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SYNTHESIS

Marine shelf habitat: biogeography and evolution

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ABSTRACT

We synthesize the evolutionary implications of recent advances in the fields of phylogeography, biogeography and palaeogeography for shallow-water marine species, focusing on marine speciation and the relationships among the biogeographic regions and provinces of the world. A recent revision of biogeographic provinces has resulted in the recognition of several new provinces and a re-evaluation of provincial relationships. These changes, and the information that led to them, make possible a clarification of distributional dynamics and evolutionary consequences. Most of the new conclusions pertain to biodiversity hotspots in the tropical Atlantic, tropical Indo-West Pacific, cold-temperate North Pacific, and the cold Southern Ocean. The emphasis is on the fish fauna, although comparative information on invertebrates is utilized when possible. Although marine biogeographic provinces are characterized by endemism and thus demonstrate evolutionary innovation, dominant species appear to arise within smaller centres of high species diversity and maximum interspecies competition. Species continually disperse from such centres of origin and are readily accommodated in less diverse areas. Thus, the diversity centres increase or maintain species diversity within their areas of influence, and are part of a global system responsible for the maintenance of biodiversity over much of the marine world.

Keywords

Accommodation, centres of origin, dispersal, endemism, evolution, marine biogeography, marine provinces, phylogeography, speciation.

INTRODUCTION

During the past 15 years, hundreds of articles pertaining to the distribution and evolution of marine species have been published. Most of these publications are limited in geographic scope, but, when considered along with more wide-ranging works, they have allowed us to re-examine biogeographic relationships in the Atlantic Ocean, Indo-West Pacific, North Pacific and Southern Ocean. For example, the movement of species among the warm Atlantic provinces is now better understood. We know more about the function of the Indo-Pacific Barrier between the Pacific and Indian Oceans; the North Pacific can be identified as the primary source for contemporary cold-temperate biotas; and evolution in the Southern Hemisphere's cold-temperate and cold Antarctic waters has enriched the Southern Ocean to a much greater degree than previously suspected.

Three biogeographic models have been proposed for the origins of marine biodiversity: centre of origin (Briggs, 2003, 2005), centre of accumulation (Ladd, 1960; Jokiel & Martinelli, 1992), and a centre of overlap between the Pacific and Indian Ocean faunas (Woodland, 1983). We contend that there is most support for the centre of origin model, with a flow of species from high-diversity centres that enhances species abundance in outlying communities (Mora *et al.*, 2003; Briggs, 2006). Other studies, however, have shown that some migration may take place towards the diversity centre (Bellwood & Wainwright, 2002; Hobbs *et al.*, 2009; Eble *et al.*, 2011a; Gaither *et al.*, 2011a).

The biogeographic provinces discussed herein are shallow (< 200 m) marine regions defined by a minimum of 10% endemism. Although this cut-off is subject to criticism for being too high or too low, justifications are discussed elsewhere (Briggs, 1974; Briggs & Bowen, 2012). Here we use these marine provinces to illustrate evolutionary processes in shallow habitats that are separated by continents, ecological regimes, and vast swathes of open ocean.

ATLANTIC OCEAN

Phylogeographic analysis of the warm-water genera (reviewed in Floeter *et al.*, 2008) has allowed an improved understanding

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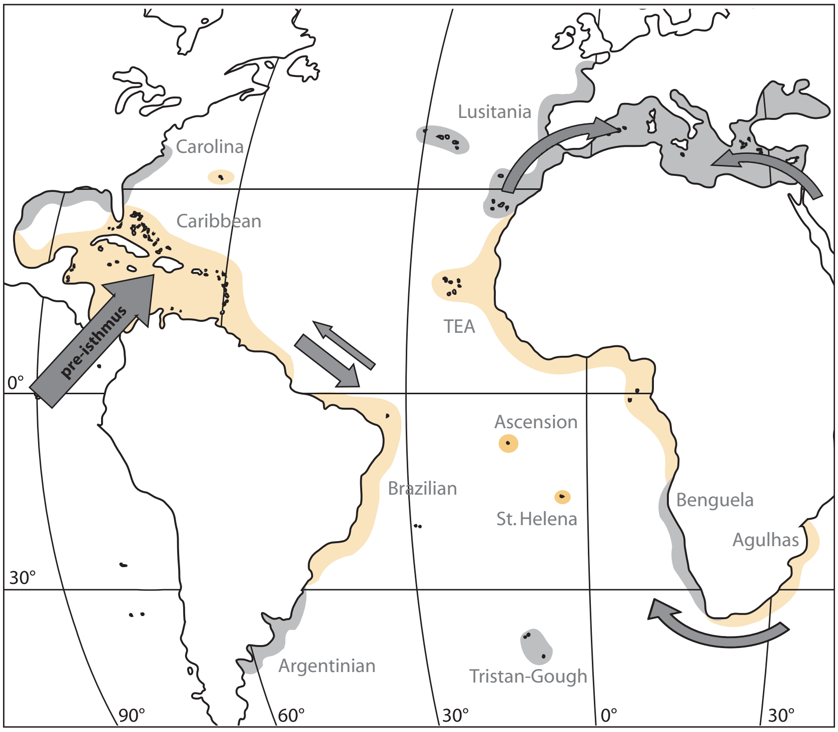

Figure 1 Map of the Atlantic showing warm-temperate biogeographic provinces (grey), tropical biogeographic provinces (gold), and the biogeographic pathways that contribute to biodiversity in these provinces. Named locations refer to provinces. Parallel arrow sizes indicate relative size of migratory flows. These pathways include the Tethys Sea relicts, which arrived prior to 12 Ma through what is now the Mediterranean Sea; the New World fauna that was isolated from the East Pacific by the rise of the Isthmus of Panama about 3 Ma; and the Indian Ocean fauna, which occasionally contributes biodiversity via southern Africa. The fourth source of marine biodiversity in these provinces is new species that arise *in situ*, primarily in the Caribbean hotspot. Abbreviation: TEA, Tropical East Atlantic.

of the evolution and distribution of the Atlantic fauna. We can now identify four origins of Atlantic genera: (1) Tethys (relictual) origins prior to the collision of Africa and Europe about 12–20 million years ago (Ma) (Dercourt *et al.*, 1986), (2) origins in the New World (West Atlantic–East Pacific) prior to the closure of the Isthmus of Panama about 3.1 Ma (Coates & Obando, 1996), (3) radiations within the Atlantic, and (4) invasions from the Indo-Pacific via southern Africa (Fig. 1).

The relationship among the provinces can illuminate the geographic origin of the species and the effectiveness of their dispersal across biogeographic barriers (Floeter *et al.*, 2008). For example, the freshwater discharge of the Amazon River, about 11 million years (Myr) old (Hoorn, 1996), is a soft barrier between the Caribbean (CA) and Brazilian (BR) provinces because about 348 reef fish species are shared between the two (CA, 814 species; BR, 471 species). This amounts to about 42% of the species diversity of the former and 74% of the latter. The reef specialists, species of small size, and those with limited latitudinal ranges have difficulty traversing the barrier and are much more diverse in the CA (Rocha *et al.*, 2002; Luiz *et al.*, 2012). Another soft barrier is the open-water expanse of the mid-Atlantic. The CA shares 105 reef fish species with the tropical Eastern Atlantic (TEA), and these trans-Atlantic species account for about 27% of the shallow TEA fish fauna. Similarly, the BR shares about 107 reef fish species with the TEA. Most of the trans-Atlantic species are also shared between the CA and BR, so the total number in the trans-Atlantic category is 112 (Floeter *et al.*, 2008). However, this number is likely to drop as genetic studies reveal additional cryptic species in East–West Atlantic comparisons. Based on phylogeographic surveys, Bowen *et al.* (2006a) found that 8 out of 15 Atlantic reef fishes contained cryptic evolutionary partitions.

The next most permeable boundaries are those of the open ocean to the east and west of the mid-Atlantic Ridge provinces of St Helena and Ascension (Floeter *et al.*, 2008). Those islands share 64 species with the eastern Atlantic and 71 with the western side, the majority being trans-Atlantic forms. Many of the trans-Atlantic fishes are known to accompany floating debris and have relatively large latitudinal ranges (Luiz *et al.*, 2012). Sixteen families in the TEA are composed only of these wide-ranging taxa. The soft barrier of the relatively cool Benguela Current separates the Benguela (Atlantic) and the Agulhas (Indian Ocean) provinces. At least 47 contemporary fish species have colonized from the Indian Ocean to the Atlantic (up from 24 known previously; Briggs, 1974), 38 of which are found in the TEA where they account for about 10% of that fauna (Floeter *et al.*, 2008). Phylogeographic and palaeontological studies have provided two perspectives on these Atlantic invasions. First, there may be a colonization route through the Agulhas Province west to Brazil, as the distributions of some molluscs and fishes indicate (Vermeij & Rosenberg, 1993; Rocha *et al.*, 2005a). Second, mitochondrial DNA (mtDNA) data indicate no single pulse of colonization into the Atlantic (Bowen *et al.*, 2001, 2006b; Rocha *et al.*, 2005a; Duncan *et al.*, 2006; Reece *et al.*, 2010), but rather a number of individual events that may be attributed to the cessation of cold-water upwelling (Benguela Barrier) at the end of glacial cycles, or to warm cyclonic eddies that sporadically traverse the Benguela Current (Penven *et al.*, 2001; Peeters *et al.*, 2004).

