Synthesis

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RRH: Origins of Red Sea endemism

On the origin of endemic species in the Red Sea

Joseph D. DiBattista¹,²*, J. Howard Choat³, Michelle R. Gaither⁴, Jean-Paul A. Hobbs², Diego F. Lozano-Cortés¹, Robert F. Myers⁵, Gustav Paulay⁶, Luiz A. Rocha⁷, Robert J. Toonen⁸, Mark W. Westneat⁹, Michael L. Berumen¹

¹Red Sea Research Center, Division of Biological and Environmental Science and Engineering, King Abdullah University of Science and Technology, Thuwal 23955, Saudi Arabia, ²Department of Environment and Agriculture, Curtin University, PO Box U1987, Perth, WA 6845, Australia, ³School of Marine and Tropical Biology, James Cook University, Townsville QLD 4811, Australia, ⁴School of Biological and Biomedical Sciences, Durham University, Durham DH1 3LE, United Kingdom, ⁵Seaclicks/Coral Graphics, Wellington FL 33411, USA, ⁶Florida Museum of Natural History, Gainesville, FL 32611-7800, USA, ⁷Section of Ichthyology, California Academy of Sciences, San Francisco, CA 94118, USA, ⁸Hawaii Institute of Marine Biology, Kāne‘ohe, HI 96744, USA, ⁹Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637, USA

*Correspondence: Joseph D. DiBattista, Department of Environment and Agriculture, Curtin University, PO Box U1987, Perth, WA 6845, Australia.

E-mail: josephdibattista@gmail.com
ABSTRACT

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

Location Red Sea and Western Indian Ocean.

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

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

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

**Keywords**

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

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

Recent research has demonstrated the importance of peripheral regions, such as the Red Sea, the Hawaiian Archipelago and the Marquesas Islands as “evolutionary incubators” that contribute unique genetic lineages to other regions of the Indo-West Pacific (Gaither et al., 2010, 2011; Malay & Paulay, 2010; DiBattista et al., 2011; Eble et al., 2011; Skillings et al., 2011; Hodge et al., 2012; Bowen et al., 2013; DiBattista et al., 2013). Peripheral endemism can be driven by isolation or selection, and both are of potential importance in the Red Sea. Indeed, the Red Sea is isolated by a narrow, shallow sill in the south, whereas broad areas of upwelling create a habitat barrier for reef-associated taxa in the Arabian Sea. Large spatial gradients and temporal fluctuations in physical conditions make this one of the most variable regions in the tropical marine environment, with a high potential for ecological speciation. Even greater
environmental variation is evident through glacio-eustatic cycles, with the Red Sea basin becoming isolated and hypersaline at glacial maxima. The geological and palaeo-climactic forces that gave rise to shallow water reef fauna in the Red Sea are therefore topics of biogeographical importance and the origins of the endemics are still the subject of much debate (see Rasul & Stewart, 2015). After describing the regional setting, we outline key components of this debate below.

_Geological history of the Red Sea_

The dimensions and configuration of the Red Sea reflect the influence of a combination of geological and climatic processes, which include rifting (spreading) between the African and Arabian plates, associated volcanism in the mid-Tertiary and eustatic sea level fluctuations, which intensified in the Pliocene but more so since the mid-Pleistocene (Rihm & Henke, 1998). The present day result is a narrow ocean basin with a north-south orientation, modest surface area (438,000 km$^2$) and limited continuity with the greater Indo-West Pacific as it is connected only at the Strait of Bab al Mandab (Sheppard et al., 1992). Many of the present-day Red Sea reefs have a characteristic structure of shallow flat tops, steeply sloping sides and an elongated north-south axis as a result of the geologic history in this region (Dullo & Montaggioni, 1998).

Major events that led to the present day configuration of the Red Sea were initiated by Oligocene episodes of sea floor spreading 41 to 34 Ma (Girdler & Styles, 1974). The rifting processes were associated with episodes of volcanism at the Afar Traps near present day Ethiopia, with major activity around 31 Ma near the Afar Plume (Bosworth et al., 2005). During this time, saltwater replenished the Red Sea initially from the north but subsequently from the south via episodic connections to the Mediterranean Sea and the Gulf of Aden, respectively. The
stratigraphy of this period is characterised by thick evaporate deposits interleaved with marine deposits of a northern origin indicating periods of intense evaporation interspersed with marine incursions from the Mediterranean. Uplift of the Suez area (i.e. Sinai Peninsula), driven by the collision of Eurasia with Arabia 14 Ma, shifted the location of the main oceanic connection to the south via the Gulf of Aden (Girdler & Styles, 1974; Hubert-Ferrari et al., 2003). During this period, the Red Sea environment was highly saline and unstable, subject to episodes of high temperature and evaporation and therefore unlikely to have supported a diverse tropical reef fauna.

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

The Red Sea reef fauna, having been established during the Pliocene and Pleistocene (4 to 3 Ma), is relatively recent and has been subjected to environmental variation (e.g. temperature and salinity) of a magnitude not experienced by reefs in the Indian and Pacific Oceans (Taviani, 1998). The biological impacts of this dynamic environment have been exacerbated by the distinctive reef environments of the eastern Gulf of Aden and southern Oman, which act as filters for potential colonists due to major fluctuations in temperature and primary productivity as a
result of episodic monsoonal-driven upwelling (Currie et al., 1973; Smeed, 1997; Kemp, 2000; Jung et al., 2001).

