

1 Synthesis

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4 RRH: Origins of Red Sea endemism

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6 **On the origin of endemic species in the Red Sea**

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33 **ABSTRACT**

34 **Aim** The geological and palaeo-climactic forces that produced the unique biodiversity in the Red
35 Sea are a subject of vigorous debate. Here we review evidence for and against the hypotheses
36 that: 1) Red Sea fauna was extirpated during glacial cycles of the Pleistocene and 2) coral reef
37 fauna found refuge *within* or just *outside* the Red Sea during low sea level stands when
38 conditions were inhospitable.

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40 **Location** Red Sea and Western Indian Ocean.

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42 **Methods** We review the literature on palaeontological, geological, biological and genetic
43 evidence that allow us to explore competing hypotheses on the origins and maintenance of
44 shallow water reef fauna in the Red Sea.

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46 **Results** Palaeontological (microfossil) evidence indicates that some areas of the central Red Sea
47 were devoid of most plankton during low sea level stands due to hypersaline conditions caused
48 by almost complete isolation from the Indian Ocean. However, two areas may have retained
49 conditions adequate for survival: the Gulf of Aqaba and the southern Red Sea. In addition to
50 isolation *within* the Red Sea, which separated the northern and southern faunas, a strong barrier
51 may also operate in the region: the cold, nutrient rich water upwelling at the boundary of the
52 Gulf of Aden and the Arabian Sea. Biological data are either inconclusive or support these
53 putative barriers and refugia, but no dataset that we know of rejects them. Genetic evidence
54 suggests that many endemic lineages diverged from their Indian Ocean counterparts long before

55 the most recent glaciations and/or are restricted to narrow areas, especially in the northern Red
56 Sea.

57
58 **Main conclusions** High endemism observed in the Red Sea and Gulf of Aden appears to have
59 multiple origins. A cold, nutrient-rich water barrier separates the Gulf of Aden from the rest of
60 the Arabian Sea, while a narrow strait separates the Red Sea from the Gulf of Aden, each
61 providing potential isolating barriers. Additional barriers may arise from environmental
62 gradients, circulation patterns and the constriction at the mouth of the Gulf of Aqaba. Endemics
63 that evolved within the Red Sea basin had to survive glacial times in relatively low salinity
64 refugia. It therefore appears that the unique conditions in the Red Sea basin, in addition to those
65 characteristics of the Arabian Peninsula region as a whole, drive the divergence of populations
66 via a combination of isolation and selection.

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75 **Keywords**

76 **Arabian Peninsula, biodiversity, biogeographical barriers, centre of endemism, marine**
77 **biogeography, palaeoclimate, Pleistocene, refugia, species distribution**

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79 INTRODUCTION

80 The Red Sea is a semi-enclosed basin at the north-western corner of the Indian Ocean that
81 harbours one of the highest levels of endemism for marine organisms. Although continually
82 being revised (e.g. due to cryptic species; Tornabene *et al.*, 2014), a recent review reports that
83 12.9% of fishes, 12.6% of polychaetes, 8.1% of echinoderms, 16.5% of ascidians and 5.8% of
84 scleractinian corals in the Red Sea are endemic (see DiBattista *et al.*, in press A). In the Indo-
85 West Pacific, this level of endemism is exceeded only in the Hawaiian Archipelago (25.0%;
86 Randall, 2007) and Easter Island (21.7%; Randall & Cea, 2011), with the Marquesas Islands
87 close behind (11.6%; Randall & Earle, 2000), for the well-characterised shore fish fauna. The
88 level of endemism among shore fish in the Red Sea exceeds those of all other localised hotspots
89 identified in the Indian Ocean, including the Mascarene Islands (3.4%; Fricke, 1999; Eschmeyer
90 *et al.*, 2010), the Arabian Gulf (4.0%; DiBattista *et al.*, in press A) and southern Oman (2.8%;
91 DiBattista *et al.*, in press A).

92 Recent research has demonstrated the importance of peripheral regions, such as the Red Sea,
93 the Hawaiian Archipelago and the Marquesas Islands as “evolutionary incubators” that
94 contribute unique genetic lineages to other regions of the Indo-West Pacific (Gaither *et al.*, 2010,
95 2011; Malay & Paulay, 2010; DiBattista *et al.*, 2011; Eble *et al.*, 2011; Skillings *et al.*, 2011;
96 Hodge *et al.*, 2012; Bowen *et al.*, 2013; DiBattista *et al.*, 2013). Peripheral endemism can be
97 driven by isolation or selection, and both are of potential importance in the Red Sea. Indeed, the
98 Red Sea is isolated by a narrow, shallow sill in the south, whereas broad areas of upwelling
99 create a habitat barrier for reef-associated taxa in the Arabian Sea. Large spatial gradients and
100 temporal fluctuations in physical conditions make this one of the most variable regions in the
101 tropical marine environment, with a high potential for ecological speciation. Even greater

102 environmental variation is evident through glacio-eustatic cycles, with the Red Sea basin
103 becoming isolated and hypersaline at glacial maxima. The geological and palaeo-climatic forces
104 that gave rise to shallow water reef fauna in the Red Sea are therefore topics of biogeographical
105 importance and the origins of the endemics are still the subject of much debate (see Rasul &
106 Stewart, 2015). After describing the regional setting, we outline key components of this debate
107 below.

108

109 *Geological history of the Red Sea*

110 The dimensions and configuration of the Red Sea reflect the influence of a combination of
111 geological and climatic processes, which include rifting (spreading) between the African and
112 Arabian plates, associated volcanism in the mid-Tertiary and eustatic sea level fluctuations,
113 which intensified in the Pliocene but more so since the mid-Pleistocene (Rihm & Henke, 1998).
114 The present day result is a narrow ocean basin with a north-south orientation, modest surface
115 area (438,000 km²) and limited continuity with the greater Indo-West Pacific as it is connected
116 only at the Strait of Bab al Mandab (Sheppard *et al.*, 1992). Many of the present-day Red Sea
117 reefs have a characteristic structure of shallow flat tops, steeply sloping sides and an elongated
118 north-south axis as a result of the geologic history in this region (Dullo & Montaggioni, 1998).

119 Major events that led to the present day configuration of the Red Sea were initiated by
120 Oligocene episodes of sea floor spreading 41 to 34 Ma (Girdler & Styles, 1974). The rifting
121 processes were associated with episodes of volcanism at the Afar Traps near present day
122 Ethiopia, with major activity around 31 Ma near the Afar Plume (Bosworth *et al.*, 2005). During
123 this time, saltwater replenished the Red Sea initially from the north but subsequently from the
124 south via episodic connections to the Mediterranean Sea and the Gulf of Aden, respectively. The

125 stratigraphy of this period is characterised by thick evaporate deposits interleaved with marine
126 deposits of a northern origin indicating periods of intense evaporation interspersed with marine
127 incursions from the Mediterranean. Uplift of the Suez area (i.e. Sinai Peninsula), driven by the
128 collision of Eurasia with Arabia 14 Ma, shifted the location of the main oceanic connection to
129 the south via the Gulf of Aden (Girdler & Styles, 1974; Hubert-Ferrari *et al.*, 2003). During this
130 period, the Red Sea environment was highly saline and unstable, subject to episodes of high
131 temperature and evaporation and therefore unlikely to have supported a diverse tropical reef
132 fauna.

133 Marine conditions re-established in the Red Sea during a second major phase of seafloor
134 spreading 5 to 4 Ma. This produced the deep axial trough that characterises the basin today and
135 established a more permanent connection with the Gulf of Aden through the Strait of Bab al
136 Mandab (Bailey *et al.*, 2007). The variable pattern of rifting and localised uplift since the
137 Pliocene is reflected in the latitudinal variation of reef formation. The Red Sea is characterised
138 by a vertical offshore profile and limited reefs in the northern Gulf of Aqaba, but extensive
139 shallow areas in the southern Farasan Islands and Dahlak Archipelago. The different reef
140 structures within the Red Sea are also reflected in the distinctive northern versus southern
141 distribution of the reef fauna (Winterbottom, 1985; Spalding *et al.*, 2001).

142 The Red Sea reef fauna, having been established during the Pliocene and Pleistocene (4 to 3
143 Ma), is relatively recent and has been subjected to environmental variation (e.g. temperature and
144 salinity) of a magnitude not experienced by reefs in the Indian and Pacific Oceans (Taviani,
145 1998). The biological impacts of this dynamic environment have been exacerbated by the
146 distinctive reef environments of the eastern Gulf of Aden and southern Oman, which act as filters
147 for potential colonists due to major fluctuations in temperature and primary productivity as a

148 result of episodic monsoonal-driven upwelling (Currie *et al.*, 1973; Smeed, 1997; Kemp, 2000;
149 Jung *et al.*, 2001).

150

151 *Isolation and barriers to dispersal*

152 The Red Sea reef biota is isolated from potential propagules by its narrow entrance and by the
153 environmental conditions of bordering waters. The Strait of Bab al Mandab is a narrow (29 km)
154 and shallow (137 m) channel that constitutes the only connection between the Red Sea and
155 Indian Ocean (Eshel *et al.*, 1994; Bailey, 2009). There is a seasonal variation in the ebb and flow
156 of Red Sea waters influenced by the Indian Ocean monsoon system. The water exchange
157 between the Red Sea and Gulf of Aden changes from a two-layer surface flow in the winter to a
158 three-layer flow in the summer (i.e. intrusion of Gulf of Aden Intermediate Water), with surface
159 and deeper layers often taking on very different properties (Murray & Johns, 1997; Siddall *et al.*,
160 2002; Sofianos *et al.*, 2002; Smeed, 2004; Yao *et al.*, 2014). Circulation models investigating the
161 variability of the monsoonal activity from the early Holocene (Biton *et al.*, 2010) suggest that the
162 two-layer exchange pattern remained constant throughout glaciation periods.

163 While the southern Red Sea and western Gulf of Aden are relatively similar, the eastern Gulf
164 of Aden, including northeast Africa (south of Ras Hafun), and southern Oman have markedly
165 different contemporary environments with limited reef development that pose an environmental
166 barrier for potential colonists. Currently this area experiences major fluctuations in temperature
167 and primary productivity driven by episodic monsoonal-driven upwelling (and temperatures as
168 low as 13°C; Currie *et al.*, 1973; Smeed, 1997; Kemp, 2000; Jung *et al.*, 2001). Because many
169 Red Sea endemics also occur in the Gulf of Aden (Türkay, 1996; Janssen & Taviani, 2015;
170 DiBattista *et al.*, in press A), some believe that the adjacent regions of cold water upwelling off

171 Somalia and Oman, as well as seasonal current patterns, are of greater importance as isolating
172 mechanisms than the physical isolation at Bab al Mandab (Kemp, 1998, 2000; Zajonz *et al.*,
173 2000).

