

1 Special Issue: Coral Reefs of Arabia

2 Original Article

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4 **Homogeneity of coral reef communities across 8 degrees of latitude in the Saudi**
5 **Arabian Red Sea**

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19 **Please cite this article as:** Roberts, M.B., et al., Homogeneity of coral reef communities across 8
20 degrees of latitude in the Saudi Arabian Red Sea, Marine Pollution Bulletin (2015),
21 <http://dx.doi.org/10.1016/j.marpolbul.2015.11.024>

22 **ABSTRACT:**

23 Coral reef communities between 26.8°N and 18.6°N latitude in the Saudi Arabian
24 Red Sea were surveyed to provide baseline data and an assessment of fine-scale
25 biogeography of communities in this region. Forty reefs along 1100 km of coastline were
26 surveyed using depth-stratified visual transects of fish and benthic communities. Fish
27 abundance and benthic cover data were analyzed using multivariate approaches to
28 investigate whether coral reef communities differed with latitude. A total of 215 fish
29 species and 90 benthic categories were recorded on the surveys. There were no
30 significant differences among locations in fish abundance, species richness, or among
31 several diversity indices. Despite known environmental gradients within the Red Sea, the
32 communities remained surprisingly similar. The communities do, however, exhibit subtle
33 changes across this span of reefs that likely reflect the constrained distributions of several
34 species of reef fish and benthic fauna.

35

36 **KEYWORDS:** Benthic cover, Biogeography, Coral reef fishes, Dissimilarity, Red
37 **Sea**

38 **INTRODUCTION:**

39 The Red Sea is located in the northwest periphery of the Indian Ocean and has
40 long been recognized as its own biogeographic region and a hotspot for biodiversity
41 (Goren & Dor, 1994; Randall, 1994; Randall, 1998) with high levels of endemism
42 (Briggs, 1974; Spalding *et al.*, 2007; Briggs, 2012; Bowen, 2013; Kulbicki *et al.*, 2013,
43 DiBattista *et al.*, *in press*). Some of the earliest tropical marine expeditions were
44 conducted in the Red Sea, where pioneering naturalists described marine fauna which
45 was also representative of the greater Indian Ocean (Forsskål 1775; Rüppell, 1828;
46 Cuvier, 1828; Ehrenberg, 1834; Klunzinger, 1870). More recently, with the exception of
47 the Gulf of Aqaba, there has been relatively little ecological research in the Red Sea
48 compared to other major tropical reef systems (Berumen *et al.*, 2013). The lack of
49 baseline information on fish populations and species ranges within much of the Red Sea
50 hinders attempts to quantify changes in the local ecology due to environmental
51 fluctuations or increasing anthropogenic influences.

52 In addition to its unique set of fauna, the Red Sea is also recognized as a mostly
53 thriving coral reef ecosystem coexisting within relatively extreme environmental
54 conditions (Sheppard *et al.*, 1992). Only the Arabian Gulf supports coral reef
55 environments that experience higher temperatures and salinity levels than those located in
56 the Red Sea (Sheppard *et al.*, 1992). However, across this long and narrow body of water,
57 which spans 17 degrees of latitude, the Red Sea is not homogenous. Sea surface
58 temperatures (SST), salinity, and nutrient concentrations exhibit latitudinal gradients and
59 fluctuate seasonally (Acker *et al.*, 2008; Ngugi *et al.*, 2012; Raitzos *et al.*, 2013). Average
60 temperatures increase southward and range from 20-28 °C (north to south) in the winter

61 and 26-32 °C (north to south) in summer. The low rainfall and freshwater influx in this
62 hot, arid region and pronounced evaporation rates result in high salinity levels (~41psu)
63 which decrease (to 36psu) near the Bab al Mandeb Strait, the only connection to the
64 Indian Ocean (Murray & Johns, 1997). Nutrient levels in the Red Sea also increase from
65 north (chlorophyll-a= 0.03 [mg m⁻³]) to south (10 [mg m⁻³]), with the most oligotrophic
66 northern waters characterized by high visibility in contrast to the more turbid southern
67 region (Sheppard & Sheppard, 1991).

68 The Red Sea has recently been described as containing two marine ecoregions
69 (Spalding *et al.*, 2007), with a division in the central Red Sea located near 20°N latitude.
70 This simplified delineation is contentious among some researchers familiar with the
71 region. Nonetheless, it provides a framework for us to test a hypothesis. While levels of
72 endemism are key characteristics for establishing broader biogeographical provinces and
73 realms (Briggs, 1974a; Briggs, 2012; Spalding *et al.*, 2007), the finer-scale marine
74 ecoregions such as those identified within the Red Sea are defined as “areas of relatively
75 homogeneous species composition, clearly distinct from adjacent systems...[and]
76 determined by a distinct suite of oceanographic or topographic features” (Spalding *et al.*,
77 2007). However, the available data from this region is focused only on a few taxonomic
78 groups. For example, regional chaetodontid and pomacanthid distributions were explored
79 by Roberts *et al.* (1992) and Righton *et al.* (1996) while Sheppard & Sheppard (1991)
80 and DeVantier & Pilcher (2000) have published studies on the distribution of
81 scleractinian assemblages within the Red Sea. While these previous studies provide
82 valuable insight to species- and family-level distributions and patterns, they may not be
83 sufficient to characterize ecoregion boundaries. Large-scale biogeographic trends provide

84 insights into broad ecological processes and relationships to changing environmental
85 conditions; understanding these trends facilitates the establishment of sound management
86 plans. The present study provides an overview of biogeographic patterns of reef
87 communities for this region.

88 The aims of this study were: 1) to determine if and to what degree offshore reef
89 communities change along a latitudinal gradient within our study area, 2) to explore the
90 presence of a within-Red Sea ecological boundary at 20°N as described by Spalding et al.
91 (2007), and 3) to provide baseline data on the biogeography of coral reef communities for
92 future comparative studies in the Red Sea. To achieve these goals, surveys were
93 conducted on coral reefs in the Saudi Arabian Red Sea spanning 1100km of latitudinal
94 coastline. Surveys assessed the abundance of reef fish species as well as benthic cover at
95 40 coral reefs. In addition to providing a valuable dataset of distributions and
96 abundances, this data lays the foundation for investigations of the mechanisms underlying
97 regional biogeography.

98

99 **METHODS**

100 *Ecological survey data collection:*

101 Our study area consisted of 40 offshore reefs along the Saudi Arabian coastline
102 between 26.8°N and 18.6°N latitude (Figure 1). Survey sites were selected to reduce the
103 confounding effects of reef type, reef slope, and within-reef location of transects. Reefs
104 were chosen based on their position at the edge of the Arabian shelf and near deep drop-
105 offs, with survey sites located near the outer reef slope on the leeward side of the reef
106 (given predominant northwesterly winds in the Red Sea, this meant that our surveys were

107 conducted on the southern ends of the reefs). Reef sites varied between 7 and 81km from
108 shore, representing the variable width of the continental shelf in the Red Sea (Figure 1).
109 The lack of any significant rainfall (yearly average less than 70mm (DeVantier & Pilcher,
110 2000)), the near absence of freshwater runoff, and minimal coastal development
111 (especially in the north) greatly reduces the confounding effects of varying reef distance
112 from shore. We define the terminology used in this study as follows. “Sub-region” refers
113 to the subdivisions of the Red Sea that we surveyed (i.e., the northern, central, or
114 southern sites within the Red Sea), “section” to refer to the groupings of reefs, and
115 finally, we refer to each individual reef site as “reef”. We surveyed four reefs per section
116 with a total of 10 sections that were further grouped into three sub-regions (Table 1).
117 These sub-regions were defined as: “northern” (n=12 reefs; 26.8°N – 24.4°N), “central”
118 (n=16 reefs; 23.8°N – 21.8°N), and “southern” (n=12 reefs; 19.8°N – 18.6°N) (see Figure
119 1 and Table 1). The groupings by sub-region were used to identify differences within our
120 study area for a biogeographic context, while the sections were used to investigate finer-
121 scale spatial variation in community indices.

