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RRH: Contemporary patterns of Red Sea endemism

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

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ABSTRACT

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

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

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

Results Within the Red Sea, we recorded 346 zooxanthellate and azooxanthellate scleractinian coral species of which 19 are endemic (5.5%). Currently 635 species of polychaetes, 211 echinoderms and 79 ascidians have been documented, with endemism rates of 12.6%, 8.1% and 16.5%, respectively. A preliminary compilation of 231 species of crustaceans and 137 species of molluscs include 10.0% and 6.6% endemism, respectively. We documented 1071 shallow fish species, with 12.9% endemic in the entire Red Sea and 14.1% endemic in the Red Sea and Gulf of Aden. Based on ecological survey data of endemic fishes, there were no major changes in species richness or abundance across 1100 km of Saudi Arabian coastline.

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

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

INTRODUCTION

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

The Red Sea

The Red Sea extends 2270 km from 30° N in the Gulf of Suez to 12° N in the Gulf of Aden. Based on existing checklists, 320 zooxanthellate scleractinian corals (Veron *et al.,* 2009) and 1078 fish species (Golani & Bogorodsky, 2010) have been identified in this region, although these values are constantly being redefined. The Red Sea harbours one of the highest levels of endemism for marine organisms, with 14% for fishes (Randall, 1994), 15% for crabs (Guinot, 1966), up to 17% for echinoderms (Price, 1982; Campbell, 1987; Dafni, 2008) and as much as 10% for scleractinian corals (Hughes *et al.*, 2002). Endemism is even higher for some conspicuous taxa, for example reaching 50% in butterflyfishes (e.g. Roberts *et al.*, 1992). This endemic region extends to the Gulf of Aden for many species, and to Oman or Socotra for fewer species (Winterbottom, 1985; Randall, 1995; Kemp, 1998, 2000; Zajonz *et al.*, 2000).

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

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

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

Data limitation in the Red Sea and Arabian Peninsula

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

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

MATERIALS AND METHODS

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

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

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

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

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

Given our interest in Red Sea endemism, we compiled species presence-absence records from the seven Marine Ecoregions of the World (MEOWs) bordering the Arabian Peninsula (modified from Spalding *et al.*, 2007): 1) Gulf of Aqaba, 2) Red Sea, 3) Gulf of Aden, 4) Socotra, 5) Southern Oman, 6) Gulf of Oman and Pakistan and 7) Arabian Gulf (see Fig. 2). In cases where data is insufficient to separate the Gulf of Aqaba or Socotra into MEOWs, they were combined with the Red Sea or Gulf of Aden, respectively. Taxonomic groups that are data deficient for an entire MEOW are omitted from regional consideration. The MEOW results are visualized using ArcGIS *vers.* 10.2 (ESRI, 2014).

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

Ecological survey of fish densities

Based on reef fish densities (May Roberts, unpub. data) we assess the abundance of 33 Red Sea endemics on 45 reefs across 1100 km of Saudi Arabian coastline surveyed between 2008 and 2011. Reefs are grouped into 10 regions from Al Wajh (26.8° N) to Ablo (18.6° N). Four replicate belt transects were made at each of four depths between the reef crest and 10 m. Each belt transect was 50 m x 4 m with the exception of smaller species (e.g. damselfishes and blennies), which were surveyed on a 50 x 1 or 2 m transect. One-way ANOVA was used to resolve latitudinal trends in mean species richness of endemics**.** Total abundance of these fishes was summed per reef and fourth root transformed to balance the effect of very abundant species, such as *Chromis dimidiata*. All statistical analyses use the vegan package in R (Oksanen *et al.*, 2014).