174

175 *Pleistocene conditions*

176 During the last (and presumably previous) glacial maxima (20 to 15 ka), the Red Sea was
177 physically isolated by the shoaling of Bab al Mandab, which was further exacerbated by
178 changing winds and marine currents associated with the Indian Ocean monsoon system (Fig. 1;
179 Siddall *et al.*, 2003; Ludt & Rocha, 2015). The result was substantially increased salinity and
180 residence times of the water masses within the Red Sea (Biton *et al.*, 2008), which led some
181 authors to suggest a scenario where the Red Sea resembled a hypersaline lake (Klausewitz,
182 1989). Such a shift in oceanographic conditions within the Red Sea is likely to have recurred
183 repeatedly during Pleistocene glaciations, and with greatest frequency and amplitude during the
184 last 430 kyr (Rohling *et al.*, 2009).

185 Even though the physical isolation of the Red Sea through the Strait of Bab al Mandab
186 increased greatly during low sea level stands, glacial impacts on Arabian Sea environments are
187 less clear. Studies on sediment cores in the Arabian Sea have shown that the upwelling was
188 increased during glacial periods (Singh *et al.*, 2011), but this point is contentious. Ivanova (2009)
189 reported the opposite effect, an intensification of upwelling during interglacial stages, based on
190 the palaeo-record of foraminifera.

191

192 *Competing hypotheses*

193 The primary unanswered question concerning Red Sea biogeography has been to what extent the
194 marine biota was able to maintain a continuous presence in the Red Sea through the major
195 environmental fluctuations of the Pleistocene. Loss of the planktonic fauna in most of the Red
196 Sea suggests extirpation of many species, but survival of some plankton and occurrence of
197 relatively old endemics with restricted ranges within the basin (e.g. Grill & Zuschin, 2001;
198 Türkay, 1996; Choat *et al.*, 2012; Janssen & Taviani, 2015; DiBattista *et al.*, in press A) suggest
199 otherwise. There are thus two distinct, but not mutually exclusive hypotheses: marine organisms
200 survived glacial conditions 1) *within* the Red Sea or 2) just *outside* of the Red Sea (i.e. Gulf of
201 Aden). In the following section we review palaeontological, biological and genetic evidence for
202 and against these hypotheses. This evidence is in turn related to hypotheses of endemism –
203 whether it is conditions in the Red Sea basin *per se* or the Arabian Peninsula region as a whole
204 that drive the divergence of populations, and how isolation and selection contribute to the
205 divergence of endemics.

206

207 **Palaeontological evidence**

208 *Core data and microfossils*

209 Deep-sea cores taken along the length of the Red Sea, including the Gulf of Aqaba, provide a
210 microfossil, isotopic, geochemical and petrographic record of environmental and biotic changes
211 over the glacial cycles of the mid to late Pleistocene (Reiss *et al.*, 1980; Almogi-Labin, 1982;
212 Hofmann *et al.*, 1998; Fenton *et al.*, 2000; Badawi *et al.*, 2005). The most striking aspect of these
213 data is that glacial maxima are associated with an “aplanktonic” period, when most, if not all,
214 planktonic foraminiferans, as well as many coccolithophorids and pteropods, disappeared,
215 indicating unsuitable environmental conditions (Fenton *et al.*, 2000). Although plankton

216 diversity decreased sharply during glacial maxima, some taxa increased in abundance, especially
217 benthic, miliolid forams, the euryhaline pteropod *Creseis acicula* and, locally, siliceous diatoms
218 and some sponges (Reiss *et al.*, 1980; Almogi-Labin *et al.*, 2008). Increases in $\delta^{18}\text{O}$,
219 development of sapropels and carbonate crusts, together with considerations of salinity tolerance
220 for extirpated and persisting microfossils, indicates that salinity levels reached and potentially
221 exceeded 50‰ (Reiss *et al.*, 1980; Hofmann *et al.*, 1998; Taviani, 1998). Temperatures also fell
222 between 3 to 5 °C, but the decrease in the diversity and abundance of planktonic microfossils is
223 primarily attributed to hypersaline conditions versus lowered temperatures (Reiss *et al.*, 1980).

224 Variation in the occurrence and diversity of microfossils in cores during glacial maxima
225 along the length of the Red Sea and Gulf of Aqaba suggests that conditions varied significantly
226 within the basin. Siliceous diatoms and sponge spicules are common during glacial maxima in
227 the northern Red Sea, suggesting upwelling, but not in cores from the Gulf of Aqaba (Reiss,
228 1980; Fenton *et al.*, 2000). Planktonic foraminiferans persisted through the last glacial maximum
229 in cores from the southern Red Sea and the northern Gulf of Aqaba, which has been interpreted
230 to indicate that salinity remained below 45‰ there (Fenton *et al.*, 2000). In contrast, salinities
231 were estimated to have reached *c.* 55‰ in most of the Red Sea basin (Fenton *et al.*, 2000). The
232 combined evidence here suggests that Red Sea fauna may have survived salinity crises of the
233 Pleistocene, particularly through refugia in the Gulf of Aqaba and southern Red Sea.

234 The drastic changes in the planktonic foraminifera communities and productivity of the Red
235 Sea (including the Gulf of Aqaba) during Pleistocene glacial periods were much greater than that
236 in the Gulf of Aden (Deuser *et al.*, 1976). The salinities in the Gulf Aden during glacial periods
237 were similar to present day salinities (36‰; Duplessy, 1982; Locke, 1986, Thunell *et al.*, 1988)
238 and, with the exception of a few species, the foraminifera and pteropod assemblages in this

239 region were similar between glacial and interglacial periods, suggesting no large changes in
240 productivity in the surface waters over the last 50 kyr (Ivanova, 1985; Locke & Thunell, 1988).
241 This cumulative evidence supports the idea that the Gulf of Aden may have served as a refuge
242 for Red Sea fauna during these times of harsh environmental conditions.

243

244 *Physical closure of the Red Sea at the Strait of Bab al Mandab*

245 A question of primary interest in the recent evolutionary history of the Red Sea fauna is the
246 possibility of complete closure of the Red Sea during periods of low sea level associated with
247 Pleistocene glacial cycles. Given that sea levels fell 115 m below present levels during five
248 periods over the last 430 kyr (Rohling *et al.*, 2009), the complete emergence of the Hanish Sill
249 (137 m depth) at Bab al Mandab is a definite possibility. That said, the current consensus is that
250 although Bab al Mandab was reduced to a narrow channel no less than 260 km in length, with a
251 minimum depth of 15 m and an approximate width of 4 km at its narrowest point, complete
252 closure probably did not occur (Bailey *et al.*, 2007; Fig. 1). Even without complete closure, the
253 restriction of water flow to the Gulf of Aden is so effective (Lambeck *et al.*, 2011) that any
254 residual flow through the narrower channel would have been insufficient to prevent major
255 increases in salinity and temperature in the Red Sea during glacial maxima.

256

257 *Climatic reconstruction of rainfall regimes*

258 Support for tolerable marine conditions in the northern and southern Red Sea comes from
259 climatic reconstructions. The Red Sea appears to be influenced by two rainfall regimes: 1) a
260 Mediterranean system in the northern Red Sea (de Menocal & Rind, 1996) and 2) a monsoonal
261 system in the southern Red Sea (Murray & Johns, 1997; Siddall *et al.*, 2002; Sofianos *et al.*,

262 2002; Smeed, 2004). Evidence of palaeorivers and palaeolakes, such as the vast Mudawwara
263 depression (2000 km²) on the border of Saudi Arabia and Jordan, can be seen across the Arabian
264 Peninsula (e.g. Parton *et al.*, 2010). Studies using oxygen isotope records have also reported the
265 occurrence of five periods of increased wetness in the Arabian Sea (10.5 to 6 ka, 82 to 78 ka, 135
266 to 120 ka, 200 to 180 ka and 325 to 300 ka; Fleitmann *et al.*, 2003). Additional evidence for
267 increased precipitation in the region comes from anthropological research. Studies show that
268 during wet periods, lakes and rivers formed, resulting in increased vegetation during the
269 Pleistocene (McLaren *et al.*, 2009; Rosenberg *et al.*, 2011; Groucutt & Petraglia, 2012). These
270 wetter periods appear to have enhanced the capacity of humans to migrate out of Africa and into
271 Arabia, and could also have had a substantial effect on the nearshore reefs of the eastern Red Sea
272 if a physical connection with the Indian Ocean persisted. That said, peaks in precipitation rarely
273 coincide with glacial periods, they favour interglacial periods instead.

274 Survival *within* the Red Sea may have been possible in the Gulf of Aqaba, owing to this area
275 being wetter (and less saline) during glacial maxima. In this scenario, southern Jordan functioned
276 as a fresh water reservoir lowering salinity in the Gulf of Aqaba to a tolerable level, as suggested
277 by the existence of palaeolakes Hasa, Jafr, Jurf ed Darawish and those in the Mudawwara and
278 Umari depressions (Rech, 2013). There is no indication, however, that the Nile ever flowed into
279 and impacted the northern Red Sea region (i.e. Gulf of Suez; Stanley & Warne, 1993; Krom *et*
280 *al.*, 2002). Regardless of rainfall level, the existence of Pleistocene reefs at 98 m depth (Hoffman
281 *et al.*, 1998) provides evidence of coral survival during advanced glacial conditions in the Gulf
282 of Aqaba (also see Fricke, 1996). Evidence from foraminifera also indicates that conditions in
283 the Gulf of Aqaba may have provided a refuge for shallow-water organisms during glacial
284 maxima (Locke & Thunell, 1988). This scenario is supported by an endemic fish fauna that is

285 restricted to the Gulf of Aqaba (4.1%, DiBattista *et al.*, in press A; but also see Winterbottom,
286 1985; Fricke *et al.*, 2014).

287 Evidence suggests that milder environmental conditions (i.e. temperature and salinity) may
288 also have prevailed in the southern Red Sea due in part to the remaining connection with the
289 Gulf of Aden. Rivers, such as the Hawash River, may have drained along the coast of Eritrea and
290 into the series of lakes feeding the Gulf of Tadjoura in Djibouti, but also further north into the
291 southern Red Sea (De Lattin, 1967). Extensive wadi systems (desert valleys or dry riverbeds),
292 most frequent in the southern Red Sea, provide “geological evidence” of increased precipitation
293 and ancient river courses (Gabriel, 1978) that may have contributed to decreased salinity in the
294 region. The exact timing of this increase in precipitation remains unclear.

295 Counter evidence to the idea of a wetter Arabian Peninsula is provided by Rohling *et al.*,
296 (2013), who report no significant rainfall associated with the Indian Ocean monsoon but do note
297 that the regions affected by summer rainfall may have shifted to the southeast margin of the
298 Arabian Peninsula (i.e. Yemen and Oman; Conroy & Overpeck, 2011). Parton *et al.* (2015)
299 argues that increased monsoonal activity occurred during Marine Isotope Stage (MIS) six (ca.
300 160 to 150 ka), MIS five (ca. 130 to 75 ka) and early MIS three (55 ka), but these were not
301 linked to particular aspects of the glacial cycle. Vast areas of the Arabian Peninsula have not
302 been explored in terms of Quaternary environmental change (Fleitmann *et al.*, 2004) or
303 geoarchaeology (Rose, 2004). Based on this equivocal evidence, we argue that even though wet
304 periods are probably not directly linked to glacial cycles and the Arabian landscape remains
305 incompletely surveyed, it is clear that the Red Sea nearshore environment was subject to high
306 variance in temperature, salinity and perhaps nearshore turbidity during the late Pleistocene.