122 At each reef, four replicate transects were laid at each of four depths: the reef
123 crest (~0m), 2m, 6m, and 10m, for a total of 16 transects per reef (as per Jones *et al.*,
124 2004). All species (Appendix S1) were counted on 50m x 4m belt transects with the
125 exception of the damselfishes (family Pomacentridae) which were surveyed within a 2m
126 belt transect, as well as the gobies (family Gobidae), blennies (family Blennidae), and
127 dottybacks (family Pseudochromidae), which were surveyed within a 1m belt due to their
128 small size and abundance. For each transect, three divers (MIM, PLM, and either GPJ or
129 MLB) observed and recorded the abundance of specific groups of fishes based on their

130 expertise. Prior to other analyses, count densities were standardized to 200m² (hereafter
131 referred to as ‘abundance’). A fourth diver (SN) conducted point-intercept benthic
132 surveys along the same 50m transects, recording the benthos at 100 random points
133 selected by a random number generator that allowed for at least two points to be within
134 the bounds of each meter of the transect to space the points out across the entire
135 transect. The substratum under each point was identified to the lowest taxonomic group
136 and morphotype where possible (Appendix S2).

137

138 *Statistical Analyses*

139 *Community indices*

140 Several community indices were assessed among the three latitudinal sub-regions
141 in our study. As each reef had the same number of transects, total abundance of all fishes
142 surveyed within a reef were used to calculate the average total abundance of fishes in
143 each of the three sub-regions (n = 12 or 16 reefs per sub-region). Total richness (S) was
144 calculated at the reef level by tallying the number of fish species recorded on all of the 16
145 transects (i.e., if a fish was seen on any transect it was counted for the reef). The
146 Shannon-Weiner diversity index (H' , log(e) scale) (Shannon & Weaver, 1963), Pielou’s
147 evenness (J') (Pielou, 1975), and Simpson’s diversity ($1-\lambda$) (Simpson, 1949) were all
148 calculated at the reef level using PRIMER-v6 (Clarke, 2006). Values of J' lie between 0-
149 1 where 0 indicates an uneven distribution of abundances among species within a site and
150 values closer to 1 show more evenly composed communities. Similarly, Simpson’s index
151 is also on a 0-1 scale, where values near 0 are interpreted as less diverse and values
152 approaching 1 signify high diversity. All of the aforementioned indices were compared

153 for significant differences among the three sub-regions using one-way way Analysis of
154 Variance (ANOVA) in R v3.03 (R Core Team, 2014).

155 *Multivariate analyses among reefs*

156 We also analyzed assemblage and biogeographic patterns in the data using non-
157 metric multi-dimensional scaling (NMDS; Kruskal & Wish, 1978) to display the relative
158 dissimilarity distances based on community compositions among the 40 reefs. For this
159 and all subsequent multivariate analyses, data were analyzed at the reef level (treating the
160 16 transects as replicates within a reef). Fish abundance data and percent benthic cover
161 data were square root transformed to balance the effect of disproportionately abundant
162 species prior to conducting the analyses. The NMDS plots were calculated using the
163 resemblance matrix of Bray-Curtis similarity coefficients (Bray & Curtis 1957; Clark and
164 Warwick, 2001). While there are many options for similarity indices, the Bray-Curtis
165 method has been shown to be sensitive to differences in community structure when using
166 species abundance data, and is thus commonly used in coral reef community studies (Burt
167 *et al.* 2011; Dornelas *et al.*, 2006; Holbrook *et al.*, 2015). Similarity coefficients are
168 calculated between assemblages of every pair of reefs using the average abundances of
169 each species within the reef. Here, the Bray-Curtis similarity coefficient S , represents the
170 similarity between reefs j and k where y_{ij} represents the average abundance of the species
171 in column i and reef j .

$$S_{jk} = 100 \left\{ 1 - \frac{\sum_{i=1}^p |y_{ij} - y_{ik}|}{\sum_{i=1}^p (y_{ij} + y_{ik})} \right\}$$

172 *Multivariate analyses among sub-regions*

173 To determine if any biogeographic differences were evident, reef sites were
174 analyzed based on the groupings by the previously defined northern, central, and southern
175 sub-regions and assessed to determine if communities were similar among sub-regions.
176 Analysis of similarity (ANOSIM; Clarke, 2001) was conducted on both the fish and
177 benthic resemblance matrices to test the null hypothesis that the community assemblages
178 were similar throughout the three sub-regions. In the ANOSIM significance test, the
179 resulting global R -value lies between -1 and 1 and reflects the degree of similarity
180 between the pairwise tests between the three sub-regions. The more similar reef
181 communities within sub-regions are to each other than to those in other sub-regions, the
182 closer the value of R approaches 1 . Positive values nearer to zero indicate that some reefs
183 between sub-regions show more similarity than reefs within the same sub-region, while a
184 negative R value would indicate that reefs between sub-regions are more similar to each
185 other than within the three sub-regions (Clarke, 2001).

186 A pairwise comparison of similarity percentages (SIMPER; Clarke, 2001) of
187 abundance data between sub-regions was used to determine which species and benthic
188 components contributed most to the differences between sub-regions. This analysis first
189 identifies the species that are most influential in characterizing a sub-region, and then
190 ranks the species that drive average dissimilarity between them. Species with greater
191 relative abundances are more heavily weighted in SIMPER calculations.

192 *Correlations between fish and benthos*

193 To test whether relationships between abundances of fish taxa versus benthic
194 components exist, we used the RELATE (Clarke, 2001) analysis with Spearman's rank

195 method. This analysis shows how well the fish resemblance matrix correlates with the
196 benthic matrix. Spearman's rank correlation (ρ) is a measure of the degree of correlation
197 between the two resemblance matrices, calculated by matching every variable in one
198 matrix to every variable in the other matrix then creating a ranking based on the
199 similarity of ρ values between benthic categories and fish species across sites. Once
200 patterns were detected, BEST (BVSTEP) analysis (Clarke, 2001) used this ranking to
201 identify which of the benthic variables most strongly correlated with fish community
202 compositions. Due to the large number of variables, we used benthic categories that
203 contributed at least 1% of dissimilarity between regions as identified by the SIMPER
204 analysis (41 of 90 categories). These analyses are commonly used to distinguish between
205 different communities and to identify geographic sub-regional breaks (Khalaf &
206 Kochzius 2002, Burt *et al.*, 2011; Sales *et al.*, 2012). All multivariate and correlation
207 analyses were conducted using PRIMER 6+ PERMANOVA software (PRIMER-E v6;
208 Clarke, 2006).