The trans-Atlantic distribution of 112 fish species demonstrates ongoing connections across multiple warm provinces (Bowen *et al.*, 2006a), or recent colonization between Atlantic provinces (Rocha *et al.*, 2005a). In most cases where a phylogeny is resolved, the dispersal took place from west to east (Muss *et al.*, 2001; Floeter *et al.*, 2008; Beldade *et al.*, 2009). The relationship across the Amazon barrier between the CA and BR indicates species flow primarily from north to south, although a few colonizations in the reverse direction have been documented (Robertson *et al.*, 2006; Rocha *et al.*, 2008). In the 21 most species-rich families, the CA has 150 genera with 24 endemic and the BR has 117 genera but with only 3 endemic. These observations, interpreted under the assumption that the greatest species richness for genera is found at their region of origin, indicate that most of the BR reef fish fauna originated in the CA.

The warm-temperate provinces of the Atlantic have been appropriately called 'impoverished outposts of adjacent tropical areas' (Floeter *et al.*, 2008). Even though such provinces are distinguished by the prerequisite endemic species (at least 10%), the families, most genera, and the majority of species are apparently derived from the adjacent tropical provinces. The Lusitania Province that borders the TEA demonstrates unusual evolutionary activity by the presence of endemic genera in several fish families (Hanel *et al.*, 2002; Levy *et al.*, 2011). In the case of the warm-temperate Carolina Province that borders the CA, most of the fauna is obviously derived from the Caribbean. The islands of Bermuda, the northernmost tropical outpost in the Western Atlantic, are clearly populated by propagules carried north by the Gulf Stream. The great diversity of the CA and the evidence for the dispersals of its fauna to the east, south and north provide clear indications that the CA, or especially the high diversity concentration within that province, has been functioning as a centre of origin for the warm provinces of the Atlantic. Within the CA, the greatest species diversity among the coastal invertebrates occurs from Cuba through the Antilles to Colombia and Venezuela (Miloslavich *et al.*, 2010). It is likely that this region is producing most of the species radiations in the Caribbean Province (see, for example, Victor & Randall, 2010).

Although the Caribbean centre has been a dominant influence on warm-province biodiversity, the tropical Atlantic has received and continues to gain diversity from other sources. The three soft barriers, Amazon, mid-Atlantic and Benguela, stimulate evolutionary partitions, as indicated by the sister taxa divided by these barriers (Bernardi *et al.*, 2000; Rocha *et al.*, 2005b, 2007). Rocha *et al.* (2008) presented phylogeographic evidence that a few species have colonized north from the BR to add to the biodiversity of the CA. Considering the soft nature of the Amazon and Benguela barriers, parapatric speciation may predominate (Rocha & Bowen, 2008), while rare colonization events across wide stretches of open ocean between the West, Central and East Atlantic reflect allopatric speciation.

At least three tropical Atlantic fish genera are considered Tethys relicts that date from 12 to 18 Ma, and the Atlantic contains numerous genera that were once part of a general New World (Western Atlantic and Eastern Pacific) fauna prior to the rise of the Panamanian Isthmus *c.* 3.1 Ma (Floeter *et al.*, 2008). About 20 of these genera, representing the most species-rich families, had apparently reached the New World via trans-Pacific migrations. Many New World genera (122) do not occur in the Eastern Atlantic, demonstrating that the Caribbean reef fishes are more closely related to those of the Eastern Pacific than to those of the Eastern Atlantic. At least 10 genera represent invasions from the Indo-West Pacific (IWP) via South Africa within the last 4.6 Myr (Floeter *et al.*, 2008). One genus, *Holacanthus*, may have invaded before 13 Ma (Alva-Campbell *et al.*, 2010). The Caribbean has 24 endemic genera and 272 endemic species, providing evidence of more evolutionary innovation in that area than in any other Atlantic province.

INDO-WEST PACIFIC

The vast expanse of the IWP is reflected in the unique distribution patterns of the fish fauna. The Indo-Polynesian Province stretches from the Society Islands to the Gulf of Oman, about halfway around the planet (Fig. 2). For the reef fishes, Allen (2008) calculated an average range of 9,357,070 km^2, an area roughly the size of China. Only 10.8% of the 3919 IWP species occupy areas smaller than 120,000 km^2. Mundy *et al.* (2010), in a report on the fishes of the US Phoenix and Line Islands, found that 69.1% of the species ranged from the Indian Ocean (usually from East Africa) to their study location at the eastern edge of the south-west Pacific; 6.3% were restricted to the Pacific Plate; and 3.8% were circumtropical. The configuration of the Indo-Polynesian Province is determined by the distribution of archipelagos. No oceanic gap greater than 800 km exists between the Society Islands and the Western Pacific Ocean (Schultz *et al.*, 2008), and favourable ocean currents (Mora *et al.*, 2012) result in high genetic connectivity in reef-associated species (Lessios *et al.*, 2003; DiBattista *et al.*, 2011; Eble *et al.*, 2011a).

Considerable research has been focused on the 'Indo-Pacific Barrier' between the Eastern Indian Ocean and the Western Pacific (Barber *et al.*, 2000; Williams *et al.*, 2002; Gaither *et al.*, 2010). The two oceans are connected by means of an Indonesian throughflow via the Makassar Strait,

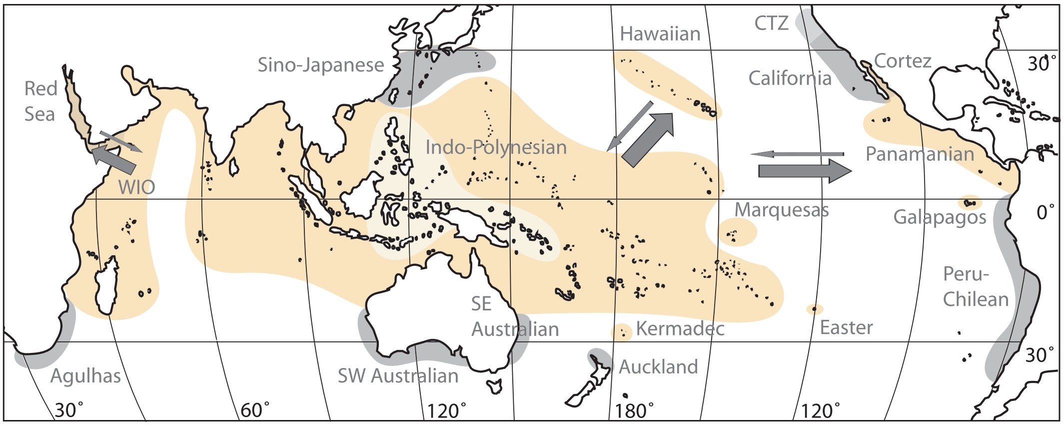

Figure 2 Map of the Indo-Pacific showing warm-temperate provinces (in grey) and tropical provinces (in gold). The Coral Triangle biodiversity hotspot is indicated by lighter gold. The California Transition Zone (CTZ) within the Oregon and California provinces is indicated by light grey. Arrows at the North Pacific and Red Sea indicate a primary flow of species out to peripheral biogeographic provinces (centre of origin model), but also a secondary flow from the peripheral provinces in towards the biodiversity hotspot of the Coral Triangle (centre of accumulation model). Abbreviation: WIO, Western Indian Ocean.

but during the last glaciation, *c.* 18,000 years ago, sea levels were about 130 m lower than present (Chappell & Shackleton, 1986; Voris, 2000). Hence the Indonesian throughflow was greatly reduced during Pliocene–Pleistocene glaciations, which decreased the opportunities for exchange. As a result, some sister species in the two oceans apparently originated during the glacial interruptions of gene flow (Randall, 1998). At present, some of these sister species have renewed contact in the eastern Indian Ocean, especially around the islands of Christmas and Cocos/Keeling, which host hybrids in some cases (Hobbs *et al.*, 2009; DiBattista *et al.*, 2012). In a review of phylogeographic evidence for this Indo-Pacific Barrier, Gaither *et al.* (2010) reported genetic distinctions within 15 of 18 species (fish, crustaceans, echinoderms). However, in several cases the genetic breaks are no larger than observed elsewhere in species ranges for fishes (Horne *et al.*, 2008) and crustaceans (Barber *et al.*, 2006). In other cases, ancient evolutionary partitions are apparent for fishes (McMillan & Palumbi, 1995; Read *et al.*, 2006; Gaither *et al.*, 2011a) and invertebrates (Lavery *et al.*, 1996; Lessios *et al.*, 2001; Kirkendale & Meyer, 2004). Veron (1995) considered the coral fauna of the eastern Indian Ocean to be continuous with that of the West Pacific.

