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Comparative phylogeography of the western Indian Ocean reef fauna

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ABSTRACT

Assessing patterns of connectivity at the community and population levels is relevant to marine resource management and conservation. The present study reviews this issue with a focus on the western Indian Ocean (WIO) biogeographic province. This part of the Indian Ocean holds more species than expected from current models of global reef fish species richness. In this study, checklists of reef fish species were examined to determine levels of endemism in each of 10 biogeographic provinces of the Indian Ocean. Results showed that the number of endemic species was higher in the WIO than in any other region of the Indian Ocean. Endemic species from the WIO on the average had a larger body size than elsewhere in the tropical Indian Ocean. This suggests an effect of peripheral speciation, as previously documented in the Hawaiian reef fish fauna, relative to other sites in the tropical western Pacific. To explore evolutionary dynamics of species across biogeographic provinces and infer mechanisms of speciation, we present and compare the results of phylogeographic surveys based on compilations of published and unpublished mitochondrial DNA sequences for 19 Indo-Pacific reef-associated fishes (rainbow grouper *Cephalopholis argus*, scrawled butterflyfish *Chaetodon meyeri*, bluespot mullet *Crenimugil* sp. A, humbug damselfish *Dascyllus abudafur*/*Dascyllus aruanus*, areolate grouper *Epinephelus areolatus*, blacktip grouper *Epinephelus fasciatus*, honeycomb grouper *Epinephelus merra*, bluespotted cornetfish *Fistularia commersonii*, cleaner wrasse *Labroides* sp. 1, longface emperor *Lethrinus* sp. A, bluestripe snapper *Lutjanus kasmira*, unicornfishes *Naso brevirosris*, *Naso unicornis* and *Naso vlamingii*, blue-spotted maskray *Neotrygon kuhlii*, largescale mullet *Planiliza macrolepis*, common parrotfish *Scarus psicattus*, crescent grunter *Terapon jarbua*, whitetip reef shark *Triaenodon obesus*) and three coastal Indo-West Pacific invertebrates (blue seastar *Linckia laevigata*, spiny lobster *Panulirus homarus*, small giant clam *Tridacna maxima*). Heterogeneous and often unbalanced sampling design, paucity of data in a number of cases, and among-species discrepancy in phylogeographic structure precluded any generalization regarding phylogeographic patterns. Nevertheless, the WIO might have been a source of haplotypes in some cases and it also harboured an endemic clade in at least one case. The present survey also highlighted likely cryptic species. This may eventually affect the accuracy of the current checklists of species, which form the basis of some of the recent advances in Indo-West Pacific marine ecology and biogeography.

1. Introduction

1.1. Background

Marine biologists define biogeographic provinces as regions of the ocean characterized by the presence of distinct communities that are thought to have some cohesion at the evolutionary

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timescale and found to be distinct from adjacent provinces (Spalding et al., 2007; Briggs and Bowen, 2012, and references therein). Thus-called marine biogeographic provinces generally harbour a proportion of endemic species. The extent of biogeographic provinces generally coincides with geologic and/or oceanographic boundaries (Spalding et al., 2007; and references therein; Briggs and Bowen, 2012; Obura, 2012; Veron et al., 2015). Quantitative delineation of biogeographic provinces based on 169 reef fish checklists from across all tropical oceans (Kulbicki et al., 2013a) showed less clear-cut province boundaries, than those described in the above surveys. The delimitation of biogeographic provinces is viewed as important to help establish patterns of connectivity at the community and the population levels, which in turn has relevance in resource management and conservation (Spalding et al., 2007; Obura, 2012; Kulbicki et al., 2013a; Veron et al., 2015).

Ocean currents transport larvae of sedentary marine species, allowing the connection of geographically-distant habitats suitable for adults. Larval transportation also enables sedentary marine species to colonize new habitats (e.g., recent volcanic islands), and to recolonize habitats where the species have been extirpated. Although the direction and intensity of currents may determine levels of contemporary gene flow, a species' geographic structure over evolutionary time is more likely to be influenced by geographic distance between suitable habitats (Crandall et al., 2014). Albeit not a primary determinant of distribution range size, variability in pelagic larval duration may partly contribute to differences in the distribution of reef fish species in the Indo-Pacific, as species with longer larval duration have a greater chance to disperse over habitats unsuitable to adults than those with shorter pelagic larval duration (Scheltema, 1968; Woodland, 1990; Lester et al., 2007; Treml et al., 2012; Luiz et al., 2013). Adult body size is another factor affecting a species' distribution range (Luiz et al., 2013). Larger adults have higher reproductive output and higher-quality offspring (Beldade et al., 2012; Hixon et al., 2014), which enhances the probability of achieving long-distance dispersal. At the intraspecific level, higher larval survival rate potentially translates into higher dispersal ability which in turn translates into potential for higher gene flow between populations. Population genetic differentiation decreases with pelagic larval duration in the tropical Indo-West Pacific fish family Siganidae (Lemer et al., 2007), where geographic range size also increases with pelagic larval duration (Woodland, 1990). Tropical Pacific fishes from families Chaetodontidae, Labridae and Pomacentridae show a similar correlation (Lester and Ruttenberg, 2005; Lester et al., 2007). Selkoe and Toonen (2011) found that pelagic larval duration and genetic differentiation estimates, i.e. S. Wright's *Fst* and the slope of the isolation-by-distance correlation (Rousset, 1997), typically reflect scales of dispersal if the sampling design is adequate. Gene flow counteracts genetic differentiation by natural selection and genetic drift (Slatkin, 1985), thus hampering adaptation to local conditions.