209

210 **RESULTS**

211 *Community indices*

212 A total of 268,313 individuals were counted representing 215 species from the 40
213 reefs (Appendix S1). However, nine fish taxa were subsequently removed from further
214 analysis because they were not identified to species and an additional four species, all
215 within the family Mullidae, were also excluded, as they were not counted in all of the
216 survey periods (Appendix S3). The remaining 202 fish species, representing 110 genera
217 and 26 families were used for subsequent analyses (Appendix S1 and S2).

218 Total abundance was not significantly different across sub-regions (one-way
219 ANOVA, $F_{2,37}=2.76$, $p=0.0764$). Similarly, the other community indices showed no
220 significant differences among sub-regions. These included mean species richness (one-
221 way ANOVA, $F_{3,37} = 1.319$, $p=0.280$) (Figure 2b), Shannon's diversity (H') (one-way
222 ANOVA, $F_{2,37} = 0.585$, $p = 0.562$), Pielou's evenness (J') (one-way ANOVA, $F_{2,37} =$
223 0.437 , $p=0.649$), and Simpson's index ($1-\lambda'$) (one-way ANOVA, $F_{2,37} = 1.487$, $p =0.239$
224 (Figure 2b-d).

225 Among the individual reefs, the highest and lowest values of Shannon's diversity,
226 Pielou's evenness, and Simpson's index were within the central sub-region. *Abu Terr* reef
227 in the region of North Jeddah had the highest indices with $H'=3.15$, $J'=0.69$, and $1-$
228 $\lambda'=0.91$, while the lowest values were found on *Shib Shabarir* in the Seven Sisters area
229 with $H'=1.37$, $J'=0.31$, and $1-\lambda'=0.56$ (Table 2).

230 *Fish assemblage multivariate analyses across reefs and between sub-regions*

231 The NMDS plot (Figure 3) for fishes within reefs revealed the clustering of
232 northern and southern sites separated by a wide band of central reef sites, generally
233 showing a gradual progression of community assemblages from north to south. Pairwise
234 ANOSIM tests by sub-region also confirmed significant differences between the three
235 sub-regions ($p<0.001$, $R=0.321$) (Table 2). The benthic NMDS plot (Figure 3) also shows
236 clustering of reef sites based on sub-regions. Benthic ANOSIM results confirmed that
237 sub-regional clusters are significant ($p<0.001$, $R=0.632$) with all pairwise tests yielding P
238 values of 0.001 (Table 3).

239 However, in the SIMPER pairwise comparisons, four species (*Pseudanthias*
240 *squamipinnis*, *Chromis dimidiata*, *Chromis flavaxilla*, and *Pseudochromis fridmani*) were

241 consistently identified as being the primary drivers of between-sub-region dissimilarity
242 (Table 2). The three sub-regions were also characterized by a similar assemblage of
243 fishes with the same 19 species making up the top 25 most influential species driving the
244 similarities within each of the three sub-regions (Table 4). None of the three sub-regions
245 were found to have a notably distinct assemblage structure based on pairwise
246 dissimilarity values. SIMPER results show that benthic categories driving the top 25% of
247 differences in the ANOSIM were more diverse than the combinations that drive
248 differences in the fish ANOSIM (Tables 2 and 3). Percent contribution levels were also
249 more even and were generally higher among these benthic factors than contributions
250 found in the fish community (Tables 2 and 3). As in the fish assemblages, low
251 dissimilarity values indicate relatively low levels of differences among sub-regions.

252 *Correlations between fish and benthos*

253 The RELATE analysis showed a significant positive correlation between patterns
254 in the fish assemblages and the corresponding benthic communities ($p < 0.001$, $\rho = 0.386$).
255 The SIMPER analysis identified that 41 of the 90 benthic categories contributed at least
256 1% to dissimilarity in benthic communities. We therefore used BEST (BVSTEP) to
257 examine these 41 benthic variables in order to identify which benthic variables may have
258 contributed to shifts in the fish assemblages. However, this analysis did not find a benthic
259 variable or a combination of benthic variables that correlated significantly ($p = 0.07$) with
260 the changes in fish assemblages across latitude.

261

262 **DISCUSSION**

263 Previous large-scale studies of biogeographic patterns were conducted primarily
264 on near shore reefs in the Red Sea and had revealed a trend of higher diversity in what
265 corresponds to the northern and central sub-regions in our study (Roberts *et al.*, 1992;
266 Sheppard & Sheppard, 1991). These studies also identified overall latitudinal changes in
267 the species composition of selected taxa such as the chaetodontids, pomacanthids and
268 sclerictinians (Roberts *et al.*, 1992; Sheppard & Sheppard, 1991). Our extensive surveys
269 of 40 reefs along 1100km of the Saudi Arabia Red Sea coast encompassing 110 genera of
270 fishes and 90 benthic categories, presents a novel dataset representing offshore reef
271 communities. Though we do not directly compare our data to the findings in previous
272 literature on inshore reefs, our study revealed that across latitude, offshore reef fish
273 assemblages were generally more homogenous in nature. While there were subtle
274 assemblage shifts along this gradient, they were not strong enough to be reflected in five
275 common indices, none of which differed significantly among the three sub-regions.
276 Nevertheless, reefs within the same area generally cluster closely together in an overall
277 latitudinal pattern. Patterns found in the fish assemblages also appear to be related to
278 benthic composition, but the exact drivers are difficult to identify. We did not find strong
279 evidence for the current location of the within-Red Sea ecoregion boundary designated by
280 Spalding *et al.* (2007) at 20°N.

281 The great deal of homogeneity and relatively small differences in the species that
282 characterize the reefs throughout our study area are in contrast to earlier studies on near-
283 shore reefs and contradict the delineations of distinct bioregions assigned in the MEOWS
284 (Roberts *et al.*, 1992; Spalding *et al.*, 2007). Subtle shifts are, however, apparent in the
285 fish assemblage ordination clustering the reefs in a generally latitudinal order. Northern

286 reefs, as well as some southern reefs, were highly clustered within their respective sub-
287 regions while many central and some southern reefs were grouped together also
288 indicating a gradual latitudinal shift. These patterns can be attributed to the several
289 species that have restricted ranges within the Red Sea, an effect already reported within
290 the chaetodontid family (Roberts *et al.*, 1992). Several butterflyfishes exhibit
291 distributions that are confined to either the northern, southern, or central sub-regions
292 (e.g., Roberts *et al.* 1992). Although there were no apparent major habitat changes that
293 would limit these distributions, a more thorough examination of specific case studies and
294 habitat associations might reveal further connections

295 There is no standard value for a threshold of difference vs. similarity, however, it
296 is our opinion that the results indicate relatively homogenous communities (cf. Burt *et al.*,
297 2011). We did not find evidence supporting the current division of the Red Sea into two
298 bioregions at 20 °N latitude, based on the definition used by Spalding *et al.* (2007). The
299 lack of separate clusters between sites across this delineation (between central and
300 southern sub-regions) and the uniformity in species driving the similarities within sub-
301 regions indicated a generally homogeneous assemblage along this span of coastline. We
302 also found that dissimilarities (though significant) were half that of similar studies
303 comparing coral reef fish assemblages across other similarly defined bioregions that
304 displayed substantially higher dissimilarity percentages (e.g., 72-85%) (Burt *et al.*, 2011).
305 This was further corroborated by the high resemblance of the fishes (19 of the 25 species
306 identified by SIMPER analyses) that contribute to the similarity between each sub-region.
307 Across this stretch of the Red Sea, while the dissimilarities may be significant,
308 communities remained relatively similar. Results from the ANOSIM analysis indicated

309 that fish assemblages were more similar between adjacent sub-regions than other
310 pairwise comparisons. The benthic communities formed clear clusters but with less
311 evidence of a latitudinal pattern. However, subsequent BEST analyses and careful
312 examination of the reef ordination show patterns with similar clustering between the two
313 data sets.