307

308 **Biological evidence**

309 *Salinity tolerances for marine organisms*

310 During glacial maxima, salinity in the Red Sea was more than 10‰ higher than current levels
311 (which are 37 to 41‰), and much greater in the central and northern regions (reaching up to 55
312 to 57‰) than in the southern region (which remained below 45‰) (Thunell *et al.*, 1988;
313 Geiselhart, 1998). These episodes of elevated salinity corresponded with the virtual
314 disappearance of planktonic foraminifera in parts of the Red Sea (Locke & Thunell, 1988),
315 however other marine species may have persisted (e.g. some fish can tolerate salinities up to
316 60‰; Bayly, 1972). The Red Sea biota thrives today at salinities near 42‰ in the Gulf of Aqaba,
317 but species rapidly drop out between 45‰ to 50‰ in marginal lagoons (Kinsman, 1964; Por,
318 1972, 2008). For corals, the key habitat-forming organism that currently supports much of the
319 Red Sea biodiversity, the upper threshold to salinity tolerance appears to be 50‰, with few
320 corals surviving salinities in excess of 45‰ (Coles, 2003). Some shallow water
321 macroinvertebrates can tolerate high salinities (> 50‰; Por, 1972) and may have persisted in
322 parts of the Red Sea during interglacial periods. There is also evidence that endemic deep water
323 bivalves persisted and evolved during glacial periods (Türkay, 1996), whereas shallow water
324 species contracted to refugia outside of the Red Sea (Grill & Zuschin, 2001). Thus, evidence
325 suggests that tolerance to elevated salinities allowed some species to survive through glacial
326 cycles within the Red Sea and evolve into endemics.

327

328 *Species distributions and distribution of sister taxa*

329 The most compelling evidence for survival of endemics *within* the Red Sea comes from the large
330 number of species that appear to be restricted to the basin (DiBattista *et al.*, in press A). Whereas

331 some of these species may have been overlooked outside the basin and others could have become
332 recently restricted, the sheer diversity of species suggests that some have persisted in the Red Sea
333 through glacial periods.

334 Sister taxon relationships provide further evidence for the origin of Red Sea endemics. The
335 Red Sea reef fish fauna are relatively well-characterised (Golani & Bogorodsky, 2010), and
336 consist primarily of species of Indo-West Pacific origin in addition to a small number of species
337 (along with some Arabian Peninsula endemics) that lack clearly identifiable close relatives. The
338 latter groups are likely relicts of palaeo-Mediterranean Tethyan ancestry that persisted in the
339 north-western Indian Ocean long after the mass extinction of their Mediterranean relatives in the
340 late Miocene (i.e. Messinian salinity crisis, *c.* 6 Ma; Krijgsman *et al.*, 1999). An updated list of
341 Red Sea endemics with presumed geminate sister species of reef fish are provided in Table 1.
342 We excluded species with no known close relatives given that these may be Tethyan relicts. We
343 focused on fish because this is the group with the most resolved taxonomy among the reef fauna.
344 The final list was constructed by examining the list of endemic species and choosing those pairs
345 that we had some knowledge of, or could systematically check within the literature for,
346 information on presumed relationships. In some, but not all cases, the information is backed by
347 molecular evidence, and the naming convention follows Eschmeyer (2014) unless otherwise
348 noted.

349 Klausewitz (1989) provided a framework for classifying the historical origins of Red Sea fish
350 based on the relative age of differentiation: 1) postglacial fish that invaded the basin during the
351 past 10 kyr, 2) interglacial fish that invaded during earlier interglacial periods and 3) fish with a
352 high degree of differentiation that invaded much earlier and persisted in the basin. Although
353 Klausewitz (1989) considered the question of the viability of the Red Sea as a habitat for tropical

354 reef fish during glacial maxima to be unresolved, he also suggested that the southern part of the
355 Red Sea could have served as a refuge. Whereas current ecological conditions in the southern
356 Red Sea may not be ideal for many species, it is clear that a number of them effectively disperse
357 through the Bab al Mandab barrier in both directions. It therefore seems more likely that
358 speciation of true Red Sea endemics (those not found in the Gulf of Aden), with clearly
359 identifiable Indo-West Pacific sister species, occurred when isolation of the basin was greater if
360 not complete. Furthermore, we now know that the relative ages of differentiation of many
361 endemics in the Red Sea precede the end of the last interglacial, and in rare cases the entire
362 Pleistocene (examples from Table 1: *Chlorurus gibbus* and *C. strongylocephalus* [0.5 Ma],
363 Choat *et al.*, 2012; *Chromis dimidiata* and *C. fieldi* [0.95 Ma], Randall & DiBattista, 2013;
364 *Etrumeus golanii* and *E. wongratanai* [1.65 Ma], DiBattista *et al.*, 2012; *Pomacentrus*
365 *albicaudatus* and *P. adelus* [~3.5 Ma], Litsios *et al.*, 2012; *Thalassoma rueppellii* and *T.*
366 *quinquevitatum* [~12.5 Ma], Hodge *et al.*, 2014).

367 The presence of refugia *outside* of the Red Sea is supported by the distribution of reef fish
368 and other marine organisms in the region. While 138 of the 189 (73%) Red Sea endemics are
369 only known from the Red Sea, 45 (24%) occur in the Red Sea and Gulf of Aden, which indicates
370 that the Gulf of Aden represents a biogeographical extension of the Red Sea (Kemp, 1998;
371 DiBattista *et al.*, in press A). Moreover, 13.5% of Red Sea to Gulf of Aden endemics (e.g.
372 *Myripristis xanthacra*, *Neopomacentrus xanthurus*, *Pristotis cyanostigma*) are restricted to the
373 southern portion of the Red Sea (DiBattista *et al.*, in press A), presumably due to a greater
374 similarity between environments. The Gulf of Aden may therefore have served as a refuge for
375 local endemics during periods of lowered sea level and hypersalinity within the Red Sea.

376

377 **Genetic evidence**

378 *Phylogenetic dispersion and taxonomic sampling*

379 Time-calibrated phylogenetic trees for coral reef fish allows an examination of the evolutionary
380 history of the Red Sea fauna. Phylogenetic hypotheses for angelfish (Gaither *et al.*, 2014),
381 butterflyfish (Fessler & Westneat, 2007; Bellwood *et al.*, 2010), damselfish (Cooper *et al.*, 2009;
382 Frédéricich *et al.*, 2013), parrotfish (Choat *et al.*, 2012) and wrasses (Westneat & Alfaro, 2005), as
383 well as integrated higher-level phylogenies among reef fish (Hodge *et al.*, 2014), provide
384 templates for exploring the historical patterns of biogeography in the Red Sea in two ways. First,
385 calibrated phylogenetic time trees provide estimates of the timing of the origin of species groups,
386 and can further bracket the minimum and maximum timing of splits between species pairs.
387 Second, phylogenetic trees combined with regional species composition data enable exploration
388 of the evolutionary history of community composition.

389 Phylogenetic analyses show that Red Sea reef fish, including endemic species, have
390 repeatedly evolved within major reef fish groups over the past 25 Myr, have primarily evolved
391 from Indian Ocean relatives and represent highly “over-dispersed” communities sampled from
392 the phylogenies of reef fish families. Using a multi-family fish phylogeny, Hodge *et al.* (2014)
393 showed that Red Sea endemic reef fish species have originated frequently and steadily over the
394 past 16 Myr, with most endemics originating within the past 5 Myr. Using a time-calibrated
395 phylogeny of the butterflyfish, Fessler & Westneat (2007) showed that four of the six Red Sea
396 endemics split from their sister species 4 to 1 Ma, and perhaps even more recently. Similarly,
397 endemic Red Sea parrotfish have originated within the past 4 Myr, and several species within the
398 past 500 kyr (Choat *et al.*, 2012). Pomacentridae (see Fig. 2) show a more complex pattern of
399 deeper origins for Red Sea species, as well as more recent speciation in the region, with time

400 calibrations of some Red Sea components dating back as much as 25 Myr across the
401 Miocene/Oligocene boundary.

402 Red Sea coral reef fish communities can be viewed as having been “sampled” from the
403 phylogenies of major family groups (Webb *et al.*, 2002; Emerson & Gillespie, 2008; Rabosky *et*
404 *al.*, 2011). The assembly of Red Sea reef fish in several families (Chaetodontidae, Labridae, and
405 Pomacentridae) is a non-random sample from the phylogenetic history of these groups (Fig. 2;
406 M.W. Westneat, unpub. data). For the damselfish, the Red Sea community is composed of
407 members of almost all major clades, and endemics have arisen from various parts of the
408 phylogeny (Fig. 2). This pattern is considered phylogenetically over-dispersed, with a
409 significantly negative net relatedness index (-2.2). Such patterns are characteristic of systems
410 with high competition for resources or species interactions based on key ecological traits
411 (Emerson & Gillespie, 2008). These patterns may also be explained by an alternate hypothesis
412 where endemics are related to widespread species rather than to each other as a result of little
413 adaptive radiation in the Red Sea.

414 Phylogenetic patterns suggest that periods of inhospitable conditions in the Red Sea, from the
415 Miocene through the Pleistocene, were survived by many lineages. Current phylogenetic time
416 tree resolution among species does not usually have the accuracy to resolve species origins on
417 the order of thousands of years, but some of the youngest speciation events in the Red Sea
418 occurred within the past 50 kyr. Most of the Red Sea reef fish community, including many
419 endemics, however, originated much earlier. Future work should broaden our sample of time-
420 calibrated phylogenies for fishes, explore trait evolution that may have driven the patterns of
421 over dispersion that are emerging, test for adaptive radiation and attempt to integrate species-

422 level phylogenetic patterns with finer-scale phylogeographical studies to increase resolution on
423 the timing of recent splits in this dynamic region.

424

425 *Phylogeography and population genetics*

426 Phylogeographical analyses are powerful tools for detecting population level divergences,
427 identifying cryptic lineages and providing insight into historical processes that may not be
428 apparent from contemporary species distributions or higher-level phylogenies (Palumbi, 1997;
429 Avise, 2000). Most phylogeographical studies of broadly distributed species indicate some level
430 of genetic distinction of Red Sea populations (Table 2), and a few studies have resulted in the
431 description of new species endemic to the region (e.g. Terranova *et al.*, 2007; DiBattista *et al.*,
432 2012). There are only a handful of cases where Red Sea populations demonstrate little to no
433 genetic distinction from populations in the Indian Ocean, including the widespread checkerboard
434 wrasse (*Halichoeres hortulanus*; DiBattista *et al.*, 2013), the bluestripe snapper (*Lutjanus*
435 *kasmira*; DiBattista *et al.*, 2013), the African coris wrasse (*Coris cuvieri*; P. Ahti, pers. comm.)
436 and several species of elasmobranchs (Spaet *et al.*, 2015) (Table 2). Red Sea populations of
437 lionfish (*Pterois miles* and *Dendrochirus brachypterus*) also show no distinction, however,
438 limited sample sizes preclude a final conclusion (Kochzius *et al.*, 2003; Kochzius & Blohm,
439 2005).