1.2. The western Indian Ocean (WIO) province

The present study focuses on the western Indian Ocean (WIO) province, the westernmost of the tropical Indo-West Pacific domain. The WIO province is defined here as the oceanic region bounded by the eastern coast of Africa from Somalia to Mozambique and extending to the East so as to include the Seychelles and Mascarene archipelagoes. This approximately coincides with Obura's (2012) and Spalding et al.'s (2007) definitions of the Western Indian Ocean province. Briggs and Bowen (2012) did not mention the WIO as a particular biogeographic province in terms of endemism or as a diversity hotspot.

The reef fish fauna of the WIO has attracted increased interest from the scientific community. Smith and Heemstra (1986) described a large proportion of the species occurring in South Africa and adjacent waters (Mozambique, Madagascar). Subsequently, a number of country-based checklists have been proposed in this region (e.g. Iles Eparses, the Comores archipelago, Seychelles, Mascarene Islands). These species checklists were used to delineate biogeographic regions (Kulbicki et al., 2013a), and to relate species richness to a number of large-scale environmental factors, including sea-surface temperature, island size and its degree of isolation, distance from the Coral Triangle, and reef area (Parravicini et al., 2013). These studies, along with previous work on reef fish macro-ecology (Santini and Winterbottom, 2002; Bellwood et al., 2012; Kulbicki et al., 2013b; Mouillot et al., 2013), suggest that the WIO has some specific characteristics. In particular, this part of the Indian Ocean holds more species than expected from modelling based on geomorphologic, biogeographic and environmental explanatory variables (Parravicini et al., 2013; Pellissier et al., 2014). This leads us to hypothesize that the WIO represents either a species sink, a center of origin, or a zone of overlap. Possible routes of migration for reef fishes include along the eastern African coast, from the Maldives–Chagos archipelagoes towards the Seychelles, or from temperate southern Africa towards the North-East. Obura (2012) (p. 1) posits that diversity patterns in WIO corals are consistent with the oceanography of the western Indian Ocean, "*reflecting inflow of the South Equatorial Current, maintenance of high diversity in the northern Mozambique Channel, and export from this central region to the north and south, and to the Seychelles and Mascarene islands.*" This amounts to suggesting that the WIO may harbour specific communities that both receive and export species.

1.3. Comparative phylogeography as an approach to test biogeographic hypotheses

Community assembly, the sum of the processes leading to the aggregation of species in ecological communities (Emerson and Gillespie, 2008), results from intricate interactions at the regional and local scales (Ricklefs, 1987; Leibold et al., 2004, 2010). Community assembly is affected by the dynamics of diversification, which drives the biodiversity build-up in a regional pool, and by the ecological dynamics within communities, which limits the number of species that coexist (Hubert et al., 2015). Historical biogeography has traditionally focused on the contribution of geological and paleoecological landscape histories on species diversification at the regional scale (Nelson and Platnick, 1981; Myers and Giller, 1988; Ricklefs and Schluter, 1993). For this, the distributions of species have been analysed to detect coinciding geographical boundaries, which in turn have been linked to known past events (Cracraft and Prum, 1988; Morrone, 1994; Morrone and Escalante, 2002). The introduction of genetic markers into historical biogeography has led to the development of comparative phylogeography, which aims at uncovering shared patterns in the distribution of intraspecific genetic diversity (Avise, 2000). Phylogeography offers the tools and concepts to study the historical processes that may be responsible for the contemporary geographic distributions of gene genealogies. Thus, phylogeography addresses some of the conservation issues that are at the core of modern marine biogeography. This approach has proven to be informative in exploring evolutionary dynamics of species across biogeographical boundaries and in revealing the temporal dynamics underpinning the coincidence of species distributions (Bermingham and Moritz, 1998; Hubert et al., 2007; Lee and Johnson, 2009). Phylogeographic subdivisions generally corroborate biogeographic provinces based on species lists, with a notable exception at the Indian-Pacific boundary (Briggs and Bowen, 2012). Studying phylogeographic structure (i.e., generally at the intraspecific level) allows one to test