1

2 **Variation in coral rubble cryptofauna is scale-dependent and driven by small-scale**

3 **habitat characteristics.**

4

5 Lisa S. Goberdhan[1*], Craig M. Robertson[1], Jack P. Egerton[1], Michael D. Fox[2], Maggie D.

6 Johnson[2], Nicholas A. J. Graham[3], and Gareth J. Williams[1]

7

8 [1]School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB, UK

9 [2]Marine Science Program, King Abdullah University of Science and Technology 239556900,

10 Thuwal, Kingdom of Saudi Arabia

11 [3]Lancaster Environment Centre, Lancaster University, LA1 4YQ, UK

12

13

14

15

16

17

18

19

20

21

22

l.goberdhan@bangor.ac.uk

23 **ABSTRACT**

24 Motile cryptofauna living in dead coral rubble represent some of the greatest biodiversity and

25 basal energetic resources on tropical coral reefs. Yet, we know relatively little about how and

26 why coral rubble cryptofauna communities change over space and time. As human impacts

27 increase the degradation of living hard corals to dead coral rubble on many reefs worldwide,

28 understanding the communities that will succeed in these degraded environments, and the

29 factors paramount to their success, becomes increasingly central to coral reef ecology and

30 conservation. Using a remote and uninhabited oceanic atoll in the Pacific Ocean, we quantified

31 the natural spatial variability in motile cryptofauna diversity and community structure in coral

32 rubble across scales (m to km) and tested whether variability at smaller scales could be

33 explained by gradients in microhabitat. We show that coral rubble cryptofauna communities

34 are most variable at intra-site scales (m) rather than inter-site scales (100s m) or between reef

35 zones (km scales). We also show that a substantial amount of variation in cryptofauna density

36 (55%) and phyla-level community structure (31%) is explained by small-scale habitat

37 characteristics, specifically the substrate type below the rubble and the variability in macroalgal

38 cover on individual rubble pieces. Our findings highlight the need to study small-scale

39 processes that are relevant to motile cryptofauna and their community interactions if we are to

40 elucidate the structuring forces of these diverse cryptic assemblages on coral reefs.

41

42 **KEYWORDS:**

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

44

45

46

l.goberdhan@bangor.ac.uk

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

l.goberdhan@bangor.ac.uk

72 (Rogers et al. 2014, 2018, Morais et al. 2020, Tebbett et al. 2023). As a result, the role coral

73 rubble plays in overall reef ecosystem structure and function has become a focus of research in

74 recent years (Rasser & Riegl 2002, Biondi et al. 2020, Ceccarelli et al. 2020, Kenyon et al.

75 2020, Masucci et al. 2021, Wolfe et al. 2021).

76 Despite a seemingly barren and featureless appearance, coral rubble forms complex

77 microhabitats that host a diversity of life including microbes and biofilms, sessile and

78 encrusting taxa, and motile cryptobenthic fishes and invertebrates (Gischler & Ginsburg 1996,

79 Enochs 2012, Kramer et al. 2014). Invertebrate motile cryptofauna (hereafter motile

80 cryptofauna) like crabs, shrimps, molluscs, and polychaetes, comprise the highest density and

81 diversity of animals directly associated with coral reef substrates (Plaisance et al. 2009). Their

82 diversity and abundance enable them to perform a wide range of functional roles including

83 scavenging, predation, cleaning fishes, sediment clearing, bioturbation and parasitism (Keable

84 1995, Becker & Grutter 2004, Stewart et al. 2006, Pollock et al. 2013). One of their more

85 influential roles is arguably as a significant basal energetic resource to higher level consumers

86 (Glynn 2011, Kramer et al. 2013a, 2014, 2017) and they are well represented among the gut

87 contents of many reef fishes (Randall 1967, Kramer et al. 2015, Casey et al. 2019a).

88

89 Motile cryptofauna density, biomass and productivity are more than an order of magnitude

90 greater in dead corals and coral rubble than within live coral colonies (Enochs & Manzello

91 2012, Fraser et al. 2021, Stella et al. 2022). Due to their disproportionate abundance in coral

92 rubble and the increasing prevalence of coral rubble on reefs, motile cryptofauna will likely

93 play an increasingly important role in coral reef food webs and ecosystem functioning (Fraser

94 et al. 2021, Stella et al. 2022, Wolfe et al. 2023b). This is well supported by modelling

95 projections that predict an initial increase in secondary productivity of benthic invertebrates on

96 degraded reefs which may temporarily support reef trophodynamics (Rogers et al. 2014, 2018).

l.goberdhan@bangor.ac.uk

97 However, despite their ubiquity, motile cryptofauna remain one of the most understudied

98 groups of organisms on coral reefs. Their small size, cryptic nature and the methodological

99 difficulties involved with quantitative sampling, means they remain poorly described and

100 underrepresented in ecological studies (Reaka-Kudla 1997, Small et al. 1998, Dennis &

101 Aldhous 2004, Plaisance et al. 2011). This represents a substantial gap in our understanding of

102 community organisation for some of the greatest metazoan biodiversity on coral reefs.

103 In many ecosystems, ecological communities are most variable at small spatial scales (cm to

104 m) driven in part by gradients in microhabitat structure (Underwood & Chapman 1996,

105 Coleman 2002, Anderson et al. 2005, Harris et al. 2015). For example in woodlands and

106 rainforests, small-scale features like branch thickness, leaf density (Halaj et al. 2000) and leaf

107 litter quality (Lassau et al. 2005) drive invertebrate abundance and community structure.

108 Similarly, the high density, biomass and productivity of motile cryptofauna in coral rubble may

109 be due to the increased complexity of interstitial spaces (Wolfe et al. 2023a) and the micro-

110 structural complexity provided by encrusting taxa like macroalgae and turf algae living on the

111 rubble (Kramer et al. 2013b, Roff et al. 2013, Lavender et al. 2017). However, motile

112 cryptofauna in coral rubble have typically been described across broader spatial scales (10s m

113 to km) that compare community structure between reef habitats and depths, and investigations

114 into their driving forces focused on site-level gradients in wave exposure (Takada et al. 2012,

115 Masucci et al. 2021) and water quality (Takada et al. 2008). While these studies show

116 generalisable patterns at broader scales, it remains unclear at what scales motile crytopfauna

117 are most variable and what role, if any, microhabitat structure plays in dictating these patterns.

118 Here, our overarching aims were to quantify the variability in motile cryptofauna diversity and

119 community structure (total density, biomass, and community composition at three taxonomic

120 resolutions) in coral rubble across scales (m to km) and test whether variability at smaller scales

121 could be explained by gradients in microhabitat. We partition community composition into

l.goberdhan@bangor.ac.uk

122   three taxonomic levels (phyla, order and family) to determine how much variation can be

123   explained by microhabitat factors across these incremental increases in underlying ecological

124   complexity. We did this at a remote, uninhabited coral reef atoll system that lacks the

125   confounding effects of direct local human impacts on reef ecosystem structure and function. In

126   doing so, we provide key insights into the natural variability of motile cryptofauna living in

127   coral rubble across scales.

128

129   **2. MATERIALS AND METHODS**

130   **2.1 Study site**

131   Palmyra Atoll National Wildlife Refuge is the northernmost atoll in the Northern Line Islands,

132   central Pacific. It consists of 12 km^2 of land area and 47.2 km^2 of subtidal reef (Williams et al.

133   2011). Palmyra has no permanent human population and is part of the Pacific Remote Islands

134   Marine National Monument and is protected under United States federal law. Palmyra's remote

135   location and its protected status provides the unique opportunity to study the natural variability

136   of ecosystems with minimal direct human impacts.

137   **2.2 Defining and surveying coral rubble habitats**

138   Nine sites were surveyed around Palmyra in October to November 2022 (Fig. 1). Six of these

139   sites were located on the wave sheltered backreef and three were on the wave exposed forereef

140   (the reef slope facing the open ocean). Of the backreef sites, three were located on the open

141   western terrace, and the remaining three were located on the closed eastern side of the atoll

142   (Fig. 1). Considering that wave exposure can influence benthic community dynamics (Williams

143   et al., 2011; Williams et al., 2013), we hypothesised that there would be a difference in motile

144   cryptofauna community structure between the open western terrace sites and closed eastern

145   sites. Overall, these sites were selected based on two factors: 1) their spatial breadth across the

l.goberdhan@bangor.ac.uk

146   atoll which, given the concurrent gradients in other benthic communities like corals (Williams

147   et al. 2011, 2013) should encompass a wide range of cryptofauna communities, and 2) that all

148   these sites contained 'rubble patches', defined here as accumulations of dead coral rubble ≥ 1

149   m in length and width. During reconnaissance surveys on the backreef, we observed two

150   physically distinct rubble habitat types, likely formed by different physical mechanisms. Type

151   1, which we referred to as 'reef rubble', were rubble patches interspersed between other benthic

152   habitats (e.g., live coral) on the coral-dominated reef (Fig. 1). Type 2, which we referred to as

153   'rubble beds', were featureless mass accumulations of coral rubble that spanned > 1 km in

154   extent (Fig. 1), similar to rubble flats described at One Tree Reef in the southern Great Barrier

155   Reef (Shannon et al. 2012). We hypothesised that the smaller 'reef rubble' patches were formed

156   by the physical destruction of corals within close proximity, whereas the larger 'rubble beds'

157   were the result of rubble accumulation over greater distances by strong hydrodynamic action.

158   Once deposited, rubble within rubble beds may undergo further fragmentation through physical

159   reworking (Shannon et al. 2012). We hypothesised that if reef rubble and rubble beds were

160   indeed different rubble habitat types, then they may contain different cryptofauna communities.

161   No rubble beds were located on the forereef, likely due its sloping geomorphology whereby

162   rubble accumulates as a talus at the foot of the slope at great depths (Scoffin 1993), beyond the

163   accessible survey limits of this study.

164   Within each rubble habitat type (n = 2 habitat types), a 0.5 m^2 quadrat was haphazardly placed

165   over rubble and cryptofauna and rubble characteristic data were collected (described below).

166   This was repeated twice within each rubble habitat type (n = 3 quadrats) of each reef zone (i.e.

167   n = 6 quadrats per backreef site; n = 3 quadrats per forereef site).

