

1 Special Paper

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3 LRH: J. D. DiBattista *et al.*

4 RRH: Contemporary patterns of Red Sea endemism

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6 **A review of contemporary patterns of endemism for shallow water reef fauna in the Red**

7 **Sea**

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35 **ABSTRACT**

36 **Aim** The Red Sea is characterised by a unique fauna and historical periods of desiccation,  
37 hypersalinity and intermittent isolation. The origin and contemporary composition of reef-  
38 associated taxa in this region can illuminate biogeographical principles about vicariance and the  
39 establishment (or local extirpation) of existing species. Here we aim to: 1) outline the  
40 distribution of shallow water fauna between the Red Sea and adjacent regions, 2) explore  
41 mechanisms for maintaining these distributions and 3) propose hypotheses to test these  
42 mechanisms.

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44 **Location** Red Sea, Gulf of Aden, Arabian Sea, Arabian Gulf and Indian Ocean

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46 **Methods** Updated checklists for scleractinian corals, fishes and non-coral invertebrates were  
47 used to determine species richness in the Red Sea and the rest of the Arabian Peninsula, and  
48 assess levels of endemism. Fine-scale diversity and abundance of reef fish within the Red Sea  
49 were explored using ecological survey data.

50

51 **Results** Within the Red Sea, we recorded 346 zooxanthellate and azooxanthellate scleractinian  
52 coral species of which 19 are endemic (5.5%). Currently 635 species of polychaetes, 211  
53 echinoderms and 79 ascidians have been documented, with endemism rates of 12.6%, 8.1% and  
54 16.5%, respectively. A preliminary compilation of 231 species of crustaceans and 137 species of  
55 molluscs include 10.0% and 6.6% endemism, respectively. We documented 1071 shallow fish  
56 species, with 12.9% endemic in the entire Red Sea and 14.1% endemic in the Red Sea and Gulf

57 of Aden. Based on ecological survey data of endemic fishes, there were no major changes in  
58 species richness or abundance across 1100 km of Saudi Arabian coastline.

59

60 **Main conclusions** The Red Sea biota appears resilient to major environmental fluctuations and  
61 is characterised by high rates of endemism with variable degrees of incursion into the Gulf of  
62 Aden. The nearby Omani and Arabian Gulfs also have variable environments and high levels of  
63 endemism, but these are not consistently distinct across taxa. The presence of physical barriers  
64 do not appear to explain species distributions, which are more likely determined by ecological  
65 plasticity and genetic diversity.

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81 **Keywords: Arabian Peninsula, biodiversity, biogeographical barriers, centre of endemism,**  
82 **coral reef, ecological processes, faunal checklist, marine biogeography**

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## 84 **INTRODUCTION**

85 Biogeographical regions with exceptional taxonomic diversity and high levels of endemism are  
86 known as biodiversity hotspots and by definition are high conservation priorities (Myers *et al.*,  
87 2000). These hotspots support a disproportionately high percentage of biodiversity including  
88 unique species and evolutionary novelty. While the Indo-Malay Archipelago (i.e. Coral Triangle)  
89 is the centre of species richness for many coral reef organisms (Briggs, 2005; Hoeksema, 2007;  
90 Veron *et al.*, 2009), endemism hotspots as expressed in percentage of unique fauna tend to occur  
91 in isolated or peripheral regions (Roberts *et al.*, 2002; Hughes *et al.*, 2002). For Indo-Pacific reef  
92 fishes, the highest endemism can be found in the Hawaiian Islands, Easter Island, Marquesas  
93 Islands, Mascarene Islands and the Red Sea (Mora *et al.*, 2003; Allen, 2008; Briggs & Bowen,  
94 2012; Kulbicki *et al.*, 2013). Recent research has also demonstrated the importance of peripheral  
95 regions, such as the Hawaiian Archipelago, the Marquesas Islands and the Red Sea in exporting  
96 unique genetic lineages to other regions (Gaither *et al.*, 2011; Malay & Paulay, 2010; Eble *et al.*,  
97 2011; Bowen *et al.*, 2013; DiBattista *et al.*, 2013).

98

### 99 **The Red Sea**

100 The Red Sea extends 2270 km from 30° N in the Gulf of Suez to 12° N in the Gulf of Aden.  
101 Based on existing checklists, 320 zooxanthellate scleractinian corals (Veron *et al.*, 2009) and  
102 1078 fish species (Golani & Bogorodsky, 2010) have been identified in this region, although  
103 these values are constantly being redefined. The Red Sea harbours one of the highest levels of

104 endemism for marine organisms, with 14% for fishes (Randall, 1994), 15% for crabs (Guinot,  
105 1966), up to 17% for echinoderms (Price, 1982; Campbell, 1987; Dafni, 2008) and as much as  
106 10% for scleractinian corals (Hughes *et al.*, 2002). Endemism is even higher for some  
107 conspicuous taxa, for example reaching 50% in butterflyfishes (e.g. Roberts *et al.*, 1992). This  
108 endemic region extends to the Gulf of Aden for many species, and to Oman or Socotra for fewer  
109 species (Winterbottom, 1985; Randall, 1995; Kemp, 1998, 2000; Zajonz *et al.*, 2000).

110 The unique fauna of the Red Sea is coupled with a turbulent geological history and unusual  
111 environmental conditions, including minimal freshwater inflow, high rates of evaporation,  
112 latitudinal gradients in environmental variables (temperature, salinity and nutrients) and a narrow  
113 (18 km) and shallow (137 m) connection with the Indian Ocean at the Strait of Bab al Mandab.  
114 Water exchange between the Red Sea and Indian Ocean was repeatedly restricted during  
115 Pleistocene glacial cycles when sea level lowered as much as 140 m (Braithwaite, 1987; Rohling  
116 *et al.*, 1998). Isolation of the Red Sea fauna is probably reinforced by cold-water upwelling off  
117 the northeast African and southern Arabian coasts (Smeed, 1997; Kemp, 2000). A turbid-water  
118 region south of 19 to 20° N in the Red Sea may also limit larval dispersal, a hypothesis supported  
119 by the disjunct distribution of some reef fish species (Roberts *et al.*, 1992) and coral genera (F.  
120 Benzoni, pers. comm.), as well as genetic differentiation between populations of coral reef  
121 organisms (Froukh & Kochzius, 2008, Nanninga *et al.*, 2014; Giles *et al.*, 2015; but see Robitzch  
122 *et al.*, 2015).