Isolation and barriers to dispersal

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

While the southern Red Sea and western Gulf of Aden are relatively similar, the eastern Gulf of Aden, including northeast Africa (south of Ras Hafun), and southern Oman have markedly different contemporary environments with limited reef development that pose an environmental barrier for potential colonists. Currently this area experiences major fluctuations in temperature and primary productivity driven by episodic monsoonal-driven upwelling (and temperatures as low as 13°C; Currie et al., 1973; Smeed, 1997; Kemp, 2000; Jung et al., 2001). Because many Red Sea endemics also occur in the Gulf of Aden (Türkay, 1996; Janssen & Taviani, 2015; DiBattista et al., in press A), some believe that the adjacent regions of cold water upwelling off
Somalia and Oman, as well as seasonal current patterns, are of greater importance as isolating mechanisms than the physical isolation at Bab al Mandab (Kemp, 1998, 2000; Zajonz et al., 2000).

Pleistocene conditions

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

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

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

**Palaeontological evidence**

*Core data and microfossils*

Deep-sea cores taken along the length of the Red Sea, including the Gulf of Aqaba, provide a microfossil, isotopic, geochemical and petrographic record of environmental and biotic changes over the glacial cycles of the mid to late Pleistocene (Reiss et al., 1980; Almogi-Labin, 1982; Hofmann et al., 1998; Fenton et al., 2000; Badawi et al., 2005). The most striking aspect of these data is that glacial maxima are associated with an “aplanktonic” period, when most, if not all, planktonic foraminifera, as well as many coccolithophorids and pteropods, disappeared, indicating unsuitable environmental conditions (Fenton et al., 2000). Although plankton
diversity decreased sharply during glacial maxima, some taxa increased in abundance, especially benthic, miliolid forams, the euryhaline pteropod *Creseis acicula* and, locally, siliceous diatoms and some sponges (Reiss *et al*., 1980; Almogi-Labin *et al*., 2008). Increases in δ¹⁸O,

development of sapropels and carbonate crusts, together with considerations of salinity tolerance for extirpated and persisting microfossils, indicates that salinity levels reached and potentially exceeded 50‰ (Reiss *et al*., 1980; Hofmann *et al*., 1998; Taviani, 1998). Temperatures also fell between 3 to 5 °C, but the decrease in the diversity and abundance of planktonic microfossils is primarily attributed to hypersaline conditions versus lowered temperatures (Reiss *et al*., 1980).

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

The drastic changes in the planktonic foraminifera communities and productivity of the Red Sea (including the Gulf of Aqaba) during Pleistocene glacial periods were much greater than that in the Gulf of Aden (Deuser *et al*., 1976). The salinities in the Gulf Aden during glacial periods were similar to present day salinities (36‰; Duplessy, 1982; Locke, 1986, Thunell *et al*., 1988) and, with the exception of a few species, the foraminifera and pteropod assemblages in this
region were similar between glacial and interglacial periods, suggesting no large changes in productivity in the surface waters over the last 50 kyr (Ivanova, 1985; Locke & Thunell, 1988). This cumulative evidence supports the idea that the Gulf of Aden may have served as a refuge for Red Sea fauna during these times of harsh environmental conditions.

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

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

Climatic reconstruction of rainfall regimes

Support for tolerable marine conditions in the northern and southern Red Sea comes from climatic reconstructions. The Red Sea appears to be influenced by two rainfall regimes: 1) a Mediterranean system in the northern Red Sea (de Menocal & Rind, 1996) and 2) a monsoonal system in the southern Red Sea (Murray & Johns, 1997; Siddall et al., 2002; Sofianos et al.,
Evidence of palaeorivers and palaeolakes, such as the vast Mudawwara depression (2000 km²) on the border of Saudi Arabia and Jordan, can be seen across the Arabian Peninsula (e.g. Parton et al., 2010). Studies using oxygen isotope records have also reported the occurrence of five periods of increased wetness in the Arabian Sea (10.5 to 6 ka, 82 to 78 ka, 135 to 120 ka, 200 to 180 ka and 325 to 300 ka; Fleitmann et al., 2003). Additional evidence for increased precipitation in the region comes from anthropological research. Studies show that during wet periods, lakes and rivers formed, resulting in increased vegetation during the Pleistocene (McLaren et al., 2009; Rosenberg et al., 2011; Groucutt & Petraglia, 2012). These wetter periods appear to have enhanced the capacity of humans to migrate out of Africa and into Arabia, and could also have had a substantial effect on the nearshore reefs of the eastern Red Sea if a physical connection with the Indian Ocean persisted. That said, peaks in precipitation rarely coincide with glacial periods, they favour interglacial periods instead.

Survival within the Red Sea may have been possible in the Gulf of Aqaba, owing to this area being wetter (and less saline) during glacial maxima. In this scenario, southern Jordan functioned as a fresh water reservoir lowering salinity in the Gulf of Aqaba to a tolerable level, as suggested by the existence of palaeolakes Hasa, Jafr, Jurf ed Darawish and those in the Mudawwara and Umari depressions (Rech, 2013). There is no indication, however, that the Nile ever flowed into and impacted the northern Red Sea region (i.e. Gulf of Suez; Stanley & Warne, 1993; Krom et al., 2002). Regardless of rainfall level, the existence of Pleistocene reefs at 98 m depth (Hoffman et al., 1998) provides evidence of coral survival during advanced glacial conditions in the Gulf of Aqaba (also see Fricke, 1996). Evidence from foraminifera also indicates that conditions in the Gulf of Aqaba may have provided a refuge for shallow-water organisms during glacial maxima (Locke & Thunell, 1988). This scenario is supported by an endemic fish fauna that is
restricted to the Gulf of Aqaba (4.1%, DiBattista et al., in press A; but also see Winterbottom, 1985; Fricke et al., 2014).