168

169   **2.3 Quantifying coral rubble cryptofauna communities**

l.goberdhan@bangor.ac.uk

170   Within each 0.5 m^2 quadrat, approximately 1 L of coral rubble was scooped to an average depth

171   of 5 – 10 cm directly from the rubble patch surface using a plastic beaker. Each scoop of rubble

172   was immediately placed in double-bagged sealable plastic bags underwater and returned to the

173   lab for processing. At the lab, each rubble scoop was emptied into a bucket and flushed with

174   fresh water three times. After each flushing, the water was poured through a 1x1 mm mesh net

175   to retrieve cryptofauna individuals. This method was effective in capturing fauna >1 mm, but

176   excluded fauna <1 mm, meaning the total density and diversity of organisms documented here

177   is likely underestimated.

178   Using a dissecting microscope, each cryptofauna individual was identified to phylum, order

179   and family and measured to the nearest 0.1 mm using standard linear measurements (carapace

180   width for crab-like crustaceans, carapace length for shrimp-like crustaceans, longest distance

181   of shell length for molluscs diameter for echinoderms with radial symmetry, and length for all

182   types of worms. Individuals were blotted dry and weighed to the nearest whole mg on an

183   analytical balance (± 0.0001mg). Total cryptofauna density (individuals L^{-1}), biomass, and

184   community composition were determined for each rubble patch (n = 45 scoops in total).

185   **2.3 Quantifying rubble habitat characteristics**

186   Within each 0.5 m^2 quadrat, eight pieces of rubble were haphazardly collected (n = 24 – 48

187   pieces per site) and used to estimate the following rubble morphological parameters: (a) length

188   (longest span in any direction), (b) mean width (n = 2 – 3 measurements per rubble piece), (c)

189   number of branches (referred to here as 'branchiness'), and (d) mean branch length. The

190   substrate type found immediately below the rubble layer (e.g. sand, dead *Halimeda* pellets, or

191   more rubble) was recorded, and provided an additional rubble habitat characteristic.

192   Of the rubble pieces collected, the cover of sessile organisms growing on each individual piece

193   of rubble was quantified. Sessile communities can differ between the top and underside of

l.goberdhan@bangor.ac.uk

194 rubble pieces due largely to differences in light exposure, interstitial sediment, and water

195 movement (Choi & Ginsburg 1983, Gischler & Ginsburg 1996, Kenyon 2021). We therefore

196 photographed each rubble piece from both sides using a Olympus TG-6 camera and used these

197 images to quantify the proportional cover of: encrusting algae (mainly crustose coralline algae

198 (CCA), *Peysonnelia*), turf algae, macroalgae (including *Dictyota*, *Lobophora* and *Halimeda*),

199 sessile invertebrates (including live coral and sponges), and bare surface (if the surface

200 appeared bare or covered in micro and endolithic algae). We did this using the guides function

201 in Microsoft Powerpoint. A 66 x 38 grid (in which each grid cell = 0.5 cm) was placed over

202 each image. The number of cells occupied by each sessile group on both sides of each rubble

203 piece was counted.The proportion of each sessile group on a rubble piece was calculated by

204 dividing the total number of grid cells occupied by the sessile group by the total number of grid

205 cells occupied by the respective rubble piece.

2.5 Statistical analyses

2.5.1 Testing for differences in cryptofauna communities on the backreef

208 We tested for an effect of backreef site groupings (fixed factor, 2 levels: open western terrace

209 and closed eastern; with site as a random factor nested within backreef groupings) on

210 cryptofauna total density, total biomass, richness (calculated using Margalef's index)

211 (univariate responses), and community composition (multivariate response). We also

212 separately tested for an effect of rubble habitat type (fixed factor, 2 levels; with site as a random

213 factor nested within rubble habitat type) on the same community metrics.

214 We used a hierarchical nested permutational analysis of variance (PERMANOVA) (Anderson

215 2001a) using the PERMANOVA+ (Anderson et al. 2008) add-on for PRIMER-E (version 7.0)

216 (Clarke & Gorley 2015). Analyses were based on square-root transformed data, a Euclidean

217 (for total density, total biomass, Margalef's richness) and a Bray-Curtis (for community

l.goberdhan@bangor.ac.uk

218   composition) similarity matrix, and 9999 permutations of the residuals under a reduced model

219   (Anderson 2001b). Differences in dispersion amongst groups were tested using PERMDISP in

220   PRIMER-E (version 7.0) (Clarke & Gorley 2015).

221   There was no effect of backreef site groupings on cryptofauna total density, total biomass,

222   richness and community composition at each of three taxonomic levels (phylum, order and

223   family) (Table S1, Supplemental Material). Similarly, there was also no effect of rubble habitat

224   type on any of the measured community metrics. (Table S2, Supplemental Material).

225   Furthermore, there was no significant dispersal effects amongst groups (Table S3,

226   Supplemental Material). As a result, data collected on the backreef from both rubble habitat

227   types and site groupings were pooled for further analyses.

228   **2.5.2 Determining scales of variation in cryptofauna communities**

229   The cryptofauna data were assigned to three hierarchical levels of spatial organisation: 'reef

230   zone' (forereef, backreef) which spanned kilometres, 'site' (n = 9) spaced 100s of metres apart,

231   and 'quadrat' spaced metres apart at each site (n = 3 - 6 per site, n = 45 across all sites). To

232   determine which of these scales (reef zone, inter-site, intra-site) captured the most underlying

233   variation in total cryptofauna density, total biomass, and richness (univariate responses) and

234   community composition at three taxonomic resolutions (phylum, order, family) (multivariate

235   responses), we used variance components analyses. In hierarchical designs such as ours, larger

236   spatial scales necessarily have fewer degrees of freedom than smaller spatial scales. Therefore,

237   when estimating individual components of variation, estimates obtained for larger scales

238   subsequently have lower precision than estimates obtained for smaller scales. Nevertheless,

239   comparisons of the relative importance of the factors based on estimates of variance

240   components are rigorous as both analysis of variance (ANOVA) estimators and multivariate

l.goberdhan@bangor.ac.uk

241 analogues of ANOVA estimators are unbiased, so their accuracy is not affected by sample size

242 (Searle et al., 1992).

243 For the three univariate responses, we used a hierarchical nested analysis of variance

244 (ANOVA), with 'site' nested in 'reef zone'. All factors were treated as random. By treating the

245 factors as random, we tested the significance of variation between levels within each factor.

246 Assumptions of normality and homogeneity of variance for each metric was tested using a

247 Shapiro-Wilk test and Levene's test, respectively. To accommodate the unbalanced design and

248 to force non-negative variance components, a restricted maximum likelihood estimation model

249 (REML) was used to calculate the variance components. Variance for each metric is presented

250 as both absolute variance and as a percent of total variation (termed the 'magnitude of effect'

251 (Graham & Edwards 2001). This allows for both quantification of total variability attributed to

252 each spatial scale and the proportion of total variability that occurs between specific scales to

253 be determined. Levene's test was performed using the *leveneTest* function (car package) and

254 the Shapiro-Wilk test was performed using the in-built *shapiro.test* function in R 4.2.3.

255 Hierarchical ANOVAs were performed using *lmer* function (lme4 package) in R 4.2.3 (Posit

256 team 2023).

257 For the multivariate responses, we again used PERMANOVA, with 'site' nested within 'reef

258 zone', with both factors treated as random. Measures of variability at the three spatial scales,

259 reef zone (km), inter-site (100s m), and intra-site (quadrat, m), were calculated from the mean

260 squares of the PERMANOVA, using the multivariate analogue of the ANOVA variance

261 component estimators and statistical significance tested using 9999 permutations of the raw

262 data under a reduced model. PERMANOVA variance components are presented as absolute

263 variance (i.e. the square root of estimates of the variance components) (Anderson et al., 2008)

264 and as a proportion of total variability within each response variable (Underwood & Chapman,

265 1996).

l.goberdhan@bangor.ac.uk

266   Given the unbalanced sampling design, we conducted a jackknife sensitivity analysis to

267   determine if our estimates of variation were influenced by our sampling effort. We conducted

268   a traditional leave-one-out jackknife analysis (i.e. dropping only one sample from each

269   resampled dataset) and we also conducted an analysis where we dropped 18 random samples

270   from each resampled dataset. We performed these analyses on all community metrics – density,

271   biomass, richness, and community composition at all three taxonomic levels.

272   **2.5.3 Visualising rubble habitat characteristics**

273   To simultaneously visualise the correlation across all rubble habitat characteristics (rubble

274   morphometrics (rubble length, width, branchiness, branch length), cover of sessile organisms,

275   and the substrate types below the rubble patches), we used Principal Component Analysis

276   (PCA). To visualise variability of rubble morphometrics at the site and quadrat scales, we

277   calculated the coefficient of variation (CoV), a unitless measure calculated as the ratio of the

278   standard deviation to the mean.

279   **2.5.4 Testing for correlations between cryptofauna communities and rubble habitat**
280   **characteristics**

281   To test whether variations in rubble habitat characteristics explained variation in cryptofauna

282   community composition, we used a permutational distance-based multivariate multiple

283   regression model (DISTLM) (McArdle & Anderson 2001). DISTLM is used for modelling the

284   relationship between a resemblance matrix and a single (multivariate regression) or set of

285   predictor variables (multivariate multiple regression). The technique makes no prior

286   assumptions about the distribution of the response variable , and therefore normality does not

287   have to be satisfied (Anderson et al. 2008).

288   Models were constructed for three univariate responses using a Euclidean similarity matrix

289   (cryptofauna total density and total biomass, and Margalef's richness), and three multivariate

l.goberdhan@bangor.ac.uk

290   responses using a Bray-Curtis similarity matrix (community composition at the phylum, order,

291   and family taxonomic resolution). Additionally, we constructed univariate models for the four

292   most abundant taxa (*Gammarida, Amphinomidae, Eunicidae* and *Anthuridae*) and two others

293   (*Xanthidae* and *Gnathiidae*) chosen due to their ecological significance to coral reef

294   trophodynamics (Kramer et al. 2015, Artim et al. 2017, Casey et al. 2019b, Nicholson et al.

295   2020).