314 Given the lack of previously available detailed biogeographic information for
315 much of the Red Sea, and particularly offshore reefs, the placement of an ecoregion
316 boundary at 20 °N appears to be a slightly misleading conclusion arising from over-
317 simplification of previous studies (although we acknowledge that compromises by
318 Spalding *et al.* (2007) were likely necessary to keep the total number of global ecoregions
319 reasonable). Other recent investigations in the southern Red Sea provide evidence that a
320 more appropriate division may exist around 17.5 °N latitude and southwards to the strait
321 of Bab Al Mandab, where turbidity and productivity levels are much higher than the rest
322 of the Red Sea (Raitsos *et al.*, 2013). This shift in the southern Saudi Arabian Red Sea
323 coincides with a distinct habitat change. An extensive network of coral reefs known as
324 the Farasan Banks occupies the region from ~20°N to ~18°N , while to the south from
325 ~17.5°N onwards, lies the Farasan Islands. The reef communities of the Farasan Islands
326 extend into Yemeni waters and have been described as unique among Red Sea habitats
327 (Sheppard *et al.*, 1992; Turak, 2007) in that they are characterized by increasingly reduced
328 coral reef development compared to more northern Red Sea coral communities. This area
329 has shallow geomorphology that results in high SST, turbidity, and restricted water flow
330 (Turak, 2007). Although our study did not include sites in the Farasan Islands, other work
331 from this region suggests a major transition in fauna and assemblage composition. For

332 example, two recent studies have identified barriers to gene flow that match this shift in
333 environmental conditions (two-band anemonefish, Nanninga *et al.*, 2014; Carter's reef
334 sponge, Giles *et al.*, 2015). It may be more appropriate, therefore, for a within-Red Sea
335 demarcation of bioregions to be placed between the southern end of the Farasan Banks
336 and the beginning of the Farasan Islands. In addition, surveys along the Yemeni coast by
337 Turak *et al.* (2007) found that the coral assemblages of the northern reefs of Yemen are
338 more similar to the Farasan Islands while the coral assemblage in the southern area is
339 likened to the Gulf of Aden, indicating that perhaps the Gulf of Aden bioregion should
340 extend into the southern tip of the Red Sea.

341 We found that benthic communities reflected similar patterns to the fish
342 assemblages, though the ecological relationships between such large numbers of
343 variables in the analysis may mask any clear associations. The ordination in the two
344 communities as well as the RELATE analysis confirm that trends exhibited by the fish
345 assemblages were likely related to patterns found in the benthic communities.
346 Interestingly, ordination and SIMPER results showed that the northern reefs for both the
347 fish and benthos show greater uniformity, indicating consistency of communities among
348 those reefs. The northern sub-region is arguably the most environmentally challenging
349 region in the Red Sea as a result of having the overall lowest productivity (Raitsos *et al.*,
350 2013) and highest salinity (Ngugi *et al.*, 2012). It is possible that specific niche
351 specialization become necessary as environments become relatively more extreme (e.g.,
352 Moldenke, 1975). The result of more challenging environmental conditions may,
353 therefore, be increased homogeneity among the resident communities. Additionally, it is
354 also interesting that the sub-regional differences found on inshore reefs in Roberts *et al.*

355 (1992) appear to be more obvious and further north than our findings at offshore reef
356 habitats. This may suggest that the forces or gradients that determine species distribution
357 in the Red Sea communities are more influential or stronger in near-shore communities.

358 Future studies could use the data presented here as a basis for more in-depth work
359 with the aim of identifying specific mechanisms underlying the latitudinal gradient in
360 community assemblages. For example, subsequent studies may further examine reef sites
361 with greater habitat variability than the present study (e.g., comparing coastal fringing
362 reefs to offshore reefs, or sheltered vs. exposed sides of a given reef). It is likely that
363 some species exhibiting restricted ranges within the Red Sea, such as the butterflyfishes
364 and angelfishes (Roberts *et al.*, 1992), drive the observed shifts in the assemblages along
365 the latitudinal gradient we explored. There are further reef-scale biological mechanisms
366 interacting with biogeographic mechanisms to produce community variation. For
367 example, local population explosions of *Acanthaster planci*, *Drupella*, *Echinometra*, or
368 coral disease have been known to significantly alter Red Sea reef fish and coral
369 communities and habitat structure, (e.g., Antonius & Riegl, 1998; Khalil *et al.*, 2013;
370 Riegl *et al.* 2012, 2013) which likely affect the fish assemblage structure. These types of
371 disturbances have previously been suggested as a potential homogenizing force in Red
372 Sea reefs (Riegl *et al.* 2012). Future work and repeated observations will be required to
373 confirm this hypothesis.

374

375 **CONCLUSION**

376 Red Sea reef fish assemblages along the northern two-thirds of the eastern Red Sea
377 are, for the most part, composed of similar assemblages of species with no dramatic

378 changes in the general communities along this latitudinal gradient when comparing reef
379 communities on the edge of the continental shelf. Nevertheless, shifts do occur, likely
380 driven by the respective range limits of several species that are confined to either the
381 northern or southern Red Sea. While we recognize that ecoregion delineation is not a
382 fully quantitative endeavor, we recommend that the previously described zonation in
383 Spalding et al.'s Marine Ecoregions of the World within the Red Sea be reconsidered.
384 This central bioregion lacks clearly distinct species compositions on either side of its
385 borders, and as such may not be a reasonable biogeographic demarcation. Due to well-
386 established differences in abiotic conditions as well as habitat structure and
387 geomorphology, we suggest that more studies be conducted comparing the fauna between
388 the far southern region (below 18° latitude and continuing to the strait of Bab Al
389 Mandab) and the rest of the Red Sea including, the western side. While we were not able
390 to explore this possibility at the present time, our study provides a useful dataset from
391 well-distributed sites along the eastern Red Sea. Given global challenges associated with
392 “shifting baselines” (Pauly, 1995) and the emerging evidence of overfishing effects in the
393 Saudi Arabian Red Sea (e.g., Jin *et al.*, 2012; Spaet & Berumen, 2015), some form of
394 recent reference data from this region is needed. This dataset could form the basis for
395 later work to investigate finer-scale relationships between fish, benthos, and abiotic
396 factors to understand the ecological mechanisms driving biogeographic patterns within
397 the Red Sea.

398

399 **ACKNOWLEDGEMENTS**

400 This research was supported by a KAUST Competitive Research Grant (URF/1/1389-
401 01-01) and baseline research funds to MLB, as well as WHOI-KAUST Special
402 Partnership Awards (USA-00002 and KSA-00011) to SRT. For logistic and fieldwork
403 support, we thank Eric Mason and all the crew from Dream Divers, H. Jahdahli and all
404 the KAUST Coastal and Marine Resources Core Lab, Y. Kattan, K.A. Furby, J.
405 Ossolinski, K. Munday, and A.S. Al Kotob. We thank S. Vettori for statistical advice. An
406 earlier draft of this manuscript was improved by comments from J. Bouwmeester, B.
407 Bowen, J. Cochran, B. Jones, A. Kattan, and M. Morton.
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537 **SUPPORTING INFORMATION**

538 Additional Supporting Information may be found in the online version of this article:

539

540 **Appendix S1:** Summarized densities of reef fish by section, surveyed in visual belt
541 transects in the Saudi Arabian Red Sea. Values are standardized as estimated abundance
542 (\pm SE) per 200m². The 202 species presented here were used in analysis of biogeographic
543 patterns within the Saudi Arabian Red Sea. Each section is composed of 4 reefs and each
544 reef contained 16 replicate transects (i.e., presented here are the means of 64 transects for
545 each section).