123 The extent of environmental change within the Red Sea and its effects on shallow water  
124 fauna remains controversial. Some authors believe that hypersaline conditions, comparable to the  
125 present day Dead Sea (Braithwaite, 1987), extirpated most marine life during glacial maxima

126 (Sheppard *et al.*, 1992), whereas others suggest survival of a decimated fauna within isolated  
127 refugia (Goren, 1986; Klausewitz, 1989; Rohling *et al.*, 1998).

128

### 129 **Data limitation in the Red Sea and Arabian Peninsula**

130 The first step towards understanding the patterns of biodiversity is to obtain accurate species  
131 checklists and distribution maps. The seminal works of taxonomists such as Forsskål, Cuvier &  
132 Valenciennes, Rüppell, Ehrenberg, Heller and Klunzinger led to the recognition of the Red Sea  
133 as a biodiversity hotspot for marine fauna (see Fig. 1). Modern efforts to understand  
134 biogeographical processes began with the efforts of Ekman (1953) and Briggs (1974), both of  
135 whom recognized the Red Sea as an endemism hotspot. Subsequent studies have been hindered  
136 by a dearth of geographical range information (Berumen *et al.*, 2013), but recent academic  
137 investments by several countries that border the Red Sea (Mervis, 2009) has enhanced  
138 accessibility and integration of molecular and morphological research.

139 Here we define shallow water (< 200 m) species distribution patterns of the contemporary  
140 Red Sea fauna and compare these with the rest of the Arabian Peninsula and greater Indian  
141 Ocean. Our goals include: 1) outline the distribution of faunal composition in the Red Sea and  
142 adjacent regions, 2) explore mechanisms for maintaining these distributions and 3) propose  
143 working hypotheses to test these mechanisms.

144

### 145 **MATERIALS AND METHODS**

146 Databases were created from existing checklists for zooxanthellate, and when available,  
147 azooxantellate scleractinian corals (Appendix S1 for checklist and references), fishes (Appendix

148 S2 for checklist and references) and non-coral invertebrate species (annelids, arthropods,  
149 echinoderms, tunicates and molluscs; Appendix S3 for checklist and references).

150 Species names for corals and non-coral invertebrates were confirmed in the World Register  
151 of Marine Species (WoRMS Editorial Board [2014], available from  
152 <http://www.marinespecies.org> at VLIZ, accessed 2014-09-01). Fish names were confirmed using  
153 the Catalog of Fishes (Eschmeyer, 2013) and FishBase (Froese & Pauly, 2014). For corals, we  
154 excluded reports of *nomina nuda* and *dubia* species. All checklists were updated with recent  
155 taxonomic revisions where possible.

156 For fishes, only those recorded at depths less than 200 m were included in the checklist  
157 (Appendix S2). We also exclude waifs, non-neritic pelagic and mesopelagic species that  
158 vertically migrate to the surface at night, Lessepsian migrants from the Mediterranean (see  
159 Bernardi *et al.*, 2010), as well as most cases of fishes not identified to species. We include un-  
160 named species that are clearly identified and await formal description.

161 For non-coral invertebrates we focused on taxa that have been studied recently as part of  
162 King Abdullah University of Science and Technology (KAUST) biodiversity surveys (Appendix  
163 S3). Within the crustaceans and molluscs, we selected families and genera that are well known;  
164 polychaetes, echinoderms and ascidians were treated in their entirety. Records of non-coral  
165 invertebrates are updated with taxonomic literature, the WoRMS database and our collections  
166 (see Appendix S3 for references).

167 Given our interest in Red Sea endemism, we compiled species presence-absence records  
168 from the seven Marine Ecoregions of the World (MEOWs) bordering the Arabian Peninsula  
169 (modified from Spalding *et al.*, 2007): 1) Gulf of Aqaba, 2) Red Sea, 3) Gulf of Aden, 4)  
170 Socotra, 5) Southern Oman, 6) Gulf of Oman and Pakistan and 7) Arabian Gulf (see Fig. 2). In

171 cases where data is insufficient to separate the Gulf of Aqaba or Socotra into MEOWs, they were  
172 combined with the Red Sea or Gulf of Aden, respectively. Taxonomic groups that are data  
173 deficient for an entire MEOW are omitted from regional consideration. The MEOW results are  
174 visualized using ArcGIS *vers.* 10.2 (ESRI, 2014).

175 For the purpose of this review, we define endemism at multiple scales using the following  
176 terminology: 1) *Red Sea endemic*: a species only inhabiting the Red Sea (including the Gulf of  
177 Aqaba), 2) *Red Sea to Gulf of Aden endemic*: a species only found in the Red Sea and Gulf of  
178 Aden (including Socotra) and 3) *Red Sea resident*: a species inhabiting the Red Sea but also in  
179 regions outside the Red Sea and Gulf of Aden (i.e. widespread species). For the purposes of the  
180 heat maps and discussion, we also estimated the endemism for each MEOW individually. Since  
181 reef fish have been well studied compared to invertebrates, we use survey data from select reef  
182 fishes to test patterns of biodiversity and endemism *within* the Red Sea. These analyses allowed  
183 us to more broadly assess the role of environmental gradients as barriers to dispersal in the  
184 region.

