For the virtual issue, "Red Sea and Western Indian Ocean Biogeography"

Red Sea and Western Indian Ocean Biogeography

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EXECUTIVE SUMMARY

The Red Sea and Western Indian Ocean (WIO) represent iconic and strategic locations in our tropical oceans, and yet few studies address the origins, maintenance, and distribution of marine fauna of these locations. This virtual issue of the *Journal of Biogeography* (JBI) serves to illustrate the biogeographical advances in these habitats at the periphery of the vast Indo-Pacific region with an editorial introduction, 14 contributions from an international workshop, and a set of 24 papers previously published in JBI. The selection includes a number of influential research studies that present novel data, those that apply methods to synthesize general patterns, and some that utilize newer genetic methods to infer patterns of the evolutionary history of coral reef ecosystems within this region. Several key themes emerge from this collection of papers:

- There appears to be no single, repeated, or uniform explanation for the region's evolutionary history; the evolutionary path for each species appeared to be unique. It does not appear that there was a single, all-encompassing vicariance event that shaped the evolution of regional species.

- Many cryptic species have been revealed by molecular work, both in groups with ambiguous taxonomy and within the best-characterised groups. This approach clarifies patterns of regional endemism.

- Many of the previously defined or postulated biogeographical regions mirror genetic boundaries, but there are important exceptions for some species.

- There is substantial potential for regional species to serve as model study systems to address topics such as the impacts of climate change on biogeography; understanding the connections among generation of biodiversity, evolution, and the environment; and elucidating

mechanisms that maintain biodiversity and/or promote speciation in the 'marginal' seas of the WIO.

EDITORIAL

"*A moment later I was overboard. Now, in the bright midday light, the coral looked even more brilliant and colourful than the night before. Directly below me was a peach-coloured bush; from Klunzinger's writings I immediately recognized it as a cup star coral. There were violet-hued bunches of pistil coral, and between them I spotted a vermilion coenopsammia. There were luxuriant growths of dozens of species of star coral in the shape of brightly coloured balloons and blisters; snow-white thistle coral filled the hollows and staghorn coral extended their delicate rose-coloured tips. And brilliant coral fish were flitting about these fairy-tale gardens like butterflies.*"

– Hans Hass, recounting his first dives in the Red Sea, from *Challenging the Deep* (1973)

Hans Hass made his first pioneering dives within the Red Sea in 1949. He relied on works from the great naturalists dating back to the previous century, but still found great excitement in observing these fauna in their natural habitat. Since the time of Hass' explorations, much has changed. While traditional natural history expeditions still play an important role in scientific discovery, the modern era of biogeography now seeks mechanisms (or processes) to explain the observed patterns on a level that few in Klunzinger's or Hass' time could have imagined. Establishing the distribution of a species is now followed by questions of genetic similarity to conspecifics throughout their range. In some cases, the focus has shifted to understanding the spatial and temporal variability of a "hologenome" as a factor in local adaptation, recognizing that while a species may appear to be genetically homogeneous, the multitude of microorganisms, symbionts, and viruses associated with each individual may be highly variable in space and time (Zilber-Rosenberg & Rosenberg, 2008). And yet there remain some areas of

71 the world where physical acquisition of samples and deposition of these samples into natural
72 history collections still play a particularly important role in elucidating biogeographical patterns
73 (Rocha *et al.,* 2014). The Red Sea and Western Indian Ocean (WIO), for example, form a marine
74 region bordered by many countries in which the socio-economic and political realities have
75 limited access for many scientists, thus hindering a modern perspective of general biogeography
76 in the region. While local expertise and knowledge undoubtedly exist here, the accessibility of
77 this information to the international scientific community is sometimes restricted (Berumen *et*
78 *al.,* 2013; Loya *et al.,* 2014). This region is particularly interesting because it includes multiple
79 biogeographical provinces (Spalding *et al.,* 2007; Briggs & Bowen, 2012), each with distinct
80 faunal communities and suites of endemic species (e.g., DiBattista *et al*., 2016a), and these
81 provinces have numerous intersections within the region (e.g. DiBattista *et al.,* 2015a). While
82 many consider the WIO region to be "marginal" or "peripheral" habitat, it may still play an
83 important role in global biogeography (e.g., as an exporter of biodiversity) (e.g. Bowen *et al.,*
84 2013).