546 **Appendix S2:** Summarized results of benthic cover by section, surveyed in point-
547 intercept transects in the Saudi Arabian Red Sea. Values are standardized as estimated
548 percent cover (\pm SE). Categories reflect the highest level of taxonomic identification used
549 in the surveys. The 90 categories presented here were used in analysis of biogeographic
550 patterns within the Saudi Arabian Red Sea. Each section is composed of 4 reefs and each
551 reef contained 16 replicate transects (i.e., presented here are the means of 64 transects for
552 each section).

553 **Appendix S3:** Species or taxonomic categories recorded in reef fish surveys in the Saudi
554 Arabian Red Sea that were excluded from analyses. The justification for excluding each
555 category is indicated.

556

557 **BIOSKETCH**

558 The RES team (SRT, GPJ, MIM, PLM, SN, MLB) conducted these surveys as part of a
559 WHOI-KAUST partnership, with this project specifically aiming to create some form of
560 baseline data for future work at KAUST. The Reef Ecology Lab at KAUST (MBR,
561 VSNR, MLB) is interested in generally understanding Red Sea ecology, particularly in a
562 comparative context to other Indo-Pacific reef systems.

563

564 Author contributions: SRT, GPJ, MIM, PLM, SN, MLB collected the data. MBR
565 analyzed the data. SRT and MLB provided funding. MBR and MLB wrote the
566 manuscript. All authors contributed to manuscript sections or general editing.

567

568

569

570 **FIGURE LEGENDS**

571 **Figure 1.** Reef sites surveyed in the Red Sea for fish abundance and benthic cover, with
572 northern (green triangles), central (dark blue circles), and southern (cyan squares),
573 groupings of survey sites. Reefs were numbered (shown next to reefs) in order of latitude
574 and these correspond to the numbers in Table 1.

575 **Figure 2.** Community indices for fish assemblages at 40 reefs in the Saudi Arabian Red
576 Sea as recorded using ecological survey data. The 40 reefs were grouped by the three
577 sub-regions defined as: “northern” $26.8^{\circ} - 24.4^{\circ}$ N (n = 12 reefs), “central” $23.8^{\circ} - 21.8^{\circ}$
578 N (n = 16 reefs), and “southern” $19.8^{\circ} - 18.6^{\circ}$ N (n = 12). Each reef contained 16
579 transects A) Mean abundance of all recorded individuals per reef (all transects totaled at
580 each reef). B) Mean total species richness (S) recorded on each reef. C) Mean Shannon-
581 Weiner diversity index (H') (log(e) basis) values. D) Mean Pielou’s evenness (J') values.
582 All boxplots show the mean (bold line) with the upper and lower quartiles while whiskers
583 indicate the maximum and minimum values found on the reefs within each section of the
584 coastline.

585 **Figure 3.** Cluster analysis and non-metric multidimensional scaling (NMDS) of
586 reef communities at 40 reefs in the Saudi Arabian Red Sea. Each reef contained 16
587 transects on which abundance of 202 species of fishes were recorded and benthic
588 cover determined. Fish abundance data were square-root transformed prior to
589 creating the resemblance matrix. A) Cluster analysis of the 40 reefs based on fish
590 abundances. B) Cluster analysis of the 40 reefs based on percent cover of benthic
591 categories. C) NMDS of fish assemblages. The two-dimensional distance between
592 sites signifies the relative degree of difference between assemblages. D) NMDS of

593 benthic communities. Colors and shapes denote geographical assignments to one of
594 three sub-regions: Northern sites (1-12, green triangles), central sites (13-29, dark
595 blue circles), and southern sites (30-40, light blue squares).

596

597 **TABLE CAPTIONS**

598 **Table 1.** Details of 40 Saudi Arabian Red Sea coral reefs surveyed. Surveys were
599 conducted in three general sub-regions of the Red Sea. Ten regions were
600 surveyed, each comprised of four reefs. Reefs were assigned a numerical code (1-
601 40) in order of latitude and used in subsequent figures. Longitude and latitude
602 indicate survey location on reef. Distance from shore is also reported and shows
603 the straight-line distance to the nearest point on land. The total number of fish
604 species (S) recorded on 16 belt transects (4 each at the crest, 2m depth, 6m depth,
605 and 10m depth) using visual surveys are reported, along with other community
606 indices: J' , indicating Pielou's evenness; H' , representing Shannon's Diversity
607 index; and $1-\lambda$, representing Simpson's Diversity index.

608
609 **Table 2.** Similarity results of reef fish assemblages determined using SIMPER and
610 ANOSIM analyses. The tables show the species cumulatively contributing to the
611 top 25% of the dissimilarity in each pairwise comparison (SIMPER) of three sub-
612 regions from the Saudi Arabian Red Sea. Relative contribution and the cumulative
613 contribution of the top species to sub-regional dissimilarity as well as the mean
614 abundances for each species in each sub-region are shown for comparison. All other
615 species each contributed <2% of differences in assemblages. Percent dissimilarity in
616 addition to overall ANOSIM comparison results (Global R= 0.321, $p<0.001$) are
617 included alongside the pairwise results, also presented here.

618 **Table 3.** Similarity results of benthic communities determined using SIMPER and
619 ANOSIM analyses. The tables show the benthic categories cumulatively
620 contributing to the top 25% of the dissimilarity in each pairwise comparison

621 (SIMPER) of three sub-regions from the Saudi Arabian Red Sea. Relative
622 contribution and the cumulative contribution of the top benthic group to sub-
623 regional dissimilarity as well as the mean percent cover for each in the three sub-
624 regions are shown for comparison. All others contributed <2% of differences in
625 communities. Percent dissimilarity in addition to overall ANOSIM comparison
626 results (Global R= 0.632, $p < 0.001$) are included alongside the pairwise results, also
627 presented here.

628
629 **Table 4.** The most influential coral reef fishes out of the 200 species included in the
630 analysis driving *similarities* (using SIMPER analysis) between three regional sub-regions
631 which are defined as: “northern” 26.8°N – 24.4°N (n=12 reefs), “central” 23.8°N –
632 21.8°N (n=16 reefs), and “southern” 19.8°N – 18.6°N (n=12 reefs). This list is a
633 compilation of the top 25 species characteristic of each individual sub-region based on
634 the total abundance in the sub-region. Marked cells denote whether that species was
635 identified as a primary driver of similarity within that sub-region.

636

637

TABLES & FIGURES

Figure 1.