185

### 186 **Ecological survey of fish densities**

187 Based on reef fish densities (May Roberts, unpub. data) we assess the abundance of 33 Red Sea  
188 endemics on 45 reefs across 1100 km of Saudi Arabian coastline surveyed between 2008 and  
189 2011. Reefs are grouped into 10 regions from Al Wajh (26.8° N) to Ablo (18.6° N). Four  
190 replicate belt transects were made at each of four depths between the reef crest and 10 m. Each  
191 belt transect was 50 m x 4 m with the exception of smaller species (e.g. damselfishes and  
192 blennies), which were surveyed on a 50 x 1 or 2 m transect. One-way ANOVA was used to  
193 resolve latitudinal trends in mean species richness of endemics. Total abundance of these fishes



194 was summed per reef and fourth root transformed to balance the effect of very abundant species,  
195 such as *Chromis dimidiata*. All statistical analyses use the vegan package in R (Oksanen *et al.*,  
196 2014).

197

## 198 **RESULTS**

### 199 **Red Sea endemism based on MEOWs of the Arabian Peninsula**

200 **Scleractinian corals** – The Red Sea hosts 346 zooxanthellate and azooxanthellate scleractinian  
201 coral species, of which 19 are endemic (5.5%; Fig. 2a). Within the Red Sea, 307 species were  
202 found in the north/central region and 240 species were found in the southern region.  
203 For comparison, Veron *et al.* (2009) recorded 289 zooxanthellate coral species in the  
204 north/central region and higher richness in the southern region with 297 species based on similar  
205 boundaries. Additionally, Hughes *et al.* (2002) recognise 10% endemism in the Red Sea versus  
206 the 5.5% endemism identified in our study. The Arabian Gulf hosts 66 scleractinian coral species  
207 and 126 species are recorded in the Gulf of Oman. Finally, 95 species are found in the Gulf of  
208 Aden and the Arabian Sea, and 228 species, including one endemic species (0.4% endemism),  
209 are found at Socotra. In total, 394 scleractinian coral species were recorded in the Arabian  
210 Peninsula (Appendix S1).

211

212 **Fish** – The Red Sea hosts 1071 recorded fish species (versus 1760 in the entire Arabian  
213 Peninsula region) of which 138 (12.9%) are endemic to the Red Sea and 189 (14.1%) are  
214 endemic to the Red Sea and Gulf of Aden (Fig. 2b). Only 1.0%, 1.7% and 2.2% of Red Sea  
215 fishes have ranges extending to southern Oman, the Gulf of Oman or the Arabian Gulf,  
216 respectively, but no further. By comparison, Eschmeyer *et al.* (2010) recorded 1188 Red Sea fish

217 species, including 159 endemics, resulting in a comparable endemism rate of 13.6%. Goren &  
218 Dor (1994) listed 1248 species from the Red Sea. Both of these estimates, however, include all  
219 fish species as opposed to our stricter criteria, and may include unverifiable records for the latter.  
220 Similar to Fricke *et al.* (2014), we note that some of the endemic fish fauna are restricted to the  
221 Gulf of Aqaba (4.1%). This indicates an effective ecological barrier separating the Gulf of Aqaba  
222 from the rest of the Red Sea (also see Klauswitz, 1989; Sheppard *et al.*, 1992), possibly due to  
223 higher salinity in this region. This pattern may also be explained by sampling bias because  
224 87.5% of the Gulf of Aqaba endemics are from a single collection. We also note that even  
225 though the Gulf of Aden or Socotra are not considered centres of endemism (0.7% and 1.4%,  
226 respectively), the former has the second highest level of species richness in the study (Fig. 2b),  
227 and the latter appears to be a hotspot for the mixing of Red Sea and Indian Ocean fauna (see  
228 DiBattista *et al.*, 2015).

229

230 **Non-coral invertebrates** – Echinoderms are among the best studied invertebrates, with 211  
231 species recorded from the Red Sea. Of these species, 17 (8.1%) are known only from the Red  
232 Sea and 21 (10.0%) from the Red Sea to Gulf of Aden. Currently 79 ascidian species are  
233 documented from the Red Sea, with 13 (16.5%) endemic, although the rest of the Arabian  
234 Peninsula remains understudied. Among 635 polychaete species recorded from the Red Sea, 80  
235 (12.6%) are endemic and 92 (14.5%) are Red Sea to Gulf of Aden endemic. An incomplete  
236 compilation of decapods shows 231 Red Sea species, including 23 (10.0%) endemic to the Red  
237 Sea and 31 (13.4%) endemic to the Red Sea to Gulf of Aden. Although the Red Sea molluscan  
238 fauna is represented in museum collections and field guides, sampling of the Arabian Peninsula  
239 and northern Somalia is limited, and does not allow us to assess Red Sea endemism with

240 confidence. Based on the molluscs considered here, we predict 6.0% Red Sea endemism among  
241 species that occur within the Arabian Peninsula region. This figure would be higher if the Gulf of  
242 Aden were treated in the same biogeographical unit as the Red Sea. Exacerbating this lack of  
243 general knowledge is the prevalence of cryptic species among marine invertebrates, especially in  
244 groups that do not use visual systems for mate recognition (Knowlton, 1993). Integrative studies  
245 that include field and genetic approaches consistently reveal higher levels of endemism. For  
246 example, 36 species (38%) of sea cucumbers from the Red Sea to Gulf of Aden are endemic to  
247 the area based on DNA barcodes (G. Paulay, unpub. data). For molluscs, molecular data have  
248 identified new species (e.g. nudibranchs; Jörger *et al.*, 2012) and the resurrection of a historically  
249 described species (e.g. Huber & Eschner, 2011).

