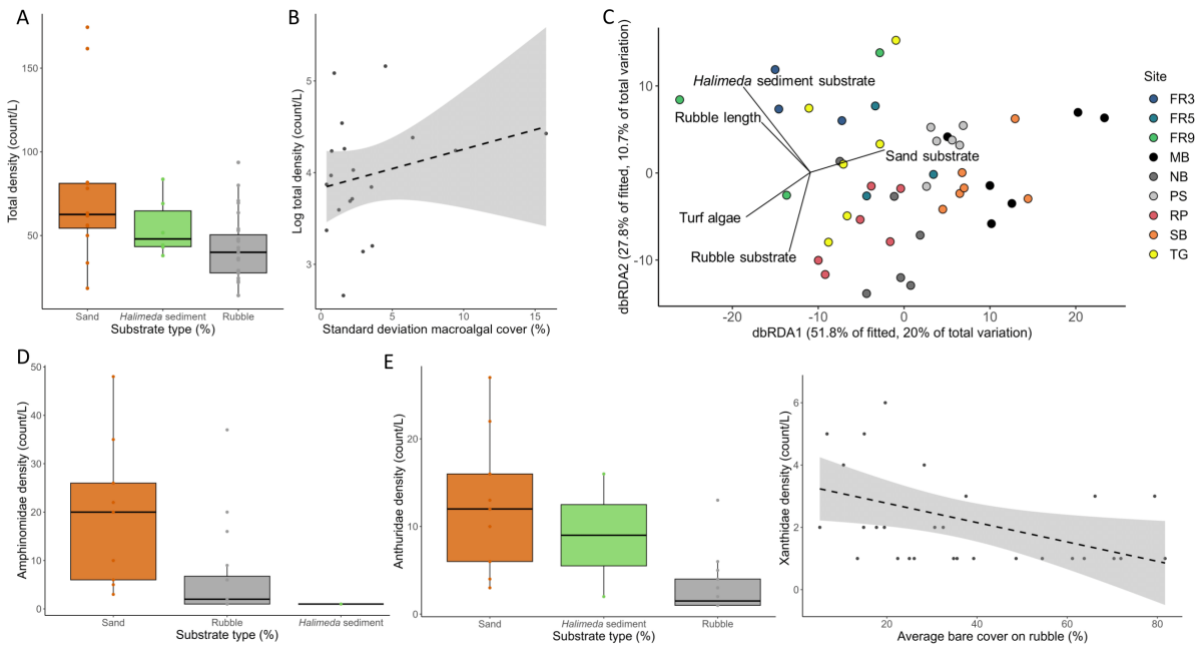

Figure 5. A) Variation of total cryptofauna density for each substrate type. Each point represents total cryptofauna density from an individual quadrat. B) Relationship between total density of cryptofauna and variability in macroalgal cover. Each point represents total cryptofauna density in an individual quadrat, and the corresponding variability of macroalgal cover on rubble pieces collected in that quadrat. C) Similarity in cryptofauna community phyla across sites at Palmyra Atoll and their proximate environmental drivers. The direction of the environmental vector lines indicates the relationship of each variable to the site groupings in multivariate space. The length of each vector line is proportional to the strength of the variance explained by that variable. D) Variation of *Amphinomidae* density measured for each substrate type. Each point represents the density of *Amphinomidae* from an individual quadrat. E) Variation of *Anthuridae* density measured for each substrate type. Each point represents the density of *Anthuridae* from an individual quadrat. F) Relationship between *Xanthidae* density with average bare surface cover on rubble. Each point represents the density of *Xanthidae* crabs in an individual quadrat, and the corresponding average bare surface cover on rubble pieces collected in that respective quadrat.

APPENDICES

Table A 1 Eleven predictors used to model cryptofauna community structure and rubble habitat characteristics. Reef zones include forereef (FR) and backreef (BR) Substrate types include *Halimeda* (calcifying alga) sediments (HS), Rubble (R), Sand (S). SD, standard deviation.