440 Levels of genetic divergence detected in these studies vary by an order of magnitude across
441 species (Table 2), indicating that colonisation of the Red Sea did not coincide with a specific
442 geologic event but perhaps multiple stochastic events. Deep phylogenetic partitions have been
443 detected in the Red Sea populations of the mud crab (*Scylla serrata*; Gopurenko *et al.* 1999;
444 Fratini & Vannini, 2002), regal angelfish (*Pygoplites diacanthus*; DiBattista *et al.*, 2013), lemon

445 sponge (*Leucetta chagosensis*; Wörheide *et al.*, 2008), yellowfin goatfish (*Mulloidichthys*
446 *flavolineatus*; Fernandez-Silva *et al.*, in press), yellowfin hind (*Cephalopholis hemistiktos*; M.
447 Priest, pers. comm.), giant clam (*Tridacna maxima*; Nuryanto & Kochzius, 2009), pronghorn
448 spiny lobster (*Panulirus penicillatus*; M. Iacchei, pers. comm.) and crown-of-thorns starfish
449 (*Acanthaster planci*; Vogler *et al.*, 2008). The oldest of these lineages may represent cryptic
450 species complexes (e.g. *A. planci* and *P. diacanthus*; Table 2). Red Sea and Indian Ocean
451 lineages in these examples are reciprocally monophyletic with no evidence of gene flow between
452 regions, and levels of divergence that represent hundreds of thousands (e.g. *P. diacanthus*) to
453 millions of years (e.g. *A. planci*). In the Sammara squirrelfish, *Neoniphon sammara*, shallower
454 divergences have been recorded that date to about 125 kyr of isolation, with near monophyly
455 (DiBattista *et al.*, 2013). Other species demonstrate significant population level structure
456 between the Red Sea and Indian Ocean, but with shared haplotypes among regions (brown
457 surgeonfish, *Acanthurus nigrofuscus*; peacock hind, *Cephalopholis argus*; threadfin butterflyfish,
458 *Chaetodon auriga*), and perhaps represent more recent colonisation of the Red Sea (DiBattista *et*
459 *al.*, 2013; also see DiBattista *et al.*, in press A).

460 Only four phylogeographical studies conducted thus far in reef fish include samples from the
461 Gulf of Aden, and these show a variable pattern that parallels what we know from species
462 distributions. The African coris wrasse (*C. cuvieri*, a Red Sea to Indian Ocean species, P. Ahti,
463 pers. comm.) and threadfin butterflyfish (*C. auriga*, an Indo-West Pacific species, DiBattista *et*
464 *al.*, in press B) demonstrate modest differentiation among Red Sea, Gulf of Aden and Indian
465 Ocean populations, whereas the other two species, the yellowfin goatfish (*M. flavolineatus*;
466 Fernandez-Silva *et al.*, in press) and the yellowfin hind (*C. hemistiktos*; M. Priest, pers. comm.),
467 have an endemic genetic lineage that extends between the Red Sea and the Gulf of Aden. We see

468 similar patterns at the species level for some invertebrates (echinoderms: G. Paulay, unpub. data;
469 coral gall crabs: S. van der Meij, pers. comm.), which are characterised by high levels of
470 endemism, with many endemics making it into the Gulf of Aden or also into the Arabian Sea.
471 This pattern suggests that many of the lineages thought to be unique to the Red Sea may be
472 found outside the basin with increased sampling. This pattern, however, does not allow us to
473 conclude whether lineages originate from glacial refugia *within* or just *outside* the Red Sea
474 owing to the potential for bidirectional post-glacial expansion.

475

476 **Conclusion and future directions**

477 Limited water exchange between the Red Sea and Indian Ocean at the Strait of Bab al Mandab
478 led to drastic changes in environmental conditions within the Red Sea during glacial maxima.
479 Coupled with regional climate shifts, the Red Sea (particularly the central region) experienced
480 fluctuations in salinity and temperature that may have presented exceptional physiological
481 challenges to resident marine life. However, apart from sediment cores from a few locations
482 indicating a loss of most planktonic organisms, there is little direct evidence supporting the
483 complete loss of species within the entire Red Sea. The spatial variability of environmental
484 conditions in the Red Sea during glacial maxima therefore requires further study, especially in
485 groups with adequate fossil records, to conclusively resolve whether one or more refugia existed
486 and how effective these were. The shallow water molluscan fauna would be a suitable target
487 given the excellent fossil record that can be interpreted in a biogeographical context (Paulay,
488 1996; Grill & Zuschin, 2001).

489 Perhaps the most compelling evidence for the persistence of some Red Sea taxa during
490 glaciation events is the genetic evidence that many endemic taxa (or lineages) diverged from

491 their Indian Ocean counterparts long before the most recent glaciations, and the restriction of
492 some endemics to narrow areas, especially in the northern Red Sea. The range of ages of Red
493 Sea endemics suggests that peripatric speciation has been an ongoing process in this region, a
494 pattern shown at other hotspots of endemism in the Indo-West Pacific (e.g. Hawaiian
495 Archipelago; Craig *et al.*, 2010) that may be the rule rather than the exception.

496 The evolutionary history of the Red Sea, Gulf of Aden and Arabian Sea is much more
497 complex than previously believed. The abrupt transition among distinctive habitats and
498 Pleistocene fluctuations in temperature, salinity and productivity have all contributed to an
499 evolutionary dynamic theatre. Future genetic work, particularly studies using advanced genomic
500 approaches (e.g. RADs, UCEs or whole genome sequencing) in this under-studied region
501 (Berumen *et al.*, 2013) could provide greater resolution to particular taxa of interest. We
502 additionally suggest that the endemism of the Red Sea may not be solely driven by isolation
503 related to the narrow strait of Bab al Mandab, but linked to other barriers in the Arabian Sea
504 punctuated with pulses of ecological selection.

505

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513

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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** Online voucher numbers for DNA sequences used in the phylogenetic analysis of
872 the Pomacentridae (also see Figure 2).

873

874 **Biosketch**

875 This paper arose from a workshop on “Red Sea and Western Indian Ocean Biogeography” in the
876 Division of Biological and Environmental Science and Engineering at King Abdullah University
877 of Science and Technology (KAUST), Saudi Arabia. The authors’ interests are based on
878 elucidating the evolutionary processes that generate and maintain marine biodiversity in the
879 tropical Indo-Pacific, with a particular focus on characterising endemism in marginal habitat like
880 the Red Sea and Western Indian Ocean.

881

882 Author contributions: J.D.D. led the writing. All other authors listed here performed literature
883 reviews and contributed to writing. R.F.M. produced a table of Red Sea endemic reef fish species
884 and their presumed sister species. M.W.W. produced a time-calibrated phylogeny for the
885 damselfish.

886

887 Editor: Richard Ladle

888

Table 1 Red Sea endemic reef fish species and their presumed sister species. Because the Gulf of Aden represents a biogeographical extension of the Red Sea province, we additionally report Red Sea to Gulf of Aden (including Socotra) endemics. We excluded species whose closest relative remains unknown or those with no known close relatives. Taxonomic names are according to the Catalog of Fishes, which is the authoritative reference for accepted nomenclature (see Eschmeyer, 2014); exceptions are listed as footnotes.

Species	Sister species	Distribution of sister species
<i>Red Sea endemic</i>		
NARKIDAE (SLEEPER RAYS)		
<i>Heteronarce bentuviai</i> (Baranes & Randall, 1989)	<i>Heteronarce garmani</i> Regan, 1921	Gulf of Aden to South Africa
TORPEDINIDAE (TORPEDOS)		
<i>Torpedo alexandrinsis</i> Mazhar, 1987	<i>Torpedo adenensis</i> Carvalho, Stehmen & Manilo, 2002	Gulf of Aden
MURAENIDAE (MORAY EELS)		
<i>Gymnothorax corallinus</i> (Klunzinger, 1871)	<i>Gymnothorax buroensis</i> (Bleeker, 1857)	Indo-Pacific
<i>Uropterygius golanii</i> McCosker & Smith, 1997	<i>Uropterygius xenodontus</i> McCosker & Smith, 1997	W Pacific
CONGRIDAE (CONGER and GARDEN EELS)		
<i>Gorgasia sillneri</i> Klausewitz, 1962	<i>Gorgasia naeocepaeus</i> (Böhlke, 1951)	W Papua & Philippines
CLUPEIDAE (HERRINGS, SPRATS, & SARDINES)		
<i>Etrumeus golanii</i> DiBattista, Randall & Bowen, 2012	<i>Etrumeus wongratanai</i> DiBattista, Randall & Bowen, 2012	Gulf of Aden to S Africa
<i>Herklotsichthys punctatus</i> (Rüppell, 1837)	<i>Herklotsichthys lossei</i> Wongratana, 1983	Arabian Gulf
SYNODONTIDAE (LIZARDFISHES)		
<i>Synodus randalli</i> Cressey, 1981	<i>Synodus fasciapelvicus</i> Randall, 2009	Indonesia and Philippines
BATRACHOIDIDAE (TOADFISHES)		
<i>Barchatus cirrhosa</i> (Klunzinger, 1871)	<i>Barchatus indicus</i> Greenfield, 2014	Gulf of Aden (N Somalia)
ATHERINIDAE (SILVERSIDES)		
<i>Atherinomorus forskalii</i> (Forster, 1801)	<i>Atherinomorus lacunosus</i> (Schneider, 1801)	Indo-Pacific (sympatric in central Red Sea)
<i>Hypoatherina golanii</i> Sasaki & Kimura, 2012	<i>Hypoatherina klunzingeri</i> Smith, 1965	W Indian Ocean (E Somalia) to S Africa
HOLOCENTRIDAE (SOLDIERFISHES & SQUIRRELFISHES)		
<i>Sargocentron marisrubri</i> Randal, Guezé & Diamant, 1989	<i>Sargocentron melanospilos</i> Bleeker, 1858	Indo-West Pacific
SYNGNATHIDAE (PIPEFISHES & SEAHORSES)		
<i>Corythoichthys</i> cf. <i>nigripectus</i> ¹	<i>Corythoichthys nigripectus</i> Herald, 1953	W Pacific
<i>Corythoichthys</i> cf. <i>schultzi</i> ¹	<i>Corythoichthys schultzi</i> Herald, 1953	W Pacific
<i>Micrognathus brevirostris</i> (Rüppell, 1838)	<i>Micrognathus pygmaeus</i> Fritzsche, 1981	Indo-West Pacific
SCORPAENIDAE (SCORPIONFISHES)		

Scorpaenodes steinitzi Klausewitz & Fröiland, 1970

APLOACTINIDAE (VELVETFISHES)

Ptarmus gallus Kossman & Rauber, 1877

SERRANOIDEA (SEABASSES)