250

### 251 **Red Sea endemism for reef fish**

252 Among reef fishes, the proportion of Red Sea endemics per family varies from 0 to 100%. The  
253 14 families with > 50% endemism have seven or fewer Red Sea species. Among families with 10  
254 or more Red Sea species, five of these have endemism values > 25% (Callionymidae,  
255 Pseudochromidae, Tripterygiidae, Monacanthidae and Tetraodontidae). When we consider the  
256 Red Sea and Gulf of Aden combined, this value increases for several families or sub-families  
257 including the Pseudochromidae (from 33.3% to 64.3%), Apogonidae (15.3% to 25.3%) and  
258 Scarinae (11.1% to 32.0%). Endemism is apparent for the Chaetodontidae only when the Red  
259 Sea and Gulf of Aden region are considered together (0% to 12.0%, but 32.0% for the entire  
260 Arabian Peninsula region), which contradicts the 50% endemism reported in Roberts *et al.*  
261 (1992). The variable proportion of endemic species across taxonomic groups indicates that the  
262 evolutionary processes have affected groups of reef fish differently. These results must be

263 interpreted with caution given that presence-absence data may be biased for highly dispersive  
264 species that appear in locations where they are functionally absent.

265

### 266 **Reef fish density data**

267 Based on 33 Red Sea to Gulf of Aden endemic reef fish species, there were no major changes in  
268 species richness or abundance among 10 sub-regions (Figs 3 and 4). One-way ANOVA analyses  
269 revealed no consistent significant change with latitude or direction across our survey area.

270 Indeed, out of 99 comparisons between northern, central and southern regions for all species,  
271 only 16 were significant at  $P < 0.05$ . This trend was most apparent in the numerically dominant  
272 species (e.g. *Chromis dimidiata*, *Thalassoma rueppellii*, *Pseudochromis fridmani*). Such findings  
273 contradict previous evidence for biogeographical barriers in the central Red Sea (Khalaf &  
274 Kochzius, 2002; Spalding *et al.*, 2007; but see Kulbicki *et al.*, 2013). This central delineation  
275 may instead represent an “average” boundary for many of the species that show distributional  
276 shifts.

277

### 278 **DISCUSSION**

279 The Red Sea hosts a distinct coral reef fauna with consistently high endemism for shallow water  
280 organisms (> 10% in fishes, annelids, arthropods and chordates). Looking across the region,  
281 levels of both biodiversity and endemism are highest in the Red Sea for fishes and scleractinian  
282 corals (Fig. 2). The pattern is more complicated for the non-coral invertebrates, with a trend of  
283 highest diversity and endemism in the Red Sea, Gulf of Oman and Arabian Gulf (Fig. 2). This  
284 confirms the status of the Red Sea as a significant region of endemism for coral reef biota at the

285 western periphery of the Indo-Pacific. Reef fishes provide the most complete information for  
286 investigating the processes that underlie patterns of endemism.

287 Two features dominate the biogeography of Red Sea reefs. Firstly, the biota has persisted  
288 through major environmental alterations, especially with respect to temperature and salinity  
289 (DiBattista *et al.*, 2013). Episodic restrictions of the Strait of Bab al Mandab during the  
290 Pleistocene produced an environment that was very different from contemporary conditions,  
291 which in turn would eliminate or extirpate many species throughout the Red Sea. Indeed, we did  
292 not detect any differences in species richness or community composition of the endemic reef  
293 fishes across the Red Sea based on our survey data. Secondly, the Red Sea biota are not confined  
294 by consistent geographic boundaries, with some endemics penetrating varying distances into the  
295 Gulf of Aden and the northern Arabian Sea. Pelagic larval duration (PLD) does not appear to be  
296 an important determinant of geographic range size in most instances (Victor & Wellington, 2000;  
297 Lester & Ruttenberg, 2005; Macpherson *et al.*, 2006; Luiz *et al.*, 2013), especially for peripheral  
298 regions such as the East Pacific (Robertson, 2001; Zapata & Herrón, 2002; Lessios & Robertson,  
299 2006). Thus neither differences in larval duration nor the presence of physical barriers likely  
300 define the distributions of reef fishes in the Red Sea. We consider the details of these issues  
301 below.

302

### 303 **What are the processes maintaining putative barriers to dispersal for the Red Sea?**

#### 304 *a. Environmental gradients*

305 The contemporary Red Sea is a spatially heterogeneous ecosystem based on gradients in salinity  
306 (range: 35 to 41 ppt), temperature (range: 21 to 34 °C) and primary productivity (Chlorophyll a  
307 [chl-a] range: 0.5 to 4.0 mg/m<sup>3</sup>) (Sofianos, 2003; Raitzos *et al.*, 2013) from north to south.

308 Besides spatial variation there are seasonal differences among regions. Temperature variation in  
309 the northern (20 to 30°N) and southern (12 to 16°N) Red Sea is much higher (annual range ~10  
310 °C) than in the central Red Sea (annual range ~5 °C). Salinity in the Gulf of Suez and Gulf  
311 Aqaba also have higher annual ranges (2 to 4 ppt) than the rest of the Red Sea (< 1 ppt). The  
312 oligotrophic waters of the north (chl-a range: 0.1 to 0.35 mg/m<sup>3</sup>) contrast with the eutrophic  
313 waters in the south, which vary considerably (chl-a range: 0.5 to 5.0 mg/m<sup>3</sup>) due to seasonal  
314 influx of nutrient rich waters from the Gulf of Aden.

315 Reef fish species richness, abundance and composition appear to be evenly distributed across  
316 eight degrees of latitude and 1100 km of Saudi coastline (Fig. 3 and 4), spanning a gradient with  
317 significant temporal and spatial variation in the physical environment. We lack data, however,  
318 from the Gulf of Aqaba in the far north (but see Khalaf & Kochzius, 2002), and more critically  
319 from the Farasan Islands (Saudi Arabia into Yemen) in the far south (Fig. 3). The Farasan Islands  
320 are characterised by shallow sand banks, sparsely distributed reef and eutrophic conditions  
321 compared to the sloping, oligotrophic reefs for the rest of the Red Sea (Sheppard & Sheppard,  
322 1991; Raitzos *et al.*, 2013). Central and southern Red Sea regions in this study did, however,  
323 support a few species not recorded from the northern region (Fig. 4). This agrees with previous  
324 work that shows some species, such as the damselfish *Neopomacentrus miryae* and the wrasse  
325 *Paracheilinus octotaenia* are abundant in the northern Red Sea, but virtually absent in the  
326 southern part (Ormond & Edwards, 1987; Sheppard *et al.*, 1992; also see Winterbottom, 1985).  
327 The unique environmental features of the Farasan Islands in the far south suggests that fish  
328 communities there would also differ from the assemblages to the north and should be a focal  
329 point for further study.