296   Prior to model fitting, the predictor variables were investigated for co-linearity using draftsman

297   plots and Pearson's (r) pairwise correlations. For the rubble morphometrics and sessile

298   organism cover, each variable's mean value correlated with its respective standard deviation (r

299   > 0.7). We chose to retain the standard deviation for each predictor rather than the mean, with

300   two exceptions: the mean number of branches was retained (we deemed this more reflective of

301   each individual rubble piece's structural complexity) and mean bare surface cover since its

302   standard deviation also correlated with the standard deviation of encrusting algae. The

303   remaining eleven predictors (Table A1, Appendix) were included in the model-fitting process.

304   Each predictor was log-transformed, normalised (to account for the differences in units and

305   ranges among the predictors) and fitted conditionally in a step-wise manner to the cryptofauna

306   community resemblance matrix. Tests were based on 9999 permutations of the residuals under

307   the reduced model (Anderson 2001a). Model selection was based on Akaike's Information

308   Criterion (Akaike 1998) with a second-order bias correction applied (AICc) (Hurvich & Tsai

309   1989) to account for the relatively high number of predictor variables relative to the response

310   variable replication. Once the optimal model was selected, we further investigated the

311   underlying relationships between the response and top contributing predictor variables using

312   distance-based redundancy analysis (dbRDA) (McArdle & Anderson 2001) (for the

313   multivariate models) and boxplots and scatter plots (for the univariate models).

314

l.goberdhan@bangor.ac.uk

315 **3. RESULTS**

316 **3.1 Cryptofauna communities in coral rubble (density, biomass, richness, community**

317 **composition)**

318 Across our samples, we identified 2603 individual motile cryptofauna from 6 phyla, 28 orders,

319 and 57 families (Fig. 2; Table S4 in Supplemental Material)). Mean (± 1 standard error) density

320 of cryptofauna across all quadrats (n = 45) was 58 ± 5.3 individuals L^{-1} (range = 17 – 194

321 individuals L^{-1}), mean biomass was 1.4 ± 0.21 mg (range = 0.03 – 5.01 mg), mean number of

322 families was 13 ± 0.5 (range 6 – 21), and mean richness was 3.2 ± 5.3 (range 1.3 – 5.1).

323 The Arthropoda (primarily crustaceans) and Annelida (polychaetes) were the most abundant

324 phyla, representing 47% and 36% of all individuals, respectively (Fig. 2). The most abundant

325 orders were Amphipoda, Isopoda, Amphinomida and Eunicida, which also contained the most

326 abundant families *Gammarida, Anthuridae, Amphinomidae* and *Eunicidae*. The phylum

327 Mollusca dominated, representing 71% of the total cryptofauna biomass, with the family

328 *Cypraeidae* (cowries) and order Neogastropoda contributing 48% and 18% to total biomass,

329 respectively. The second top contributing phylum Echinodermata represented 11% of total

330 biomass, with the family Holothuriidae (sea cucumbers) representing 9% of total biomass. The

331 phyla Arthropoda and Annelida encompassed the greatest number of families identified, with

332 21 and 20 families, respectively.

333 **3.2 Scales of variation in cryptofauna density, biomass, and richness (univariate)**

334 Across the intra-site (m), inter-site (100s m) and reef zone (km) scales we examined,

335 cryptofauna density, biomass and richness were always greatest at the smallest intra-site scale

336 (Fig. 3, Table S5 in Supplemental Material). Variation in total cryptofauna density was greatest

337 at intra-site and inter-site scales, representing 51% and 49% of the total variation, respectively

338 (Fig. 3A). Variability in total cryptofauna biomass was greatest at the intra-site and reef zone

l.goberdhan@bangor.ac.uk

339   scales, representing 55% and 35% of the total variation, respectively. Variability in total

340   richness was greatest at the intra- and inter-site scale, representing 64% and 36% of the total

341   variation, respectively.

342   There was significant variation in total cryptofauna density at the inter-site (100s m) scale

343   (ANOVA; $F_{7,44} = 7.07$, $p < 0.001$) but not at the reef zone (km) scale (ANOVA; $F_{1,44} = 0.52$, p

344    $= 0.480$). Similarly, there was significant variation in cryptofauna richness at the inter-site (100s

345   m) scale (ANOVA; $F_{7,44} = 2.84$, $p = 0.018$) but not at the reef zone (km) scale (ANOVA; $F_{1,44}$

346    $= 0.26$, $p = 0.613$). In contrast, there was significant variation in total cryptofauna biomass at

347   the reef zone (km) scale (ANOVA; $F_{1,44} = 6.70$, $p = 0.014$) but not at the inter-site (100s m)

348   scale (ANOVA; $F_{7,44} = 1.04$, $p = 0.420$).

349

350   **3.3 Scales of variation in cryptofauna community composition (multivariate)**

351   At all three taxonomic resolutions, cryptofauna community variability decreased as scale

352   increased. Variability was greatest at the intra-site (quadrat, m) scale, and then decreased at the

353   inter-site scale (100s m), and then again at the reef zone scale (km) (Fig. 3B). Variability at the

354   intra-site scale also increased as taxonomic resolution increased (from phylum, to order to

355   family), while the proportion of variability at the inter-site and reef zone scale was unaffected

356   by taxonomic resolution (Fig. 3B). There was significant variation in community composition

357   at both the reef zone and inter-site scale at all three taxonomic resolutions (Table S6 in

358   Supplemental Material).

359   Patterns of univariate and multivariate variation across the three spatial scales were matched

360   by the jackknife analysis estimates, reinforcing that the largest portion of variation was always

361   found at the smallest spatial scale despite an unbalanced sampling design. As expected, the

362   largest spatial scale (reef zone, km) had the least precision for estimating variance components

l.goberdhan@bangor.ac.uk

363   (Table S7, Supplemental Material). Whilst in this study it was logistically necessary to have

364   only two levels at the largest spatial scale (km), it is advised for future studies to have a greater

365   number of levels at the largest spatial scale (reducing the number of lower-level replicates, if

366   necessary) to improve the precision of variance components estimates across spatial scales

367   ranging kilometres.

368   **3.4 Summary of rubble habitat characteristics**

369   Across our samples, mean (± 1 standard error) rubble length was 7.1 ± 3.4 cm, and mean rubble

370   thickness was 2.3 ± 1.4 cm. The mean number of branches was 1.0 ± 1.2, and mean branch

371   length was 0.9 ± 1.4 cm (Fig. 4). Encrusting algae was the most dominant sessile organism

372   living on rubble, with a mean cover of 52.7 ± 30.8 %, followed by bare surface (39.2 ± 30.9

373   %). Three substrate types were recorded below the sampled rubble. The most common was

374   more rubble (found under 62% of quadrats), followed by sand at three out of the six backreef

375   sites (27% of quadrats), and *Halimeda* sediment was found predominantly at forereef sites

376   (11% of quadrats) (Fig. 4).

377   There were correlations among the rubble habitat characteristics (Fig. 4). Sandy substrates

378   strongly correlated with bare surface cover on rubble, whilst rubble substrates strongly

379   correlated with encrusting algae on rubble. Rubble morphological characteristics were

380   uncorrelated or had weak correlations with substrate type and algal cover. Some sites had low

381   intra-site variability in rubble morphological characteristics, whereas others were much more

382   variable. For example, the southwest backreef (site: PS, Fig. 1) was consistently characterised

383   by sandy substrates and rubble pieces with a higher percentage of bare surface cover (Fig. 4,

384   note the low overall dispersion among replicates). In contrast some sites, like the northwest

385   backreef (site: TG, Fig. 1), showed high intra-site variability in rubble habitat characteristics,

386 and were characterised by rubble substrates and rubble pieces with a higher percentage of

387 encrusting algae (Fig. 4).

388 **3.5 Correlations between cryptofauna communities and rubble habitat characteristics**

389 Substrate type below the rubble, variability in macroalgae and turf algae cover, variability in

390 rubble thickness, and the average number of rubble branches together explained 54.8 % of the

391 total variation in cryptofauna density (Table 1). Of these five predictors, substrate type and

392 variability in macroalgae cover were the top performing predictors, explaining 21.7% and

393 17.6% of the total variation in cryptofauna density, respectively. Cryptofauna density was

394 greatest over sandy substrates (compared to rubble or *Halimeda* sediment substrates) and

395 showed a positive trend with variability in macroalgal cover (Fig. 5A, B). In contrast, rubble

396 habitat characteristics did not explain as much of the variation in cryptofauna biomass (9.3 %

397 variation explained) or cryptofauna richness (17.4 % variation explained) (Table 1).

398 Substrate type, variability in rubble length and variability in turf algae cover best explained

399 variations in cryptofauna community composition (Fig. 5B). At the phylum level, these three

400 predictors explained 31.4% of the total variation in cryptofauna community composition, with

401 substrate type explaining the most variation (22.3%) (Table 1). As taxonomic resolution

402 increased model performance decreased, with rubble habitat characteristics explaining just

403 12.7% and 5.4% of the cryptofauna community composition at the order and family level,

404 respectively (Table 1).

405 Variations in rubble habitat characteristics correlated with variations in the density of the four

406 most abundant cryptofauna organisms in our samples (Table 1). Variability in rubble length

407 and substrate type explained 22% of the total variation in *Gammarida* (Arthropoda) density,

408 while substrate type and variability in macroalgae cover explained 33% of the total variation in

409 *Anthuridae* (Arthropoda) density. Similarly, substrate type, variability in macroalgae cover and

410 variability in rubble length explained 36% of the total variation in *Amphinomidae* (Annelida)

411 density (Table 1). Both *Anthuridae* and *Amphinomidae* were best predicted by substrate type

412 (20.8 and 23%, respectively), with the density of both groups greatest over sandy substrates

413 (Fig. 5C, D). Variability in turf algae cover and various rubble morphometrics including

414 variability rubble thickness, mean number of branches and variability in length, explained 30%

415 of the total variation in *Eunicidae* (Annelida) density. However, no single predictor explained

416 more than 12% of the total variation and two explained less than 5% (Table 1). As such, these

417 relationships were not explored further. Variations in *Xanthidae* (crab) density were best

418 explained by the cover of bare substrate on rubble, variability in turf algae cover, encrusting

419 algae cover and macroalgae cover, together explaining 47% of the total variation in *Xanthidae*

420 density (Table 1). The cover of bare substrate on rubble alone explained 23.9%; *Xanthidae*

421 density decreased as the cover of bare substrate on the rubble increased (Fig. 5E). Finally,

422 rubble habitat characteristics did not explain any appreciable variation in *Gnathiidae* density

423 (Table 1).