Given that the Indo-Pacific Barrier lies within the well-defined Indo-Polynesian Province, this is the primary example of a marine phylogeographic break that is not concordant with biogeographic boundaries. Perhaps too few species have diverged at the barrier to attain the 10% endemism threshold for distinct provinces (Briggs & Bowen, 2012). Alternatively, the Eastern Indian and Western Pacific sections may eventually be distinguished as provinces if phylogeographic breaks translate into taxonomic descriptions. Two considerations are pertinent here.

1. The putative Indo-Pacific Barrier is different from other biogeographic barriers, most of which have been present for millions of years, in that it switches on and off with *c.*100,000-year oscillations (Rocha *et al.*, 2007). This allows the unique possibility of overlap by distinct faunas.
2. The presence of sister (Indian and Pacific) taxa hybridizing in the Indian Ocean indicates that the Pacific fauna is expanding westwards along the diversity gradient (Craig, 2008; Hobbs *et al.*, 2009). Hence the Indo-Pacific Barrier is ephemeral over evolutionary time and diffuse on a geographic scale *in contemporary time*, and is spread across 25° longitude from the Sunda Shelf to Cocos/Keeling Island.

We conclude that the Eastern Indian Ocean may have been a valid biogeographic province at the height of the last glaciation (18,000 years ago), but this distinction has been swamped by repeated invasions from the West Pacific.

Coral triangle

Within the Indo-Polynesian Province lies the Coral Triangle (CT), which supports the greatest diversity of species, genera and families in the marine world. The geographic position of the CT (East Indies Triangle), including the Philippines, Indonesia and New Guinea, was first delineated by Briggs (1987), followed by Hoeksema (2007) and Veron *et al.* (2009). This area by itself cannot be considered a distinct biogeographic province because the adjoining areas, although demonstrating reduced species diversity, do not as a rule host species that are not also found in the CT. Several groups of fishes and molluscs are represented by their most advanced (apomorphic) species in the CT (Briggs, 1984). Additional research on several tropical fish families indicated that the high-diversity reefs are occupied by the more advanced species, while the basal forms tend to occur in peripheral habitats or at greater depths (Briggs, 2004).

While the CT had been celebrated for high species diversity for many years, Allen & Adrim (2003) and Allen (2008) were the first to examine fish diversity patterns within the CT, with subsequent updates by Allen & Erdmann (2009) and Fraser & Allen (2011). The Bird's Head region of Indonesia at the extreme western end of New Guinea contains the world's highest diversity of fishes, with at least 1426 species. The same region contains the world's highest coral species diversity, with 574 species (Veron *et al.*, 2009). For the CT in its entirety, there are at least 605 coral species or about 76% of the world's total (798), including 15 endemic species. Reef fishes include 2228 species in the CT, representing 37.1% of the world total (about 6000 species) with an endemism rate of 7.8% (235 species); most of the endemic species are concentrated in the eastern part of the CT.

Short-range endemic fishes in the CT are clustered in four areas, indicating four localities of species origination (Allen, 2008). A comparative phylogeographic study of three stomatopod species within the CT also supported lineage diversification involving physical separation (Barber *et al.*, 2006). The *Echinolittorina* snails within the CT exhibit a mosaic of restricted allopatric species (Williams & Reid, 2004). Timm *et al.* (2008) observed five lineages of anemonefishes representing different regions of the CT. Lourie *et al.* (2005) found strong geographic partitioning in the CT among mtDNA lineages in seahorse species. Most recently, Carpenter *et al.* (2011) provided maps of concordant phylogeographic breaks in the CT. Such observations indicate that the CT does not comprise a single centre of origin but rather consists of multiple centres. It is possible that all three speciation modes (allopatric, sympatric, parapatric) may be functional in this region. However, a recent review of speciation in reef fishes noted that parapatric speciation is a common (and possibly prevalent) mode of diversification (Rocha & Bowen, 2008). Briggs (2007) suggested that speciation in the CT may be primarily sympatric, but it would be difficult to detect the difference between the sympatric and parapatric processes. Both are driven by natural selection, in contrast to the allopatric process for which the initial division is entirely mechanical (Coyne & Orr, 2004).

If there is little or no difference in the speciation process that takes place in the CT and elsewhere, then the ability of the CT to function as a centre of origin must be due to other causes. Six biogeographic patterns indicate a continuous flow of species outwards from the centre (Briggs, 2005). In addition, there are many widely distributed or circumtropical species that probably originated in the centre, including the sharks *Sphyrna lewini* (Daly-Engel *et al.*, 2012) and *Triaenodon obesus* (Whitney *et al.*, 2011). Mironov (2006) proposed that centres of origin have three developmental stages: accumulation, diversification and dispersal. This sequence nicely fits the history of the CT: an accumulation from the Tethys Sea via the Arabian Sea, and possibly from the New World, in the early Miocene; a diversification due to the rapid buildup of species in the late Miocene; and the current dispersal stage beginning *c.* 10 Ma (Briggs, 2007; Renema *et al.*, 2008). Cowman & Bellwood (2011, 2013) have also recognized this sequence, indicating that the CT has functioned as a refugium as well as a wellspring of biodiversity. Therefore, it is apparent that the CT has served as both a museum and a cradle of diversity, *but the museum came first and the cradle second.* The concept of the CT as both a museum and a cradle may augment earlier theories that involved accumulation only, an overlap of Indian Ocean and Western Pacific faunas, and the mid-domain hypothesis (Connolly *et al.*, 2003).

Fossil studies have shown that, throughout the Phanerozoic (540 Ma to present), shallow reefs have functioned as cradles of evolution and sources of biodiversity for benthic invertebrates (Kiessling *et al.*, 2010). During the Cenozoic (65 Ma to present), reefs have also apparently driven the diversification of teleost fishes (Alfaro *et al.*, 2007; Cowman & Bellwood, 2013). A general characteristic of centres of origin is an enhanced level of competition that produces species with the highest competitive, defensive and reproductive performance. From these centres of innovation, novel lineages spread out, bringing increases in ecosystem productivity that already existed in the centres (Vermeij, 2005). This outward flow effect was demonstrated by Karlson *et al.* (2004), who examined local coral reef communities along a 10,000-km transect from the CT to Polynesia. A strong linear relationship between local and regional species diversity was demonstrated throughout. The authors concluded that regional enrichment was pervasive and influenced both rich and poor communities.

Dispersive species

In comparison to the Caribbean Centre, whose influence is confined to the Atlantic Ocean, numerous species produced by the CT have extended their ranges into other oceans (Figs 1 & 2). To the east, these dominant species extend through the Indian Ocean and into the Red Sea, and southwards along the East African coast to the Cape of Good Hope. From the Red Sea, more than 300 species including more than 60 fishes have invaded the Mediterranean by means of the Suez Canal (Goren & Galil, 2005). In addition, at least 47 fishes and numerous invertebrates have penetrated the Atlantic by rounding the tip of South Africa (Floeter *et al.*, 2008). To the west, along the shores of the Eastern Pacific and nearby islands, 80 fishes, 61 gastropod molluscs, and 95% of the corals are recent immigrants from the IWP (Robertson *et al.*, 2004; http://biogeodb.stri.si.edu/sftep/).

It was previously believed that dispersal from centres of origin was unidirectional – outwards into areas where the biota was poorer and the competition lower (Briggs, 1995). Although strictly eastward trans-Pacific migrations are indicated for molluscs (Vermeij, 1978; Emerson, 1991), some fish species have proved capable of crossing the East Pacific Barrier from east to west. Twenty-two shore fish species are presently known to be westward migrants, and 16 of them are recorded from the Hawaiian Islands (Lessios & Robertson, 2006). Some fish species accompany floating debris and thus can transgress barriers that otherwise may be impassable for shore species. In addition, several lines of evidence now indicate that peripheral provinces can export propagules back towards the CT, including Hawaii (Bay *et al.*, 2004; Eble *et al.*, 2011b; Gaither *et al.*, 2011b) and the Red Sea (DiBattista *et al.*, 2013), consistent with the accumulation model.

NORTH PACIFIC

The cold-temperate North Pacific Ocean functions as an important evolutionary engine, producing fauna and flora that have been able to transgress biogeographic boundaries and become established elsewhere (Briggs, 2003). By this means, lineages that originated in the North Pacific have an enormous influence on the biology of the cold-temperate and cold waters of the world, including the deep sea.

The trans-Arctic interchange between the North Pacific and the North Atlantic was well under way by *c.* 3.5 Ma, with biogeographic consequences described by Vermeij (1991, 2004). He identified 265 molluscan species that had invaded from the Pacific to the Atlantic, and only 24 that had invaded in the opposite direction, a ratio of more than 9:1. Despite this influx into the Atlantic, modern molluscan species diversity in the North Pacific is approximately twice as great as that in the Atlantic. Hence, the asymmetry of the invasion cannot be explained solely by the 2:1 ratio in species diversity. The diversity of fish species is about 3:1 for the North Pacific relative to the North Atlantic (Briggs, 1974).