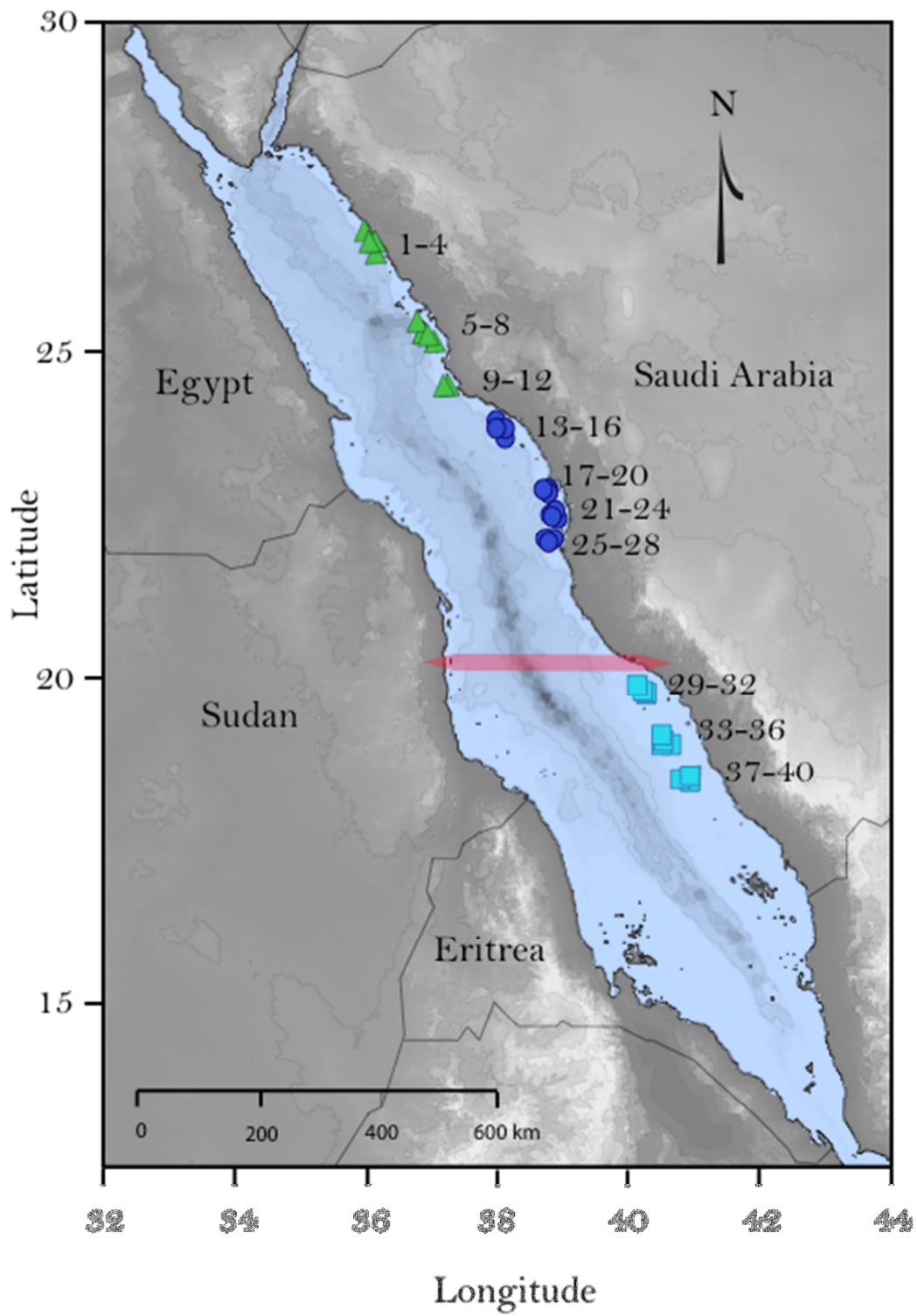


Figure 2

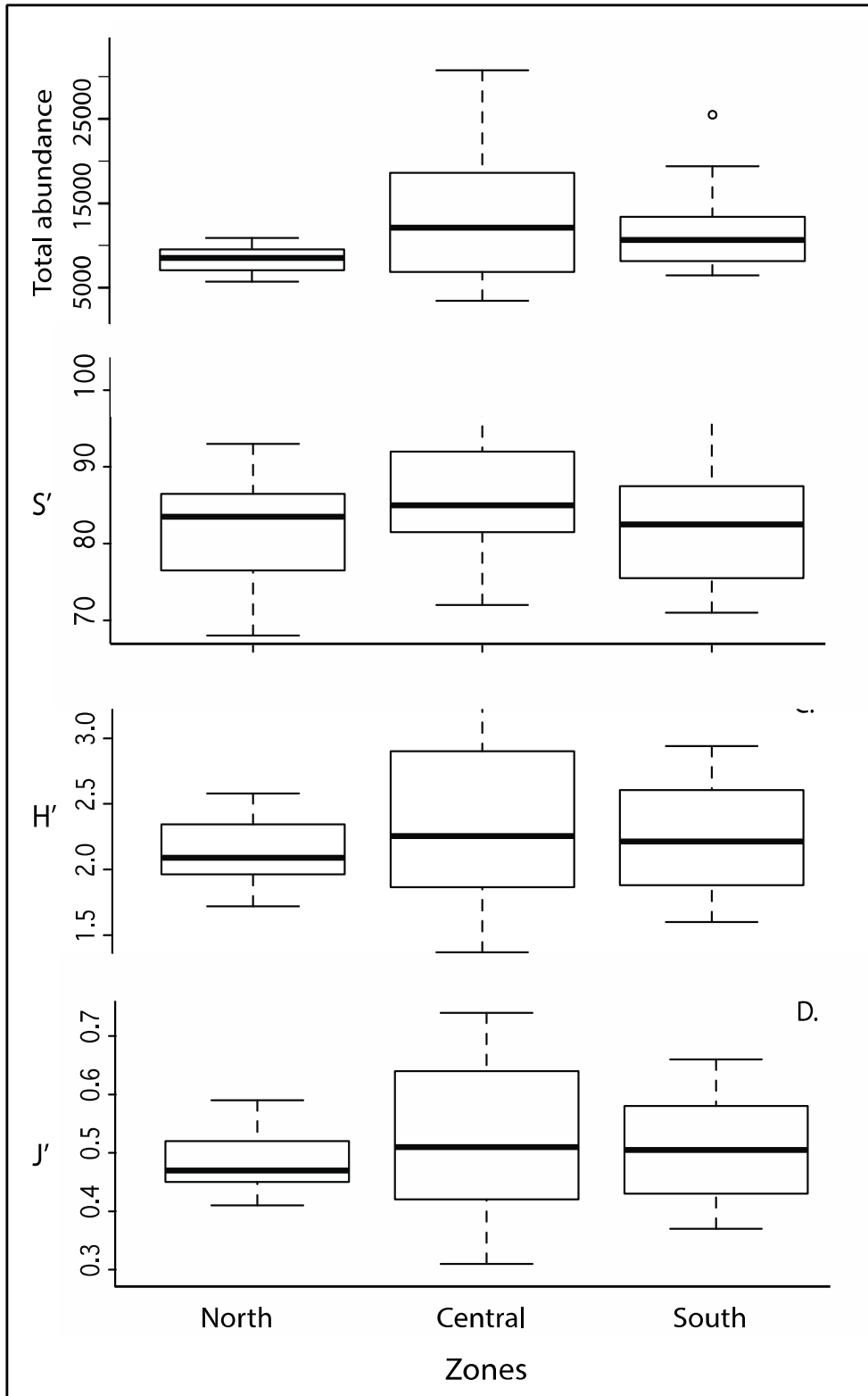


Figure 3.