Plectropomus marisrubri Randall & Hoese, 1986

Pseudanthias taeniatus (Klunzinger, 1855)

Pseudogramma megamycterum Randall & Baldwin, 1997

PSEUDOCHROMIDAE (DOTTYBACKS)

Pseudochromis fridmani Klausewitz, 1968

Pseudochromis pesi Lubbock, 1975

PLESIOPIDAE (PRETTYFINS/LONGFINS)

Acanthoplesiops cappuccino Gill, Bogorodsky & Mal, 2013

OPISTHOGNATHIDAE (JAWFISHES)

Stalix davidsheni Klausewitz, 1985

APOGONIDAE (CARDINALFISHES)

Cheilodipterus pygmaios Gon, 1993

Taeniamia lineolata (Cuvier, 1828)

MALACANTHIDAE (SAND TILEFISHES)

Hoplotalilus oreni Clark & Ben-Tuvia, 1973

CAESIONIDAE (FUSILIERS)

Caesio suevica Klunzinger, 1884

SPARIDAE (SEA BREAMS)

Argyrops megalommatus (Klunzinger, 1870)

Diplodus noct (Valenciennes, 1830)

PEMPHERIDAE (SWEEPERS)

Parapriacanthus guentheri (Klunzinger, 1871)

POMACENTRIDAE (DAMSELFISHES)

Chromis dimidiata (Klunzinger, 1871)

Chromis pelloura Randall & Allen, 1982

Pomacentrus albicaudatus Baschieri-Salvadori, 1955

LABRIDAE (WRASSES)

Chlorurus gibbus (Rüppell, 1829)

Scorpaenodes parvipinnis (Garrett, 1864)

Ptarmus jubatus (Smith, 1935)

Plectropomus pessuliferus (Fowler, 1904)

Pseudanthias townsendi (Boulenger, 1897)

Pseudogramma astigmum Randall & Baldwin, 1997

Pseudochromis sankeyi Lubbock, 1975

Pseudochromis melas Lubbock, 1977

Acanthoplesiops indicus (Day, 1888)

Stalix histrio Jordan & Snyder, 1902

Cheilodipterus quinquelineatus (Cuvier, 1828)

Taeniamia flavofasciata (Gon & Randall, 2003)

Hoplotalilus fourmanoiri Smith, 1964

Caesio xanthonota Bleeker, 1853

Argyrops filamentosus (Valenciennes, 1830)

Diplodus capensis (Smith, 1884)

Parapriacanthus ransonneti Steindachner, 1870

Chromis fieldi Randall & DiBattista, 2013

Chromis axillaris (Bennett, 1831)

Pomacentrus adeli Allen, 1991

Chlorurus strongylocephalus (Bleeker, 1864)

Indo-Pacific

E Africa to Natal, S Africa

Indian Ocean and Fiji

Gulf of Aden to Gulf of Oman

Indo-Pacific

S Red Sea and Gulf of Aden

E Africa

Indian Ocean

W Pacific

Indo-Pacific (sympatric in Red Sea)

E Africa to Madagascar

Indonesia, Brunei, and Solomon Islands

Indian Ocean (sympatric S of Gulf of Aqaba)

W Indian Ocean, including Gulf of Aden

W Indian Ocean, including Gulf of Aden

Indo-West Pacific, including Gulf of Aden

Indian Ocean, including Gulf of Aden

Somalia to S Mozambique and Mauritius

Andaman Sea to W Pacific

Indian Ocean, including Gulf of Aden

<i>Cirrhilabrus blatteus</i> Springer & Randall, 1974	<i>Cirrhilabrus lanceolatus</i> Randall & Masuda, 1991	W Pacific
<i>Iniistius</i> n sp cf <i>balwini</i> ²	<i>Iniistius baldwini</i> (Jordan & Evermann, 1903)	Indo-West Pacific
<i>Macropharyngodon marisrubri</i> Randall, 1978	<i>Macropharyngodon bipartitus</i> Smtih 1957	W Indian Ocean, including Gulf of Aden
<i>Thalassoma rueppellii</i> (Klunzinger, 1828)	<i>Thalassoma quinquevittatum</i> (Lay & Bennett, 1839)	Indo-Pacific, including Gulf of Aden
TRICHONOTIDAE (SAND-DIVERS)		
<i>Limnichthys marisrubri</i> Fricke & Golani, 2012	<i>Limnichthys nitidus</i> (Smith, 1958)	Indian Ocean
TRIPTERYGIIDAE (TRIPLEFINS)		
<i>Enneapterygius altipinnis</i> Clark, 1980	<i>Enneapterygius tutuilae</i> Jordan & Seale, 1906	Indo-W Pacific
BLENNIIDAE (BLENNIES)		
<i>Alticus magnusi</i> (Klausewitz, 1964)	<i>Alticus kirki</i> (Günther, 1868)	WC Indian Ocean, including Gulf of Aden
<i>Entomacrodus solus</i> Williams & Bogorodsky 2010	<i>Entomacrodus epalzeocheilos</i> (Bleeker, 1859)	Indo-Pacific
<i>Istiblennius rivulatus</i> (Rüppell 1830)	<i>Istiblennius dussumieri</i> (Valenciennes, 1836)	Indo-Pacific
GOBIIDAE (GOBIES)		
<i>Oxyurichthys petersi</i> (KLunzinger, 1871)	<i>Oxyurichthys papuensis</i> (Valenciennes, 1837)	Indo-West Pacific
<i>Tomiyamichthys dorsostigma</i> Bogorodsky, Kovacic & Randall, 2011	<i>Tomiyamichthys smithi</i> (Chen & Fang, 2003)	W Pacific
TRICHIURIDAE (HAIRTAILS)		
<i>Evoxymetopon moricheni</i> Fricke, & Golani & Appelbaum-Golani 2014	<i>Evoxymetopon taeniatus</i> Gill, 1863	W Pacific & W Atlantic
MONACANTHIDAE (FILEFISHES/LEATHERJACKETS)		
<i>Oxymonacanthus halli</i> Marshall, 1952	<i>Oxymonacanthus longirostris</i> (Bloch & Schneider, 1801)	Indo-Pacific, excluding Arabian Peninsula
<i>Paraluteres arqat</i> Clark & Gohar, 1953	<i>Paraluteres</i> n sp ³	Andaman Sea
<i>Thamnoconus erythraensis</i> Bauchot & Mauge, 1978	<i>Thamnoconus modestoides</i> (Barnard, 1927)	Indo-West Pacific
TETRAODONTIDAE (PUFFERFISH)		
<i>Arothron diadematus</i> (Rüppell, 1829)	<i>Arothron nigropunctatus</i> (Bloch & Schneider, 1801)	Indo-Pacific, including Gulf of Aden
<u><i>Red Sea to Gulf of Aden endemic</i></u>		
HOLOCENTRIDAE (SOLDIERFISHES & SQUIRELFISHES)		
<i>Myripristis xanthacra</i> Randall & Gueze, 1981	<i>Myripristis hexagona</i> (Lacepède, 1802)	Indo-West Pacific
PLATYCEPHALIDAE (FLATHEADS)		
<i>Thysanophrys springeri</i> Knapp, 2013	<i>Thysanophrys chiltonae</i> (Schultz, 1966)	Indo-West Pacific
SERRANOIDEA (SEABASSES)		
<i>Diploprion drachi</i> Esteve, 1955	<i>Diploprion bifasciatum</i> Cuvier, 1828	Indo-West Pacific to Maldives
<i>Epinephelus geoffroyi</i> (Klunzinger, 1870) ⁴	<i>Epinephelus chlorostigma</i> (Valenciennes, 1828)	Indo-Pacific, including Gulf of Aden

<i>Epinephelus summana</i> (Forsskål, 1775)	<i>Epinephelus caeruleopunctatus</i> (Bloch, 1790)	Indo-West Pacific
PSEUDOCHROMIDAE (DOTTYBACKS)		
<i>Chlidichthys auratus</i> Lubbock, 1975	<i>Chlidichthys johnvoelckeri</i> Smith, 1953	East Africa
<i>Pseudochromis sankeyi</i> Lubbock, 1975	<i>Pseudochromis fridmani</i> Klausewitz, 1968	N to C Red Sea
APOGONIDAE (CARDINALFISHES)		
<i>Cheilodipterus lachneri</i> Klausewitz, 1959	<i>Cheilodipterus arabicus</i> (Gmelin [ex Forsskål], 1789)	Red Sea and W Indian Ocean
<i>Nectamia zebrinus</i> (Fraser, Randall & Lachner, 1999)	<i>Nectamia luxuria</i> Fraser, 2008	Indo-West Pacific to Maldives
MULLIDAE (GOATFISHES)		
<i>Parupeneus forsskali</i> (Fourmanior & Gueze, 1976)	<i>Parupeneus barberinus</i> (Lacepède, 1801)	Indo-Pacific
PEMPHERIDAE (SWEEPERS)		
<i>Pempheris flavicycla marisrubri</i> (Randall, Bogorodsky & Alpermann, 1977)	<i>Pempheris flavicycla flavicycla</i> (Randall, Bogorodsky & Alpermann, 1977)	W Indian Ocean
CHAETODONTIDAE (BUTTERFLYFISHES)		
<i>Chaetodon fasciatus</i> Forsskål, 1775	<i>Chaetodon lunula</i> (Lacepède, 1802)	Indo-Pacific
<i>Chaetodon paucifasciatus</i> Ahl, 1923	<i>Chaetodon madagascariensis</i> Cuvier, 1831	W Indian Ocean
POMACENTRIDAE (DAMSELFISHES)		
<i>Amblyglyphidodon flavilatus</i> Allen & Randall, 1981	<i>Amblyglyphidodon indicus</i> Allen & Randall, 2002	Indian Ocean
<i>Neopomacentrus xanthurus</i> Allen & Randall, 1981	<i>Neopomacentrus nemurus</i> (Bleeker, 1857)	W Pacific
<i>Pristotis cyanostigma</i> Rüppell, 1835	<i>Pristotis obtusirostris</i> (Günther, 1862)	Indo-Pacific
LABRIDAE (WRASSES)		
<i>Cetoscarus bicolor</i> (Rüppell, 1829) ⁵	<i>Cetoscarus ocellatus</i> (Valenciennes, 1840)	Indo-West Pacific
<i>Cheilinus abudjubbe</i> Rüppell, 1835	<i>Cheilinus chlororurus</i> (Bloch, 1791)	Indo-Pacific
<i>Cheilinus quinquecinctus</i> Rüppell, 1835	<i>Cheilinus fasciatus</i> (Bloch, 1791)	Indo-Pacific
<i>Coris variegata</i> (Rüppell, 1835)	<i>Coris batuensis</i> (Bleeker, 1856)	Indian Ocean
<i>Gomphosus caeruleus klunzingeri</i> Klausewitz, 1962	<i>Gomphosus caeruleus caeruleus</i> Lacepede, 1801	Indian Ocean
<i>Hemigymnus sexfasciatus</i> Rüppell, 1835	<i>Hemigymnus fasciatus</i> (Bloch, 1792)	Indo-West Pacific
TRICHONOTIDAE (SAND-DIVERS)		
<i>Trichonotus nikii</i> Clark & Schmidt, 1966	<i>Trichonotus marleyi</i> (Smith, 1936)	W Indian Ocean
BLENNIIDAE (BLENNIES)		
<i>Antennablennius</i> n sp ⁶	<i>Antennablennius variopunctatus</i> (Jatzow & Lenz, 1898)	W Indian Ocean, including Gulf of Aden
SIGANIDAE (RABBITFISHES/SPINEFOOTS)		
<i>Siganus rivulatus</i> (Forsskål, 1775)	<i>Siganus sutor</i> (Valenciennes, 1835)	Indian Ocean, including Gulf of Aden
<i>Siganus stellatus</i> (Forskål, 1775)	<i>Siganus laqueus</i> von Bonde, 1934	Indian Ocean