Although the area of the North Pacific shelf occupied by boreal waters is larger than the equivalent part of the North Atlantic, it is not twice as large, so size alone does not seem to be sufficient to account for the difference in species diversity. Because the North Atlantic is a smaller ocean with a smaller heat budget, it is more susceptible to the influence of ice from the Arctic Basin, and it was exposed to lower temperatures during the Pliocene glacial stages. Extinctions during that epoch were higher in the North Atlantic than in the North Pacific, but primary productivity in the latter may also have been greater (Vermeij, 1989). Owing to the presence of the Bering land bridge, the North Pacific was not exposed to the Arctic Basin during the glacial stages. This protection from temperature extremes, along with a larger area and higher primary production, may have been important in promoting the greater diversity in the North Pacific.

Although the trans-Arctic migrations are best known through the molluscan surveys of Vermeij (1991, 2004), almost all groups of North Atlantic macroinvertebrates and fishes include species of North Pacific ancestry. For example, the fish families Salmonidae, Osmeridae, Zoarcidae, Hexagrammidae, Cottidae, Agonidae, Liparididae, Stichaeidae and Pholididae probably originated in the North Pacific but contributed one or more species to the North Atlantic. However, the cod family Gadidae evolved in the Atlantic and contributed three species to the North Pacific. Among the marine mammals, fur seals (family Otariidae) and walruses (family Odobenidae) originated in the North Pacific (Carroll, 1988); true seals (family Phocidae) may also have originated in the North Pacific (Fyler *et al.*, 2005).

The North Pacific Centre has contributed a broad variety of organisms to the cold-temperate Southern Hemisphere. The migrations took place primarily via isothermic submergence, whereby species could maintain a suitable temperature by moving beneath the tropics at great depth. Lindberg (1991) proposed that some temperate organisms, confined to shallow water, may have migrated by using upwelling systems as stepping stones across the tropics. Most cases of interhemispheric migration involve populations that have been separated long enough to have become distinct species or genera. The fish genus *Sebastes* (family Scorpaenidae) is extraordinarily diverse in the North Pacific, represented by at least 65 species in the north-east Pacific, 27 in the north-west Pacific, and 7 in the Gulf of California. In addition, four exist in the North Atlantic, and at least three in the Southern Hemisphere originated from a single dispersal south along the west coast of the Americas within the past 200,000 years (Rocha-Olivares *et al.*, 1999). A genetic analysis by Hyde & Vetter (2007) indicated that the genus originated in the north-west Pacific in the mid-Miocene and dispersed in synchrony with high-latitude cooling.

Two other fish families of North Pacific origin are represented by numerous species around the Antarctic continent, namely the Liparididae (snailfishes) and the Zoarcidae (eelpouts). Both are capable of penetrating deep water and probably migrated south using isothermic submergence. Andriashev (1986, 1991) showed that the shallow water liparidids evidently reached the North Atlantic during the trans-Arctic interchange. However, members of the deep-water liparidid genus *Paraliparis* dispersed to the Antarctic along the west coast of the Americas. From the Antarctic, the genus colonized northwards along the mid-Atlantic Ridge and thence to the Arctic Basin. As a result, the liparidid fauna of the Arctic–North Atlantic owes its origin to two migratory groups: the shallow-water genera came directly through the Arctic Ocean, while the deep-water paraliparids dispersed south to the Antarctic via the Eastern Pacific, then north to the Arctic Basin via the Atlantic.

The Zoarcidae has speciated extensively in Antarctic and sub-Antarctic waters (Anderson, 1988). The family Cottidae (sculpins) originated in the North Pacific and is represented in the Southern Ocean by the single genus *Antipodocottus* (Nelson, 1985). The large brown algae or kelps of the order Laminariales belong to four families, all of them found in the North Pacific. Estes & Steinberg (1988) concluded that the centre of origin for the order was in the North Pacific and that the southern species must have reached their present ranges via dispersal. Bolton (2010) located the putative kelp ancestors in northern Japan. Indeed, the contemporary Arctic marine flora is largely of Pacific origin (Adey *et al.*, 2008). The crab genus *Cancer* originated in the North Pacific, spread to the North Atlantic, and then reached the Southern Hemisphere by isothermic submersion. Phylogeographic analyses indicate that this trans-Arctic invasion took place 6–12 Ma and that the dispersal to New Zealand occurred *c.* 6 Ma (Harrison & Crespi, 1999). For high-latitude molluscan faunas, Crame (1996) identified 27 cases of bipolar (Arctic/Antarctic) or bi-temperate distributions. In several cases where ancestral locations could be resolved, the genera had evidently originated in the North Pacific.

In general, the predominant interhemispheric dispersals in the Pacific Ocean have taken place from north to south. This, together with the strong North Pacific influence in the Arctic–North Atlantic, indicates that the rich fauna and flora of the former have produced many species that have dispersed across biogeographic boundaries and become established elsewhere. The North Pacific has had a profound influence on the composition of the marine ecosystems in the Arctic, North Atlantic, temperate Southern Ocean and Antarctic, and has also been a source of species that inhabit the deep sea (Zezina, 1997).

East–west differences

The Bering Sea is a broad, shallow basin almost completely enclosed to the north and bordered by the Alaska Peninsula and the Aleutian islands to the south. The absence of obvious barriers might lead one to expect a homogeneous marine fauna, but several investigators, beginning with Andriashev (1939), have recognized significant differences across this sea. Numerous species, considered to be endemic to one side or the other, are documented among the anomuran crabs, polychaetes, ascidians and fishes (Briggs, 1974). The more recent literature pertaining to amphi-Pacific relationships has been reviewed by Ilves & Taylor (2007). On the western side, the complex geological history, with periodic isolations of the Sea of Japan and the Okhotsk Sea, was probably important in generating diversity (Figure 3 in Briggs & Bowen, 2012). The fish families Cottidae, Zoarcidae and Liparididae, the genera *Oncorhynchus* and *Sebastes* (Hyde & Vetter, 2007), and numerous molluscan genera probably underwent major radiations in that area. In contrast, the fish family Embiotocidae (surf perches) and the gastropod genera *Nucella* and *Littorina* may have originated on the eastern side (Ilves & Taylor, 2007). So, the North Pacific has two diversity hotspots, each demonstrating evolutionary innovation.

SOUTHERN OCEAN

Griffiths *et al.* (2009) prompted a major revision of Southern Ocean biogeography, demonstrating that all provinces cluster into three primary groupings: southern South America, New Zealand–Australia, and Antarctic. There is a strong similarity between South America and the Antarctic, far greater than either has with New Zealand–Australia. The sub-Antarctic islands of Kerguelen, Crozet and Prince Edward show a South American signature for the bryozoans and bivalves, but the gastropods are affiliated with the Antarctic. The New Zealand sub-Antarctic islands (Figure 5 in Briggs & Bowen, 2012) have a strong New Zealand relationship except for the cheilostomes (bryozoans), which are affiliated with Antarctic fauna. New Zealand has the richest fauna and highest endemism: 1376 gastropods (65% endemic) and 380 bivalves (52% endemic), although these numbers include a few warm-temperate species. MacDiarmid & Patuawa (2010) reported even higher endemism for gastropods (87%) and bivalves (85%). These results were surprising, as it was previously thought that South America hosted the richest cold-temperate fauna in the Southern Ocean. After New Zealand, the Tasmania Province is the next richest, with extremely high endemism among 869 gastropods and 232 bivalves (93%) (Griffiths *et al.*, 2009).

In comparison, the Antarctic has 543 known gastropods (73% endemic) and 141 bivalves (49% endemic). The gastropods were the only class to indicate a difference between East and West Antarctica, with areas of overlap in the Weddell and Bellingshausen seas. The influence of the circumpolar West Wind Drift (WWD) was most pronounced in the cheilostomes, cyclostomes and bivalves, whereby South American species had been transported all the way to Kerguelen and intervening islands (Figure 6 in Briggs & Bowen, 2012). That influence probably also extends to Macquarie Island but recent data are lacking. For many invertebrates, kelp rafts may be an important dispersal mechanism (Smith, 2002). At least one fish species, *Chionodraco rastrospinosus*, has a circum-Antarctic distribution (Papetti *et al.*, 2012).

The documentation by Griffiths *et al.*'s (2009) of high individual endemism for the Falkland Islands, southern Argentina, southern Chile and Tierra del Fuego is astonishing and unprecedented. All four of these localities lie in geographic proximity (Figure 4 in Briggs & Bowen, 2012), with comparable temperatures and climate, and they were previously thought to have no substantial faunal differences. Now, however, their invertebrate faunas indicate that each is a separate province, an outstanding biogeographic enigma. Although the Falklands are slightly separated, about 460 km from South America, the other three are contiguous. Why should Tierra del Fuego exhibit 28% endemism in bivalves and 18% in gastropods, when it is separated from the rest of the continent only by the narrow Strait of Magellan? Some of the Falkland endemism might be explained by its history of once having been close to Africa and then moving with South America as that continent separated from Africa (McDowall, 2005), but there is no tectonic evidence that Tierra del Fuego was separated from the rest of South America.