RESULTS

Red Sea endemism based on MEOWs of the Arabian Peninsula

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

Fish – The Red Sea hosts 1071 recorded fish species (versus 1760 in the entire Arabian Peninsula region) of which 138 (12.9%) are endemic to the Red Sea and 189 (14.1%) are endemic to the Red Sea and Gulf of Aden (Fig. 2b). Only 1.0%, 1.7% and 2.2% of Red Sea fishes have ranges extending to southern Oman, the Gulf of Oman or the Arabian Gulf, respectively, but no further. By comparison, Eschmeyer *et al.* (2010) recorded 1188 Red Sea fish species, including 159 endemics, resulting in a comparable endemism rate of 13.6%. Goren & Dor (1994) listed 1248 species from the Red Sea. Both of these estimates, however, include all fish species as opposed to our stricter criteria, and may include unverifiable records for the latter. Similar to Fricke *et al.* (2014), we note that some of the endemic fish fauna are restricted to the Gulf of Aqaba (4.1%). This indicates an effective ecological barrier separating the Gulf of Aqaba from the rest of the Red Sea (also see Klausewitz, 1989; Sheppard *et al.*, 1992), possibly due to higher salinity in this region. This pattern may also be explained by sampling bias because 87.5% of the Gulf of Aqaba endemics are from a single collection. We also note that even though the Gulf of Aden or Socotra are not considered centres of endemism (0.7% and 1.4%, respectively), the former has the second highest level of species richness in the study (Fig. 2b), and the latter appears to be a hotspot for the mixing of Red Sea and Indian Ocean fauna (see DiBattista *et al.*, 2015).

Non-coral invertebrates – Echinoderms are among the best studied invertebrates, with 211 species recorded from the Red Sea. Of these species, 17 (8.1%) are known only from the Red Sea and 21 (10.0%) from the Red Sea to Gulf of Aden. Currently 79 ascidian species are documented from the Red Sea, with 13 (16.5%) endemic, although the rest of the Arabian Peninsula remains understudied. Among 635 polychaete species recorded from the Red Sea, 80 (12.6%) are endemic and 92 (14.5%) are Red Sea to Gulf of Aden endemic. An incomplete compilation of decapods shows 231 Red Sea species, including 23 (10.0%) endemic to the Red Sea and 31 (13.4%) endemic to the Red Sea to Gulf of Aden. Although the Red Sea molluscan fauna is represented in museum collections and field guides, sampling of the Arabian Peninsula and northern Somalia is limited, and does not allow us to assess Red Sea endemism with confidence. Based on the molluscs considered here, we predict 6.0% Red Sea endemism among species that occur within the Arabian Peninsula region. This figure would be higher if the Gulf of Aden were treated in the same biogeographical unit as the Red Sea. Exacerbating this lack of general knowledge is the prevalence of cryptic species among marine invertebrates, especially in groups that do not use visual systems for mate recognition (Knowlton, 1993). Integrative studies that include field and genetic approaches consistently reveal higher levels of endemism. For example, 36 species (38%) of sea cucumbers from the Red Sea to Gulf of Aden are endemic to the area based on DNA barcodes (G. Paulay, unpub. data). For molluscs, molecular data have identified new species (e.g. nudibranchs; Jörger *et al.*, 2012) and the resurrection of a historically described species (e.g. Huber & Eschner, 2011).

Red Sea endemism for reef fish

Among reef fishes, the proportion of Red Sea endemics per family varies from 0 to 100%. The 14 families with > 50% endemism have seven or fewer Red Sea species. Among families with 10 or more Red Sea species, five of these have endemism values > 25% (Callionymidae, Pseudochromidae, Tripterygiidae, Monacanthidae and Tetraodontidae). When we consider the Red Sea and Gulf of Aden combined, this value increases for several families or sub-families including the Pseudochromidae (from 33.3% to 64.3%), Apogonidae (15.3% to 25.3%) and Scarinae (11.1% to 32.0%). Endemism is apparent for the Chaetodontidae only when the Red Sea and Gulf of Aden region are considered together (0% to 12.0%, but 32.0% for the entire Arabian Peninsula region), which contradicts the 50% endemism reported in Roberts *et al.* (1992). The variable proportion of endemic species across taxonomic groups indicates that the evolutionary processes have affected groups of reef fish differently. These results must be interpreted with caution given that presence-absence data may be biased for highly dispersive species that appear in locations where they are functionally absent.