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

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

Salinity tolerances for marine organisms

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

Species distributions and distribution of sister taxa

The most compelling evidence for survival of endemics within the Red Sea comes from the large number of species that appear to be restricted to the basin (DiBattista et al., in press A). Whereas
some of these species may have been overlooked outside the basin and others could have become
recently restricted, the sheer diversity of species suggests that some have persisted in the Red Sea
through glacial periods.

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

Klausewitz (1989) provided a framework for classifying the historical origins of Red Sea fish
based on the relative age of differentiation: 1) postglacial fish that invaded the basin during the
past 10 kyr, 2) interglacial fish that invaded during earlier interglacial periods and 3) fish with a
high degree of differentiation that invaded much earlier and persisted in the basin. Although
Klausewitz (1989) considered the question of the viability of the Red Sea as a habitat for tropical
reef fish during glacial maxima to be unresolved, he also suggested that the southern part of the Red Sea could have served as a refuge. Whereas current ecological conditions in the southern Red Sea may not be ideal for many species, it is clear that a number of them effectively disperse through the Bab al Mandab barrier in both directions. It therefore seems more likely that speciation of true Red Sea endemics (those not found in the Gulf of Aden), with clearly identifiable Indo-West Pacific sister species, occurred when isolation of the basin was greater if not complete. Furthermore, we now know that the relative ages of differentiation of many endemics in the Red Sea precede the end of the last interglacial, and in rare cases the entire Pleistocene (examples from Table 1: *Chlorurus gibbus* and *C. strongylocephalus* [0.5 Ma], Choat *et al.*, 2012; *Chromis dimidiata* and *C. fieldi* [0.95 Ma], Randall & DiBattista, 2013; *Etrumeus golanii* and *E. wongratanai* [1.65 Ma], DiBattista *et al.*, 2012; *Pomacentrus albicaudatus* and *P. adelus* [~3.5 Ma], Litsios *et al.*, 2012; *Thalassoma rueppellii* and *T. quinquevitattum* [~12.5 Ma], Hodge *et al.*, 2014).

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

Phylogenetic dispersion and taxonomic sampling

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

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

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

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

Phylogeography and population genetics

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

Levels of genetic divergence detected in these studies vary by an order of magnitude across species (Table 2), indicating that colonisation of the Red Sea did not coincide with a specific geologic event but perhaps multiple stochastic events. Deep phylogenetic partitions have been detected in the Red Sea populations of the mud crab (*Scylla serrata*; Gopureenko et al. 1999; Fratini & Vannini, 2002), regal angelfish (*Pygoplites diacanthus*; DiBattista et al., 2013), lemon
sponge (*Leucetta chagosensis*; Wörheide et al., 2008), yellowfin goatfish (*Mulloidichthys flavolineatus*; Fernandez-Silva et al., in press), yellowfin hind (*Cephalopholis hemistiktos*; M. Priest, pers. comm.), giant clam (*Tridacna maxima*; Nuryanto & Kochzius, 2009), pronghorn spiny lobster (*Panulirus penicillatus*; M. Iacchei, pers. comm.) and crown-of-thorns starfish (*Acanthaster planci*; Vogler et al., 2008). The oldest of these lineages may represent cryptic species complexes (e.g. *A. planci* and *P. diacanthus*; Table 2). Red Sea and Indian Ocean lineages in these examples are reciprocally monophyletic with no evidence of gene flow between regions, and levels of divergence that represent hundreds of thousands (e.g. *P. diacanthus*) to millions of years (e.g. *A. planci*). In the Sammara squirrelfish, *Neoniphon sammara*, shallower divergences have been recorded that date to about 125 kyr of isolation, with near monophyly (DiBattista et al., 2013). Other species demonstrate significant population level structure between the Red Sea and Indian Ocean, but with shared haplotypes among regions (brown surgeonfish, *Acanthurus nigrofuscus*; peacock hind, *Cephalopholis argus*; threadfin butterflyfish, *Chaetodon auriga*), and perhaps represent more recent colonisation of the Red Sea (DiBattista et al., 2013; also see DiBattista et al., in press A).

Only four phylogeographical studies conducted thus far in reef fish include samples from the Gulf of Aden, and these show a variable pattern that parallels what we know from species distributions. The African coris wrasse (*C. cuvieri*, a Red Sea to Indian Ocean species, P. Ahti, pers. comm.) and threadfin butterflyfish (*C. auriga*, an Indo-West Pacific species, DiBattista et al., in press B) demonstrate modest differentiation among Red Sea, Gulf of Aden and Indian Ocean populations, whereas the other two species, the yellowfin goatfish (*M. flavolineatus*; Fernandez-Silva et al., in press) and the yellowfin hind (*C. hemistiktos*; M. Priest, pers. comm.), have an endemic genetic lineage that extends between the Red Sea and the Gulf of Aden. We see
similar patterns at the species level for some invertebrates (echinoderms: G. Paulay, unpub. data; coral gall crabs: S. van der Meij, pers. comm.), which are characterised by high levels of endemism, with many endemics making it into the Gulf of Aden or also into the Arabian Sea. This pattern suggests that many of the lineages thought to be unique to the Red Sea may be found outside the basin with increased sampling. This pattern, however, does not allow us to conclude whether lineages originate from glacial refugia within or just outside the Red Sea owing to the potential for bidirectional post-glacial expansion.