85 Herein we introduce a special virtual issue in the Journal of Biogeography (JBI) titled
86 "Red Sea and Western Indian Ocean Biogeography". The overall aim of the present virtual issue
87 is to highlight advances in our understanding of marine biogeography in this fascinating region.
88 The virtual issue arises largely as the result of a workshop convened by the King Abdullah
89 University of Science and Technology (KAUST) in Saudi Arabia to bring together expertise on
90 regional biogeography in early 2014. As a leading journal in this field, JBI was a logical place to
91 house the proceedings of this workshop. The virtual issue highlights previously published works
92 in JBI and provided the impetus for new papers to find a common repository. It currently
93 includes 24 previously published papers and 14 papers specifically submitted to the thematic

issue and it creates the opportunity to add additional papers to the collection as they are published.

The Red Sea and WIO are reported to host endemism and biodiversity hotspots. Two review papers capture the past and present patterns of endemism surrounding the Arabian Peninsula. DiBattista *et al.* (2016a) summarize the patterns of endemism for several broad taxonomic groups, finding consistently high levels of endemism within the Red Sea and variable patterns in adjacent regions. Turning to the question of how these patterns of endemism arose, DiBattista *et al.* (2016b) explore competing hypotheses but conclude that there is no single explanation. Focusing on the corals of the Indian Ocean, Obura (2016) reaches a similar conclusion; multiple origins of diversity are likely responsible for the current biogeographical patterns. McClanahan (2015) offers a perspective on applications of such biogeographical patterns in connection with management efforts to conserve reef fisheries; based on data from seven southwestern Indian Ocean countries, he proposes a "portfolio approach" that spreads risk by managing a variety of habitats and locations, but with a particular focus on protecting biomass in high-compliance areas.

Several studies in this virtual issue focus on wide-ranging phylogeographical patterns, placing the region in a much broader context. Ahti *et al.* (2016) examine cosmopolitan wrasses, finding that Indian Ocean and Pacific Ocean sister species may be better described as subspecies. Waldrop *et al.* (2016) highlight the evolution of range-restricted butterflyfish species (Red Sea and NW Indian Ocean) and isolated populations (Hawai'i), concluding that genetic divergence is high among these peripheral biogeographical provinces. On the other hand, in a wide-ranging butterflyfish species, DiBattista *et al.* (2015b) find that genetic differentiation among studied populations was insufficient to justify a species- or subspecies-level distinction of a previously

proposed Red Sea subspecies, despite different colour morphs across its range (*i.e.*, the two colour morphs do not sort into reciprocally monophyletic groups of mtDNA haplotypes). Fernandez-Silva *et al.* (2016) examine a goatfish species and find that phylogeographical breaks are congruent with existing boundaries of biogeographical provinces, and that these peripheral biogeographical provinces may represent evolutionary incubators for reef fishes (*sensu* Bowen *et al*., 2013). Broadening the taxonomic scope, Iacchei *et al.* (2016) find similar concordance of phylogeographical and biogeographical barriers in the spiny lobster. Higher resolution studies such as Priest *et al.* (2016) explore fine-scale genetic and life history patterns in a grouper around the Arabian Peninsula, suggesting that cryptic speciation exists as a result of biogeographical barriers within the Arabian region. Van der Ven *et al.* (2015) explore population genetics of an *Acropora* coral species along the Kenyan and Tanzanian coasts, concluding that high connectivity was most likely explained by local oceanographic features rather than by geographical distance. Within the Red Sea, Reimer *et al.* (2016) examine the type (i.e., clade) of symbiotic algae residing in a zoantharian host and find that the local thermal regime is the most likely driver of their distribution. As invasive species become even hotter topics in various parts of the world, the role of the Red Sea fauna in the Lessepsian invasion of the Mediterranean is examined by Bariche *et al.* (2015), who use DNA barcoding to identify numerous cases of invasive fishes. Bariche *et al*. (2015) revealed some possible cases of previously unrecognized invasions as well as invasions by cryptic species. The authors found some taxa with unresolved taxonomic status, highlighting the need for updated and vouchered genetic libraries for the region.

Our selection of papers from the JBI archives highlights seminal work on the origin of tropical marine species (Briggs, 2000) and a realignment of biogeographical provinces (Briggs &