330

331 *b. Species specific differences in dispersal and colonisation*

332 Robertson (2001) found that endemic reef fishes could not be differentiated by PLD estimates  
333 from similar species with broad distributions. The conclusion that PLD values are not reliable  
334 indicators of range size is further supported by analyses of reef fish taxa with very different  
335 larval dispersal characteristics that traverse the vast Eastern Pacific Barrier (> 6000 km) in both  
336 directions (Lessios & Robertson, 2006). PLDs as a basis for estimating the dispersal potential in  
337 coral reef fishes is also the subject of ongoing debate (Riginos *et al.*, 2011; Selkoe & Toonen,  
338 2011).

339 To test the hypothesis that dispersal limitation is not driving small range sizes in the Red Sea  
340 endemics, larval input could be quantified in adjacent but divergent environments. This could be  
341 tested with light traps, crest nets or the In-Situ Ichthyoplankton Imaging System (ISIIS; Cowen  
342 & Guigand, 2008) for fish larvae, or settlement plates (and complimentary genetics) for corals  
343 and non-coral invertebrates (e.g. Plaisance *et al.*, 2011). These methods should be accompanied  
344 by visual surveys to document the abundance and distribution of recently settled recruits,  
345 juveniles and adults. Monitoring survivorship of recruits should be included because traits that  
346 increase survivorship appear important in promoting persistence following range extensions  
347 (Luiz *et al.*, 2013).

348

349 *c. Available resources and recruitment*

350 Recruitment failure is a potentially important driver of the localized distribution and abundance  
351 patterns of Red Sea or regional endemics. For example, distributions may be extremely localized  
352 in Gulf of Aden and Oman endemic parrotfishes, such as *Scarus arabicus* and *Scarus zufar*,  
353 whereas other regional endemics (*Scarus ferrugineus*) extend through the entire environmental

354 gradient of the Red Sea and northern Arabian Sea (Choat *et al.*, 2012). It is unlikely that  
355 dispersal capacity is the limiting factor in these species distributions. Testing of recruitment  
356 failure hypotheses requires a capacity to identify recruitment habitats and the age structure and  
357 condition of endemic species over their distributional range. Genomic and stable isotope  
358 analyses provide options to resolve ontogenetic interactions between the relevant species and  
359 suitable habitats.

360

#### 361 *d. Phylogenetic community structure in the Red Sea*

362 Phylogenetic hypotheses are now available for a wide range of reef organisms, including  
363 endemic and more widespread species that occur in the Red Sea (e.g. Fessler & Westneat, 2007).  
364 Exploring patterns of phylogenetic community assembly at multiple scales (Kooyman *et al.*,  
365 2011) will resolve the role of environmental filtering, competition and specific climatic factors in  
366 shaping Red Sea coral reef ecosystems.

367 Several families of Red Sea reef fishes are ideal for phylogenetic community assembly  
368 analysis, including the wrasses and parrotfishes (Labridae), damselfishes (Pomacentridae) and  
369 butterflyfishes (Chaetodontidae) (Westneat & Alfaro, 2005; Fessler & Westneat, 2007; Cooper *et al.*,  
370 2009; Cowman *et al.*, 2009; Choat *et al.*, 2012; Hodge *et al.*, 2014; DiBattista *et al.*, in  
371 press). The first step is to examine phylogenetic dispersion of Red Sea reef fishes on their  
372 respective trees and then examine phylogenetic distance among members of the community. The  
373 endemic Red Sea species appear to be derived from many different parts of their family trees,  
374 indicating that the factors driving Red Sea endemism impact multiple clades with different  
375 ecologies. Measures of phylogenetic under- and over-dispersion can reveal patterns of faunal



376 exchange with the Indian Ocean and the timing of Red Sea endemism among multiple reef  
377 organisms (see Hodge *et al.*, 2014).

378

379 *e. Physical barriers to dispersal: One theory to define species distributions and gene flow*

380 Physical barriers to dispersal of marine biota are less evident than amongst terrestrial ecosystems  
381 (Mayr, 1954). In terms of habitat patchiness, both the eastern and western coasts of the Red Sea  
382 are lined with continuous fringing coral reefs from north to south. Also, the Red Sea is quite  
383 narrow, only 234 km at its widest point, and so this may enhance dispersal across the deep open  
384 centre, which is possibly an effective barrier only to shallow benthic species with limited  
385 dispersal (Leese *et al.*, 2008; Munday *et al.*, 2009).

386 Another physical barrier, albeit ephemeral in nature, is the shallow (137 m) Strait of Bab al  
387 Mandab in the south, which reduces water exchange between the Red Sea and the Indian Ocean  
388 during glacial maxima (Rohling *et al.*, 1998; Siddall *et al.*, 2003; Bailey, 2009). This historical  
389 barrier may be responsible for some of the observed endemics, although the origination of  
390 several reef fish taxa (and their coral reef hosts) in the Red Sea predates the Pleistocene (Benzie,  
391 1999; Choat *et al.*, 2012; Duchene *et al.*, 2013; Hodge *et al.*, 2014).

392 Within the Red Sea, the narrow (6 km) and shallow (242 to 270 m) Straits of Tiran between  
393 the Gulf of Aqaba and Red Sea proper can also act as a physical barrier. The deep and narrow  
394 fjord-like Gulf of Aqaba is 180 km long and is 25 km at its widest point, and the depth can reach  
395 1800 m but averages 800 m. Hot and dry desert flank the semi-enclosed basin, which result in a  
396 high evaporation rate, high salinity (41 ppt) and a thermohaline circulation that drives water  
397 exchange with the Red Sea (Reiss & Hottinger, 1984). Water residence time in the upper 300 m  
398 of the Gulf of Aqaba varies from only a few months up to two years. The amount of Red Sea

399 water reaching the northern tip of the Gulf of Aqaba is therefore estimated to be only 1% of that  
400 at the Straits of Tiran (Wolf-Vecht *et al.*, 1992).