The very diverse Antarctic icefishes (suborder Notothenioidei), including eight families, 44 genera and 129 species (Eastman, 2005), dominate the ichthyofauna, often comprising 80–90% of the species in Antarctic fish catches. A notothenioid fossil from the late Eocene of Seymour Island reinforces the theory of an Antarctic origin of this group (Balushkin, 1994). However, a molecular phylogeny indicates a close relationship among the notothenioids, zoarcids and gadids (cods) (Verde *et al.*, 2006), indicating that the notothenioids may have originated in the North Pacific along with the zoarcids, or else both may have originated in the Antarctic.

A molecular phylogeny of the notothenioids (Near & Cheng, 2008) reveals a specialized, high Antarctic group comprising about 20 genera. In contrast, there is a basal group of four genera (*Bovichtus*, *Cottoperca*, *Pseudaphritis*, *Eleginops*) that have a peripheral distribution in the surrounding cold-temperate marine waters as well as in freshwater in South America and Australia. This kind of phylogenetic pattern, where the more advanced groups occupy the centre and the more primitive groups are found at the periphery, indicates a centre of origin.

As a centre of origin, the Antarctic may have had its greatest impact on the abyssal (4000–6000 m) and hadal (6000–10,900 m) zones. In addition to the production of species that have invaded other areas, the Antarctic has provided a refugium for phylogenetic relicts. The most generalized gadiform fishes (family Muraenolepidae) include four species on the shelf and slopes of the Antarctic and sub-Antarctic, which thus inhabit the southern periphery of the order (Howe, 1990). The lantern fishes (family Myctophidae) originated in the tropical waters of the Tethys Sea, but the three most primitive genera are now confined to the Antarctic and sub-Antarctic (Andriashev, 1988). For the invertebrates, Antarctica has been described as one of the last strongholds of the brachiopods, together with the hexactinellid sponges and several bivalve genera (Crame, 1996).

EVOLUTIONARY CONSEQUENCES AND CONSERVATION IMPLICATIONS

There are relatively few impenetrable barriers to facilitate allopatric speciation in the sea, aside from the tectonic rise of landmasses and the imposition of ocean temperature zones. Hence the soft (weak or intermittent) barriers predominate and promote differentiation. There is now good evidence that natural selection can maintain adaptations in local populations despite ongoing gene flow (Gillespie, 1998; Rocha *et al.*, 2005b) and that this process can ultimately lead to speciation (Doebeli & Dieckmann, 2003). Many broadly distributed marine organisms exist as mosaics of partially isolated subpopulations separated by soft barriers. Thus, when speciation does take place it may most often occur via the parapatric mode, when natural selection overwhelms the homogenizing effects of gene flow (Rocha & Bowen, 2008).

As more information is gathered about the consequences of marine invasions and about local versus regional relationships, it is becoming obvious that native species in less diverse ecosystems almost invariably make accommodations to accept colonizers from more diverse systems (Briggs, 2010). Usually, the native species persist by retaining parts of their original habitats. Accommodations constitute the basic mechanism that is responsible for the operation of certain global dynamics, including the spread of dominant species as well as the maintenance or increase of biodiversity in areas peripheral to diversity centres. Invasions may be as crucial to the short-term health of communities and ecosystems as mutations are to the long-term evolution of populations and species (Vermeij, 2005).

The observed lack of contemporary marine extinctions (Dulvy *et al.*, 2008) means that the continued accommodation of invader species may increase overall biodiversity in peripheral ecosystems (Briggs, 2011). Marine extinctions are not the result of species invasions but are concentrated in a series of pulses after drastic environmental changes. The most recent pulse occurred at the beginning of the Pleistocene, *c.* 1.5 Ma (Jablonski, 2008). If the global warming trend continues, it may result in another pulse of marine extinction. There are numerous small populations, remnants of much larger ones, as a result of overfishing during the past 50 years. These, as well as new species evolving in the high-diversity centres, deserve extraordinary conservation measures.

CONCLUSIONS

The realignment of marine biogeographic regions and provinces, plus many recent publications, has allowed a better understanding of evolutionary processes in the marine fauna. For the Atlantic Ocean, we now have a much improved concept of the directions and magnitude of species dispersal, both within the ocean basin and from external sources. In the Caribbean Province, the Antilles from Cuba to northern South America possess the greatest species diversity and probably function as the evolutionary centre, although there is evidence that some Brazilian Province species have been able to invade the Caribbean. A few tropical species from the Western Indian Ocean have colonized the Atlantic by rounding the Cape of Good Hope at infrequent times when ocean conditions favoured westward transport.

In the IWP, the huge Indo-Polynesian Province, which extends halfway around the world, contains the peak of global biodiversity in the Coral Triangle (CT). The CT apparently contributes to biodiversity via speciation along several pathways, while another area of speciation, the episodic Indo-Pacific Barrier, contributes to biodiversity via transient allopatry. Within the CT, phylogeographic research has revealed numerous geographic boundaries and the production of short-range species, indicating evolutionary innovation. The CT appears to have undergone a temporal progression from biodiversity accumulation to speciation to outward dispersal. This dispersal function has influenced the entire global marine tropics and has extended into warm-temperate waters at higher latitudes. Similarly, the North Pacific provinces have contributed species to and added to the diversity of the world's cold-temperate and cold (polar) regions. In the Southern Ocean, the Antarctic and sub-Antarctic provinces act as centres of origin for some families but also as relict havens for others. In southern South America, four newly recognized provinces (Southern Chile, Tierra del Fuego, Southern Argentina, Falkland Islands) exhibit faunal independence yet lie adjacent to one another, providing a biogeographic puzzle that begs for solution.

Overall, the geographic locations of the newer species and the directions of dispersal identify centres of successful speciation in the IWP, North Pacific, Western Atlantic and the high-latitude Southern Ocean. These centres or hotspots generally occur as relatively small areas within large provinces.

We conclude that the dynamic global system of invasions and colonizations is based on the continual outward flow of species from high-diversity centres and the accommodation of such invaders by the native species in outlying communities. Finally, we note that many species persist as small remnants of huge populations that were overfished, and emphasize that these, as well as new species in the high-diversity centres, are compelling conservation priorities.

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REFERENCES

Adey, W.H., Lindstrom, S.C., Hommersand, M.H. & Muller, K.M. (2008) The biogeographic origin of Arctic endemic seaweeds: a thermogeographic view. *Journal of Phycology*, **44**, 1384–1394.

Alfaro, M.E., Santini, F. & Brock, C.D. (2007) Do reefs drive diversification in marine teleosts? Evidence from the pufferfish and their allies (Order Tetraodontiformes). *Evolution*, **61**, 2104–2126.

Allen, G.R. (2008) Conservation hotspots of biodiversity and endemism for Indo-Pacific coral reef fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **18**, 541–556.

Allen, G.R. & Adrim, M. (2003) Coral reef fishes of Indonesia. *Zoological Studies*, **42**, 1–72.

Allen, G.R. & Erdmann, M.V. (2009) Reef fishes of the Bird's Head Peninsula, West Papua, Indonesia. *Check List*, **5**, 587–628.

Alva-Campbell, R., Floeter, S.R., Robertson, D.R., Bellwood, D.R. & Bernardi, G. (2010) Molecular phylogenetics and evolution of *Holacanthus* angelfishes (Pomacanthidae). *Molecular Phylogenetics and Evolution*, **56**, 456–461.

Anderson, M.E. (1988) Studies on the Zoarcidae (Teleostei: Perciformes) of the southern hemisphere 2. Two new genera and two new species from South America. *Proceedings California Academy of Sciences*, **45**, 267–276.

Andriashev, A.P. (1939) *The fishes of the Bering Sea and its neighboring waters, origin and zoogeography*. Leningrad University Press, Leningrad.

Andriashev, A.P. (1986) *Review of the snailfish genus* Paraliparis *(Scorpaeniformes: Liparididae) of the Southern Ocean*. Koeltz, Koenigstein.

Andriashev, A.P. (1988) Problem of geographic and bathymetric distribution of primitive forms in the group distribution range. *Biologya Morya*, **5**, 3–9.

Andriashev, A.P. (1991) Possible pathways of *Paraliparis* (Pisces: Liparididae) and some other North Pacific secondarily deep-sea fishes into North Atlantic and Arctic depths. *Polar Biology*, **11**, 213–218.

Balushkin, A.V. (1994) Fossil notothenioid, and not gadiform, fish *Proeleginops grandeastmanorum* gen. nov. sp. nov. (Perciformes, Notothenioidei, Eleginopidae) from the late Eocene found in Seymour Island (Antarctica). *Voprosy Ikhtiologii*, **34**, 298–307.

Barber, P.H., Palumbi, S.R., Erdmann, M.V. & Moosa, M.K. (2000) A marine Wallace's line? *Nature*, **406**, 692–693.

Barber, P.H., Erdmann, M.V. & Palumbi, S.R. (2006) Comparative phylogeography of three codistributed stomatopods: origins and timing of regional lineage diversification in the Coral Triangle. *Evolution*, **60**, 1825–1839.

Bay, L.K., Choat, J.H., van Herwerden, L. & Robertson, D.R. (2004) High genetic diversities and complex genetic structure in an Indo-Pacific tropical reef fish (*Chlorurus sordidus*): evidence of an unstable evolutionary past? *Marine Biology*, **144**, 757–767.