**Conclusion and future directions**

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

Perhaps the most compelling evidence for the persistence of some Red Sea taxa during glaciation events is the genetic evidence that many endemic taxa (or lineages) diverged from
their Indian Ocean counterparts long before the most recent glaciations, and the restriction of some endemics to narrow areas, especially in the northern Red Sea. The range of ages of Red Sea endemics suggests that peripatric speciation has been an ongoing process in this region, a pattern shown at other hotspots of endemism in the Indo-West Pacific (e.g. Hawaiian Archipelago; Craig et al., 2010) that may be the rule rather than the exception.

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

ACKNOWLEDGEMENTS

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REFERENCES


**SUPPORTING INFORMATION**

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

**Appendix S1** Online voucher numbers for DNA sequences used in the phylogenetic analysis of the Pomacentridae (also see Figure 2).
Biosketch

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

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

Editor: Richard Ladle
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.

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

**PSEUDDOCHROMIDAE (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)**
Hoplolatilus 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)

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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)
Hoplolatilus 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 adelus Allen, 1991
Chlorurus strongylocephalus (Bleeker, 1864)
Cirrhilabrus blatteus Springer & Randall, 1974
Inisius n sp cf balwini2
Macropharyngodon marisrubri Randall, 1978
Thalassoma rueppelli (Kunzinger, 1828)

TRICHTONOTIDAE (SAND-DIVERS)
Limnichthys marisrubri Fricke & Golani, 2012

TRIPERTYGIIDAE (TRIPLEFINS)
Enneapterygus altipinnis Clark, 1980

BLENNIIDAE (BLENNIES)
Alticus magnusi (Klausewitz, 1964)
Entomacrodus solus Williams & Bogorodsky 2010
Istiblennius rivulatus (Rüppell 1830)

GOBIIDAE (GOBIES)
Oxyurichthys petersi (KLunzinger, 1871)
Tomiyamichthys dorsostigma Bogorodsky, Kovacic & Randall, 2011

TRICHIURIDAE (HAIRTAILS)
Evoxymetopon moricheni Fricke, & Golani & Appelbaum-Golani 2014

MONACANTHIDAE (FILEFISHES/LEATHERJACKETS)
Oxymonacanthus halli Marshall, 1952
Paraluteres arqat Clark & Gohar, 1953
Thamnoconus erythraensis Bauchot & Mauge, 1978

TETRAODONTIDAE (PUFFERFISH)
Arothron diadematus (Rüppell, 1829)

Red Sea to Gulf of Aden endemic

HOLOCENTRIDAE (SOLDIERFISHES & SQUIRRELFISHES)
Myripristis xanthaca Randall & Gueze, 1981

PLATYCEPHALIDAE (FLATHEADS)
Thysanophrys springeri Knapp, 2013

SERRANOIDEA (SEABASSES)
Diploprion drachi Esteve, 1955
Epinephelus geoffroyi (Kunzinger, 1870)4

Cirrhilabrus lanceolatus Randall & Masuda, 1991
Inisius baldwini (Jordan & Evermann, 1903)
Macropharyngodon bipartitus Smith 1957
Thalassoma quinquevitattum (Lay & Bennett, 1839)

Limnichthys nitidus (Smith, 1958)

Enneapterygus tutulae Jordan & Seale, 1906

Alticus kirki (Günther, 1868)
Entomacrodus epalzeocheilos (Bleeker, 1859)
Istiblennius dussumieri (Valenciennes, 1836)

Oxyurichthys papuensis (Valenciennes, 1837)
Tomiyamichthys smithi (Chen & Fang, 2003)

Evoxymetopon taeniatus Gill, 1863

Oxymonacanthus longirostris (Bloch & Schneider, 1801)
Thamnoconus modestoides (Barnard, 1927)

Arothron nigropunctatus (Bloch & Schneider, 1801)

Myripristis hexagona (Lacepède, 1802)
Thysanophrys chilonae (Schultz, 1966)

Diploprion bifasciatum Cuvier, 1828
Epinephelus chlorostigma (Valenciennes, 1828)

Indo-Pacific, including Gulf of Aden

W Pacific

Indo-West Pacific

W Indian Ocean, including Gulf of Aden

Indo-Pacific, including Gulf of Aden

Indian Ocean

Indo-W Pacific

WC Indian Ocean, including Gulf of Aden

Indo-Pacific

Indo-Pacific

W-West Pacific

W Pacific

Indo-Pacific, excluding Arabian Peninsula

Andaman Sea

Indo-West Pacific

Indo-Pacific, including Gulf of Aden

Indo-West Pacific

Indo-West Pacific

Indo-West Pacific to Maldives

Indo-Pacific, including Gulf of Aden
Epinephelus summana (Forsskål, 1775)

**PSEUDOCHROMIDAE (DOTTYBACKS)**

Chlidichthys auratus Lubbock, 1975
Pseudochromis sankeyi Lubbock, 1975

**APOGONIDAE (CARDINALFISHES)**

Cheilodipterus lachneri Klausewitz, 1959
Nectamia zebrinus (Fraser, Randall & Lachner, 1999)

**MULLIDAE (GOATFISHES)**

Parupeneus forsskali (Fourmanior & Gueze, 1976)

**PHEMPHERIDAE (SLEEPERS)**

Pempheris flavicycla marisrubri (Randall, Bogorodsky & Alpermann, 2013)

**CHÆTODONTIDAE (BUTTERFLYFISHES)**

Chaetodon fasciatus Forsskål, 1775
Chaetodon paucifasciatus Ahl, 1923

**POMACENTRIDAE (DAMSELFISHES)**

Amblyglyphidodon flavilatus Allen & Randall, 1981
Neopomacentrus xanthurus Allen & Randall, 1981
Pristotis cyanostigma Rüppell, 1835