401 Genetics provides one way to examine connectivity and effective barriers (e.g. Baums *et al.*,  
402 2006; Crandall *et al.*, 2012; Liggins *et al.*, 2013; Selkoe *et al.*, 2014). Most genetic connectivity  
403 studies have focused on broad-scale comparisons between the Red Sea and greater Indo-Pacific.  
404 For example, Froukh & Kochzius (2008) identified a genetic partition in the damselfish *Chromis*  
405 *viridis* between the Red Sea and Indonesia, whereas studies on lionfish (*Pterois* spp.) using  
406 similar mtDNA sequence methods find no difference (Kochzius *et al.*, 2003; Kochzius & Blohm  
407 2005). A study on mtDNA sequence divergence between fishes from the Red Sea and Japan  
408 revealed high divergences for *Apogon cyanosoma*, *Gerres oyena*, *Sargocentron rubrum*,  
409 *Spratelloides delicatulus* and *Terapon jarbua* (5.8% to 18.8%), possibly indicating cryptic  
410 species (Tikochinski *et al.*, 2013). The Indo-Pacific damselfish *Dascyllus aruanus* demonstrated  
411 differentiation between Red Sea and Western Indian Ocean (WIO) samples based on mtDNA  
412 and microsatellite markers (Liu *et al.*, 2014). However, the Goldband Goatfish, *Upeneus*  
413 *mollucensis*, did not show any mtDNA differentiation on this scale (Tikochinski *et al.*, 2013).  
414 Another recent study of Red Sea resident reef fish showed a range of connectivity with the WIO,  
415 from species with almost no differentiation (*Halichoeres hortulanus* and *Lutjanus kasmira*) to  
416 species with ancient genetic separations (*Neoniphon sammara* and *Pygoplites diacanthus*)  
417 (DiBattista *et al.*, 2013). Research on invertebrates (*Acanthaster planci*: Vogler *et al.*, 2008;  
418 *Panulirus penicillatus*: M. Iacchei, pers. comm.; *Pocillopora* spp., Pinzón *et al.*, 2013; *Scylla*  
419 *serrata*: Fratini & Vannini, 2002, *Tridacna maxima*: Nuryanto & Kochzius, 2009; Holothuroids:  
420 G. Paulay, unpub. data) support a genetic distinction of Red Sea versus Indian Ocean  
421 populations. These combined results indicate sustained isolation between the Red Sea and WIO

422 populations for several hundred thousand years. The diversity of outcomes is also likely a  
423 reflection of taxonomic differences in life histories and habitat requirements that have evolved  
424 over millions of years.

425

## 426 **Conclusion and future perspectives**

427 Since 2000, 58 new endemic species have been described in the Red Sea indicating that a vast  
428 gap remains between recognised taxonomy and existing biodiversity (Table 1). Most descriptions  
429 are based on morphological data highlighting the need for increased sampling in understudied  
430 regions of the Red Sea (i.e. along its western shores and the far south) where new species await  
431 discovery. Recent genetic tools add momentum to the discovery of cryptic species, which can be  
432 very difficult to distinguish based on morphological characters (Knowlton, 1993; Bickford *et al.*,  
433 2007), leading to underestimates of species diversity. Exceptional examples are seen in primitive  
434 bony fishes such as the round herrings (genus *Etrumeus*). Recent morphological and  
435 phylogenetic studies reveal seven divergent mitochondrial lineages within a single putative  
436 species (DiBattista *et al.*, 2012; Randall & DiBattista, 2012; DiBattista *et al.*, 2014), most of  
437 which are distributed in allopatry, and all of which are now described as distinct species.  
438 Phylogenetic frameworks are also fruitful testing grounds for biogeographical hypotheses by  
439 relating differences in life-history, ecology, physiology and behaviour among closely (and more  
440 distantly) related species (see DiBattista *et al.*, in press).

441 Molecular tools are proving useful for the identification of cryptic lineages in endemism  
442 hotspots such as Hawai'i (Randall *et al.*, 2011), the Marquesas Islands (Szabo *et al.*, 2014) and  
443 the Red Sea (Randall & DiBattista, 2013). In the Red Sea, only 10% of the new species  
444 descriptions listed in Table 1 were corroborated using molecular data, but this includes three new

445 species of fish (DiBattista *et al.*, 2012; Herler *et al.*, 2013; Koeda *et al.*, 2014) and a coral  
446 (Terraneo *et al.*, 2014). As molecular tools are applied more broadly, endemism in the region  
447 will continue to rise. But certainly broadscale sampling is necessary to discover the cryptic  
448 evolutionary lineages hidden in species previously thought to be widespread (e.g. Williams &  
449 Reid, 2004; Vogler *et al.*, 2008; Williams *et al.*, 2011, 2012; Hoareau *et al.*, 2013; Postaire *et al.*,  
450 2014). Undersampled areas include the Andaman Sea, Bangladesh, India, Myanmar, Somalia  
451 and much of the Red Sea (particularly Eritrea and Yemen). This deficiency is partly due to long-  
452 term political instability, although some regions like Western Australia are politically stable but  
453 undersampled (e.g. Poore *et al.*, 2014).

454       Based on the regional picture of endemism and the underlying processes that produce them, a  
455 primary question is what prevents Red Sea endemics from spreading eastward. Indeed, the Red  
456 Sea is in contact with the Arabian Sea and WIO through the Gulf of Aden. It is unlikely that Red  
457 Sea and regional endemics are confined to particular areas due to either physiological constraints  
458 or a limited dispersal capacity. Moreover, the Red Sea reef biota have been and are currently  
459 subject to a demanding and highly variable environment. A number of taxa display an abrupt  
460 southern boundary to their distribution extending only to the Strait of Bab al Mandab, whereas  
461 others extend beyond the Gulf of Aden to the northern coast of Oman. In this sense the southern  
462 boundary of the Red Sea is selectively porous, allowing some species to establish populations in  
463 the different reef environments of the northern Arabian Sea. Both Red Sea and Omani reef  
464 environments are highly variable, and for this reason, environmental variation *per se* in the Gulf  
465 of Aden is unlikely to constitute a distributional barrier; rather ecological factors may dominate.