424

425 **4. DISCUSSION**

426 Coral rubble cryptofauna represent an abundant basal energetic resource that support higher

427 trophic level consumers and overall coral reef biodiversity (Kramer et al. 2016, Wolfe et al.

428 2021, Stella et al. 2022). Yet, we know relatively little about how and why coral rubble

429 cryptofauna communities change over space and time. Here we show that coral rubble

430 cryptofauna communities are most variable at intra-site scales (m) rather than inter-site scales

431 (100s m) or between reef zones (km scales). We also show that a substantial amount of variation

432 in cryptofauna density and phyla-level community composition is explained by small-scale

433 habitat characteristics, including the substrate type below the rubble and the variability in

434 macroalgal cover on individual rubble pieces. Our findings highlight the need to study small-

l.goberdhan@bangor.ac.uk

435 scale processes that are relevant to individual cryptofauna organisms and their community

436 interactions if we are to elucidate the structuring forces of these diverse cryptic assemblages on

437 coral reefs.

4.1 Scales of variation in cryptofauna communities in coral rubble

439 Across the intra-site (m), inter-site (100s m) and between reef zone (km) scales we examined,

440 all cryptofauna community parameters measured were most variable at the smallest intra-site

441 scale. This is congruent with benthic invertebrate assemblages in other ecological systems. For

442 example, in temperate systems, benthic invertebrates inhabiting kelp holdfasts are most

443 variable at metre scales, from holdfast to holdfast (Anderson et al. 2005), while in the deep sea,

444 infaunal communities change substantially more with differences in sediment depth layers than

445 with differences associated to larger geographical or bathymetrical scales (Ingels & Vanreusel

446 2013). Similarly, invertebrate assemblages on temperate rocky shores are most variable at

447 centimetre to metre scales (Underwood & Chapman 1996, Benedetti-Cecchi 2001, Fraschetti

448 et al. 2005). On tropical coral reefs, other benthic groups also tend to show the greatest

449 variability at smaller spatial scales. For example, algal turf assemblages are most variable at

450 centimetre scales rather than at metre or kilometre scales (Harris et al. 2015). Understanding

451 the primary spatial scales at which organisms interact with one another and their environment

452 is an essential basis to identifying the processes that dictate community structure (Underwood

453 & Chapman 1996). These commonalities across trophic levels and ecological systems suggest

454 that small-scale processes contribute a substantial amount to driving benthic community

455 organisation in the marine environment (Coleman 2002, Fraschetti et al. 2005).

456 Beyond the intra-site scale, the univariate responses of cryptofauna communities (overall

457 density, biomass and richness) showed different patterns of variation across spatial scales.

458 Variation in cryptofauna density and richness were both significant at the inter-site scale (100s

459   m) but not at the reef zone scale (km). However, variance components for cryptofauna density

460   were almost equivalent at the intra-site (m) and inter-site scales. This suggests that quantifying

461   processes acting at metres to 100s of metres should capture a large proportion of variation in

462   cryptofauna density in coral rubble. In contrast though, variance components for cryptofauna

463   richness at the intra-site scale was almost double that at the inter-site scale, suggesting that

464   processes acting at the metre scale or smaller influence the diversity of cryptofauna organisms.

465   Variation in cryptofauna biomass was significant at the reef zone scale (km) and at the intra-

466   site scale (m), but not significant at the inter-site scale (100s m). Further, the majority of

467   variance components were divided between the reef zone scale (km) and intra-site scale (m).

468   This suggests that broad-scale (km scale) processes may have direct influences on small-scale

469   processes that in turn structure cryptofauna biomass in coral rubble.

470   In contrast to univariate responses (cryptofauna density, biomass and richness), the multivariate

471   community responses showed consistent patterns of variation across spatial scales. Cryptofauna

472   community composition was significantly different across inter-site and reef zone scales,

473   suggesting that small-scale (m) to larger-scale (km) processes dictate community structure.

474   Variance components at the intra-site scale increased with increasing taxonomic resolution, a

475   similar finding observed for benthic invertebrates in temperate kelp holdfasts (Anderson et al.

476   2005) and temperate soft sediments (Vanderklift et al. 1996, Olsgard et al. 1998), and reflects

477   the increased ecological information gained via lower-level taxonomic resolution. At the inter-

478   site scale, differences in variance components across taxonomic resolutions were marginal.

479   Similarly at the reef zone scale, phylum-level community composition had the greatest variance

480   components, with marginal differences between order- and family-level variance components.

481   This suggests that processes acting at kilometres and 100s of metres structure cryptofauna

482   communities at a broad taxonomic level (phylum in this case) with not much change in

483   community variance with increasing taxonomic resolution.

l.goberdhan@bangor.ac.uk

484 While these findings are novel for cryptofauna communities inhabiting rubble on tropical coral

485 reefs, the diversity of the sampled assemblages in this study (57 families from six phyla) is

486 comparably much lower than studies from Australia where greater than 122 families occur at

487 individual study sites (Stella et al. 2022, Wolfe et al. 2023b). Due to its remoteness and size,

488 island biogeography theory may explain the lower species richness found at Palmyra Atoll

489 compared to Australia (Maragos & Williams, 2011), however there are methodological

490 limitations within this study that may have influenced this as well. While we identified most

491 organisms to family, some individuals were grouped at the phylum level (e.g. Ribbon worms:

492 Nemertea), while others were grouped at the order level (e.g. the gastropod Mollusca:

493 Neogastropoda, Littorinimorpha). Furthermore, the density and biomass of coral rubble

494 cryptofauna can be dominated by Harpacticoid copepods that are <1 mm in size (Fraser et al.

495 2021, Wolfe et al. 2023a) and that would have been missed by our sampling approach.

496 Therefore, it is likely the abundance and biodiversity of motile cryptofauna we describe here is

497 underestimated. Despite this, the diversity of cryptofauna (57 families) is impressive

498 considering that of the two most frequently studied marine organisms at Palmyra Atoll – hard

499 corals and non-cryptic reef-associated fish – there are only 26 families and 31 families recorded

500 respectively (Williams et al. 2008, Caselle & Carlsen unpubl. data). This finding underscores

501 the significance of cryptofauna as a source of biodiversity on Palmyra's coral reefs, and the

502 need for further study into their functional importance.

503 **4.2 Association of cryptofauna with rubble habitat characteristics**

504 The substrate type below the sampled rubble best explained variation in cryptofauna density,

505 including variation in the two most abundant organisms - annelids *Amphinomidae* and

506 arthropods *Anthuridae*. In particular, we found sandy substrates below coral rubble supported

507 increased cryptofauna density compared to either more rubble substrate or *Halimeda* sediment

508 (the calcium carbonate pellets left by the calcifying macroalga *Halimeda*). While sandy habitats

l.goberdhan@bangor.ac.uk

509   on coral reefs have comparably low rates of community production (Brock & Smith 1983,

510   Johnstone et al. 1990, Kramer et al. 2014), here we demonstrate that sandy substrates covered

511   by coral rubble can support diverse cryptofauna communities.

512   The rubble pieces are likely providing structurally complex, habitable substrate and algal and

513   other organic matter food resources (Klumpp et al. 1988, Enochs & Manzello 2012, Takada et

514   al. 2012, 2014). Also sand, while not a structurally complex habitat, does retain algal and

515   detrital resources (Johnstone et al. 1990, Kramer et al. 2014). A high proportion of the

516   organisms found within dead coral substrates are deposit feeders and omnivores (Enochs 2012,

517   Kramer et al. 2017). Across the three substrate types we recorded, sand may act as the best sink

518   for organic matter from the overlaying rubble. This may explain the increased densities of

519   *Amphinomidae* and *Anthuridae* we observed living in rubble that overlaid a sandy substrate.

520   *Amphinomidae* are an omnivorous group of polychaetes with a preference for colonising

521   environments with accumulations of decaying organic matter (Fauchald & Jumars 1979,

522   Cosentino & Giacobbe 2011, Schulze et al. 2017). *Anthuridae* are anecdotally suggested to be

523   detritivores, carnivores, browsers or filter feeders (Poore & Bruce 2012), and so too may benefit

524   from the increased food resources likely found in sandy substrates. Whilst dead *Halimeda*

525   sediments could potentially perform the same trapping function of organic matter as sand, at

526   Palmyra Atoll this substrate type is typically characteristic of the forereef zone. Strong surge

527   may frequently stir up and redeposit this sediment (Williams et al. 2011), thus reducing its

528   ability to retain organic content. The arrangement of rubble overlaying sand may represent a

529   'sweet spot' to rubble cryptofauna. It marries the habitat-provisioning of rubble and its

530   relatively extensive surface area colonised by a variety of algal and encrusting taxa that

531   promotes detrital resources, with the retainment ability of sand, providing a food-rich

532   environment to fauna inhabiting rubble.

l.goberdhan@bangor.ac.uk

533 Variation in motile crytofauna community composition at the phylum level was also best

534 explained by the substrate type below the sampled rubble. Increasing taxonomic resolution

535 (from phyla to family) resulted in a substantial reduction in the explanatory power of rubble

536 habitat characteristics. This is not surprising given that the strength of community-environment

537 relationships often differ depending on the taxonomic resolution of the community data (Lu et

538 al. 2016). For example at a course taxonomic resolution, variations in benthic invertebrate

539 communities in temperate fjords closely reflect gradients in anthropogenic pollution, whereas

540 the same communities viewed at the species-level correlate more with small-scale habitat

541 characteristics like sediment grain size (Warwick 1988a b). From the perspective of these tiny

542 organisms, the rubble characteristics measured here may represent broad-scale habitat features

543 that allow phyla-level taxa with similar traits to occupy the same niche space. However, perhaps

544 to understand community organisation of coral rubble motile cryptofauna at a finer taxonomic

545 resolution requires an appreciation of other small-scale processes, like organism dispersal

546 capabilities, competition, predation or finer-scale habitat characteristics like the availability and

547 quality of organic matter (Pacala & Levin 1997, Harris et al. 2015, Lu et al. 2016).