Beldade, R., Heiser, J.B., Robertson, D.R., Gasparini, J.L., Floeter, S.R. & Bernardi, G. (2009) Historical biogeography and speciation in the Creole wrasses (Labridae, *Clepticus*). *Marine Biology*, **156**, 679–687.

Bellwood, D.R. & Wainwright, P.C. (2002) The history and biogeography of fishes on coral reefs. *Coral reef fishes: dynamics and diversity in a complex ecosystem* (ed. by P.F. Sale), pp. 5–32. Academic Press, San Diego, CA.

Bernardi, G., Robertson, D.R., Clifton, K.E. & Azzurro, E. (2000) Molecular systematics, zoogeography, and evolutionary ecology of the Atlantic parrotfish genus *Sparisoma*. *Molecular Phylogenetics and Evolution*, **15**, 292–300.

Bolton, J.J. (2010) The biogeography of kelps (Laminariales, Phaeophyceae): a global analysis with new insights from recent advances in molecular phylogenetics. *Helgoland Marine Research*, **64**, 263–279.

Bowen, B.W., Bass, A.L., Rocha, L.A., Grant, W.S. & Robertson, D.R. (2001) Phylogeography of the trumpetfish (*Aulostomus* spp.): ring species complex on a global scale. *Evolution*, **55**, 1029–1039.

Bowen, B.W., Bass, A.L., Muss, A.J., Carlin, J. & Robertson, D.R. (2006a) Phylogeography of two Atlantic squirrelfishes (family Holocentridae): exploring pelagic larval duration and population connectivity. *Marine Biology*, **149**, 899–913.

Bowen, B.W., Muss, A., Rocha, L.A. & Grant, W.S. (2006b) Shallow mtDNA coalescence in Atlantic pygmy angelfishes (genus *Centropyge*) indicates a recent invasion from the Indian Ocean. *Journal of Heredity*, **97**, 1–12.

Briggs, J.C. (1974) *Marine zoogeography*. McGraw-Hill, New York.

Briggs, J.C. (1984) *Centres of origin in biogeography*. Biogeography Monograph No. 1, University of Leeds, Leeds, UK.

Briggs, J.C. (1987) Antitropical distributions and evolution in the Indo-West Pacific Ocean. *Systematic Zoology*, **36**, 237–247.

Briggs, J.C. (1995) *Global biogeography*. Elsevier, Amsterdam.

Briggs, J.C. (2003) Marine centres of origin as evolutionary engines. *Journal of Biogeography*, **30**, 1–18.

Briggs, J.C. (2004) Older species: a rejuvenation on coral reefs? *Journal of Biogeography*, **31**, 525–530.

Briggs, J.C. (2005) The marine East Indies: diversity and speciation. *Journal of Biogeography*, **32**, 1517–1522.

Briggs, J.C. (2006) Proximate sources of marine biodiversity. *Journal of Biogeography*, **33**, 1–10.

Briggs, J.C. (2007) Marine longitudinal biodiversity: causes and conservation. *Diversity and Distributions*, **13**, 544–555.

Briggs, J.C. (2010) Marine biology: the role of accommodation in shaping marine biodiversity. *Marine Biology*, **157**, 2117–2126.

Briggs, J.C. (2011) Marine extinctions and conservation. *Marine Biology*, **158**, 485–488.

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

Carpenter, K.E., Barber, P.H., Crandall, E.D., Ablan-Lagman, M.C.A., Ambariyanto, Mahardika, G.N., Manjaji-Matsumoto, B.M., Juinio-Meñez, M.A., Santos, M.D., Starger, C.J. & Toha, A.H.A. (2011) Comparative phylogeography of the Coral Triangle and implications for marine management. *Journal of Marine Biology*, **2011**, Article ID 396982, pp. 1–14. doi:10.1155/2011/396982.

Carroll, R.L. (1988) *Vertebrate paleobiology and evolution*. W.H. Freeman, New York.

Chappell, J. & Shackleton, N.J. (1986) Oxygen isotopes and sea level. *Nature*, **324**, 137–140.

Coates, A.G. & Obando, J.A. (1996) The geologic evolution of the Central American isthmus. *Evolution and environment in tropical America* (ed. by J. Jackson, A.F. Budd and A.G. Coates), pp. 21–56. University of Chicago Press, Chicago.

Connolly, S.R., Bellwood, D.R. & Hughes, T.P. (2003) Indo-Pacific biodiversity of coral reefs: deviations from a mid-domain model. *Ecology*, **84**, 2178–2190.

Cowman, P.F. & Bellwood, D.R. (2011) Coral reefs as drivers of cladogenesis: expanding coral reefs, cryptic extinction events, and the development of biodiversity hotspots. *Journal of Evolutionary Biology*, **24**, 2543–2562.

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.

Coyne, J.A. & Orr, H.A. (2004) *Speciation*. Sinauer Associates, Sunderland, MA.

Craig, M.T. (2008) The goldrim surgeonfish (*Acanthurus nigricans*; Acanthuridae) from Diego Garcia, Chagos Archipelago: first record for the central Indian Ocean. *Zootaxa*, **1850**, 65–68.

Crame, J.A. (1996) Evolution of high-latitude molluscan faunas. *Origins and evolutionary radiation of the Mollusca* (ed. by J. Taylor), pp. 119–131. Oxford University Press, Oxford.

Daly-Engel, T.S., Seraphin, K.D., Holland, K.N., Coffey, J.P., Nance, H.A., Toonen, R.J. & Bowen, B.W. (2012) Global phylogeography with mixed-marker analysis reveals male-mediated dispersal in the endangered scalloped hammerhead shark (*Sphyrna lewini*). *PLoS ONE*, **7**, e29986.

Dercourt, J., Zonenshain, L.P., Ricou, L.E., Kazmin, V.G., Le Pichon, X., Knipper, A.L., Grandiaquet, C., Sbortshikov, J.M., Geyassant, J., Lepvrier, C., Pechersky, D.H., Boulin, J., Sibuet, J.-C., Savostin, L.A., Sorokhtin, O., Westphal, M., Bazhenov, M.L., Lauer, J.P. & Biju-Duval, B. (1986) Geological evolution of the Tethys belt from the Atlantic to the Pamirs since the LIAS. *Tectonophysics*, **123**, 241–315.

DiBattista, J.D., Wilcox, C., Craig, M.T., Rocha, L.A. & Bowen, B.W. (2011) Phylogeography of the Pacific Blueline Surgeonfish *Acanthurus nigroris* reveals a cryptic species in the Hawaiian Archipelago. *Journal of Marine Biology*, **2011**, Article ID 839134, pp. 1–17. doi:10.1155/2011/839134.

DiBattista, J.D., Craig, M.T., Rocha, L.A., Feldheim, K.A. & Bowen, B.W. (2012) Phylogeography of the Indo-Pacific butterfly fishes, *Chaetodon meyeri* and *Chaetodon ornatissimus*: sister species reveal different evolutionary histories and discordant results from mtDNA and microsatellites. *Journal of Heredity*, **103**, 617–629.

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*, doi:10.1111/jbi.12068.

Doebeli, M. & Dieckmann, U. (2003) Speciation along environmental gradients. *Nature*, **421**, 259–264.

Dulvy, N.K., Pinnegar, J.K. & Reynolds, J.D. (2008) Holocene extinctions in the sea. *Holocene extinctions* (ed. by S.T. Turvey), pp. 129–150. Oxford University Press, Oxford.

Duncan, K.M., Martin, A.P., Bowen, B.W. & de Couet, D.H. (2006) Global phylogeography of the scalloped hammerhead shark (*Sphyrna lewini*). *Molecular Ecology*, **15**, 2239–2251.

Eastman, J.T. (2005) The nature of the diversity of Antarctic fishes. *Polar Biology*, **28**, 93–107.

Eble, J.A., Rocha, L.A., Craig, M.T. & Bowen, B.W. (2011a) Not all larvae stay close to home: long-distance dispersal in Indo-Pacific reef fishes, with a focus on the Brown Surgeonfish (*Acanthurus nigrofuscus*). *Journal of Marine Biology*, **2011**, Article ID 518516, pp. 1–12. doi:10.1155/2011/518516.

Eble, J.A., Toonen, R.J., Sorensen, L.L., Papastamatiou, Y. & Bowen, B.W. (2011b) Escaping paradise: larval export from Hawaii in an Indo-Pacific reef fish, the yellow tang (*Zebrasoma flavescens*). *Marine Ecology Progress Series*, **428**, 245–258.

Emerson, W.K. (1991) First records for *Cymatium mundum* (Gould) in the Eastern Pacific Ocean, with comments on the zoogeography of the tropical trans-Pacific tonnacean and non-tonnacean prosobranch gastropods with Indo-Pacific faunal affinities in west American waters. *The Nautilus*, **105**, 62–80.

Estes, J.A. & Steinberg, P.D. (1988) Predation, herbivory and kelp evolution. *Paleobiology*, **14**, 19–36.