466       The geological history and differences in oceanographic regime between the Red Sea, Gulf  
467 of Aden, Oman and the Arabian Gulf have resulted in very different reef ecosystems. This

468 spectrum ranges from sites in the Red Sea dominated by corals that have evolved in high  
469 temperature and relatively clear water environments to rocky reefs dominated by upwelling  
470 episodes in the Gulf of Aden and northern Arabian Sea. Some reef fish taxa, for example, with  
471 very different larval characteristics (e.g. *Acanthurus sohal* and *Scarus ferrugineus*) are able to  
472 extend beyond the Red Sea while others (e.g. *Acanthurus gahhm* and *Chlorurus gibbus*) remain  
473 restricted to the north of Bab al Mandab. This suggests a taxon specific capacity to recruit to the  
474 distinctive reef systems of Oman and the genetic endowment to respond to the environments  
475 encountered there. Thus, present day boundaries at the southern Red Sea will be porous and  
476 determined by differing degrees of ecological plasticity and genetic diversity in taxa that  
477 penetrate beyond the Red Sea and into the Gulf of Aden.

478 Our primary argument for this ecological filter follows Keith *et al.* (2015): what appears to  
479 be geographic barriers are defined by traits indicative of establishment (i.e. habitat switching)  
480 and persistence but not necessarily dispersal (also see Keith *et al.*, 2011; Luiz *et al.*, 2013). This  
481 hypothesis predicts that while a number of species may disperse beyond the southern boundary  
482 of the Red Sea, the capacity to establish populations reflects the extent to which both phenotypic  
483 plasticity and genetic endowment of the potential colonisers allows successful settlement, post  
484 settlement survival and recruitment to novel environments. Individuals successfully colonising  
485 reef habitats ecologically distinct from that of the parental population would be those with the  
486 capacity to respond to the novel selective environments. Genetic analyses designed to  
487 differentiate between drift and natural selection (i.e. RAD-seq methods; Willette *et al.*, 2014) in  
488 driving differences between parental and colonising populations would be an appropriate  
489 research design. The prediction is that species that successfully recruit beyond the distributional  
490 boundaries of the parental population will display strong signatures of selection. A critical

491 feature would be to determine if such colonising populations represent an independent  
492 evolutionary trajectory driven by divergent selection in the environment encountered by the  
493 colonists. This is the approach taken by Gaither *et al.* (2015) in a comparative analysis of Indo-  
494 Pacific surgeonfish that successfully colonised the divergent reef environment of the Marquesas  
495 Islands, and would therefore be appropriate to apply more broadly to other reef fauna.

496

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510

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867

## 868 **SUPPORTING INFORMATION**

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

870

### 871 **Appendix S1**

872 Updated checklist of corals from the Arabian Peninsula region, including source references.

873

874 **Appendix S2**

875 Updated checklist of shore fish from the Arabian Peninsula region, including footnotes and  
876 source references.

877

878 **Appendix S3**

879 Updated checklist of non-coral invertebrate phyla (annelids, arthropods, echinoderms, tunicates  
880 and molluscs) from the Arabian Peninsula region, including source references.

881

882 **Biosketch**

883 The authors include researchers with a vast range of expertise including ecological surveys,  
884 testing evolutionary models, resolving life history traits that influence dispersal, population  
885 separations in reef organisms and informing marine conservation initiatives in the greater Indo-  
886 Pacific region.

887

888 Author contributions: All authors listed here contributed data, analysed the data or wrote sections  
889 of the paper.

890

891 Editor: David Bellwood

892

Species	taxonomic authority
<b>Vertebrata</b>	
<i>Acanthoplesiops cappuccino</i>	Gill, Bogorodsky & Mal, 2013
<i>Adelotremus leptus</i>	Smith-Vaniz & Rose, 2012
<i>Amblyeleotris neglecta</i>	Jaafar & Randall, 2009
<i>Aseraggodes kruppi</i>	Randall, Bogorodsky & Mal, 2013
<i>Aseraggodes macronasus</i>	Randall, Bogorodsky & Mal, 2013
<i>Bryaninops spongicolus</i>	Suzuki, Bogorodsky & Randall, 2012
<i>Cabillus nigrostigmus</i>	Kovacic & Bogorodsky, 2013
<i>Enneapterygius qirmiz</i>	Holleman & Bogorodsky, 2012
<i>Entomacrodus solus</i>	Williams & Bogorodsky, 2010
<i>Etrumeus golanii</i>	DiBattista, Randall & Bowen, 2012
<i>Eviota geminata</i>	Greenfield & Bogorodsky, 2014
<i>Eviota oculopiperita</i>	Greenfield & Bogorodsky, 2014
<i>Evoxymetopon moricheni</i>	Fricke, Golani & Appelbaum-Golani, 2014
<i>Gobiodon ater</i>	Herler, Bogorodsky & Suzuki, 2013
<i>Gobiodon bilineatus</i>	Herler, Bogorodsky & Suzuki, 2013
<i>Gymnapogon melanogaster</i>	Gon & Golani, 2002
<i>Gymnothorax baranesi</i>	Smith, Brokovich & Einbinder, 2008
<i>Gymnoxenisthmus tigrellus</i>	Gill, Bogorodsky & Mal, 2014
<i>Heteroeleotris dorsovittata</i>	Kovacic, Bogorodsky & Mal, 2014
<i>Heteroeleotris psammophila</i>	Kovacic & Bogorodsky, 2014
<i>Hippocampus debelius</i>	Gomon & Kuitert, 2009
<i>Hypoatherina golanii</i>	Sasaki & Kimura, 2012
<i>Limnichthys marisrubri</i>	Fricke & Golani, 2012
<i>Opisthognathus dipharus</i>	Smith-Vaniz, 2010
<i>Pempheris tominagai</i>	Koeda, Yoshino & Tachihara, 2014
<i>Pseudamiops springeri</i>	Gon, Bogorodsky & Mal, 2013
<i>Pteragogus clarkae</i>	Randall, 2013
<i>Pteragogus trispilus</i>	Randall, 2013
<i>Siphamia goreni</i>	Gon & Allen, 2012
<i>Soleichthys dori</i>	Randall & Munroe, 2008
<i>Symphysanodon disii</i>	Khalaf & Krupp, 2008