**LABRIDAE (WRASSES)**

Cetoscarus bicolor (Rüppell, 1829)
Cheilinus abudjubbe Rüppell, 1835
Cheilinus quinquecinctus Rüppell, 1835
Coris variegata (Rüppell, 1835)
Gomphosus caeruleus caeruleus Lacepede, 1801
Hemigymnus sexfasciatus Rüppell, 1835

**TRICHONOTIDAE (SAND-DIVERS)**

Trichonotus nikii Clark & Schmidt, 1966

**BLENNIIDAE (BLENNIES)**

Antennamblenius n sp

**SIGANIDAE (RABBITFISHES/SPINEFOOTS)**

Siganus rivulatus (Forsskål, 1775)
Siganus stellatus (Forsskål, 1775)
### ACANTHURIDAE (SURGEONFISHES & UNICORNFISHES)

<table>
<thead>
<tr>
<th>Species</th>
<th>Author</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthurus gahhm</td>
<td>Forsskål, 1775</td>
<td>Indo-Pacific</td>
</tr>
<tr>
<td>Acanthurus nigricauda</td>
<td>Duncker &amp; Mohr, 1929</td>
<td>Indo-Pacific</td>
</tr>
</tbody>
</table>

### BALISTIDAE (TRIGGERFISHES)

<table>
<thead>
<tr>
<th>Species</th>
<th>Author</th>
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</tr>
</thead>
<tbody>
<tr>
<td>Sufflamen albicaudatum</td>
<td>(Rüppell, 1829)</td>
<td>Indo-Pacific</td>
</tr>
<tr>
<td>Sufflamen chrysopterum</td>
<td>(Bloch &amp; Schneider, 1801)</td>
<td>Indo-Pacific</td>
</tr>
</tbody>
</table>

### TETRAODONTIDAE (PUFFERFISH)

<table>
<thead>
<tr>
<th>Species</th>
<th>Author</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canthigaster margaritata</td>
<td>(Rüppell, 1826)</td>
<td>Indian Ocean, including Gulf of Aden</td>
</tr>
<tr>
<td>Canthigaster petersii</td>
<td>(Bianconi, 1854)</td>
<td></td>
</tr>
</tbody>
</table>