Reef fish density data

Based on 33 Red Sea to Gulf of Aden endemic reef fish species, there were no major changes in species richness or abundance among 10 sub-regions (Figs 3 and 4). One-way ANOVA analyses revealed no consistent significant change with latitude or direction across our survey area. Indeed, out of 99 comparisons between northern, central and southern regions for all species, only 16 were significant at $P < 0.05$. This trend was most apparent in the numerically dominant species (e.g. *Chromis dimidiata*, *Thalassoma rueppellii*, *Pseudochromis fridmani*). Such findings contradict previous evidence for biogeographical barriers in the central Red Sea (Khalaf & Kochzius, 2002; Spalding *et al.*, 2007; but see Kulbicki *et al.*, 2013). This central delineation may instead represent an "average" boundary for many of the species that show distributional shifts.

DISCUSSION

The Red Sea hosts a distinct coral reef fauna with consistently high endemism for shallow water organisms (> 10% in fishes, annelids, arthropods and chordates). Looking across the region, levels of both biodiversity and endemism are highest in the Red Sea for fishes and scleractinian corals (Fig. 2). The pattern is more complicated for the non-coral invertebrates, with a trend of highest diversity and endemism in the Red Sea, Gulf of Oman and Arabian Gulf (Fig. 2). This confirms the status of the Red Sea as a significant region of endemism for coral reef biota at the western periphery of the Indo-Pacific. Reef fishes provide the most complete information for investigating the processes that underlie patterns of endemism.

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

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

a. Environmental gradients

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

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

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

b. Species specific differences in dispersal and colonisation

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

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

c. Available resources and recruitment

Recruitment failure is a potentially important driver of the localized distribution and abundance patterns of Red Sea or regional endemics. For example, distributions may be extremely localized in Gulf of Aden and Oman endemic parrotfishes, such as *Scarus arabicus* and *Scarus zufar,* whereas other regional endemics (*Scarus ferrugineus*) extend through the entire environmental gradient of the Red Sea and northern Arabian Sea (Choat *et al.*, 2012). It is unlikely that dispersal capacity is the limiting factor in these species distributions. Testing of recruitment failure hypotheses requires a capacity to identify recruitment habitats and the age structure and condition of endemic species over their distributional range. Genomic and stable isotope analyses provide options to resolve ontogenetic interactions between the relevant species and suitable habitats.

d. Phylogenetic community structure in the Red Sea

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

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

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

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

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

Within the Red Sea, the narrow (6 km) and shallow (242 to 270 m) Straits of Tiran between the Gulf of Aqaba and Red Sea proper can also act as a physical barrier. The deep and narrow fjord-like Gulf of Aqaba is 180 km long and is 25 km at its widest point, and the depth can reach 1800 m but averages 800 m. Hot and dry desert flank the semi-enclosed basin, which result in a high evaporation rate, high salinity (41 ppt) and a thermohaline circulation that drives water exchange with the Red Sea (Reiss & Hottinger, 1984). Water residence time in the upper 300 m of the Gulf of Aqaba varies from only a few months up to two years. The amount of Red Sea water reaching the northern tip of the Gulf of Aqaba is therefore estimated to be only 1% of that at the Straits of Tiran (Wolf-Vecht *et al.*, 1992).