Bowen, 2012, 2013). We include studies that apply phylogenetic or phylogeographical methods in order to advance our understanding of drivers of speciation and subsequent dispersal in reef fish (Cowman & Bellwood, 2013; DiBattista *et al.*, 2013; Gaither & Rocha, 2013; Hodge *et al.*, 2014; Ludt & Rocha, 2015; Hodge & Bellwood, 2016), non-coral invertebrates (Reid *et al.*, 2006; Hoareau *et al.*, 2013), or corals (Pinzón *et al.*, 2013) and their symbionts (LaJeunesse *et al.*, 2010). Collectively, these studies show that there are not "one size fits all" generalities for patterns of speciation and genetic connectivity within the WIO. Rather, each taxon may have its own unique evolutionary history (even congeners may have different histories) with correspondingly unique mechanisms. We additionally include studies focused on an important transition zone along the South African coastline (Bustamante & Branch, 1996; Primo & Vazquez, 2004; Teske *et al.*, 2014), studies teasing apart key processes affecting both ancient (Fernandes *et al.*, 2006) and more recent migration (Roberts *et al.*, 1992; Golani, 1993; Kiflawi *et al.*, 2006) within and out of the Red Sea, studies focused on the isolating effects of the Arabian Sea upwelling (Kemp, 1998; Schils & Coppejans, 2003), a study using holothuroids as a model to understand zoographical patterns in the Western Indian Ocean (Samyn & Tallon, 2005), and studies that remind us we must not now nor ever forget to consider the ecology of a system when defining biogeographical boundaries (Choat, 2006).

Our sincere gratitude goes to the Editor-in-Chief (Peter Linder, who handled the transition in the role from Rob Whittaker); the handling editors for individual papers in the virtual issue; and numerous authors and reviewers, whom all created and shaped the content of the final contribution. Input from Dr Michelle Gaither and three anonymous reviewers improved this introductory note. The virtual issue represents a major step forward in our ability to consider the

"big picture" supporting the origins and maintenance of marine fauna in the Red Sea and WIO, thus following in the footsteps of the likes of Klunzinger and other regional explorers.

"I suspected that the Red Sea still had a lot to reveal to us, a lot which had remained hidden from me on my first visit. I was to be proved right."

– Hans Hass, from *Challenging the Deep* (1973)

References

Ahti, P.A., Coleman, R.R., DiBattista, J.D., Berumen, M.L., Rocha, L.A. & Bowen, B.W. (2016) Phylogeography of Indo-Pacific reef fishes: sister wrasses *Coris gaimard* and *C. cuvieri* in the Red Sea, Indian Ocean and Pacific Ocean. *Journal of Biogeography*, **43,** 1103–1115.

Bariche, M., Torres, M., Smith, C., Sayar, N., Azzurro, E., Baker, R. & Bernardi, G. (2015) Red Sea fishes in the Mediterranean Sea: a preliminary investigation of a biological invasion using DNA barcoding. *Journal of Biogeography*, **42,** 2363–2373.

Berumen, M.L., Hoey, A.S., Bass, W.H., Bouwmeester, J., Catania, D., Cochran, J.E., Khalil, M.T., Miyake, S., Mughal, M.R., Spaet, J.L.Y. & Saenz-Agudelo, P. (2013) The status of coral reef ecology research in the Red Sea. *Coral Reefs*, **32,** 737–748.

Bowen, B.W., Rocha, L.A., Toonen, R.J., Karl, S.A. & The TOBO Laboratory (2013) The origins of tropical marine biodiversity. *Trends in Ecology & Evolution*, **28,** 359–366.

Briggs, J.C. (2000) Centrifugal speciation and centres of origin. *Journal of Biogeography*, **27,** 1183–1188.

Briggs, J.C. & Bowen, B.W. (2012) A realignment of marine biogeographic provinces with particular reference to fish distributions. *Journal of Biogeography*, **39,** 12–30.

Briggs, J.C. & Bowen, B.W. (2013). Marine shelf habitat: biogeography and evolution. *Journal of Biogeography*, **40,** 1023–1035.

Bustamante, R. & Branch, G. (1996) Large scale patterns and trophic structure of southern African rocky shores: the roles of geographic variation and wave exposure. *Journal of Biogeography*, **23,** 339–351.

Choat, J.H. (2006) Phylogeography and reef fishes: bringing ecology back into the argument.

Journal of Biogeography, **33,** 967–968.

Cowman, P.F. & Bellwood, D.R. (2013) The historical biogeography of coral reef fishes: global patterns of origination and dispersal. *Journal of Biogeography*, **40,** 209–224.

DiBattista, J.D., Berumen, M.L., Gaither, M.R., Rocha, L.A., Eble, J.A., Choat, J.H., Craig, M.T., Skillings, D.J. & Bowen, B.W. (2013) After continents divide: comparative phylogeography of reef fishes from the Red Sea and Indian Ocean. *Journal of Biogeography*, **40,** 1170–1181.

DiBattista, J.D., Rocha, L.A., Hobbs, J.P., He, S., Priest, M.A., Sinclair-Taylor, T.H., Bowen, B.W. & Berumen, M.L. (2015a) When biogeographical provinces collide: hybridization of reef fishes at the crossroads of marine biogeographical provinces in the Arabian Sea. *Journal of Biogeography*, **42,** 1601–1614.