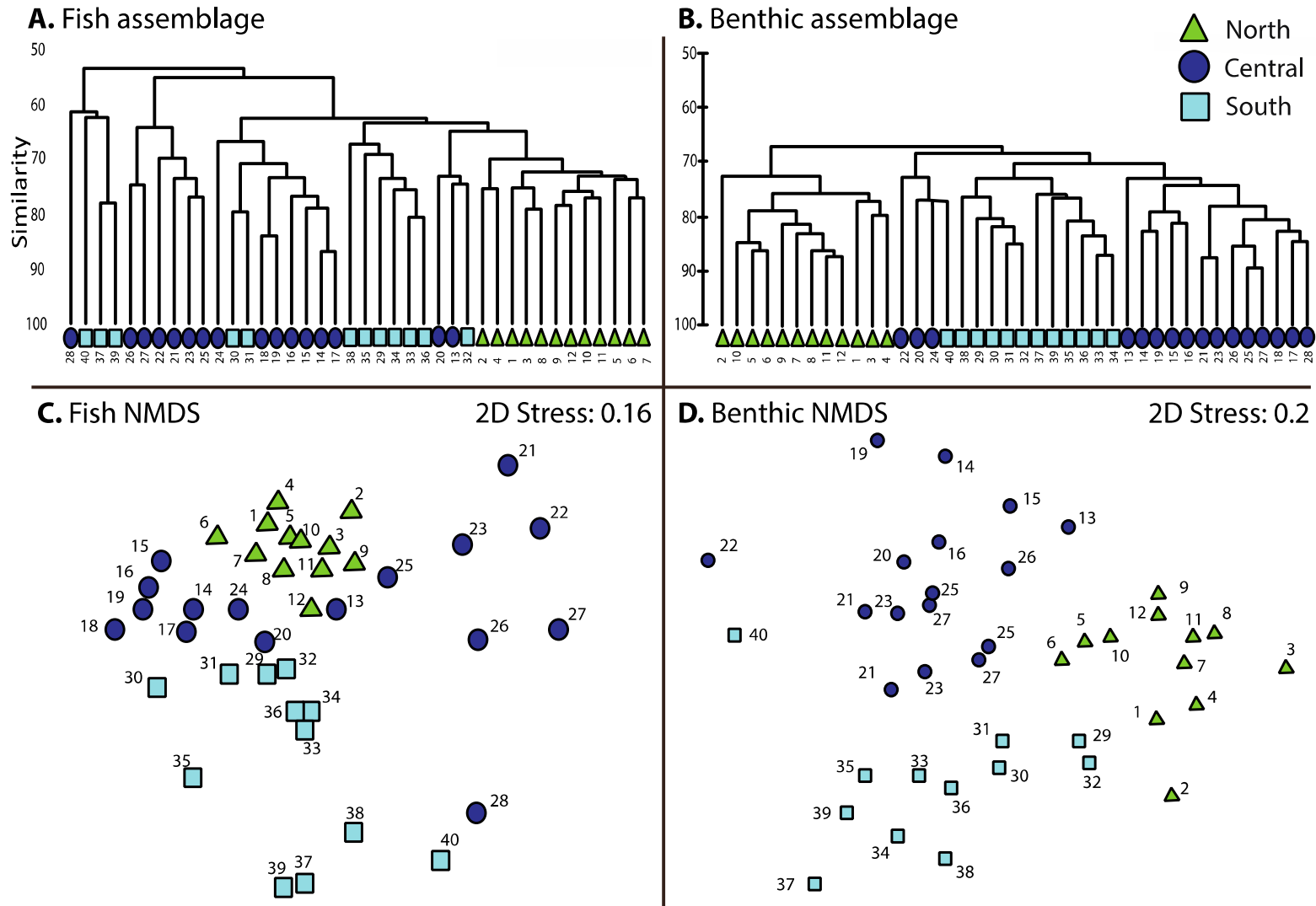


Table 1.

Sub-region	Reef ID #	Section	Reef Name	Latitude	Longitude	Survey Year	Dist.(km)	S	J'	H'(loge)	1-Lambda'
North	1	Wajh	Pele 1	26.80908	35.89095	2011	16.0	68	0.41	1.72	0.62
	2	Wajh	Skharu Luhs 1	26.62883	36.25481	2011	8.10	93	0.51	2.30	0.72
	3	Wajh	Skharu Luhs 3	26.40832	36.26557	2011	9.6	87	0.47	2.09	0.71
	4	Wajh	Skharu Luhs 2	26.37708	36.25453	2011	9.6	86	0.50	2.23	0.78
	5	Wajh Bank	Wajh Bank 1	25.39082	36.68348	2011	34.3	85	0.58	2.58	0.80
	6	Wajh Bank	Wajh Bank 2	25.27030	36.85697	2011	25.2	78	0.47	2.07	0.74
	7	Wajh Bank	Wajh Bank 3	25.24035	36.93472	2011	19.3	82	0.47	2.09	0.70
	8	Wajh Bank	Wajh Bank 4	25.15465	36.91172	2011	27.5	75	0.44	1.88	0.64
	9	Umm Lujj	Marker 7 - 1	24.45313	37.19970	2011	7.0	88	0.53	2.39	0.75
	10	Umm Lujj	Marker 7 - 2	24.44277	37.20667	2011	20.5	86	0.46	2.05	0.70
	11	Umm Lujj	Marker 7 - 3	24.43110	37.22140	2011	20.7	72	0.43	1.82	0.61
	12	Umm Lujj	Marker 7 - 4	24.727	37.151	2011	20.2	82	0.59	2.58	0.81
Central	13	Seven Sisters	Abu Galawa	23.86382	37.88830	2008	27.9	85	0.38	1.70	0.56
	14	Seven Sisters	No Name	23.83428	37.89798	2008	30.1	81	0.42	1.86	0.70
	15	Seven Sisters	Shi'b Shabarir	23.78768	37.93590	2008	33.1	83	0.31	1.37	0.56
	16	Seven Sisters	Shib Sufmami	23.75252	37.96917	2008	33.2	72	0.38	1.64	0.69
	17	Rabigh	Maria's Reef	22.85080	38.72097	2008	16.0	85	0.43	1.89	0.70
	18	Rabigh	Khamsa 2	22.79837	38.61450	2008	28.6	78	0.46	2.01	0.78
	19	Rabigh	Noura	22.74988	38.61977	2008	31.2	79	0.47	2.06	0.79
	20	Rabigh	Bayeda long	22.72068	38.79622	2008	17.8	86	0.42	1.87	0.67