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2. Initially misidentified as *I. melanopus*; Randall *et al.* (in press)
4. Randall *et al.* (2013)
5. Randall (2005)
Table 2 Phylogeographic studies comparing Red Sea (RS) and Indian Ocean (IO) populations. Species, DNA fragment analysed, $\Phi_{ST}$ 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>DNA fragment</th>
<th>$\Phi_{ST}$, $F_{ST}$ or % divergence</th>
<th>Reciprocally monophyletic</th>
<th>Source of tissue samples</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lutjanus kasmira</em> (bluestripe snapper)</td>
<td>COI, Cyt b</td>
<td>$F_{ST} = 0.05$ (1 of 6)</td>
<td>no</td>
<td>RS: Thuwal and Al Lith (KSA) IO: Diego Garcia, Seychelles, Sodwana Bay (South Africa)</td>
<td>DiBattista et al., 2013</td>
</tr>
<tr>
<td><em>Halichoeres hortulanus</em> (checkerboard wrasse)</td>
<td>COI, Cyt b</td>
<td>$F_{ST} = 0.07-0.12$ (2 of 4)</td>
<td>no</td>
<td>RS: Thuwal and Al Lith (KSA) IO: Diego Garcia, Seychelles</td>
<td>DiBattista et al., 2013</td>
</tr>
<tr>
<td><em>Cephalopholis argus</em> (peacock hind)</td>
<td>COI, Cyt b</td>
<td>$F_{ST} = 0.20-0.45$ (5 of 6)</td>
<td>no</td>
<td>RS: Thuwal and Al Lith (KSA) IO: Al Hallaniyats (Oman), Diego Garcia, Seychelles</td>
<td>DiBattista et al., 2013</td>
</tr>
<tr>
<td><em>Acanthurus nigrofuscus</em> (brown surgeonfish)</td>
<td>COI, Cyt b</td>
<td>$F_{ST} = 0.18-0.28$ (4 of 4)</td>
<td>no</td>
<td>RS: Thuwal and Al Lith (KSA) IO: Diego Garcia, Seychelles</td>
<td>DiBattista et al., 2013</td>
</tr>
<tr>
<td><em>Chaetodon auriga</em> (threadfin butterflyfish)</td>
<td>COI, Cyt b</td>
<td>$F_{ST} = 0.17-0.23$ (4 of 4)</td>
<td>no</td>
<td>RS: Thuwal and Al Lith (KSA) IO: Diego Garcia, Seychelles</td>
<td>DiBattista et al., 2013, in press B</td>
</tr>
<tr>
<td><em>Neoniphon sammara</em> (Sammaran squirrelfish)</td>
<td>COI, Cyt b</td>
<td>$F_{ST} = 0.12-0.16$ (4 of 4)</td>
<td>no</td>
<td>RS: Thuwal and Al Lith (KSA) IO: Diego Garcia, Seychelles</td>
<td>DiBattista et al., 2013</td>
</tr>
<tr>
<td><em>Scylla serrata</em> (mud crab)</td>
<td>COI</td>
<td>$F_{ST} = 0.42-1.0$ (6 of 6)</td>
<td>yes</td>
<td>RS: Jeddah (KSA) IO: Kenya, Zanzibar, Madagascar, Mauritius, South Africa</td>
<td>Frantini et al., 2002; Gopurenko et al., 1999</td>
</tr>
<tr>
<td><em>Pygoplites diacanthus</em> (regal angelfish)</td>
<td>COI, Cyt b</td>
<td>$F_{ST} = 0.65-0.67$ (2 of 2)</td>
<td>yes</td>
<td>RS: Thuwal and Al Lith (KSA) IO: Diego Garcia</td>
<td>DiBattista et al., 2013</td>
</tr>
<tr>
<td><em>Leucetta chagosensis</em> (lemon sponge)</td>
<td>ITS/18S, ATPSb</td>
<td>0.7% &lt;1.0%[^a]</td>
<td>yes</td>
<td>RS: Sinai Peninsula (Egypt) IO: Maldives</td>
<td>Wörheide et al., 2008</td>
</tr>
<tr>
<td><em>Tridacna maxima</em> (giant clam)</td>
<td>COI</td>
<td>2.5%*</td>
<td>yes</td>
<td>RS: not specified IO: Indonesia</td>
<td>Nuryanto &amp; Kochzius, 2009</td>
</tr>
<tr>
<td>Species</td>
<td>Genotype</td>
<td>Φ_{ST}</td>
<td>RS</td>
<td>IO</td>
<td>Reference</td>
</tr>
<tr>
<td>----------------------------------------------</td>
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<td>------------------------------------------------</td>
</tr>
<tr>
<td><em>Acanthaster planci</em> (crown-of-thorns starfish)</td>
<td>COI</td>
<td>8.80%</td>
<td>yes</td>
<td></td>
<td><em>Vogler et al., 2008</em></td>
</tr>
<tr>
<td><em>Mulloidichthys flavolineatus</em> (yellowstripe goatfish)</td>
<td>Cyt b</td>
<td>Φ_{ST} = 0.04-0.11 (1 of 3)</td>
<td>no</td>
<td></td>
<td><em>Fernandez-Silva et al., in press</em></td>
</tr>
<tr>
<td><em>Coris cuvieri</em> (African coris)</td>
<td>COI</td>
<td>Φ_{ST} = 0.04-0.11 (1 of 3)</td>
<td>no</td>
<td></td>
<td><em>P. Ahti, pers. comm.</em></td>
</tr>
<tr>
<td><em>Carcharhinus limbatus</em> (blacktip shark)</td>
<td>control</td>
<td>F_{ST} = 0.003 (p = 0.24)</td>
<td>no</td>
<td></td>
<td><em>Spaet et al., 2015</em></td>
</tr>
<tr>
<td><em>Carcharhinus sorrah</em> (spot-tail shark)</td>
<td>region</td>
<td>F_{ST} = 0.006 (p = 0.10)</td>
<td>no</td>
<td></td>
<td><em>Spaet et al., 2015</em></td>
</tr>
<tr>
<td><em>Rhizoprionodon acutus</em> (milk shark)</td>
<td>control</td>
<td>F_{ST} = 0.06 (p = 0.58)</td>
<td>no</td>
<td></td>
<td><em>Spaet et al., 2015</em></td>
</tr>
<tr>
<td><em>Sphyrna lewini</em> (scalloped hammerhead)</td>
<td>region</td>
<td>F_{ST} = 0.01 (p = 0.58)</td>
<td>no</td>
<td></td>
<td><em>Spaet et al., 2015</em></td>
</tr>
<tr>
<td><em>Cephalopholis hemistiktos</em> (yellowfin hind)</td>
<td>control</td>
<td>F_{ST} = 0.04-0.11 (1 of 3)</td>
<td>yes for COI</td>
<td>no for S7</td>
<td><em>M. Priest, pers. comm.</em></td>
</tr>
<tr>
<td></td>
<td>S7</td>
<td>F_{ST} = 0.41 (10 of 15 for both)</td>
<td></td>
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<tr>
<td><em>Panulirus penicillatus</em> (pronghorn spiny lobster)</td>
<td>COI</td>
<td>Φ_{ST} = 0.74 (1 of 1)</td>
<td>yes</td>
<td></td>
<td><em>M. Iacchei, pers. comm.</em></td>
</tr>
</tbody>
</table>