DiBattista, J.D., Waldrop, E., Rocha, L.A., Craig, M.T., Berumen, M.L. & Bowen, B.W. (2015b) Blinded by the bright: A lack of congruence between colour morph and phylogeography for a cosmopolitan Indo-Pacific butterflyfish, *Chaetodon auriga*. *Journal of Biogeography*, **42,** 1919–1929.

DiBattista, J.D., Roberts, M., Bouwmeester, J., Bowen, B.W., Coker, D.F., Lozano-Cortés, D.F., Choat, J.H., Gaither, M.R., Hobbs, J.P., Khalil, M., Kochzius, M., Myers, R., Paulay, G., Robitzch, V., Saenz-Agudelo, P., Salas, E., Sinclair-Taylor, T.H., Toonen, R.J., Westneat, M., Williams, S. & Berumen, M.L. (2016a) A review of contemporary patterns of endemism for shallow water reef fauna in the Red Sea. *Journal of Biogeography*, **43,** 423–439.

DiBattista, J.D., Choat, J.H., Gaither, M.R., Hobbs, J.P.A., Lozano-Cortés, D.F., Myers, R.F.,

Paulay, G., Rocha, L.A., Toonen, R.J., Westneat, M.W. & Berumen, M.L. (2016b) On the origin of endemic species in the Red Sea. *Journal of Biogeography*, **43,** 13–30.

Fernandes, C.A., Rohling, E.J. & Siddall, M. (2006) Absence of post-Miocene Red Sea land bridges: biogeographic implications. *Journal of Biogeography*, **33,** 961–966.

Fernandez-Silva, I., Randall, J.E., Coleman, R.R., DiBattista, J.D., Rocha, L.A., Reimer, J.D., Meyer, C.G. & Bowen, B.W. (2015) Yellow tails in the Red Sea: phylogeography of the Indo-Pacific goatfish *Mulloidichthys flavolineatus* reveals isolation in peripheral provinces and cryptic evolutionary lineages. *Journal of Biogeography*, **42,** 2402–2413.

Gaither, M.R. & Rocha, L.A. (2013) Origins of species richness in the Indo-Malay-Philippine biodiversity hotspot: evidence for the centre of overlap hypothesis. *Journal of Biogeography*, **40,** 1638–1648.

Golani, D. (1993) The sandy shore of the Red Sea-launching pad for Lessepsian (Suez Canal) migrant fish colonizers of the eastern Mediterranean. *Journal of Biogeography*, 579–585.

Hass, H. (1973) *Challenging the Deep. Thirty Years of Undersea Adventure*. (Translation by Osers, E., of: *In unberührte Tiefen*.). William Morrow and Company, Inc., New York. 266pp.

Loya, Y., Genin, A., el-Zibdeh, M., Naumann, M.S. & Wild, C. (2014) Reviewing the status of coral reef ecology of the Red Sea: key topics and relevant research. *Coral Reefs*, **33,** 1179.

Hoareau, T.B., Boissin, E., Paulay, G. & Bruggemann, J.H. (2013). The Southwestern Indian Ocean as a potential marine evolutionary hotspot: perspectives from comparative phylogeography of reef brittle-stars. *Journal of Biogeography*, **40,** 2167–2179.

Hodge, J.R. & Bellwood, D.R. (2016) The geography of speciation in coral reef fishes: the

relative importance of biogeographical barriers in separating sister-species. *Journal of Biogeography*. Online early.

Hodge, J.R., van Herwerden, L. & Bellwood, D.R. (2014) Temporal evolution of coral reef fishes: global patterns and disparity in isolated locations. *Journal of Biogeography*, **41,** 2115–2127.

Iacchei, M., Gaither, M.R., Bowen, B.W. & Toonen, R.J. (2016) Testing dispersal limits in the sea: range-wide phylogeography of the pronghorn spiny lobster *Panulirus penicillatus*. *Journal of Biogeography*, **43,** 1032-1044.

Kemp, J. (1998) Zoogeography of the coral reef fishes of the Socotra Archipelago. *Journal of Biogeography*, **25,** 919–933.

Kiflawi, M., Belmaker, J., Brokovich, E., Einbinder, S. & Holzman, R. (2006) The determinants of species richness of a relatively young coral-reef ichthyofauna. *Journal of Biogeography*, **33,** 1289–1294.