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

Conclusion and future perspectives

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

Molecular tools are proving useful for the identification of cryptic lineages in endemism hotspots such as Hawaiʻi (Randall *et al.*, 2011), the Marquesas Islands (Szabo *et al.*, 2014) and the Red Sea (Randall & DiBattista, 2013). In the Red Sea, only 10% of the new species descriptions listed in Table 1 were corroborated using molecular data, but this includes three new species of fish (DiBattista *et al.*, 2012; Herler *et al.*, 2013; Koeda *et al.*, 2014) and a coral (Terraneo *et al.*, 2014). As molecular tools are applied more broadly, endemism in the region will continue to rise. But certainly broadscale sampling is necessary to discover the cryptic evolutionary lineages hidden in species previously thought to be widespread (e.g. Williams & Reid, 2004; Vogler *et al.*, 2008; Williams *et al.*, 2011, 2012; Hoareau *et al.*, 2013; Postaire *et al.*, 2014). Undersampled areas include the Andaman Sea, Bangladesh, India, Myanmar, Somalia and much of the Red Sea (particularly Eritrea and Yemen). This deficiency is partly due to long-term political instability, although some regions like Western Australia are politically stable but undersampled (e.g. Poore *et al.*, 2014).

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

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

Our primary argument for this ecological filter follows Keith *et al.* (2015): what appears to be geographic barriers are defined by traits indicative of establishment (i.e. habitat switching) and persistence but not necessarily dispersal (also see Keith *et al.*, 2011; Luiz *et al.*, 2013). This hypothesis predicts that while a number of species may disperse beyond the southern boundary of the Red Sea, the capacity to establish populations reflects the extent to which both phenotypic plasticity and genetic endowment of the potential colonisers allows successful settlement, post settlement survival and recruitment to novel environments. Individuals successfully colonising reef habitats ecologically distinct from that of the parental population would be those with the capacity to respond to the novel selective environments. Genetic analyses designed to differentiate between drift and natural selection (i.e. RAD-seq methods; Willette *et al.*, 2014) in driving differences between parental and colonising populations would be an appropriate research design. The prediction is that species that successfully recruit beyond the distributional boundaries of the parental population will display strong signatures of selection. A critical feature would be to determine if such colonising populations represent an independent evolutionary trajectory driven by divergent selection in the environment encountered by the colonists. This is the approach taken by Gaither *et al.* (2015) in a comparative analysis of Indo-Pacific surgeonfish that successfully colonised the divergent reef environment of the Marquesas Islands, and would therefore be appropriate to apply more broadly to other reef fauna.

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SUPPORTING INFORMATION

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

Appendix S1

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

Appendix S2

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

Appendix S3

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

Biosketch

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

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

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Table 1 Valid scleractinian coral, fish and non-coral invertebrate endemic species described in the Red Sea from 2000 to 2014.

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

Tomiyamichthys dorsostigma	Bogorodsky, Kovacic & Randall, 2011
Upeneus davidaromi	Golani, 2001
Uranoscopus rosette	Randall & Arnold, 2012
Vanderhorstia opercularis	Randall, 2007
Annelida	
Harmothoe marerubrum	Wehe, 2006
Lepidonotus polae	Wehe, 2006
Parahalosydnopsis arabica	Wehe, 2006
Arthropoda	
Charybdis omanensis septentrionalis	Türkay & Spiridonov, 2006
Ethusa thieli	Spiridonov & Türkay, 2007
Petrolisthes aegyptiacus	Werding & Hiller, 2007
Cnidarians	
Acropora parapharaonis	Veron, 2000
Anacropora spumosa	Veron, Turak & DeVantier, 2000
Cyphastrea hexasepta	Veron, DeVantier & Turak, 2000
Echinopora irregularis	Veron, Turak & DeVantier, 2000
Echinopora tiranensis	Veron, Turak & DeVantier, 2000
Goniopora sultani	Veron, DeVantier & Turak, 2000
Montipora aspergillus	Veron, DeVantier & Turak, 2000
Montipora echinata	Veron, DeVantier & Turak, 2000
Montipora hemispherica	Veron, 2000
Montipora pachytuberculata	Veron, DeVantier & Turak, 2000
Montipora saudii	Turak, DeVantier & Veron, 2000
Pachyseris inattesa	Benzoni & Terraneo, 2014
Mollusca	
Turbo (Aspilaturbo) marisrubri	Kreipl & Alf, 2001
Tunicata	
Boltenia yossiloya	Shenkar & Lambert, 2010
Botryllus eilatensis	Shenkar & Monniot, 2006

FIGURE LEGENDS

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

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

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

25th percentiles, respectively. Vertical lines extend to the 95th (upper line) and 5th (lower line) percentiles.