Floeter, S.R., Rocha, L.A., Robertson, D.R., Joyeux, J.C., Smith-Vaniz, W.F., Wirtz, P., Edwards, A.J., Barreiros, J.P., Ferreira, C.E.L., Gasparini, J.L., Brito, A., Falcon, J.M., Bowen, B.W. & Bernardi, G. (2008) Atlantic reef fish biogeography and evolution. *Journal of Biogeography*, **35**, 22–47.

Fraser, T.H. & Allen, G.R. (2011) A new cardinalfish of the genus *Apogonichthyoides* (Perciformes, Apogonidae) from Raja Ampat Islands, with a key to species. *Zootaxa*, **3095**, 63–68.

Fyler, C.A., Reeder, T.W., Berta, A., Antonelis, G., Aguilar, A. & Androukaki, E. (2005) Historical biogeography and phylogeny of monachine seals (Pinnipedia: Phocidae) based on mitochondrial and nuclear data. *Journal of Biogeography*, **32**, 1267–1279.

Gaither, M.R., Toonen, R.J., Robertson, R.R., Planes, S. & Bowen, B.W. (2010) Genetic evaluation of marine biogeographic barriers: perspectives from two widespread Indo-Pacific snappers (*Lutjanus kasmira* and *Lutjanus fulvus*). *Journal of Biogeography*, **37**, 133–147.

Gaither, M.R., Bowen, B.W., Bordenave, T.-R., Newman, S.J., Gomez, J.A., van Herwerden, L. & Craig, M.T. (2011a) Phylogeography of the reef fish *Cephalopholus argus* (Epinephelidae) indicates Pleistocene isolation across the Indo-Pacific Barrier with contemporary overlap in the Coral Triangle. *BMC Evolutionary Biology*, **11**, 189. doi:10. 1186/1471-2148-11-189.

Gaither, M.R., Jones, S.A., Kelley, C., Newman, S.J., Sorenson, L. & Bowen, B.W. (2011b) High connectivity in the deepwater snapper *Pristipomoides filamentosus* (Lutjanidae) across the Indo-Pacific with isolation in the Hawaiian Archipelago. *PLoS ONE*, **6**, e28913.

Gillespie, J.H. (1998) *Population genetics: a concise guide*. Johns Hopkins University, Baltimore, MD.

Goren, M. & Galil, B.S. (2005) A review of the changes of the fish assemblages of Levantine inland and marine ecosystems following the introduction of non-native fishes. *Journal of Applied Ichthyology*, **21**, 1–7.

Griffiths, H.W., Barnes, D.K.A. & Linse, K. (2009) Towards a generalized biogeography of the Southern Ocean benthos. *Journal of Biogeography*, **36**, 162–177.

Hanel, R., Westneat, M. & Sturmbauer, C. (2002) Phylogenetic relationships, evolution of broodcare behavior, and geographic speciation in the wrasse tribe Labrini. *Journal of Molecular Evolution*, **55**, 776–789.

Harrison, M.K. & Crespi, B.J. (1999) Phylogenetics of *Cancer* crabs (Crustacea: Decapoda: Brachyura). *Molecular Phylogeny and Evolution*, **12**, 186–199.

Hobbs, J.-P.A., Frisch, A.J., Allen, G.R. & Van Herwerden, L. (2009) Marine hybrid hotspot at Indo-Pacific biogeographic border. *Biology Letters*, **5**, 258–261.

Hoeksema, B.W. (2007) Delineation of the Indo-Malayan centre of maximum marine biodiversity: the Coral Triangle. *Biogeography, time, and place: distributions, and islands* (ed. by W. Renema), pp. 117–178. Springer, Dordrecht.

Hoorn, C. (1996) Miocene deposits in the Amazon foreland basin. *Science*, **273**, 122–125.

Horne, J.B., van Herwerden, L., Choat, H.J. & Robertson, D.R. (2008) High population connectivity across the Indo-Pacific: congruent lack of phylogeographic structure in three reef fish congeners. *Molecular Phylogenetics and Evolution*, **49**, 629–638.

Howe, G.J. (1990) The syncranial osteology of the southern eel-cod family Muraenolepidae, with comments on its phylogenetic relationships and on the biogeography of the sub-Antarctic gadoid fishes. *Zoological Journal of the Linnean Society*, **100**, 73–100.

Hyde, J.R. & Vetter, R.D. (2007) The origin, evolution, and diversification of the rockfishes of the genus *Sebastes* (Cuvier). *Molecular Phylogenetics and Evolution*, **44**, 790–811.

Ilves, K.L. & Taylor, E.B. (2007) Evolutionary and biogeographical patterns within the smelt genus *Hypomesus* in the North Pacific Ocean. *Journal of Biogeography*, **35**, 48–64.

Jablonski, D. (2008) Extinction and the spatial dynamics of biodiversity. *Proceedings of the National Academy of Sciences USA*, **105**(Suppl. 1), 11528–11535.

Jokiel, P. & Martinelli, F.J. (1992) The vortex model of coral reef biogeography. *Journal of Biogeography*, **19**, 449–458.

Karlson, R.H., Cornell, H.V. & Hughes, T.P. (2004) Coral communities are regionally enriched along an oceanic biodiversity gradient. *Nature*, **429**, 867–870.

Kiessling, W., Simpson, C. & Foote, M. (2010) Reefs as cradles of evolution and sources of biodiversity in the Phanerozoic. *Science*, **327**, 196–198.

Kirkendale, L.A. & Meyer, C.P. (2004) Phylogeography of the *Patelloida profunda* group (Gastropoda: Lottidae): diversification in a dispersal-driven marine system. *Molecular Ecology*, **13**, 2749–2762.

Ladd, H.S. (1960) Origin of the Pacific island molluscan fauna. *American Journal of Science*, **258A**, 137–150.

Lavery, S., Moritz, C. & Fielder, D.R. (1996) Indo-Pacific population structure and evolutionary history of the coconut crab, *Birgus latro*. *Molecular Ecology*, **5**, 557–570.

Lessios, H.A. & Robertson, D.R. (2006) Crossing the impassable: genetic connections in 20 reef fishes across the eastern Pacific barrier. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 2201–2208.

Lessios, H.A., Kessing, B.D. & Pearse, J.S. (2001) Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. *Evolution*, **55**, 955–975.

Lessios, H.A., Kane, J. & Robertson, D.R. (2003) Phylogeography of the pantropical sea urchin *Tripneustes*: contrasting patterns of population structure between oceans. *Evolution*, **57**, 1026–1036.

Levy, A., Wirtz, P., Floeter, S.R. & Almada, V.C. (2011) The Lusitania Province as a center of diversification: the phylogeny of the genus *Microlipophrys* (Pisces: Blenniidae). *Molecular Phylogenetics and Evolution*, **58**, 409–413.

Lindberg, D.R. (1991) Marine biotic exchange between the northern and southern hemispheres. *Paleobiology*, **17**, 308–324.

Lourie, S.A., Green, D.M. & Vincent, A.C.J. (2005) Dispersal, habitat differences, and comparative phylogeography of Southeast Asian seahorses (Syngnathidae: *Hippocampus*). *Molecular Ecology*, **14**, 1073–1094.

Luiz, O.J., Madin, J.S., Robertson, D.R., Rocha, L.A., Wirtz, P. & Floeter, S.R. (2012) Ecological traits influencing range expansion across large oceanic dispersal barriers: insights from tropical Atlantic reef fishes. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1033–1040.

MacDiarmid, A. & Patuawa, T. (2010) Bivalves and gastropods. *The treasures of the sea: an online summary of New Zealand marine life* (ed. by A. MacDiarmid). Available at: http://www.treasuresofthesea.org.nz/bivalves-and-gastropods (accessed 11 December 2012).

McDowall, R.M. (2005) Falkland Islands biogeography: converging trajectories in the South Atlantic Ocean. *Journal of Biogeography*, **32**, 49–62.

McMillan, W.O. & Palumbi, S.R. (1995) Concordant evolutionary patterns among Indo-West Pacific butterflyfishes. *Proceedings of the Royal Society B: Biological Sciences*, **260**, 229–236.

Miloslavich, P., Díaz, J.M., Klein, E., Alvarado, J.J., Díaz, C., Gobin, J., Escobar-Briones, E., Cruz-Motta, J.J., Weil, E., Cortés, J., Bastidas, A.C., Robertson, R., Zapata, F., Martín, A., Castillo, J., Kazandjian, A. & Ortiz, M. (2010) Marine biodiversity in the Caribbean: regional estimates and distributional patterns. *PLoS ONE*, **5**, e11916.

Mironov, A.N. (2006) Centers of marine fauna distribution. *Zoologichesky Zhurnal*, **85**, 3–17.

Mora, C., Chittaro, P.M., Sale, P.F., Kritzer, J.P. & Ludsin, S.A. (2003) Patterns and processes in reef fish diversity. *Nature*, **421**, 933–936.

Mora, C., Treml, E.A., Roberts, J., Crosby, K., Roy, D. & Tittensor, D.P. (2012) High connectivity among habitats precludes the relationship between dispersal and range size in tropical reef fishes. *Ecography*, **35**, 89–96.