ACANTHURIDAE (SURGEONFISHES & UNICORNFISHES)*Acanthurus gahhm* Forsskål, 1775*Acanthurus nigricauda* Duncker & Mohr, 1929

Indo-Pacific

BALISTIDAE (TRIGGERFISHES)*Sufflamen albicaudatum* (Rüppell, 1829)*Sufflamen chrysopterum* (Bloch & Schneider, 1801)

Indo-Pacific

TETRAODONTIDAE (PUFFERFISH)*Canthigaster margaritata* (Rüppell, 1826)*Canthigaster petersii* (Bianconi, 1854)³

Indian Ocean, including Gulf of Aden

¹Kuiter (2000)²Initially misidentified as *I. melanopus*; Randall *et al.* (in press)³Allen & Erdmann (2012)⁴Randall *et al.* (2013)⁵Randall (2005)⁶Williams & Bogorodsky in Williams *et al.* (in prep).

Table 2 Phylogeographic studies comparing Red Sea (RS) and Indian Ocean (IO) populations. Species, DNA fragment analysed, Φ_{ST} and F_{ST} (as reported) or percent (%) divergence is presented with an indication whether the Red Sea and Indian Ocean populations were reciprocally monophyletic. Only COI data from DiBattista *et al.* (2013) and ITS/18S data from Wörheide *et al.* (2008) are shown. In parentheses are the number of pairwise comparisons that were statistically significant as reported in the original reference. Reciprocal monophyly implies that the Red Sea population is demographically independent.

Species	DNA fragment	Φ_{ST} , F_{ST} , or % divergence	Reciprocally monophyletic	Source of tissue samples	Reference
<i>Lutjanus kasmira</i> (bluestripe snapper)	COI, Cyt b	$F_{ST} = 0.05$ (1 of 6)	no	RS: Thuwal and Al Lith (KSA) IO: Diego Garcia, Seychelles, Sodwana Bay (South Africa)	DiBattista <i>et al.</i> , 2013
<i>Halichoeres hortulanus</i> (checkerboard wrasse)	COI, Cyt b	$F_{ST} = 0.07-0.12$ (2 of 4)	no	RS: Thuwal and Al Lith (KSA) IO: Diego Garcia, Seychelles	DiBattista <i>et al.</i> , 2013
<i>Cephalopholis argus</i> (peacock hind)	COI, Cyt b	$F_{ST} = 0.20-0.45$ (5 of 6)	no	RS: Thuwal and Al Lith (KSA) IO: Al Hallaniyats (Oman), Diego Garcia, Seychelles	DiBattista <i>et al.</i> , 2013
<i>Acanthurus nigrofuscus</i> (brown surgeonfish)	COI, Cyt b	$F_{ST} = 0.18-0.28$ (4 of 4)	no	RS: Thuwal and Al Lith (KSA) IO: Diego Garcia, Seychelles	DiBattista <i>et al.</i> , 2013
<i>Chaetodon auriga</i> (threadfin butterflyfish)	COI, Cyt b	$F_{ST} = 0.17-0.23$ (4 of 4)	no	RS: Thuwal and Al Lith (KSA) IO: Diego Garcia, Seychelles	DiBattista <i>et al.</i> , 2013, in press B
<i>Neoniphon sammara</i> (Sammara squirrelfish)	COI, Cyt b	$F_{ST} = 0.12-0.16$ (4 of 4)	no	RS: Thuwal and Al Lith (KSA) IO: Diego Garcia, Seychelles	DiBattista <i>et al.</i> , 2013
<i>Scylla serrata</i> (mud crab)	COI	$F_{ST} = 0.42-1.0$ (6 of 6)	yes	RS: Jeddah (KSA) IO: Kenya, Zanzibar, Madagascar, Mauritius, South Africa	Frantini <i>et al.</i> , 2002; Gopurenko <i>et al.</i> , 1999
<i>Pygoplites diacanthus</i> (regal angelfish)	COI, Cyt b	$F_{ST} = 0.65-0.67$ (2 of 2) <1.0% [^]	yes	RS: Thuwal and Al Lith (KSA) IO: Diego Garcia	DiBattista <i>et al.</i> , 2013
<i>Leucetta chagosensis</i> (lemon sponge)	ITS/18S, ATPSb	0.7% ^ϕ	yes	RS: Sinai Peninsula (Egypt) IO: Maldives	Wörheide <i>et al.</i> , 2008
<i>Tridacna maxima</i> (giant clam)	COI	2.5%*	yes	RS: not specified IO: Indonesia	Nuryanto & Kochzius, 2009

<i>Acanthaster planci</i> (crown-of-thorns starfish)	COI	8.80%	yes	RS: Al Wajh (KSA), Sinai Peninsula (Egypt) IO: Indonesia, Thailand, Christmas Is. and Cocos-Keeling Is. (Australia), Maldives, U.A.E., Oman, Kenya, South Africa, Reunion, Mauritius	Vogler <i>et al.</i> , 2008
<i>Mulloidichthys flavolineatus</i> (yellowstripe goatfish)	Cyt b	$\Phi_{ST} = 0-0.86$ (3 of 6)	no	RS: Eilat (Israel), Magna and Jeddah (KSA), Sudan IO: Djibouti, Madagascar	Fernandez-Silva <i>et al.</i> , in press
<i>Coris cuvieri</i> (African coris)	COI	$\Phi_{ST} = 0.04-0.11$ (1 of 3)	no	RS: north to central Red Sea (KSA) IO: Djibouti, Diego Garcia, Seychelles	P. Ahti, pers. comm.
<i>Carcharhinus limbatus</i> (blacktip shark)	control region	$F_{ST} = 0.003$ ($p = 0.24$)	no	RS: entire Red Sea coast (KSA) IO: Oman, U.A.E., Bahrain	Spaet <i>et al.</i> , 2015
<i>Carcharhinus sorrah</i> (spot-tail shark)	control region	$F_{ST} = 0.006$ ($p = 0.10$)	no	RS: entire Red Sea coast (KSA) IO: Oman, U.A.E., Bahrain	Spaet <i>et al.</i> , 2015
<i>Rhizoprionodon acutus</i> (milk shark)	control region	$F_{ST} = 0.06$ ($p = 0.58$)	no	RS: entire Red Sea coast (KSA) IO: Oman, U.A.E., Bahrain	Spaet <i>et al.</i> , 2015
<i>Sphyrna lewini</i> (scalloped hammerhead)	control region	$F_{ST} = 0.01$ ($p = 0.58$)	no	RS: entire Red Sea coast (KSA) IO: Oman, U.A.E.	Spaet <i>et al.</i> , 2015
<i>Cephalopholis hemistiktos</i> (yellowfin hind)	COI S7	$\Phi_{ST} = 0-0.85$ $F_{ST} = 0-0.41$ (10 of 15 for both)	yes for COI no for S7	RS: Magna, Thuwal, Al Lith, and Farasan Islands (KSA), Sudan IO: Djibouti, Oman, Jubail (KSA – Arabian Gulf)	M. Priest, pers. comm.
<i>Panulirus penicillatus</i> (pronghorn spiny lobster)	COI	$\Phi_{ST} = 0.74$ (1 of 1)	yes	RS: Jeddah (KSA) IO: Zanzibar, Seychelles, India	M. Iacchei, pers. comm.

Abbreviation: KSA, Kingdom of Saudi Arabia.

[^]calculated as 1 fixed difference in 634 bp

[♠]calculated as 7 fixed differences in 1049 bp

^{*}calculated as 12 fixed differences in 484 bp

893 **FIGURE LEGENDS**

894 **Figure 1** The Arabian Peninsula region at present-day sea level (a) and when sea level was 120
895 m lower (b), such as during the last glacial maximum approximately 18 kya. Notice that during
896 times of lowered sea level there was reduced shelf area available for coral reefs and other
897 shallow water coastal communities. The southern Red Sea consisted of a long narrow trough
898 nearly completely cut off from the Gulf of Aden at its southern terminus and the Arabian Gulf
899 was non-existent. At the resolution used here, there would be almost no visual difference for
900 shorelines between 100 and 200 m below present day levels. Note the well-defined locations of
901 the Mudawwara Depression (circle symbol) and Umari Depression (square symbol) near the
902 border of present-day Jordan and Saudi Arabia, which provide evidence of palaeorivers and
903 palaeolakes in the region. Satellite-based imagery was courtesy of NASA, and modified by R.F.
904 Myers.

905

906 **Figure 2** Time-calibrated phylogenetic tree for 224 species of damselfish (family
907 Pomacentridae), with biogeographical provinces mapped onto the topology. Colour coding is as
908 follows: red = Red Sea endemic species, green = Red Sea resident plus extended distribution
909 species, blue = Indian Ocean species, black = Pacific Ocean, Atlantic Ocean and species found
910 elsewhere. The time scale is calibrated in Myr before present.