LaJeunesse, T.C., Pettay, D.T., Sampayo, E.M., Phongsuwan, N., Brown, B., Obura, D. O., Hoegh-Guldberg, O. & Fitt, W. K. (2010) Long-standing environmental conditions, geographic isolation and host–symbiont specificity influence the relative ecological dominance and genetic diversification of coral endosymbionts in the genus *Symbiodinium*. *Journal of Biogeography*, **37,** 785–800.

Ludt, W.B. & Rocha, L.A. (2015) Shifting seas: the impacts of Pleistocene sea-level fluctuations on the evolution of tropical marine taxa. *Journal of Biogeography*, **42,** 25–38.

McClanahan, T.R. (2015) Biogeography versus resource management: how do they compare when prioritizing the management of coral reef fish in the south-western Indian Ocean? *Journal of Biogeography*, **42,** 2414–2426.

Obura, D.O. (2016) An Indian Ocean centre of origin revisited: Palaeogene and Neogene influences defining a biogeographic realm. *Journal of Biogeography*, **43,** 229–242.

Pinzón, J.H., Sampayo, E., Cox, E., Chauka, L.J., Chen, C.A., Voolstra, C.R. & LaJeunesse, T.C. (2013) Blind to morphology: genetics identifies several widespread ecologically common species and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). *Journal of Biogeography*, **40,** 1595–1608.

Priest, M.A., DiBattista, J.D., McIlwain, J.L., Taylor, B.M., Hussey, N.E. & Berumen, M.L. (2016) A bridge too far: dispersal barriers and cryptic speciation in an Arabian Peninsula grouper (*Cephalopholis hemistiktos*). *Journal of Biogeography*, **43,** 820–832.

Primo, C. & Vazquez, E. (2004) Zoogeography of the southern African ascidian fauna. *Journal of Biogeography*, **31,** 1987–2009.

Reid, D.G., Lal, K., Mackenzie-Dodds, J., Kaligis, F., Littlewood, D.T.J. & Williams, S.T. (2006) Comparative phylogeography and species boundaries in Echinolittorina snails in the central Indo-West Pacific. *Journal of Biogeography*, **33,** 990–1006.

Reimer, J.D., Herrera, M., Gatins, R., Kattan, A., Roberts, M. & Berumen, M.L. (2016) Latitudinal variation in the symbiotic dinoflagellate *Symbiodinium* of the common reef zoantharian *Palythoa tuberculosa* on the Saudi Arabian coast of the Red Sea. *Journal of Biogeography*. doi:10.1111/jbi.12795

Roberts, C.M., Shepherd, A.R.D. & Ormond, R.F. (1992). Large-scale variation in assemblage structure of Red Sea butterflyfishes and angelfishes. *Journal of Biogeography*, 239–250.

Rocha, L.A., Aleixo, A., Allen, G., Almeda, F., Baldwin, C.C., Barclay, M.V.L., Bates, J.M., et al. (2014) Specimen collection: An essential tool. *Science*, **344,** 814–815.

Samyn, Y. & Tallon, I. (2005) Zoogeography of the shallow-water holothuroids of the western

Indian Ocean. *Journal of Biogeography*, **32,** 1523–1538.

Schils, T. & Coppejans, E. (2003) Phytogeography of upwelling areas in the Arabian Sea. *Journal of Biogeography*, **30,** 1339–1356.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdana, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. & Robertson, J. (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience*, **57,** 573–583.

Teske, P.R., Papadopoulos, I., Barker, N.P., McQuaid, C.D. & Beheregaray, L.B. (2014) Mitonuclear discordance in genetic structure across the Atlantic/Indian Ocean biogeographical transition zone. *Journal of Biogeography*, **41,** 392–401.

van der Ven, R.M., Triest, L., De Ryck, D.J., Mwaura, J.M., Mohammed, M.S. & Kochzius, M. (2015) Population genetic structure of the stony coral *Acropora tenuis* shows high but variable connectivity in East Africa. *Journal of Biogeography*, **43,** 510–519.

Waldrop, E., Hobbs, J.P.A., Randall, J.E., DiBattista, J.D., Rocha, L.A., Kosaki, R.K., Berumen, M.L. & Bowen, B.W. (2016) Phylogeography, population structure and evolution of coral-eating butterflyfishes (Family Chaetodontidae, genus *Chaetodon*, subgenus *Corallochaetodon*). *Journal of Biogeography*, **43,** 1116–1129.

Zilber-Rosenberg, I. & Rosenberg, E. (2008) Role of microorganisms in the evolution of animals and plants: the hologenome theory of evolution. *FEMS Microbiology Reviews*, **32,** 723–735.