548 Variability in macroalgal cover was the second-best predictor of cryptofauna density in coral

549 rubble at Palmyra. This is consistent with coral rubble cryptofauna in Australia, where

550 macroalgal cover on rubble had a direct positive influence on total cryptofauna density (Wolfe

551 et al. 2023b). The physical structure of macroalgae enhances occupiable space available to

552 small benthic fauna through an increase in micro-habitat complexity that provides refuge from

553 fish predationand may enhance nutritional resource availability to herbivorous cryptofauna

554 (Stoner 1985, Roff et al. 2013, Ape et al. 2018). Furthermore, macroalgae may reduce water

555 flow, increasing the deposition of sediment (Gibbons & Griffiths 1986) rich in detritus and

556 other particulate organic matter that act as a food source to cryptofauna (Takada et al. 2012).

557 In contrast, variability in rubble thickness and the average number of branches accounted for

l.goberdhan@bangor.ac.uk

558 little variation in cryptofauna density. These findings imply that micro-complexity gained from

559 sessile organisms growing on rubble is more beneficial to cryptofauna than the structural

560 complexity of the rubble itself. However, rubble structural complexity may indirectly affect

561 crytofauna density because branchier rubble pieces tend to have higher macroalgal overgrowth

562 (Wolfe et al. 2021). While we found that the variation in rubble crab, *Xanthidae*, density was

563 not well explained by variations in algal cover on rubble, their density was negatively

564 associated with increasing bare surface cover on rubble. *Xanthidae* are omnivores with a

565 preference for algae, ranging from crustose coralline algae to turf algae (Knudsen 1960,

566 Skilleter & Anderson 1986, Kyomo 1999), suggesting their densities may be regulated in some

567 way by the abundance of sessile organisms growing on rubble.

568 With the ever-increasing degradation of living hard corals to dead coral rubble on many reefs

569 (Williams & Graham 2019), understanding the communities that will succeed in these

570 environments, and the factors paramount to their success, becomes increasingly central to coral

571 reef ecology and conservation. Motile cryptic fauna represent a significant source of coral reef

572 biodiversity and basal energetic resources to higher lever consumers, and therefore

573 understanding their role in future coral reef functioning and reef trophodynamics deserves

574 attention. The overall findings here suggest that cryptofauna communities are primarily

575 structured by small-scale processes. Habitat characteristics like the substrate type below rubble

576 and sessile organisms growing on rubble may explain broad community metrics, like density

577 and phyla-level community composition, suggesting a link with habitat complexity and food

578 availability. Future research is needed to explicitly quantify these parameters and their effects

579 in structuring motile cryptofauna communities, and how ever-changing environmental

580 conditions on contemporary reefs may impact the structure and function of these diverse cryptic

581 assemblages.

582

l.goberdhan@bangor.ac.uk

ACKNOWLEDGEMENTS

REFERENCES

Akaike H (1998) Information Theory and an Extension of the Maximum Likelihood Principle BT - Selected Papers of Hirotugu Akaike.Parzen E, Tanabe K, Kitagawa G (eds) Springer New York, New York, NY, p 199–213

Anderegg WRL, Kane JM, Anderegg LDL (2013) Consequences of widespread tree mortality triggered by drought and temperature stress. Nat Clim Chang 3:30–36.

Anderson MJ (2001a) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46.

Anderson MJ (2001b) Permutation tests for univariate or multivariate analysis of variance and regression. Can J Fish Aquat Sci 58:626–639.Anderson MJ, Diebel CE, Blom WM, Landers TJ (2005) Consistency and variation in kelp holdfast assemblages: Spatial patterns of biodiversity for the major phyla at different taxonomic resolutions. J Exp Mar Bio Ecol 320:35–56.

l.goberdhan@bangor.ac.uk

606 Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ Primer V7:Guide to Software
607   and Statistical Methods. PRIMER-E: Plymouth, UK.

608 Andringa JI, Zuo J, Berg MP, Klein R, van't Veer J, de Geus R, de Beaumont M,
609   Goudzwaard L, van Hal J, Broekman R, van Logtestijn RSP, Li Y, Fujii S, Lammers M,
610   Hefting MM, Sass-Klaassen U, Cornelissen JHC (2019) Combining tree species and
611   decay stages to increase invertebrate diversity in dead wood. For Ecol Manage 441:80–
612   88.

613 Ape F, Gristina M, Chemello R, Sarà G, Mirto S (2018) Meiofauna associated with vermetid
614   reefs: the role of macroalgae in increasing habitat size and complexity. Coral Reefs
615   37:875–889.

616 Artim JM, Hook A, Grippo RS, Sikkel PC (2017) Predation on parasitic gnathiid isopods on
617   coral reefs: a comparison of Caribbean cleaning gobies with non-cleaning
618   microcarnivores. Coral Reefs 36:1213–1223.

619 Barnhill KA, Roberts JM, Myers-Smith I, Williams M, Dexter KG, Ryan C, Wolfram U,
620   Hennige SJ (2023) Incorporating dead material in ecosystem assessments and
621   projections. Nat Clim Chang 13:113–115.

622 Becker JH, Grutter AS (2004) Cleaner shrimp do clean. Coral Reefs 23:515–520.

623 Benedetti-Cecchi L (2001) Variability in abundance of algae and invertebrates at different
624   spatial scales on rocky sea shores. Mar Ecol Prog Ser 215:79–92.

625 Biondi P, Masucci GD, Reimer JD (2020) Coral cover and rubble cryptofauna abundance and
626   diversity at outplanted reefs in Okinawa, Japan. PeerJ 8.

627 Brock RE, Smith S V. (1983) Response of coral reef cryptofaunal communities to food and
628   space. Coral Reefs 1:179–183.

l.goberdhan@bangor.ac.uk

629 Burke S, Pottier P, Lagisz M, Macartney EL, Ainsworth T, Drobniak SM, Nakagawa S

630 (2023) The impact of rising temperatures on the prevalence of coral diseases and its

631 predictability: A global meta-analysis. Ecol Lett 26:1466–1481.

632 Casey JM, Meyer CP, Morat F, Brandl SJ, Planes S, Parravicini V (2019a) Reconstructing

633 hyperdiverse food webs: Gut content metabarcoding as a tool to disentangle trophic

634 interactions on coral reefs. Methods Ecol Evol 10:1157–1170.

635 Casey JM, Meyer CP, Morat F, Brandl SJ, Planes S, Parravicini V (2019b) Reconstructing

636 hyperdiverse food webs: Gut content metabarcoding as a tool to disentangle trophic

637 interactions on coral reefs. Methods Ecol Evol 10:1157–1170.

638 Ceccarelli DM, McLeod IM, Bostrom-Einarsson L, Bryan SE, Chartrand KM, Emslie MJ,

639 Gibbs MT, Rivero MG, Hein MY, Heyward A, Kenyon TM, Lewis BM, Mattocks N,

640 Newlands M, Schlappy ML, Suggett DJ, Bay LK (2020) Substrate stabilisation and

641 small structures in coral restoration: State of knowledge, and considerations for

642 management and implementation. PLoS One 15:1–27.

643 Choi DR, Ginsburg RN (1983) Distribution of coelobites (cavity-dwellers) in coral rubble

644 across the Florida Reef Tract. Coral Reefs 2:165–172.

645 Clarke KR, Gorley RN (2015) Primer V7: User Manual/Tutorial.

646 Coker DJ, Wilson SK, Pratchett MS (2014) Importance of live coral habitat for reef fishes.

647 Rev Fish Biol Fish 24:89–126.

648 Coleman MA (2002) Small-scale spatial variability in intertidal and subtidal turfing algal

649 assemblages and the temporal generality of these patterns. J Exp Mar Bio Ecol 267:53–

650 74.

651 Cosentino A, Giacobbe S (2011) The new potential invader Linopherus canariensis

l.goberdhan@bangor.ac.uk

652   (Polychaeta: Amphinomidae) in a Mediterranean coastal lake: Colonization dynamics

653   and morphological remarks. Mar Pollut Bull 62:236–245.

654   Dennis C, Aldhous P (2004) A tragedy with many players. Nature 430:396–398.

655   Enochs IC (2012) Motile cryptofauna associated with live and dead coral substrates:

656   Implications for coral mortality and framework erosion. Mar Biol 159:709–722.

657   Enochs IC, Manzello DP (2012) Responses of cryptofaunal species richness and trophic

658   potential to coral reef habitat degradation. Diversity 4:94–104.

659   Fauchald K, Jumars P a (1979) The diet of worms: a study of polychaete feeding guilds.

660   Oceanogr Mar Biol An Annu Rev 17:193–284.

661   Fraschetti S, Terlizzi A, Cecchi-Benedetti L (2005) Patterns of distribution of marine

662   assemblages from rocky shores: evidence of relevant scales of variation. Mar Ecol Prog

663   Ser 296:13–29.

664   Fraser KM, Stuart-Smith RD, Ling SD, Edgar GJ (2021) High biomass and productivity of

665   epifaunal invertebrates living amongst dead coral. Mar Biol 168.

666   Gibbons MJ, Griffiths CL (1986) A comparison of macrofaunal and meiofaunal distribution

667   and standing stock across a rocky shore, with an estimate of their productivities. Mar

668   Biol 93:181–188.

669   Gischler E, Ginsburg RN (1996) Cavity dwellers (coelobites) under coral rubble in southern

670   Belize barrier and atoll reefs. Bull Mar Sci 58:570–589.

671   Glynn PW (2011) In tandem reef coral and cryptic metazoan declines and extinctions. Bull

672   Mar Sci 87:767–794.

673   Gove JM, Williams GJ, Lecky J, Brown E, Conklin E, Counsell C, Davis G, Donovan MK,

l.goberdhan@bangor.ac.uk

674   Falinski K, Kramer L, Kozar K, Li N, Maynard JA, McCutcheon A, McKenna SA,

675   Neilson BJ, Safaie A, Teague C, Whittier R, Asner GP (2023) Coral reefs benefit from

676   reduced land–sea impacts under ocean warming. Nature 621:536–542.