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

Appendix S1 References for updated checklist of corals from the Arabian Peninsula region.

The coral list (hermatypic and ahermatypic) included updated taxonomic information from the Red Sea region by Claereboudt & Al-Amri (2004), Benzoni (2006), Benzoni & Stefani (2012), Benzoni *et al.,* (2012, 2014), Terraneo *et al.,* (2014), Huang *et al.,* (2014a,b) and Arrigoni *et al.,* (2015). Regional distribution of coral species was completed with observations from Coles *et al.,* (1996) and Pichon *et al.,* (2010). To confirm species endemism, presence outside the Arabian region was assessed using Wallace (1999) for most *Acropora* species, Cairns (2001) for Dendrophylliidae species and Veron (2000) for all other coral taxa.

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Appendix S2 References for updated checklist of shore fish from the Arabian Peninsula region.

Footnotes for Appendix S2 fish checklist:

1) *Carcharhinus humani* – recently distinguished from *C. dussumieri* and *C. sealei* (White & Weigmann, 2014).
2) *Manta* species – most Indo-Pacific records refer to *M. alfredi*, recently resurrected from the synonymy of *M. birostris* (Marshall *et al.,* 2009); Oman photo is of *M. alfredi* (Randall, 1995), by default we use that name for older records of *Manta* spp. in the region, but both species could be present in any location. The biogeographic implications are identical, regardless of which name is used.
3) *Gymnothorax undulatus* – Red Sea population distinct (D. Smith, National Museum of Natural History, pers. com.), likely endemic but further study needed.
4) *Ariosoma sanzoi* – locality in Red Sea not known (Randall *et al.,* in press).
5) *Gorgasia* cf *preclara* – based on a reliable sighting in an MPA over a 3-year period; this species has a very distinctive and unique color pattern, tends to be deeper-dwelling and in smaller groups than most other heterocongrines.
6) *Saurida* n. sp. Russell & Golani (in prep.) - formerly mis-identified as *S. undosquamis*; Red Sea endemic (J.E. Randall & S.V. Bogorodsky, Bishop Museum & Station of Naturalists, pers. com.)
7) *Platybelone argalus platyurus* – subspecies *argalus* is widespread in the Indo-Pacific.
8) *Oxyporhamphus convexus bruuni* – s. Red Sea; s. limit 8°N; replaced by subspecies *convexus* outside our region.

9) *Corythoichthys amplexus* – likely a species complex with potential Omani endemic based on distinctive color pattern (Kuiter, 2000).

10) *Corythoichthys* n. sp. cf *nigripectus* – a Red Sea endemic misidentified as *C. nigripectus*, a w. Pacific species (Kuiter, 2000; Allen & Erdmann, 2012).

11) *Corythoichthys* n. sp. cf *schultzi* – a Red Sea endemic misidentified as *C. schultzi*, a w. Pacific species (Kuiter, 2000).

12) *Minuos andriashevi* – marginally included in Socotra based on the ne. Somalia type locality of 11.7°N, 51.4°E; apparently erroneously reported as 11.7°S and corrected without comment in Manilo & Bogorodsky (2003).

13) *Pterygotrigla (Otohime) arabica* – identification provisional for Gulf of Aden specimen (W.J. Richards, NOAA Fisheries, pers. com.).

14) *Plectranthias intermedius* – 11°33.9'N, 52°54'E to 11°38'N, 52°52'E, Meteor sta. 102, 175-337 m; locality data also for *Grammatonotus lanceolatus*.

15) *Epinephelus melanostigma* – easternmost part of Yemen, technically outside the Gulf of Aden.

16) *Archamia* is monotypic, all other species traditionally placed in *Archamia* are now in *Taeniamia* (Mabuchi *et al.,* 2014).