Mundy, B.C., Wass, R., Demartini, E., Greene, B., Zgliczynski, B., Schroeder, R.E. & Musberger, C. (2010) *Inshore fishes of Howland Island, Baker Island, Jarvis Island, Palmyra Atoll, and Kingman Reef*. Atoll Research Bulletin 585. National Museum of Natural History, Washington, D.C.

Muss, A., Robertson, D.R., Stepien, C.A., Wirtz, P. & Bowen, B.W. (2001) Phylogeography of the genus *Ophioblennius*: the role of ocean currents and geography in reef fish evolution. *Evolution*, **55**, 561–572.

Near, T.J. & Cheng, C.-H.C. (2008) Phylogenetics of notothenioid fishes (Teleostei: Acanthomorpha): inferences from mitochondrial and nuclear gene sequences. *Molecular Phylogenetics and Evolution*, **47**, 832–840.

Nelson, J.S. (1985) On the relationships of the New Zealand marine fish *Antipodocottus galatheae* with the Japanese *Stlengis misakia* (Scorpaeniformes: Cottidae). *Record of the New Zealand Oceanographic Institute*, **5**, 1–12.

Papetti, C., Pujolar, J.M., Mezzavilla, M., La Mesa, M., Rock, J., Zane, L. & Patarnello, T. (2012) Population genetic structure and gene flow patterns between populations of the Antarctic icefish *Chionodraco rastrospinosus*. *Journal of Biogeography*, **39**, 1361–1372.

Peeters, F.J.C., Acheson, R., Brummer, G.J.A., de Ruijter, W.P.M., Schneider, R.R., Ganssen, G.M., Ufkes, E. & Kroon, D. (2004) Vigorous exchange between the Indian and Atlantic Oceans at the end of the past five glacial periods. *Nature*, **430**, 661–665.

Penven, P., Lutjeharms, J.R.E., Marchesiello, P., Roy, C. & Weeks, S.J. (2001) Generation of cyclonic eddies by the Agulhas Current in the lee of the Agulhas Bank. *Geophysical Research Letters*, **28**, 1055–1058.

Randall, J.E. (1998) Zoogeography of shore fishes of the Indo-Pacific region. *Zoological Studies*, **37**, 227–268.

Read, C.I., Bellwood, D.R. & van Herwerden, L. (2006) Ancient origins of Indo-Pacific coral reef fish diversity: a case study of the leopard wrasses (Labridae: *Macropharyngodon*. *Molecular Phylogenetics and Evolution*, **38**, 808–819.

Reece, J.S., Bowen, B.W., Smith, D.G. & Larson, A.F. (2010) Molecular phylogenetics of moray eels (Muraenidae) demonstrates multiple origins of shell-crushing jaw (*Gymnomuraena, Echidna*) and multiple colonizations of the Atlantic Ocean. *Molecular Phylogenetics and Evolution*, **57**, 829–835.

Renema, W., Bellwood, D.R., Braga, J.C., Bromfield, K., Hall, R., Johnson, K.G., Lunt, P., Meyer, C.P., McMonagle, L.B., Morley, R.J., O'Dea, A., Todd, J.A., Wesselingh, F.P., Wilson, M.E.J. & Pandolfi, J.M. (2008) Hopping hotspots: global shifts in marine biodiversity. *Science*, **321**, 654–657.

Robertson, D.R., Grove, J.S. & McCosker, J.E. (2004) Tropical transpacific shore fishes. *Pacific Science*, **58**, 507–565.

Robertson, D.R., Karg, F., de Moura, R.L., Victor, B.C. & Bernardi, B. (2006) Mechanisms of speciation and faunal enrichment in Atlantic parrotfishes. *Molecular Phylogenetics and Evolution*, **40**, 795–807.

Rocha, L.A. & Bowen, B.W. (2008) Speciation in coral reef fishes. *Journal of Fish Biology*, **72**, 1101–1121.

Rocha, L.A., Bass, A.L., Robertson, D.R. & Bowen, B.W. (2002) Adult habitat preferences, larval dispersal, and the comparative phylogeography of three Atlantic surgeonfishes (Teleostei: Acanthuridae). *Molecular Ecology*, **11**, 243–252.

Rocha, L.A., Robertson, D.R., Rocha, C.R., Van Tassell, J.L., Craig, M.T. & Bowen, B.W. (2005a) Recent invasion of the tropical Atlantic by an Indo-Pacific coral reef fish. *Molecular Ecology*, **14**, 3921–3928.

Rocha, L.A., Robertson, D.R., Roman, J. & Bowen, B.W. (2005b) Ecological speciation in tropical reef fishes. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 573–579.

Rocha, L.A., Craig, M.T. & Bowen, B.W. (2007) Phylogeography and the conservation genetics of coral reef fishes. *Coral Reefs*, **26**, 501–512.

Rocha, L.A., Rocha, C.R., Robertson, D.R. & Bowen, B.W. (2008) Comparative phylogeography of Atlantic reef fishes indicates both origin and accumulation of diversity in the Caribbean. *BMC Evolutionary Biology*, **8**, 157. doi:10.1186/1471-2148-8-157.

Rocha-Olivares, A., Rosenblatt, R.H. & Vetter, R.D. (1999) Cryptic species of rockfishes (*Sebastes*: Scorpaenidae) in the Southern Hemisphere inferred from mitochondrial lineages. *Journal of Heredity*, **90**, 404–411.

Schultz, J.K., Feldheim, K.A., Gruber, S.H., Ashley, M.V., McGovern, T.M. & Bowen, B.W. (2008) Global phylogeography and seascape genetics of the lemon sharks (genus *Negaprion*). *Molecular Ecology*, **17**, 5336–5348.

Smith, S.D.A. (2002) Kelp rafts in the Southern Ocean. *Global Ecology and Biogeography*, **11**, 67–69.

Timm, J., Figiel, M. & Kochzius, M. (2008) Contrasting patterns in species boundaries and evolution of anemonefishes (Amphiprioninae, Pomacentridae) in the centre of marine biodiversity. *Molecular Phylogenetics and Evolution*, **49**, 268–276.

Verde, C., Balestrieri, M., de Pascale, D., Pagnozzi, D., Lecointre, G. & di Prisco, G. (2006) The oxygen transport system in three species of the boreal fish family Gadidae. *Journal of Biological Chemistry*, **281**, 22073–22084.

Vermeij, G.J. (1978) *Biogeography and adaptation*. Harvard University Press, Cambridge, MA.

Vermeij, G.J. (1989) Geographical restriction as a guide to the causes of extinction: the case of the cold northern oceans during the Neogene. *Paleobiology*, **15**, 335–356.

Vermeij, G.J. (1991) Anatomy of an invasion: the trans-Arctic interchange. *Paleobiology*, **17**, 281–307.

Vermeij, G.J. (2004) *Nature: an economic history*. Princeton University Press, Princeton, NJ.

Vermeij, G.J. (2005) Invasion as expectation. *Species invasions: insights into ecology, evolution, and biogeography* (ed. by D.F. Sax, J.J. Stachowicz and S.D. Gaines), pp. 315–339. Sinauer Associates, Sunderland, MA.

Vermeij, G.J. & Rosenberg, G. (1993) Giving and receiving: the tropical Atlantic as donor and recipient region for invading species. *American Malacological Bulletin*, **10**, 181–194.

Veron, J.E.N. (1995) *Corals in space and time*. Cornell University Press, Ithaca, NY.

Veron, J.E.N., DeVantier, L.M., Turak, E., Green, A.L., Kininmonth, S., Stafford-Smith, M. & Peterson, N. (2009) Delineating the Coral Triangle. *Galaxea*, **11**, 91–100.

Victor, B.C. & Randall, J.E. (2010) *Gramma dejongi*, a new basslet (Perciformes: Grammatidae) from Cuba, a sympatric sibling species of *G. loreto*. *Zoological Studies*, **49**, 865–871.

Voris, H.K. (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography*, **27**, 1153–1167.

Whitney, N.M., Robbins, W.D., Schultz, J.K., Bowen, B.W. & Holland, K.N. (2011) Oceanic dispersal in a sedentary reef shark (*Triaenodon obesus)*: genetic evidence for extensive connectivity without a pelagic larval stage. *Journal of Biogeography*, **39**, 1144–1156.

Williams, S.T. & Reid, D.G. (2004) Speciation and diversity on tropical rocky shores: a global phylogeny of snails of the genus *Echinolittorina*. *Evolution*, **58**, 2227–2251.

Williams, S.T., Jara, J., Gomez, E. & Knowlton, N. (2002) The marine Indo-West Pacific break: contrasting the resolving power of mitochondrial and nuclear genes. *Integrative and Comparative Biology*, **42**, 941–952.

Woodland, D.J. (1983) Zoogeography of the Siganidae (Pisces): an interpretation of distribution and richness patterns. *Bulletin of Marine Science*, **33**, 713–717.

Zezina, O.N. (1997) Biogeography of the bathyal zone. *Advances in Marine Biology*, **32**, 389–420.

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