677 Graham MH, Edwards MS (2001) Statistical significance versus fit: estimating the

678   importance of individual factors in ecological analysis of variance. Oikos 93:505–513.

679 Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-

680   driven regime shifts versus rebound potential in coral reefs. Nature 518:94–97.

681 Halaj J, Ross DW, Moldenke AR (2000) Importance of Habitat Structure to the Arthropod

682   Food-Web in Douglas-Fir Canopies. Oikos 90:139–152.

683 Harris JL, Lewis LS, Smith JE (2015) Quantifying scales of spatial variability in algal turf

684   assemblages on coral reefs. Mar Ecol Prog Ser 532:41–57.

685 Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum

686   JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison

687   H, Hobbs J-PA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM,

688   Pratchett M, Schoepf V, Torda G, Wilson SK (2018) Spatial and temporal patterns of

689   mass bleaching of corals in the Anthropocene. Science (80-) 359:80–83.

690 Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J,

691   van de Leemput IA, Lough JM, Morrison TH, Palumbi SR, van Nes EH, Scheffer M

692   (2017) Coral reefs in the Anthropocene. Nature 546:82–90.

693 Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples.

694   Biometrika 76:297–307.

695 Ingels J, Vanreusel A (2013) The importance of different spatial scales in determining

696   structural and functional characteristics of deep-sea infauna communities.

l.goberdhan@bangor.ac.uk

697   Biogeosciences 10:4547–4563.

698   Johnstone R, Koop K, Larkum A (1990) Physical aspects of coral reef lagoon sediments in
699   relation to detritus processing and primary production. Mar Ecol Prog Ser 66:273–283.

700   Jonsson BG, Kruys N, Ranius T (2005) Ecology of species living on dead wood - Lessons for
701   dead wood management. Silva Fenn 39:289–309.

702   Keable SJ (1995) Structure of the marine invertebrate scavenging guild of a tropical reef
703   ecosystem: field studies at Lizard Island, Queensland, Australia. J Nat Hist 29:27–45.

704   Kenyon TM (2021) From rubble to reef: The physical and biological dynamics of coral reef
705   rubble beds. University of Queensland

706   Kenyon TM, Doropoulos C, Dove S, Webb GE, Newman SP, Sim CWH, Arzan M, Mumby
707   PJ (2020) The effects of rubble mobilisation on coral fragment survival, partial mortality
708   and growth. J Exp Mar Bio Ecol 533:151467.

709   Klumpp D, McKinnon A, Mundy C (1988) Motile cryptofauna of a coral reef: abundance,
710   distribution and trophic potential. Mar Ecol Prog Ser 45:95–108.

711   Knudsen JW (1960) Aspects of the Ecology of the California Pebble Crabs (Crustacea:
712   Xanthidae). Ecol Monogr 30:165–185.

713   Kramer MJ, Bellwood DR, Bellwood O (2014) Benthic crustacea on coral reefs: A
714   quantitative survey. Mar Ecol Prog Ser 511:105–116.

715   Kramer MJ, Bellwood DR, Taylor RB, Bellwood O (2017) Benthic Crustacea from tropical
716   and temperate reef locations: differences in assemblages and their relationship with
717   habitat structure. Coral Reefs 36:971–980.

718   Kramer MJ, Bellwood O, Bellwood DR (2016) Foraging and microhabitat use by crustacean-

719   feeding wrasses on Coral Reefs. Mar Ecol Prog Ser 548:277–282.

720 Kramer MJ, Bellwood O, Bellwood DR (2013a) The trophic importance of algal turfs for

721   coral reef fishes: The crustacean link. Coral Reefs 32:575–583.

722 Kramer MJ, Bellwood O, Bellwood DR (2013b) The trophic importance of algal turfs for

723   coral reef fishes: The crustacean link. Coral Reefs 32:575–583.

724 Kramer MJ, Bellwood O, Fulton CJ, Bellwood DR (2015) Refining the invertivore: diversity

725   and specialisation in fish predation on coral reef crustaceans. Mar Biol 162:1779–1786.

726 Kristensen LD, Stenberg C, Støttrup JG, Poulsen LK, Christensen HT, Dolmer P, Landes A,

727   Røjbek M, Thorsen SW, Holmer M, Deurs M V., Grønkjær P (2015) Establishment of

728   blue mussel beds to enhance fish habitats. Appl Ecol Environ Res 13:783–798.

729 Kyomo J (1999) Feeding patterns, habits and food storage in Pilumnus vespertilio

730   (Brachyura: Xanthidae). Bull Mar Sci 65:381–389.

731 Larsson S, Danell K (2001) Science and the Management of Boreal Forest Biodiversity.

732   Scand J For Res 16:5–9.

733 Lassau SA, Hochuli DF, Cassis G, Reid CAM (2005) Effects of habitat complexity on forest

734   beetle diversity: do functional groups respond consistently? Divers Distrib 11:73–82.

735 Lavender JT, Dafforn KA, Bishop MJ, Johnston EL (2017) Small-scale habitat complexity of

736   artificial turf influences the development of associated invertebrate assemblages. J Exp

737   Mar Bio Ecol 492:105–112.

738 Lu H-P, Yeh Y-C, Sastri AR, Shiah F-K, Gong G-C, Hsieh C (2016) Evaluating community–

739   environment relationships along fine to broad taxonomic resolutions reveals

740   evolutionary forces underlying community assembly. ISME J 10:2867–2878.

l.goberdhan@bangor.ac.uk

741   Maragos, J.E., Williams, G.J. (2011) Pacific Coral Reefs: An Introduction. In: Hopley, D

742   (eds.) Encyclopedia of Modern Coral Reefs. Encyclopedia of Earth Sciences Series.

743   Springer, Dordrecht

744   Masucci GD, Biondi P, Reimer JD (2021) Impacts of coastal armouring on rubble mobile

745   cryptofauna at shallow coral reefs in Okinawa, Japan. Plankt Benthos Res 16:237–248.

746   McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: A

747   comment on distance-based redundancy analysis. Ecology 82:290–297.

748   Morais J, Morais R, Tebbett SB, Bellwood DR (2022) On the fate of dead coral colonies.

749   Funct Ecol 36:3148–3160.

750   Morais RA, Depczynski M, Fulton C, Marnane M, Narvaez P, Huertas V, Brandl SJ,

751   Bellwood DR (2020) Severe coral loss shifts energetic dynamics on a coral reef. Funct

752   Ecol 34:1507–1518.

753   Nicholson MD, Hendrick GC, Packard AJ, Strobel DL, Vondriska C, Sikkel PC (2020)

754   Vertical limits of host infestation by gnathiid isopods (Isopoda: Gnathiidae) parasitic on

755   Caribbean coral reef fishes. J Crustac Biol 40:866–871.

756   Odum HT, Odum EP (1955) Trophic Structure and Productivity of a Windward Coral Reef

757   Community on Eniwetok Atoll. Ecol Monogr 25:291–320.

758   Olsgard F, Somerfield PJ, Carr MR (1998) Relationships between taxonomic resolution,

759   macrobenthic community patterns and disturbance. Mar Ecol Prog Ser 172:25–36.

760   Pacala SW, Levin SA (1997) Biologically generated spatial pattern and the coexistence of

761   competing species.

762   Plaisance L, Caley MJ, Brainard RE, Knowlton N (2011) The Diversity of Coral Reefs: What

763   Are We Missing? PLoS One 6:e25026.

l.goberdhan@bangor.ac.uk

764 Plaisance L, Knowlton N, Paulay G, Meyer C (2009) Reef-associated crustacean fauna:

765   Biodiversity estimates using semi-quantitative sampling and DNA barcoding. Coral

766   Reefs 28:977–986.

767 Pollock FJ, Katz SM, Bourne DG, Willis BL (2013) Cymo melanodactylus crabs slow

768   progression of white syndrome lesions on corals. Coral Reefs 32:43–48.

769 Poore GCB, Bruce NL (2012) Global diversity of marine isopods (except Asellota and

770   crustacean symbionts). PLoS One 7:e43529.

771 Posit team (2023) No Title.

772 Randall JE (1967) Food habits of reef fishes of the West Indies.

773 Rasser MW, Riegl B (2002) Holocene coral reef rubble and its binding agents. Coral Reefs

774   21:57–72.

775 Reaka-Kudla M (1997) The Global Biodiversity of Coral Reefs: A Comparison with

776   Rainforests. In: *Biodiversity II: Understanding and Protecting our Biological Resources*.

777   Reaka-Kudla M, Wilson DE, Wilson OE (eds) Joseph Henry Press, Washington, p 83–

778   108

779 Roff G, Wabnitz CCC, Harborne AR, Mumby PJ (2013) Macroalgal associations of motile

780   epifaunal invertebrate communities on coral reefs. Mar Ecol 34:409–419.

781 Rogers A, Blanchard JL, Mumby PJ (2018) Fisheries productivity under progressive coral

782   reef degradation. J Appl Ecol 55:1041–1049.

783 Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of Coral Reef Fisheries to a Loss of

784   Structural Complexity. Curr Biol 24:1000–1005.

785 Saldaña PH, Angelini C, Bertness MD, Altieri AH (2023) Dead foundation species drive

786 ecosystem dynamics. Trends Ecol Evol.

787 Schulze A, Grimes CJ, Rudek TE (2017) Tough, armed and omnivorous: Hermodice

788 carunculata (Annelida: Amphinomidae) is prepared for ecological challenges. J Mar Biol

789 Assoc United Kingdom 97:1075–1080.

790 Scoffin TP (1993) The geological effects of hurricanes on coral reefs and the interpretation of

791 storm deposits. Coral Reefs 12:203–221.

792 Shannon A, Power H, Webster J, Vila-Concejo A (2012) Evolution of Coral Rubble Deposits

793 on a Reef Platform as Detected by Remote Sensing. Remote Sens 5:1–18.

794 Searle R.S., Casella, G., McCulloch, C.E. (1992) Variance Components. John Wiley and

795 Sons, Toronto.

796 Skilleter GA, Anderson DT (1986) Functional morphology of hte Chelipeds, mouthparts and

797 gastric mill of Ozius truncatus (Milne Edwards) (Xanthidae) and Leptograpsus

798 variegatus (Fabricius) (Grapsidae) (Brachyura). Mar Freshw Res 37:67–79.