17) *Ostorhinchus fasciatus* – misidentified as *Apogon quadrifasciatus* in most literature, true *O. fasciatus* might be confined to Australia (Fraser, 2005; Allen & Erdmann, 2012).

18) *Sillago* n. sp. cf *erythraea* – Red Sea population formerly misidentified as *S. erythraea*; endemic (J. E. Randall, Bishop Museum, pers. com.)

19) “*Alepes*” *kleinii* – formerly placed in *Alepes*, the species *kleinii* requires a new genus (J.E. Randall, Bishop Museum, pers. com.).

20) *Argyrops filamentosus* – Red Sea records based on misidentification of *A. megalommatus* a Red Sea endemic being re-described by Y. Iwatsuki (S. Bogorodsky & J.E. Randall, Station of Naturalists & Bishop Museum, pers. com.).

21) *Pempheris* n. spp. – four new species described in forthcoming volume on fishes of the western Indian Ocean (J. E. Randall, Bishop Museum, pers. com.).

22) *Pempheris flavicycla* – 2 subspecies, *flavicycla* in e. Gulf of Aden, *marisrubri* in Djibouti.

23) *Plectroglyphododon leucozonus cingulus* – subspecies *leucozonus* is widespread Indo-Pacific.

24) *Chrysiptera unimaculatus* – WIO population likely distinct from Pacific, genetic studies are needed (Kuiter & Tonozuka, 2001).

25) *Bodianus* cf *trilineatus* – formerly misidentified as *B. trilineatus*; Red Sea material is either *B. rubrisos* or possibly new (J.E. Randall, Bishop Museum, pers. com.).

26) *Pteragogus* n. sp. cf *pelycus* – Red Sea endemic formerly misidentified as *P. pelycus* (J.E. Randall, Bishop Museum, pers. com.).

27) *Iniistius* n. sp. cf *melanopus* – Red Sea endemic formerly misidentified as *I. melanopus* (J.E. Randall, Bishop Museum, pers. com.).

28) *Suezichthys caudovittatus* – ranges to ne Somalia only slightly south of the Horn of Africa.

29) *Parapercis simulata* – Safaga, Egypt only in Red Sea; 11.0°N off Somalia.

30) *Parapercis somaliensi*s – Gulf of Aqaba in 350 m (Baranes & Golani, 1993) and Cape Gwardafuy, Somalia in 50 to 70 m. Records of *P. somaliensis* outside the region are based on misidentifications of other closely related species.

31) *Antennablennius* n. sp. – J.T. Williams & S.V. Bogorodsky (in prep.).

32) *Amblyeleotris sungami* – visual survey record from Glorieuse Island requires verification, likely a misidentification.

33) *Amblyeleotris triguttata* – photographed in Kenya by R. Myers.

34) *Schindleria* unid. sp. – tentatively regarded as a monotypic family; outside the region, three species have been named but many more are indicated on DNA (Abu El-Regal & Kon, 2008).

35) *Zebrasoma xanthurum* – reports from the Maldives and Sri Lanka are considered to be based on non-reproducing waifs (Kuiter, 1998; Randall, 2001).

36) *Sufflamen chrysopterum* – Red Sea records (visual and photographic) are very sporadic and may represent waifs, if not mis-identifications of the very similar geminate sister species *S. albicaudatum*.

Notes:

The following species that may occur marginally south of Cape Gwardafuy (Horn of Africa) but north of about 8 to 10°S are here considered to be Greater Arabian Peninsula endemics and within either the Gulf of Aden or Socotra Archipelago areas:

Oxyporhamphus convexus bruuni
Minuos andriashevi
Plectranthias intermedius
Cephalopholis hemistiktos

Epinephelus gabrielae
Epinephelus stolizkae
Grammatonotus lanceolatus
Cirrhitichthys calliurus
Pseudochromis nigrovittatus
Pomadasys taeniatus
Chromis flavaxilla
Neopomacentrus xanthurus
Suezichthys caudovittata
Scarus fuscopurpurea
Parapercis simulata
Parapercis somaliensis
Callionymus margaritae

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