*Tomiyamichthys dorsostigma* Bogorodsky, Kovacic & Randall, 2011  
*Upeneus davidaromi* Golani, 2001  
*Uranoscopus rosette* Randall & Arnold, 2012  
*Vanderhorstia opercularis* Randall, 2007

**Annelida**

*Harmothoe marerubrum* Wehe, 2006  
*Lepidonotus polae* Wehe, 2006  
*Parahalosydropsis arabica* Wehe, 2006

**Arthropoda**

*Charybdis omanensis septentrionalis* Türkay & Spiridonov, 2006  
*Ethusa thieli* Spiridonov & Türkay, 2007  
*Petrolisthes aegyptiacus* Werding & Hiller, 2007

**Cnidarians**

*Acropora parapharaonis* Veron, 2000  
*Anacropora spumosa* Veron, Turak & DeVantier, 2000  
*Cyphastrea hexasepta* Veron, DeVantier & Turak, 2000  
*Echinopora irregularis* Veron, Turak & DeVantier, 2000  
*Echinopora tiranensis* Veron, Turak & DeVantier, 2000  
*Goniopora sultani* Veron, DeVantier & Turak, 2000  
*Montipora aspergillus* Veron, DeVantier & Turak, 2000  
*Montipora echinata* Veron, DeVantier & Turak, 2000  
*Montipora hemispherica* Veron, 2000  
*Montipora pachytuberculata* Veron, DeVantier & Turak, 2000  
*Montipora saudii* Turak, DeVantier & Veron, 2000  
*Pachyseris inattesa* Benzoni & Terraneo, 2014

**Mollusca**

*Turbo (Aspilaturbo) marisrubri* Kreipl & Alf, 2001

**Tunicata**

*Boltenia yossiloya* Shenkar & Lambert, 2010  
*Botryllus eilatensis* Shenkar & Monniot, 2006

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894 **FIGURE LEGENDS**

895 **Figure 1** Number of valid Red Sea endemic scleractinian coral ( $N = 19$ ), fish ( $N = 138$ ) or non-  
896 coral invertebrate ( $N = 91$ ) species described from 1741 to 2014 with seminal works noted.

897

898 **Figure 2** Species richness and level of endemism (%) for (a) scleractinian corals, (b) fish, (c)  
899 annelids, (d) arthropods, (e) echinoderms, (f) tunicates and (g) molluscs within each of the seven  
900 Marine Ecoregions of the World (MEOWs) bordering the Arabian Peninsula (modified from  
901 Spalding *et al.*, 2007): 1) Gulf of Aqaba, 2) the Red Sea; 3) Gulf of Aden, 4) Socotra, 5)  
902 Southern Oman; 6) Gulf of Oman and Pakistan and 7) Arabian Gulf. In cases where there is no  
903 data for a MEOW, the region was coloured white; MEOWs coloured grey have zero values. In  
904 cases where data was insufficient to separate the Gulf of Aqaba and Socotra MEOW sub-regions,  
905 they were assigned the same colour as their primary MEOW Red Sea or Gulf of Aden,  
906 respectively.

907

908 **Figure 3** Mean species richness of endemic fishes from (a) Red Sea and (b) Red Sea to Gulf of  
909 Aden based on a maximum of 33 conspicuous species, estimated from sites within the Red Sea  
910 from latitude  $26.8^{\circ}$  N (Al Wajh) to  $18.6^{\circ}$  N (Ablo). In most cases, there were four reefs surveyed  
911 in each of the 10 regions, exceptions include Thuwal (five reefs) and Al Lith (eight reefs). North,  
912 central, and southern Red Sea partitions defined as Al Wajh to the Seven Sisters ( $26.8^{\circ}$  N to  
913  $23.8^{\circ}$  N), Rabigh to Jeddah ( $22.8^{\circ}$  N to  $21.8^{\circ}$  N) and Al Lith to Ablo ( $19.9^{\circ}$  N to  $18.6^{\circ}$  N) are  
914 shaded light red, light blue and light green, respectively. Black horizontal bars on the box plot  
915 represent the median of each group. Upper and lower bounds of the boxes represent the 75<sup>th</sup> and

916 25<sup>th</sup> percentiles, respectively. Vertical lines extend to the 95<sup>th</sup> (upper line) and 5<sup>th</sup> (lower line)  
917 percentiles.

918

919 **Figure 4** Fourth-root transformed average abundance of Red Sea to Gulf of Aden endemic reef  
920 species ( $N = 33$ ) along with standard deviation in the north, central and southern Red Sea  
921 partitions defined as Al Wajh to the Seven Sisters (26.8° N to 23.8° N), Rabigh to Jeddah (22.8°  
922 N to 21.8° N) and Al Lith to Ablo (19.9° N to 18.6° N), respectively. Bars within the figure were  
923 derived from average abundances among transects (area dependent on fish species and thus  
924 corrected for) within reefs for each of the three partitions. All fish species have been ordered  
925 most to least abundant and further grouped by family in taxonomic order (Chaetodontidae [red],  
926 Pomacentridae [orange], Labridae [yellow], Scaridae [green], Pseudochromidae [teal] and all  
927 others considered [blue]).