	21	Thuwal	3 Stick Reef	22.45928	38.90508	2008	18.2	82	0.74	3.28	0.94
	22	Thuwal	Al Mutarbej	22.42913	38.94718	2008	13.5	98	0.70	3.19	0.93
	23	Thuwal	Al Mutarbej South	22.39037	38.91820	2008	16.4	87	0.65	2.91	0.88
	24	Thuwal	Shi'b Nazar	22.37217	38.89715	2008	18.7	90	0.59	2.67	0.84
	25	North Jeddah	Madafi	22.05675	38.76688	2008	17.7	85	0.55	2.45	0.79
	26	North Jeddah	South reef	21.93408	38.86485	2008	9.17	98	0.58	2.65	0.84
	27	North Jeddah	Coral gardens	21.86748	38.75643	2008	20.9	95	0.63	2.89	0.91
	28	North Jeddah	Abu Terr	21.86605	38.85972	2008	12.3	94	0.69	3.15	0.91
South	29	Al-Lith	Mar Mar	19.84335	39.93358	2009	47.4	101	0.48	2.23	0.75
	30	Al-Lith	Dohra Island	19.82893	39.89853	2009	51.1	73	0.41	1.76	0.69
	31	Al-Lith	Al-Jadir	19.78848	39.95683	2009	49.4	87	0.41	1.81	0.63
	32	Al-Lith	Long Reef	19.76643	39.89223	2009	56.2	78	0.37	1.60	0.61
	33	Al-Qunfidhah	AQ4	19.15483	40.30113	2009	71.3	71	0.51	2.16	0.75
	34	Al-Qunfidhah	AQ3	19.10642	40.31775	2009	73.8	89	0.59	2.65	0.81
	35	Al-Qunfidhah	Murabit 1	19.02432	40.31792	2009	77.6	79	0.57	2.49	0.84
	36	Al-Qunfidhah	Petit Murabit	19.00238	40.28493	2009	81.5	73	0.45	1.95	0.66
	37	Ablo	Ablo 4	18.70673	40.65362	2009	57.0	88	0.57	2.56	0.84
	38	Ablo	Ablo 1	18.67510	40.73922	2009	50.1	85	0.66	2.94	0.89
	39	Ablo	Ablo 3	18.66772	40.65928	2009	58.9	82	0.50	2.20	0.75
	40	Ablo	Ablo 2	18.66500	40.81282	2009	41.6	83	0.62	2.75	0.82

Table 2

Sub-regions Compared:	Species	% Contribution to Dissimilarity	% Cumulative Contribution	Sub-region 1 mean abundance	Sub-region 2 mean abundance
North and Central	<i>Pseudoanthias squamipinnis</i>	7.9	7.9	5.2	9.3
Average dissimilarity = 38.4%	<i>Chromis dimidiata</i>	7.5	15.3	16.2	16.5
ANOSIM:	<i>Pseudochromis fridmani</i>	4.8	20.1	5.7	6.1
Global R=0.212, p=0.009	<i>Chromis flavaxilla</i>	3.6	23.6	4.7	5.4
	<i>Chromis viridis</i>	2.9	26.5	2.1	2.5
North and South	<i>Chromis dimidiata</i>	5.1	5.1	16.2	17.9
Average dissimilarity = 39.2%	<i>Pseudoanthias squamipinnis</i>	4.9	10.0	5.2	6.6
ANOSIM:	<i>Chromis flavaxilla</i>	4.5	14.5	4.7	7.6
Global R=0.651, p=0.001	<i>Eviota guttata</i>	3.4	17.9	0.3	3.5
	<i>Pseudochromis fridmani</i>	2.8	20.7	5.7	5.8
	<i>Chromis viridis</i>	2.5	23.2	2.1	2.2
	<i>Chrysiptera unimaculata</i>	2.3	25.4	0.3	2.3
Central and South	<i>Chromis dimidiata</i>	7.0	7.0	16.5	17.9
Average dissimilarity = 42.96%	<i>Pseudoanthias squamipinnis</i>	7.0	14.0	9.3	6.6
ANOSIM:	<i>Pseudochromis fridmani</i>	4.0	18.0	6.1	5.8
Global R=0.260, p=0.001	<i>Chromis flavaxilla</i>	3.8	21.8	5.4	7.6
	<i>Eviota guttata</i>	2.6	24.3	0.8	3.5
	<i>Chromis viridis</i>	2.4	26.7	2.5	2.2

Table 3

Sub-regions Compared:	Species	% Contribution to Dissimilarity	% Cumulative Contribution	Sub-region 1 mean abundance	Sub-region 2 mean abundance
North and Central Average dissimilarity =35.9% ANOSIM: Global R=0.702, p=0.001	<i>Xeniidae</i>	5.2	5.2	2	3.3
	Coralline (encrusting flat)	4.9	10.1	2.5	3.7
	Rubble (turf on rubble)	4.5	14.7	1.3	0.2
	<i>Millepora</i>	4.4	19	2.1	0.9
	Coralline (turf algae on rock)	3.8	22.8	6.5	5.9
	Sand	3.6	26.4	1.1	2.1
North and South Average dissimilarity = 36.8% ANOSIM: Global R=0.7, p=0.001	Coralline (encrusting flat)	4.9	4.9	2.5	3.7
	Coralline (turf algae on rock)	4.1	9	6.5	6
	Rubble (turf on rubble)	3.8	12.8	1.3	0.2
	Sponges (encrusting flat)	3.7	16.5	1.9	2.6
	<i>Millepora</i>	3.5	20	2.1	1.1
	<i>Porites</i> (encrusting columnar)	3.5	23.5	1.1	0
	<i>Acropora</i> (digitate)	3.4	27	1.7	0.6
Central and South Average dissimilarity = 34.5% ANOSIM: Global R=0.501, p=0.001	Coralline (encrusting flat)	4.6	4.6	3.7	3.7
	<i>Xeniidae</i>	4.5	9.1	3.3	2.7
	<i>Sinularia</i>	3.9	13	1.7	0.7
	Sand	3.9	16.9	2.1	1.3
	Sponges (encrusting flat)	3.8	20.6	2.3	2.6
	Coralline (turf algae on rock)	3.6	24.3	5.9	6

Table 4

Top 25 species		North	Central	South
1	<i>Acanthurus nigrofuscus</i>	x	x	x
2	<i>Acanthurus sohal</i>	x	x	x
3	<i>Amblyglyphidodon indicus</i>	x	x	x
4	<i>Centropyge multispinis</i>	x	x	x
5	<i>Chaetodon austriacus</i>	x	x	x
6	<i>Chromis dimidiata</i>	x	x	x
7	<i>Chromis flavaxilla</i>	x	x	x
8	<i>Cirripectes castaneus</i>	x	x	x
9	<i>Ctenochaetus striatus</i>	x	x	x
10	<i>Gobiodon rivulatus</i>	x	x	x
11	<i>Gomphosus caeruleus</i>	x	x	x
12	<i>Halichoeres hortulanus</i>	x	x	x
13	<i>Labroides dimidiatus</i>	x	x	x
14	<i>Pomacentrus sulfureus</i>	x	x	x
15	<i>Pseudoanthias squamipinnis</i>	x	x	x
16	<i>Pseudocheilinus hexataenia</i>	x	x	x
17	<i>Pseudochromis fridmani</i>	x	x	x
18	<i>Pygoplites diacanthus</i>	x	x	x
19	<i>Thalassoma rueppellii</i>	x	x	x
20	<i>Chaetodon paucifasciatus</i>	x		
21	<i>Pseudocheilinus evanidus</i>	x		
22	<i>Naso elegans</i>	x	x	
23	<i>Plectroglyphidodon lucozonus</i>	x	x	
24	<i>Zebrasoma desjardini</i>	x	x	
25	<i>Chaetodon auriga</i>		x	
26	<i>Chromis viridis</i>		x	
27	<i>Heniochus intermedius</i>		x	
28	<i>Myripristis murdjan</i>	x		x
29	<i>Paracirrhites forsteri</i>	x		x
30	<i>Thalassoma lunare</i>		x	x
31	<i>Cephalopholis hemistiktos</i>			x
32	<i>Chrysiptera unimaculata</i>			x
33	<i>Eviota guttata</i>			x
34	<i>Plectroglyphidodon lacrymatus</i>			x
% Cumulative contribution		76%	72%	72%