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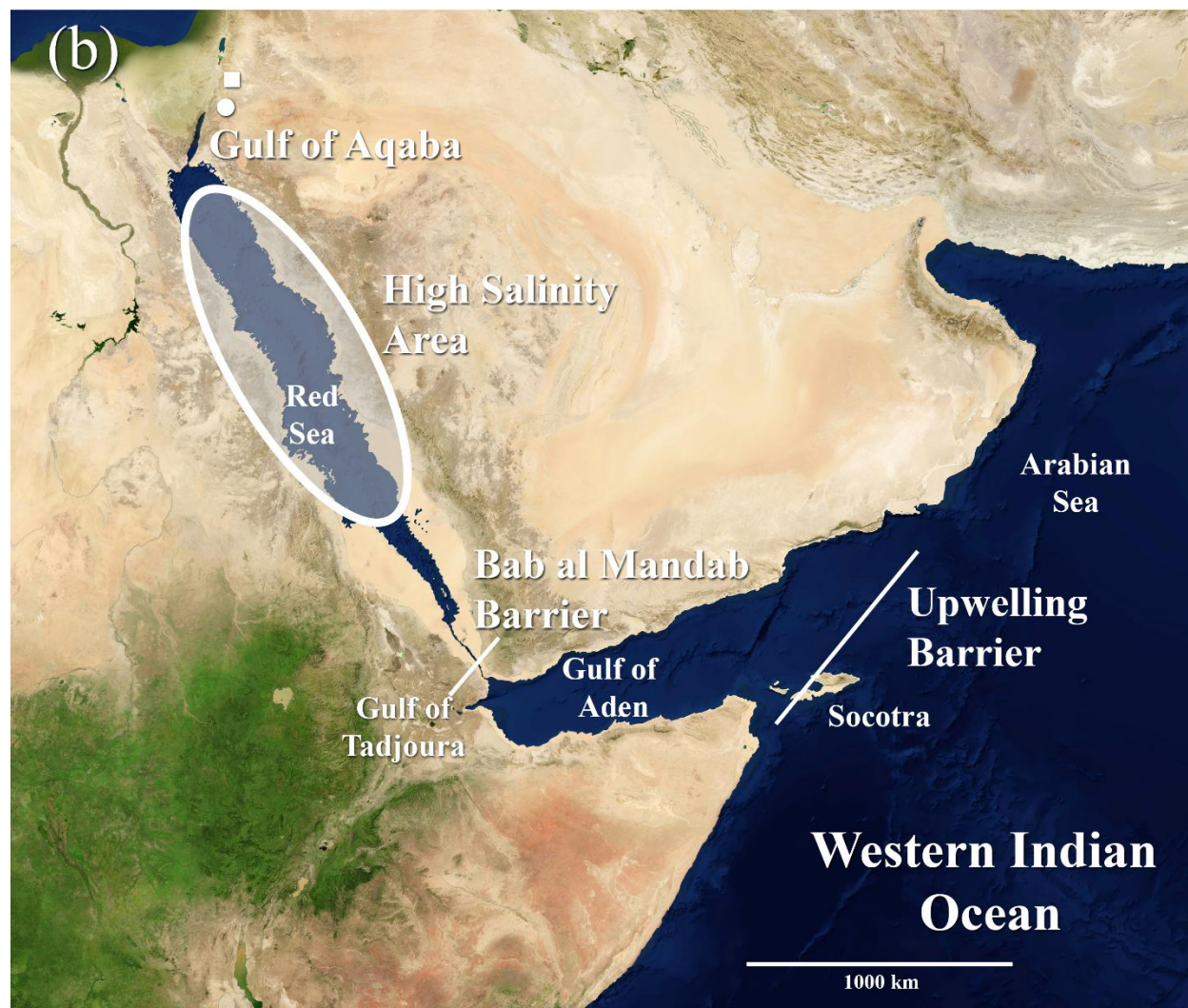
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Table 1 Red Sea endemic reef fish species and their presumed sister species. Because the Gulf of Aden represents a biogeographical extension of the Red Sea province, we additionally report Red Sea to Gulf of Aden (including Socotra) endemics. We excluded species whose closest relative remains unknown or those with no known close relatives. Taxonomic names are according to the Catalog of Fishes, which is the authoritative reference for accepted nomenclature (see Eschmeyer, 2014); exceptions are listed as footnotes.

Species	Sister species	Distribution of sister species
<i>Red Sea endemic</i>		
NARKIDAE (SLEEPER RAYS)		
<i>Heteronarce bentuviai</i> (Baranes & Randall, 1989)	<i>Heteronarce garmani</i> Regan, 1921	Gulf of Aden to South Africa
TORPEDINIDAE (TORPEDOS)		
<i>Torpedo alexandrinsis</i> Mazhar, 1987	<i>Torpedo adenensis</i> Carvalho, Stehmen & Manilo, 2002	Gulf of Aden
MURAENIDAE (MORAY EELS)		
<i>Gymnothorax corallinus</i> (Klunzinger, 1871)	<i>Gymnothorax buroensis</i> (Bleeker, 1857)	Indo-Pacific
<i>Uropterygius golanii</i> McCosker & Smith, 1997	<i>Uropterygius xenodontus</i> McCosker & Smith, 1997	W Pacific
CONGRIDAE (CONGER and GARDEN EELS)		
<i>Gorgasia sillneri</i> Klausewitz, 1962	<i>Gorgasia naeocepaeus</i> (Böhlke, 1951)	W Papua and Philippines
CLUPEIDAE (HERRINGS, SPRATS, & SARDINES)		
<i>Etrumeus golanii</i> DiBattista, Randall & Bowen, 2012	<i>Etrumeus wongratanai</i> DiBattista, Randall & Bowen, 2012	Gulf of Aden to South Africa
<i>Herklotsichthys punctatus</i> (Rüppell, 1837)	<i>Herklotsichthys lossei</i> Wongratana, 1983	Arabian Gulf
SYNODONTIDAE (LIZARDFISHES)		
<i>Synodus randalli</i> Cressey, 1981	<i>Synodus fasciapelvicus</i> Randall, 2009	Indonesia and Philippines
BATRACHOIDIDAE (TOADFISHES)		
<i>Barchatus cirrhosa</i> (Klunzinger, 1871)	<i>Barchatus indicus</i> Greenfield, 2014	Gulf of Aden (N Somalia)
ATHERINIDAE (SILVERSIDES)		
<i>Atherinomorus forskalii</i> (Forster, 1801)	<i>Atherinomorus lacunosus</i> (Schneider, 1801)	Indo-Pacific (sympatric in C Red Sea)
<i>Hypoatherina golanii</i> Sasaki & Kimura, 2012	<i>Hypoatherina klunzingeri</i> Smith, 1965	W Indian Ocean (E Somalia) to South Africa
HOLOCENTRIDAE (SOLDIERFISHES & SQUIRRELFISHES)		
<i>Sargocentron marisrubri</i> Randal, Guezé & Diamant, 1989	<i>Sargocentron melanospilos</i> Bleeker, 1858	Indo-West Pacific
SYNGNATHIDAE (PIPEFISHES & SEAHORSES)		
<i>Corythoichthys</i> cf <i>nigripectus</i> ¹	<i>Corythoichthys nigripectus</i> Herald, 1953	W Pacific
<i>Corythoichthys</i> cf <i>schultzi</i> ¹	<i>Corythoichthys schultzi</i> Herald, 1953	W Pacific
<i>Micrognathus brevirostris</i> (Rüppell, 1838)	<i>Micrognathus pygmaeus</i> Fritzsche, 1981	Indo-West Pacific
SCORPAENIDAE (SCORPIONFISHES)		
<i>Scorpaenodes steinitzi</i> Klausewitz & Fröiland, 1970	<i>Scorpaenodes parvipinnis</i> (Garrett, 1864)	Indo-Pacific
APLOACTINIDAE (VELVETFISHES)		
<i>Ptarmus gallus</i> Kossman & Rauber, 1877	<i>Ptarmus jubatus</i> (Smith, 1935)	E Africa to Natal, South Africa
SERRANOIDEA (SEABASSES)		
<i>Plectropomus marisrubri</i> Randall & Hoese, 1986	<i>Plectropomus pessuliferus</i> (Fowler, 1904)	Indian Ocean and Fiji
<i>Pseudanthias taeniatus</i> (Klunzinger, 1855)	<i>Pseudanthias townsendi</i> (Boulenger, 1897)	Gulf of Aden to Gulf of Oman
<i>Pseudogramma megamycterum</i> Randall & Baldwin, 1997	<i>Pseudogramma astigmum</i> Randall & Baldwin, 1997	Indo-Pacific

PSEUDOCROMIDAE (DOTTYBACKS)*Pseudochromis fridmani* Klausewitz, 1968*Pseudochromis pesi* Lubbock, 1975*Pseudochromis sankeyi* Lubbock, 1975*Pseudochromis melas* Lubbock, 1977

S Red Sea and Gulf of Aden

E Africa

PLESIOPIDAE (PRETTYFINS/LONGFINS)*Acanthoplesiops cappuccino* Gill, Bogorodsky & Mal, 2013*Acanthoplesiops indicus* (Day, 1888)

Indian Ocean

OPISTHOGNATHIDAE (JAWFISHES)*Stalix davidsheni* Klausewitz, 1985*Stalix histrio* Jordan & Snyder, 1902

W Pacific

APOGONIDAE (CARDINALFISHES)*Cheilodipterus pygmaios* Gon, 1993*Taeniamia lineolata* (Cuvier, 1828)*Cheilodipterus quinquelineatus* (Cuvier, 1828)*Taeniamia flavofasciata* (Gon & Randall, 2003)

Indo-Pacific (sympatric in Red Sea)

E Africa to Madagascar

MALACANTHIDAE (SAND TILEFISHES)*Hoplolatilus oreni* Clark & Ben-Tuvia, 1973*Hoplolatilus fourmanoiri* Smith, 1964

Indonesia, Brunei, and Solomon Islands

CAESIONIDAE (FUSILIERS)*Caesio suevica* Klunzinger, 1884*Caesio xanthonota* Bleeker, 1853

Indian Ocean (sympatric S of Gulf of Aqaba)

SPARIDAE (SEA BREAMS)*Argyrops megalommatus* (Klunzinger, 1870)*Diplodus noct* (Valenciennes, 1830)*Argyrops filamentosus* (Valenciennes, 1830)*Diplodus capensis* (Smith, 1884)

W Indian Ocean, including Gulf of Aden

W Indian Ocean, including Gulf of Aden

PEMPHERIDAE (SWEEPERS)*Parapriacanthus guentheri* (Klunzinger, 1871)*Parapriacanthus ransonneti* Steindachner, 1870

Indo-West Pacific, including Gulf of Aden

POMACENTRIDAE (DAMSELFISHES)*Chromis dimidiata* (Klunzinger, 1871)*Chromis pelloura* Randall & Allen, 1982*Pomacentrus albicaudatus* Baschieri-Salvadori, 1955*Chromis fieldi* Randall & DiBattista, 2013*Chromis axillaris* (Bennett, 1831)*Pomacentrus adelus* Allen, 1991

Indian Ocean, including Gulf of Aden

Somalia to S Mozambique and Mauritius

Andaman Sea to W Pacific

LABRIDAE (WRASSES)*Chlorurus gibbus* (Rüppell, 1829)*Cirrhilabrus blatteus* Springer & Randall, 1974*Iniiistius* n sp cf *balwini*²*Macropharyngodon marisrubri* Randall, 1978*Thalassoma rueppellii* (Klunzinger, 1828)*Chlorurus strongylocephalus* (Bleeker, 1864)*Cirrhilabrus lanceolatus* Randall & Masuda, 1991*Iniiistius baldwini* (Jordan & Evermann, 1903)*Macropharyngodon bipartitus* Smtih 1957*Thalassoma quinquevitattum* (Lay & Bennett, 1839)

Indian Ocean, including Gulf of Aden

W Pacific

Indo-West Pacific

W Indian Ocean, including Gulf of Aden

Indo-Pacific, including Gulf of Aden

TRICHONOTIDAE (SAND-DIVERS)*Limnichthys marisrubri* Fricke & Golani, 2012*Limnichthys nitidus* (Smith, 1958)

Indian Ocean

TRIPTERYGIIDAE (TRIPLEFINS)*Enneapterygius altipinnis* Clark, 1980*Enneapterygius tutuilae* Jordan & Seale, 1906