799 Small AM, Adey WH, Spoon D (1998) Are current estimates of coral reef biodiversity too

800 low? The view through the window of a microcosm. Atoll Res Bull:1–20.

801 Stavi I, Zaady E, Gusarov A, Yizhaq H (2021) Dead shrub patches as ecosystem engineers in

802 degraded drylands. J Geogr Sci 31:1187–1204.

803 Stella JS, Wolfe K, Roff G, Rogers A, Priest M, Golbuu Y, Mumby PJ (2022) Functional and

804 phylogenetic responses of motile cryptofauna to habitat degradation. J Anim Ecol

805 91:2203–2219.

806 Stewart HL, Holbrook SJ, Schmitt RJ, Brooks AJ (2006) Symbiotic crabs maintain coral

807 health by clearing sediments. Coral Reefs 25:609–615.

l.goberdhan@bangor.ac.uk

808 Stoner AW (1985) Penicillus capitatus: an algal island for macrocrustaceans. Mar Ecol Prog

809   Ser 26:279–287.

810 Takada Y, Abe O, Shibuno T (2008) Cryptic assemblages in coral-rubble interstices along a

811   terrestrial-sediment gradient. Coral Reefs 27:665–675.

812 Takada Y, Abe O, Shibuno T (2012) Variations in cryptic assemblages in coral-rubble

813   interstices at a reef slope in Ishigaki Island, Japan. Fish Sci 78:91–98.

814 Takada Y, Ikeda H, Hirano Y, Saigusa M, Hashimoto K, Abe O, Shlbuno T (2014)

815   Assemblages of cryptic animals in coral rubble along an estuarine gradient spanning

816   mangrove, seagrass, and coral reef habitats. Bull Mar Sci 90:723–740.

817 Tebbett SB, Connolly SR, Bellwood DR (2023) Benthic composition changes on coral reefs

818   at global scales. Nat Ecol Evol 7:71–81.

819 Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution of intertidal

820   invertebrates. Oecologia 107:212–224.

821 Vanderklift MA, Ward TJ, Jacoby CA (1996) Effect of reducing taxonomic resolution on

822   ordinations to detect pollution-induced gradients in macrobenthic infaunal assemblages.

823   Mar Ecol Prog Ser 136:137–145.

824 Warwick R (1988a) Analysis of community attributes of the macro-benthos of

825   Frierfjord/Langesundfjord at taxonomic levels higher than species. Mar Ecol Prog Ser

826   46:167–170.

827 Warwick RM (1988b) The level of taxonomic discrimination required to detect pollution

828   effects on marine benthic communities. Mar Pollut Bull 19:259–268.

829 Williams GJ, Graham NAJ (2019) Rethinking coral reef functional futures. Funct Ecol

830   33:942–947.

l.goberdhan@bangor.ac.uk

831 Williams GJ, Knapp IS, Maragos JE, Davy SK (2011) Proximate environmental drivers of

832   coral communities at Palmyra Atoll: Establishing baselines prior to removing a WWII

833   military causeway. Mar Pollut Bull 62:1842–1851.

834 Williams GJ, Smith JE, Conklin EJ, Gove JM, Sala E, Sandin SA (2013) Benthic

835   communities at two remote Pacific coral reefs: effects of reef habitat, depth, and wave

836   energy gradients on spatial patterns. PeerJ 1:e81.

837 Wolfe K, Desbiens AA, Mumby PJ (2023a) Emigration patterns of motile cryptofauna and

838   their implications for trophic functioning in coral reefs. 1–14.

839 Wolfe K, Kenyon TM, Desbiens A, de la Motte K, Mumby PJ (2023b) Hierarchical drivers of

840   cryptic biodiversity on coral reefs. Ecol Monogr:1–27.

841 Wolfe K, Kenyon TM, Mumby PJ (2021) The biology and ecology of coral rubble and

842   implications for the future of coral reefs. Coral Reefs 40:1769–1806.

843

844 **TABLES**

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

850

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

l.goberdhan@bangor.ac.uk

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

l.goberdhan@bangor.ac.uk

***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

851

852

853 **FIGURES**

854

855

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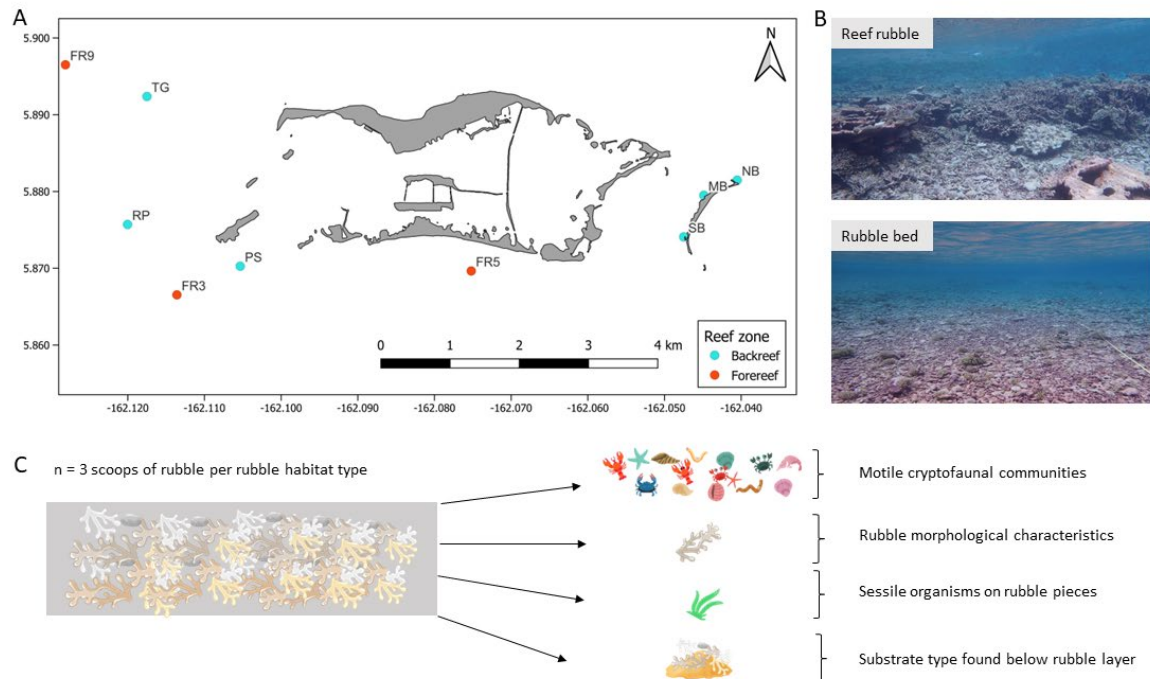
Figure 1. A) Location of survey sites (n = 9) around Palmyra Atoll, central Pacific. B) Two distinct rubble habitats were identified within reef zones (n = 2 for backreef; n = 1 for forereef). C) Coral rubble collected within quadrats (n = 3) from each rubble habitat per site to characterise rubble cryptofauna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