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
FIGURE LEGENDS

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

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Sister species</th>
<th>Distribution of sister species</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Red Sea endemic</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>NARKIDAE (SLEEPER RAYS)</strong></td>
<td></td>
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<tr>
<td>Heteronarce bentuviai (Baranes &amp; Randall, 1989)</td>
<td>Heteronarce garmani Regan, 1921</td>
<td>Gulf of Aden to South Africa</td>
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<tr>
<td><strong>TORPEDINIDAE (TORPEDOS)</strong></td>
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<tr>
<td>Torpedo alexandrinsis Mazhar, 1987</td>
<td>Torpedo adenensis Carvalho, Stehmen &amp; Manilo, 2002</td>
<td>Gulf of Aden</td>
</tr>
<tr>
<td><strong>MURAENIDAE (MORAY EELS)</strong></td>
<td></td>
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<tr>
<td>Gymnothorax corallinus (Klunzinger, 1871)</td>
<td>Gymnothorax buroensis (Bleeker, 1857)</td>
<td>Indo-Pacific</td>
</tr>
<tr>
<td>Uropterygius golanii McCosker &amp; Smith, 1997</td>
<td>Uropterygius xenodontus McCosker &amp; Smith, 1997</td>
<td>W Pacific</td>
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<tr>
<td><strong>CONGRIDAE (CONGER and GARDEN EELS)</strong></td>
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<tr>
<td>Gorgasia silmeri Klauserwitz, 1962</td>
<td>Gorgasia naeoepeaeus (Böhle, 1951)</td>
<td>W Papua and Philippines</td>
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<tr>
<td><strong>CLUPEIDAE (HERRINGS, SPRATS, &amp; SARDINES)</strong></td>
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<tr>
<td>Herklotsichthys punctatus (Rüppell, 1837)</td>
<td>Herklotsichthys lossei Wongratana, 1983</td>
<td>Arabian Gulf</td>
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<td><strong>SYNODONTIDAE (LIZARDFISHES)</strong></td>
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<tr>
<td>Synodus randalli Cressey, 1981</td>
<td>Synodus fasciapelicus Randall, 2009</td>
<td>Indonesia and Philippines</td>
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<td><strong>BATCHROIDIDAE (TOADFISHES)</strong></td>
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<tr>
<td>Barchatus cirrhosa (Klunzinger, 1871)</td>
<td>Barchatus indicus Greenfield, 2014</td>
<td>Gulf of Aden (N Somalia)</td>
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<td><strong>ATHERINIDAE (SILVERSIDES)</strong></td>
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<tr>
<td>Atherinomorus forskalii (Forster, 1801)</td>
<td>Atherinomorus lacunosus (Schneider, 1801)</td>
<td>Indo-Pacific (sympatric in C Red Sea)</td>
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<tr>
<td>Hypoherina golanii Sasaki &amp; Kimura, 2012</td>
<td>Hypoherina klunzingeri Smith, 1965</td>
<td>W Indian Ocean (E Somalia) to South Africa</td>
</tr>
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<td><strong>HOLOCENTRIDAE (SOLDIERFISHES &amp; SQUIRRELFISHES)</strong></td>
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<tr>
<td>Sargocentron marisrubri Randal, Guenzé &amp; Diamant, 1989</td>
<td>Sargocentron melanospilos Bleeker, 1858</td>
<td>Indo-West Pacific</td>
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<td><strong>SYNGNATHIDAE (PIPEFISHES &amp; SEAHORSES)</strong></td>
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<td>Corythoichthys cf nigripexus</td>
<td>Corythoichthys nigripexus Herald, 1953</td>
<td>W Pacific</td>
</tr>
<tr>
<td>Corythoichthys cf schultzi</td>
<td>Corythoichthys schultzi Herald, 1953</td>
<td>W Pacific</td>
</tr>
<tr>
<td>Micrognathus brevirostris (Rüppell, 1838)</td>
<td>Micrognathus pygmaeus Fritzche, 1981</td>
<td>Indo-West Pacific</td>
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<tr>
<td><strong>SCORPAENIDAE (SCORPIONFISHES)</strong></td>
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<tr>
<td>Scorpaenodes steinitzi Klausewitz &amp; Fröiland, 1970</td>
<td>Scorpaenodes parvipinnis (Garrett, 1864)</td>
<td>Indo-Pacific</td>
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<td><strong>APLOACTINIDAE (VELVETFISHES)</strong></td>
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<td>Ptarmus gallus Kossmann &amp; Rauber, 1877</td>
<td>Ptarmus jubatus (Smith, 1935)</td>
<td>E Africa to Natal, South Africa</td>
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<td><strong>SERRANOIDEA (SEABASSES)</strong></td>
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<tr>
<td>Plectropomus marisrubri Randall &amp; Hoese, 1986</td>
<td>Plectropomus pessuliferus (Fowler, 1904)</td>
<td>Indian Ocean and Fiji</td>
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<tr>
<td>Pseudanthias taeniatas (Klunzinger, 1855)</td>
<td>Pseudanthias townsendi (Boulenger, 1897)</td>
<td>Gulf of Aden to Gulf of Oman</td>
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<td>Pseudogramma megamycterum Randall &amp; Baldwin, 1997</td>
<td>Pseudogramma astigmum Randall &amp; Baldwin, 1997</td>
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<td>Family</td>
<td>Genus</td>
<td>Species</td>
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<td><strong>PSEUDOCHROMIDAE</strong></td>
<td><em>Pseudochromis</em> fridmani</td>
<td>Klausewitz, 1968</td>
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<td><em>Pseudochromis</em> pesi</td>
<td>Lubbock, 1975</td>
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<td><strong>PLESIOPIDAE</strong></td>
<td><em>Acanthoplesiops</em> cappuccino</td>
<td>Gill, Bogorodsky &amp; Mal, 2013</td>
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<td><em>Acanthoplesiops</em> indicus</td>
<td>(Day, 1888)</td>
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<td><strong>OSTEOCHROMIDAE</strong></td>
<td><em>Stalix</em> davidsheni</td>
<td>Klausewitz, 1985</td>
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<td><strong>APOGONIDAE</strong></td>
<td><em>Cheilodipterus</em> pygmaeus</td>
<td>Gon, 1993</td>
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<td><em>Taeniamia</em> lineolata</td>
<td>Cuvier, 1828</td>
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<td><strong>MALACANTHIDAE</strong></td>
<td><em>Hoplolatilus</em> oreni</td>
<td>Clark &amp; Ben-Tuvia, 1973</td>
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<td><strong>CAESIONIDAE</strong></td>
<td><em>Caesio</em> suevica</td>
<td>Klunzinger, 1884</td>
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<td><strong>SPARIDAE</strong></td>
<td><em>Argyrops</em> megalomatus</td>
<td>Klunzinger, 1870</td>
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<td><em>Diplodus</em> noct</td>
<td>Valenciennes, 1830</td>
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<td><strong>PEMPHERIDAE</strong></td>
<td><em>Parapriacanthus</em> guentheri</td>
<td>Klunzinger, 1871</td>
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<td><strong>POMACENTRIDEA</strong></td>
<td><em>Chromis</em> dimidiata</td>
<td>(Klunzinger, 1871)</td>
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<td><em>Chromis</em> pelloura</td>
<td>Randall &amp; Allen, 1982</td>
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<td><em>Pomacentrus</em> albidus</td>
<td>Baschieri-Salvadori, 1955</td>
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<td><strong>LABRIDAE</strong></td>
<td><em>Chlorurus</em> gibbus</td>
<td>Rüppell, 1829</td>
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<td><em>Cirrhilabrus</em> latteus</td>
<td>Springer &amp; Randall, 1974</td>
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<td></td>
<td><em>Inimius</em> sp cf balwini²</td>
<td>Jordan &amp; Evermann, 1903</td>
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<td><em>Macropharyngodon</em> marisrubri</td>
<td>Randall, 1978</td>
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<td><em>Thalassoma</em> ruepellii</td>
<td>Klunzinger, 1828</td>
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<td><strong>TRICHONOTIDAE</strong></td>
<td><em>Limnichthys</em> marisrubri</td>
<td>Fricke &amp; Golani, 2012</td>
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<td><strong>TRIPTERYGIIDAE</strong></td>
<td><em>Enneapterygius</em> altipinnis</td>
<td>Clark, 1980</td>
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<td><strong>BLENNIIDAE</strong></td>
<td><em>Alticus</em> magnusi</td>
<td>(Klausewitz, 1964)</td>
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<td><em>Alticus</em> kirki</td>
<td>Günther, 1868</td>
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<td><em>Entomacrodus</em> solus</td>
<td>Williams &amp; Bogorodsky, 2010</td>
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<td><em>Istiblennius</em> rivulatus</td>
<td>Rüppell 1830</td>
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<td><strong>GOBIIDAE</strong></td>
<td><em>Oxyurichthys</em> petersi</td>
<td>Klunzinger, 1871</td>
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</table>
**Tomiyamichthys dorsostigma** Bogorodsky, Kovacic & Randall, 2011