Indo-West Pacific

BLENNIIDAE (BLENNIES)*Alticus magnusi* (Klausewitz, 1964)*Entomacrodus solus* Williams & Bogorodsky, 2010*Istiblennius rivulatus* (Rüppell 1830)*Alticus kirki* (Günther, 1868)*Entomacrodus epalzeocheilos* (Bleeker, 1859)*Istiblennius dussumieri* (Valenciennes, 1836)

WC Indian Ocean, including Gulf of Aden

Indo-Pacific

Indo-Pacific

GOBIIDAE (GOBIES)*Oxyurichthys petersi* (KLunzinger, 1871)*Oxyurichthys papuensis* (Valenciennes, 1837)

Indo-West Pacific

<i>Tomiyamichthys dorsostigma</i> Bogorodsky, Kovacic & Randall, 2011	<i>Tomiyamichthys smithi</i> (Chen & Fang, 2003)	W Pacific
TRICHIURIDAE (HAIRTAILS)		
<i>Evoxymetopon moricheni</i> Fricke, Golani & Appelbaum-Golani 2014	<i>Evoxymetopon taeniatus</i> Gill, 1863	W Pacific and W Atlantic
MONACANTHIDAE (FILEFISHES/LEATHERJACKETS)		
<i>Oxymonacanthus halli</i> Marshall, 1952	<i>Oxymonacanthus longirostris</i> (Bloch & Schneider, 1801)	Indo-Pacific, excluding Arabian Peninsula
<i>Paraluteres arqat</i> Clark & Gohar, 1953	<i>Paraluteres</i> n sp ³	Andaman Sea
<i>Thamnoconus erythraensis</i> Bauchot & Mauge, 1978	<i>Thamnoconus modestoides</i> (Barnard, 1927)	Indo-West Pacific
TETRAODONTIDAE (PUFFERFISH)		
<i>Arothron diadematus</i> (Rüppell, 1829)	<i>Arothron nigropunctatus</i> (Bloch & Schneider, 1801)	Indo-Pacific, including Gulf of Aden
<u>Red Sea to Gulf of Aden endemic</u>		
HOLOCENTRIDAE (SOLDIERFISHES & SQUIRRELFISHES)		
<i>Myripristis xanthacra</i> Randall & Gueze, 1981	<i>Myripristis hexagona</i> (Lacepède, 1802)	Indo-West Pacific
PLATYCEPHALIDAE (FLATHEADS)		
<i>Thysanophrys springeri</i> Knapp, 2013	<i>Thysanophrys chiltonae</i> (Schultz, 1966)	Indo-West Pacific
SERRANOIDEA (SEABASSES)		
<i>Diploprion drachi</i> Esteve, 1955	<i>Diploprion bifasciatum</i> Cuvier, 1828	Indo-West Pacific to Maldives
<i>Epinephelus geoffroyi</i> (Klunzinger, 1870) ⁴	<i>Epinephelus chlorostigma</i> (Valenciennes, 1828)	Indo-Pacific, including Gulf of Aden
<i>Epinephelus summana</i> (Forsskål, 1775)	<i>Epinephelus caeruleopunctatus</i> (Bloch, 1790)	Indo-West Pacific
PSEUDOCROMIDAE (DOTTYBACKS)		
<i>Chlidichthys auratus</i> Lubbock, 1975	<i>Chlidichthys johnvoelckeri</i> Smith, 1953	East Africa
<i>Pseudochromis sankeyi</i> Lubbock, 1975	<i>Pseudochromis fridmani</i> Klausewitz, 1968	N to C Red Sea
APOGONIDAE (CARDINALFISHES)		
<i>Cheilodipterus lachneri</i> Klausewitz, 1959	<i>Cheilodipterus arabicus</i> (Gmelin [ex Forsskål], 1789)	Red Sea and W Indian Ocean
<i>Nectamia zebrinus</i> (Fraser, Randall & Lachner, 1999)	<i>Nectamia luxuria</i> Fraser, 2008	Indo-West Pacific to Maldives
MULLIDAE (GOATFISHES)		
<i>Parupeneus forsskali</i> (Fourmanior & Gueze, 1976)	<i>Parupeneus barberinus</i> (Lacepède, 1801)	Indo-Pacific
PEMPHERIDAE (SWEEPERS)		
<i>Pempheris flavicycla marisrubri</i> (Randall, Bogorodsky & Alpermann, 2013)	<i>Pempheris flavicycla flavicycla</i> (Randall, Bogorodsky & Alpermann, 2013)	W Indian Ocean
CHAETODONTIDAE (BUTTERFLYFISHES)		
<i>Chaetodon fasciatus</i> Forsskål, 1775	<i>Chaetodon lunula</i> (Lacepède, 1802)	Indo-Pacific
<i>Chaetodon paucifasciatus</i> Ahl, 1923	<i>Chaetodon madagascariensis</i> Cuvier, 1831	W Indian Ocean
POMACENTRIDAE (DAMSELFISHES)		
<i>Amblyglyphidodon flavilatus</i> Allen & Randall, 1981	<i>Amblyglyphidodon indicus</i> Allen & Randall, 2002	Indian Ocean
<i>Neopomacentrus xanthurus</i> Allen & Randall, 1981	<i>Neopomacentrus nemurus</i> (Bleeker, 1857)	W Pacific
<i>Pristotis cyanostigma</i> Rüppell, 1835	<i>Pristotis obtusirostris</i> (Günther, 1862)	Indo-Pacific
LABRIDAE (WRASSES)		
<i>Cetoscarus bicolor</i> (Rüppell, 1829) ⁵	<i>Cetoscarus ocellatus</i> (Valenciennes, 1840)	Indo-West Pacific
<i>Cheilinus abudjubbe</i> Rüppell, 1835	<i>Cheilinus chlororurus</i> (Bloch, 1791)	Indo-Pacific

<i>Cheilinus quinquecinctus</i> Rüppell, 1835	<i>Cheilinus fasciatus</i> (Bloch, 1791)	Indo-Pacific
<i>Coris variegata</i> (Rüppell, 1835)	<i>Coris batuensis</i> (Bleeker, 1856)	Indian Ocean
<i>Gomphosus caeruleus klunzingeri</i> Klausewitz, 1962	<i>Gomphosus caeruleus caeruleus</i> Lacepede, 1801	Indian Ocean
<i>Hemigymnus sexfasciatus</i> Rüppell, 1835	<i>Hemigymnus fasciatus</i> (Bloch, 1792)	Indo-West Pacific
TRICHONOTIDAE (SAND-DIVERS)		
<i>Trichonotus nikii</i> Clark & Schmidt, 1966	<i>Trichonotus marleyi</i> (Smith, 1936)	W Indian Ocean
BLENNIIDAE (BLENNIES)		
<i>Antennablennius</i> n sp ⁶	<i>Antennablennius variopunctatus</i> (Jatzow & Lenz, 1898)	W Indian Ocean, including Gulf of Aden
SIGANIDAE (RABBITFISHES/SPINEFOOTS)		
<i>Siganus rivulatus</i> (Forsskål, 1775)	<i>Siganus sutor</i> (Valenciennes, 1835)	Indian Ocean, including Gulf of Aden
<i>Siganus stellatus</i> (Forsskål, 1775)	<i>Siganus laqueus</i> von Bonde, 1934	Indian Ocean
ACANTHURIDAE (SURGEONFISHES & UNICORNFISHES)		
<i>Acanthurus gahhm</i> Forsskål, 1775	<i>Acanthurus nigricauda</i> Duncker & Mohr, 1929	Indo-Pacific
BALISTIDAE (TRIGGERFISHES)		
<i>Sufflamen albicaudatum</i> (Rüppell, 1829)	<i>Sufflamen chrysopterum</i> (Bloch & Schneider, 1801)	Indo-Pacific
TETRAODONTIDAE (PUFFERFISH)		
<i>Canthigaster margaritata</i> (Rüppell, 1826)	<i>Canthigaster petersii</i> (Bianconi, 1854) ³	Indian Ocean, including Gulf of Aden

¹Kuiter (2000)

²Initially misidentified as *I. melanopus*; Randall *et al.* (in press)

³Allen & Erdmann (2012)

⁴Randall *et al.* (2013)

⁵Randall (2005)

⁶Williams & Bogorodsky *in* Williams *et al.* (in prep).

SUPPORTING INFORMATION

On the origin of endemic species in the Red Sea

Joseph D. DiBattista, J. Howard Choat, Michelle R. Gaither, Jean-Paul A. Hobbs, Diego F. Lozano-Cortés, Robert F. Myers, Gustav Paulay, Luiz A. Rocha, Robert J. Toonen, Mark W. Westneat, and Michael L. Berumen

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

Appendix S1 GenBank accession and GI numbers for DNA sequences used in phylogenetic analysis of the Pomacentridae (see Figure 2).

Pomacentridae

12s: FJ616289 to FJ616396 (Cooper *et al.*, 2009)

16s: FJ616397 to FJ616504 (Cooper *et al.*, 2009)

ND3: FJ616505 to FJ616616 (Cooper *et al.*, 2009)

RAG1: FJ616617 to FJ616728 (Cooper *et al.*, 2009)

RAG2: FJ616729 to FJ616835 (Cooper *et al.*, 2009)

BMP4: FJ616836 to FJ616947 (Cooper *et al.*, 2009)

Cyt b: JF457872 to JF458268 (N. Hubert, Institut de Recherche pour le Développement, unpub. data)

JQ707166 to JQ707186 (Frederich *et al.*, 2012)

COI: 326455997, 312841805, 386268442, 381278444, 381278452, 328483978, 326456019, 393004003, 328483986, 375584689, 299832920, 429492384, 223366416, 223366428, 429142483, 426263640, 430007341, 326456061, 223366446, 223366480, 223366492, 393693108, 223366528, 393693114, 223366550, 393693112, 294988810, 164507045, 326456315, 312841799, 326456321, 171673952, 328484794, 223367208, 164507019, 257218521, 223367214, 326456339, 164507023, 386268520, 322402287, 164507033, 326456353, 392465170, 393004139, 326456361, 381278918, 223367234, 393005604, 328484804, 339431467, 312841733, 379134108, 326456381, 326456383, 223367252, 301036305, 326456415, 326456417, 326456423, 326456425, 359326531, 223367264, 223367286, 326456449, 223367296, 223367308, 223367306, 223367328, 223367342, 326456893, 325071210, 326456499, 223367568, 223367578, 223367582, 326456511, 223367648, 223367652, 171673956, 381279420, 386268750, 326456691, 223368376, 223368392, 375586076, 326456701, 375586316, 326456729, 375586328, 326456747, 322402289, 326456761, 326456771, 326456775, 223368698, 326456785, 400219896, 326456787, 328486924, 223368714, 400219880, 223368734, 326456835, 326456837, 312841809, 326456849, 326456863, 393757268, 386268864, 381279982, 386366917, 381279986, 386366923, 326456895, 326456915, 326456917, 386268880, 326456929, 386366939, 386268884 (includes multiple studies)