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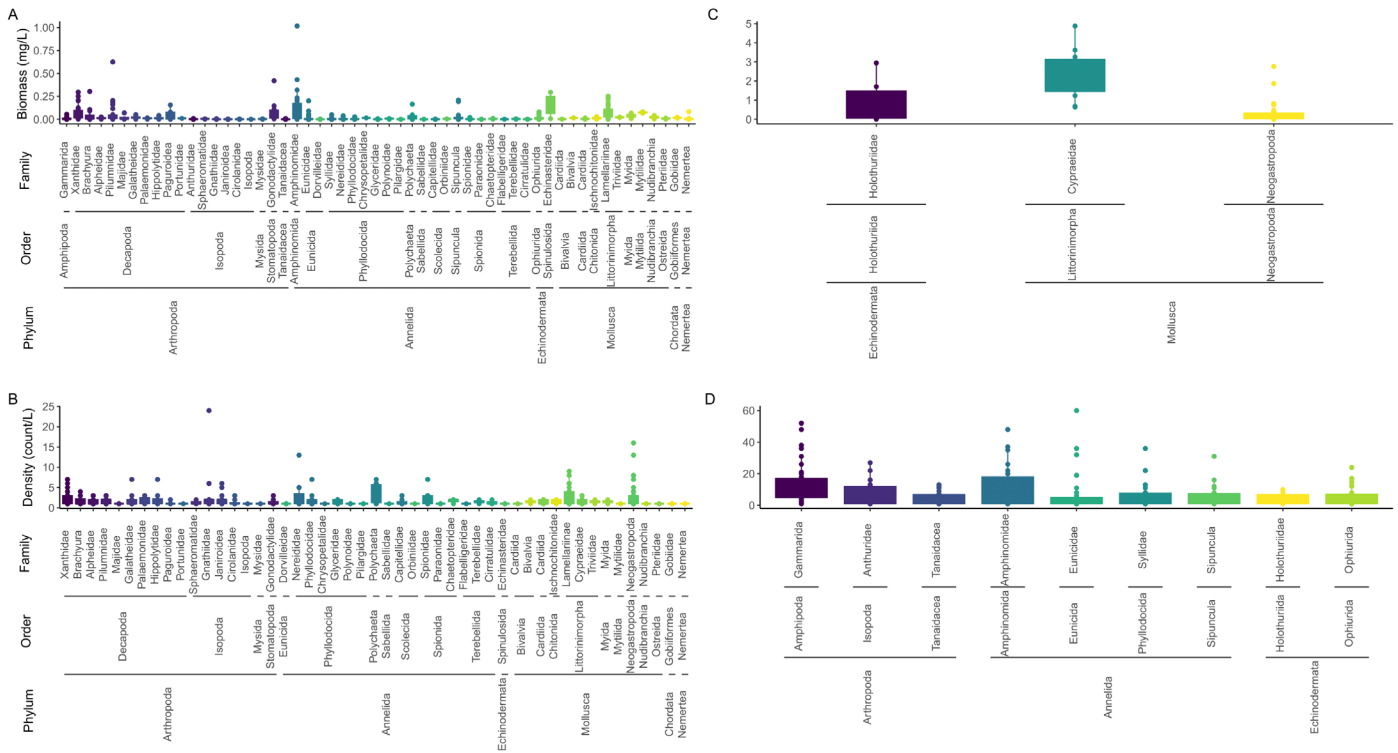
Figure 2. Biomass (A) and density (B) of motile cryptofauna living in coral rubble (n = 45 quadrats, n = 9 sites, n = 2 reef zones) at Palmyra Atoll, central Pacific. Those groups showing the highest values for both biomass and density are shown in C andD, respectively to better highlight the within-family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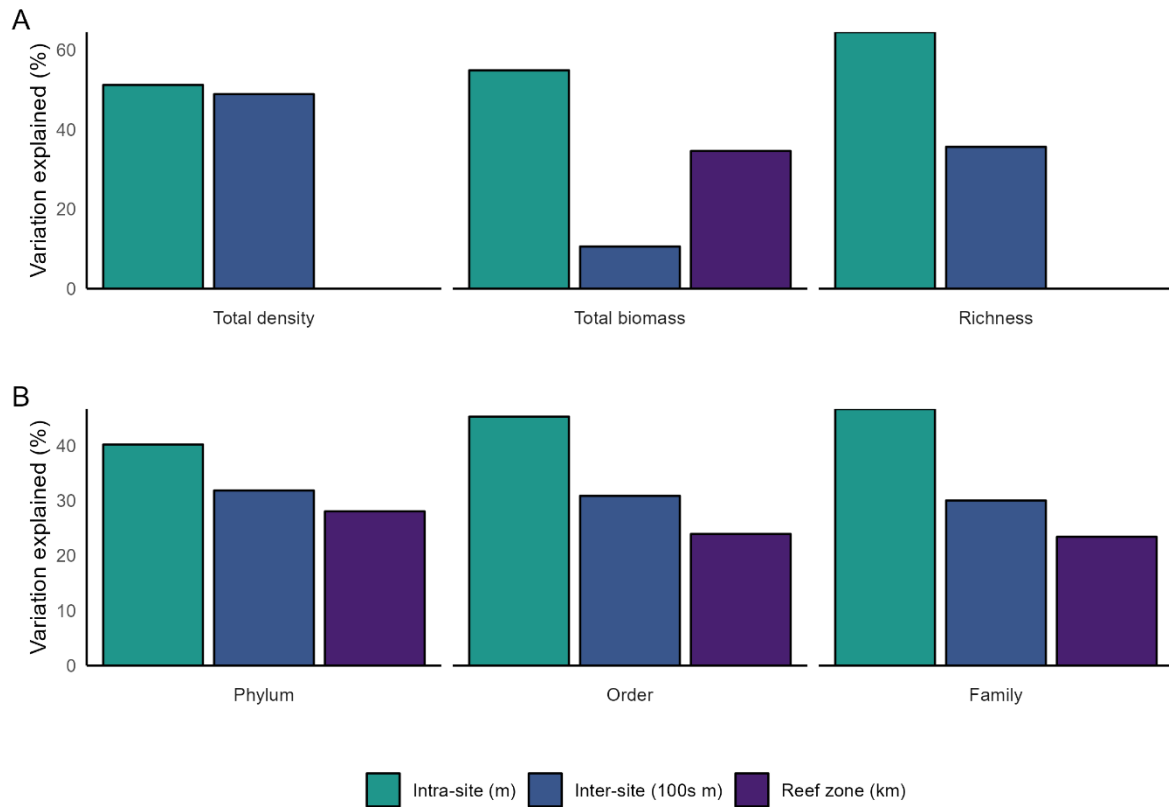
l.goberdhan@bangor.ac.uk

Variation in coral rubble cryptofauna

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.

l.goberdhan@bangor.ac.uk

881
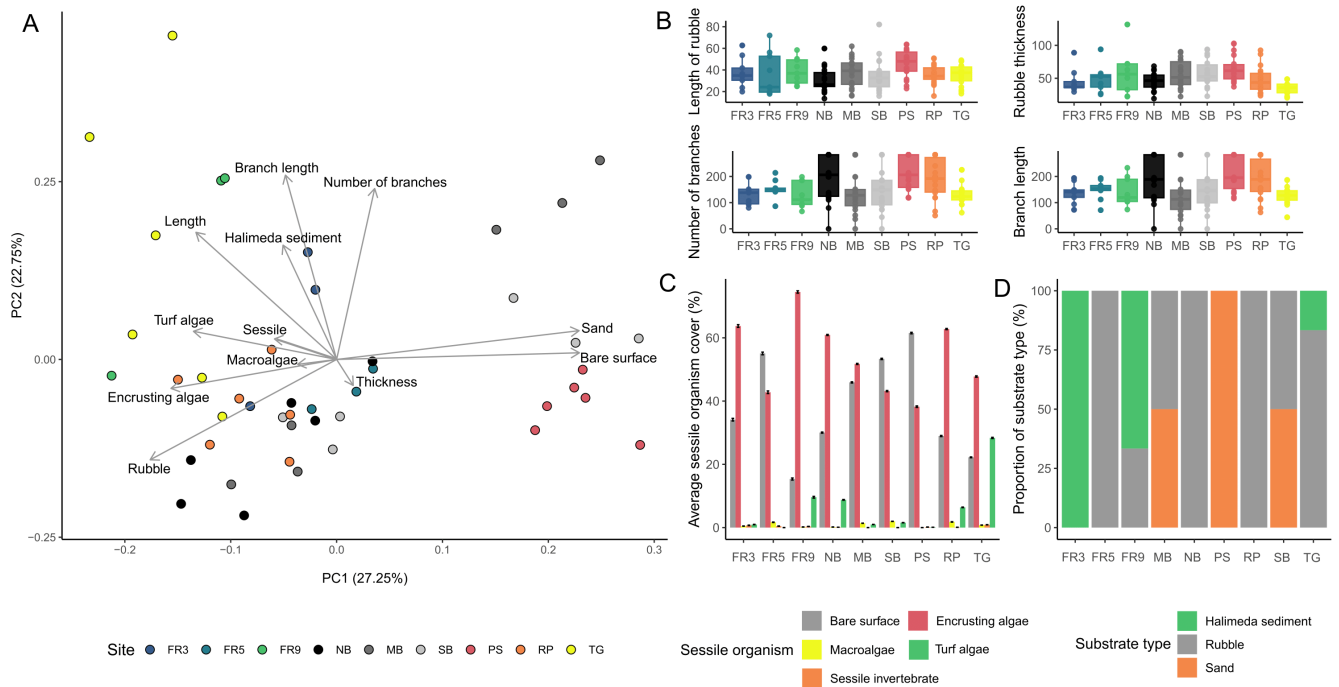
Figure 4. A) Principal components analysis (PCA) of rubble characteristics sampled from nine sites across Palmyra Atoll, central Pacific. B) Box (median and 50% quantile) and whisker (95% quantile) plots of the coefficient of variation (CoV) of rubble morphometrics across sites. Each point represents 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.

890

891

892

l.goberdhan@bangor.ac.uk
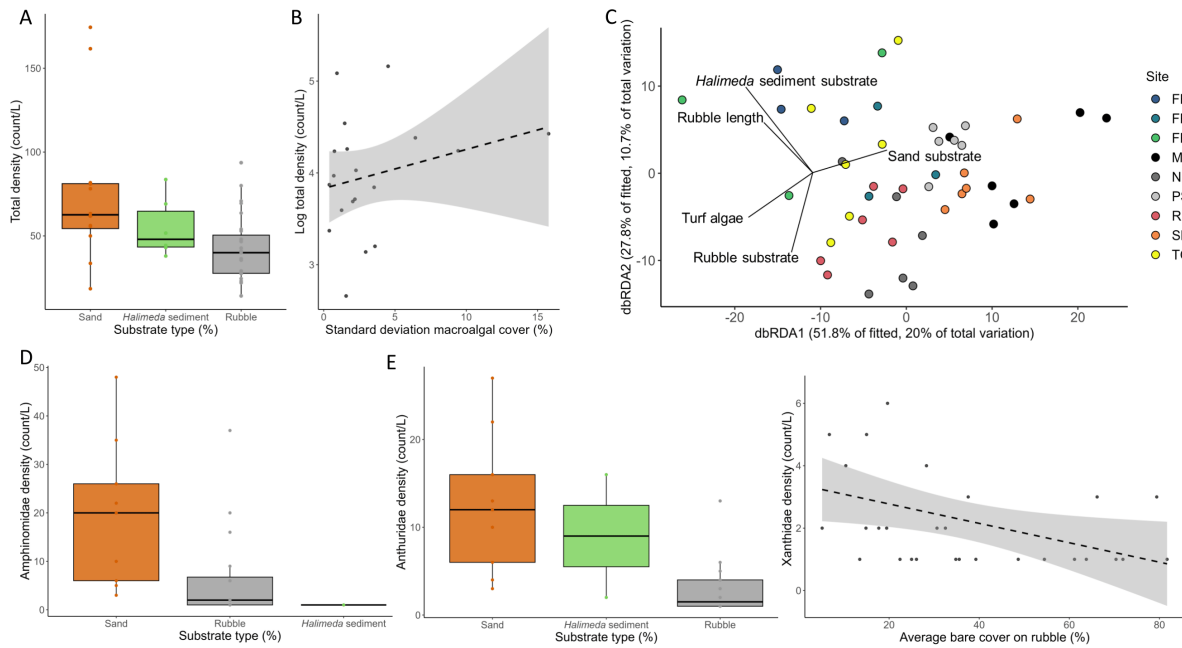
Figure 5. A) Variation of total cryptofauna density for each substrate type. Each point represents total cryptofauna density from an individual quadrat. B) Relationship between total density of cryptofauna and variability in macroalgal cover. Each point represents total cryptofauna density in an individual 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.

l.goberdhan@bangor.ac.uk

917 **APPENDICES**

918 Table A 1 Eleven predictors used to model cryptofauna community structure and rubble habitat
919 characteristics. Reef zones include forereef (FR) and backreef (BR) Substrate types include
920 *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

l.goberdhan@bangor.ac.uk

Variation in coral rubble cryptofauna

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

921

922

923

l.goberdhan@bangor.ac.uk