Reef Zone	Site	Meanno. branches	SDbranch length (cm)	SDlength (cm)	SDthickness (cm)	SDturf algae (%)	SDmacroalgae (%)	SDsessile invert (%)	SDencrust algae (%)	Meanbare (%)	Substrate

FR	FR3	0.96	1.23	4.59	1.65	0.00	1.61	0.00	30.28	35.93	HS
FR	FR3	0.79	1.70	2.91	2.04	0.00	4.22	0.00	38.42	31.74	HS
FR	FR3	0.75	1.04	2.02	1.25	5.92	0.00	10.21	24.36	34.70	R
FR	FR5	0.58	1.31	2.79	0.87	0.00	1.12	4.71	28.82	61.92	R
FR	FR5	0.71	1.15	2.63	1.39	0.00	8.68	0.00	32.47	45.79	R
FR	FR5	1.04	1.00	3.76	2.24	0.00	1.85	0.00	28.84	57.48	R
FR	FR9	0.96	2.21	3.86	0.57	3.06	0.43	0.00	24.61	23.00	HS
FR	FR9	1.25	1.58	3.37	2.45	24.78	0.00	0.00	33.11	18.22	HS
FR	FR9	0.71	1.37	2.89	1.12	20.38	1.63	3.74	24.46	4.85	R
BR	MB	0.38	0.66	3.00	1.33	0.53	5.99	0.00	12.04	21.07	R
BR	MB	0.46	0.99	2.60	1.71	0.00	6.84	0.00	22.10	34.84	R
BR	MB	0.67	1.26	1.43	1.17	0.00	1.18	0.00	18.38	34.42	R
BR	MB	1.46	1.05	3.85	1.07	9.90	0.00	0.00	24.59	53.27	S
BR	MB	1.79	1.41	1.85	0.95	6.00	5.84	0.00	21.72	61.89	S
BR	MB	2.21	1.20	2.82	1.42	0.00	2.68	0.00	21.20	69.98	S
BR	NB	0.67	1.00	2.89	1.28	2.74	0.00	0.00	26.82	42.86	R
BR	NB	0.79	1.13	2.30	1.48	5.29	0.00	0.93	20.99	37.09	R
BR	NB	1.08	1.24	2.34	1.02	2.12	0.00	2.01	21.80	58.34	R
BR	NB	0.25	0.55	1.06	0.70	10.38	0.00	0.00	19.25	19.41	R
BR	NB	0.17	1.57	2.15	0.67	23.02	2.35	0.00	23.33	14.37	R
BR	NB	0.21	0.57	1.38	1.03	20.68	1.25	0.00	18.44	8.13	R
BR	PS	0.63	0.94	1.76	1.18	0.00	0.00	0.00	36.05	51.87	S
BR	PS	0.38	0.79	2.86	1.49	0.00	0.00	0.41	31.19	50.44	S
BR	PS	0.25	0.65	2.61	1.77	0.00	0.00	0.00	33.91	74.75	S
BR	PS	0.63	1.16	2.39	1.85	0.00	0.00	0.00	38.44	60.13	S
BR	PS	0.50	1.70	2.79	1.81	1.66	0.00	0.00	38.17	59.94	S
BR	PS	0.54	1.01	3.36	2.10	1.36	0.00	4.08	23.00	71.94	S
BR	RP	0.92	1.38	2.93	1.09	5.11	0.00	1.26	25.03	37.70	R
BR	RP	0.33	0.94	3.23	1.18	17.06	0.00	0.57	21.42	21.19	R
BR	RP	0.79	1.30	2.58	1.46	8.71	0.00	0.00	22.07	14.54	R
BR	RP	0.58	0.98	2.31	1.15	15.24	0.00	0.00	32.06	31.38	R
BR	RP	0.83	1.79	2.40	1.62	19.33	19.12	0.00	25.15	27.10	R
BR	RP	0.46	1.84	3.01	1.40	12.10	16.82	0.00	28.52	41.81	R
BR	SB	0.63	1.11	2.49	1.85	12.36	9.52	0.00	19.69	36.71	R
BR	SB	0.58	1.22	2.17	1.37	0.00	2.55	0.00	25.93	48.36	R
BR	SB	0.46	0.80	2.29	1.08	0.00	9.34	0.00	16.59	49.17	R
BR	SB	0.96	1.11	2.11	1.37	1.83	0.44	0.00	19.50	76.66	S
BR	SB	0.79	1.42	2.95	1.50	4.81	3.02	0.00	31.18	63.83	S
BR	SB	1.46	0.98	1.77	1.28	0.00	2.55	0.00	33.58	45.27	S
BR	TG	0.75	1.30	2.52	0.82	13.71	0.00	3.40	22.52	21.64	R
BR	TG	0.58	0.80	2.15	0.98	26.50	0.00	0.00	24.34	20.38	R
BR	TG	0.83	1.41	2.36	0.78	21.79	0.00	7.75	28.35	21.10	R
BR	TG	1.04	2.03	4.53	0.82	19.60	0.23	2.07	19.61	28.67	R
BR	TG	1.13	2.60	6.13	0.83	24.77	0.90	0.14	28.70	23.62	R
BR	TG	2.08	1.76	4.31	0.91	1.88	12.71	2.94	26.36	17.87	HS

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