**Tomiyamichthys smithi** (Chen & Fang, 2003)

**Evoxymetopon moricheni** Fricke, Golani & Appelbaum-Golani 2014

**Evoxymetopon taeniatus** Gill, 1863

**Oxymonacanthus halii** Marshall, 1952

**Oxymonacanthus longirostris** (Bloch & Schneider, 1801)

**Paraluteres argat** Clark & Gohar, 1953

**Paraluteres n sp**

**Thamnoconus erythraensis** Bauchot & Mauge, 1978

**Thamnoconus modestoides** (Barnard, 1927)

**Arothron diadematus** (Rüppell, 1829)

**Arothron nigropunctatus** (Bloch & Schneider, 1801)

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**Indo-Pacific, excluding Arabian Peninsula

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**Evoxymetopon taeniatus** Gill, 1863

**Indo-Pacific, excluding Arabian Peninsula

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**Evoxymetopon taeniatus** Gill, 1863

**Indo-Pacific, excluding Arabian Peninsula

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**Oxymonacanthus longirostris** (Bloch & Schneider, 1801)

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**Thamnoconus modestoides** (Barnard, 1927)

**Arothron diadematus** (Rüppell, 1829)

**Arothron nigropunctatus** (Bloch & Schneider, 1801)

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**Evoxymetopon taeniatus** Gill, 1863
Cheilinus quinquecinctus Rüppell, 1835
Cheilinus fasciatus (Bloch, 1791) Indo-Pacific
Coris variegata (Rüppell, 1835)
Coris baumani (Bleeker, 1856) Indian Ocean
Gomphosus caeruleus klaunzingeri Klausewitz, 1962
Gomphosus caeruleus caeruleus Lacepede, 1801 Indian Ocean
Hemigymnus sexfasciatus Rüppell, 1835
Hemigymnus fasciatus (Bloch, 1792) Indo-West Pacific
TRICHONOTIDAE (SAND-DIVERS)
Trichonotus nikii Clark & Schmidt, 1966
Trichonotus marleyi (Smith, 1936) W Indian Ocean
BLENNIIDAE (BLENNIES)
Antennablennius n sp
Antennablennius variopunctatus (Jatzow & Lenz, 1898) W Indian Ocean, including Gulf of Aden
SIGANIDAE (RABBITFISHES/SPINEFOOTS)
Siganus rivulatus (Forsskål, 1775) Siganus sutor (Valenciennes, 1835) Indian Ocean, including Gulf of Aden
Siganus stellatus (Forsskål, 1775) Siganus laqueus von Bonde, 1934 Indian Ocean
ACANTHURIDAE (SURGEONFISHES & UNICORNFISHES)
Acanthurus gahhm Forsskål, 1775 Acanthus nigracauda Duncker & Mohr, 1929 Indo-Pacific
ACANTHURIDAE (SURGEONFISHES & UNICORNFISHES)
Sufflamen albicaudatum (Rüppell, 1829) Sufflamen chrysopterum (Bloch & Schneider, 1801) Indo-Pacific
TETRAODONTIDAE (PUFFERFISH)
Canthigaster margaritata (Rüppell, 1826) Canthigaster petersii (Bianconi, 1854) 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).
On the origin of endemic species in the Red Sea


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)
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, 223367328, 223367342, 326456893, 325071210, 326456499, 223367568, 223367578, 223367582, 326456511, 223367648, 223367652, 171673956, 381279420, 386268750, 326456691, 223368376, 223368392, 375586076, 326457001, 375586316, 326456729, 375586328, 326456747, 322402289, 326456761, 326456771, 223368698, 326456785, 400219896, 326456787, 328486924, 223368714, 400219880, 223368734, 326456835, 326456837, 326456849, 326456863, 393757268, 386268864, 381279982, 386366917, 381279986, 386366923, 326456895, 326456915, 326456917, 386268880, 326456929, 386366939, 386268884 (includes multiple studies)