A realignment of marine biogeographic provinces with particular reference to fish distributions

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INTRODUCTION

Biogeographic patterns are most useful when they identify those parts of the world that host the more unique biotas, that is, areas of evolutionary innovation or refuges where an older biota persists. Edward Forbes, in his posthumous work The Natural History of European Seas (Forbes, 1859), made three observations of lasting value: (1) each zoogeographic province is an area where there was a special manifestation of creative power, and the animals originally formed there are apt to become mixed with emigrants from other provinces; (2) each species was created only once, and individuals tend to migrate outwards from their centre of origin; and (3) provinces must, to be understood, be traced back like species to their origins in past time. Sven Ekman undertook the huge task of analysing all the pertinent literature on marine animal distribution, leading to the publication of his book Tiergeographie des Meeres (Ekman, 1935). This was followed by a revised English edition, Zoogeography of the Sea (Ekman, 1953).

Ekman (1953) considered the marine world to be composed of a series of large regions or subregions. For the continental shelf, he described regions located in warm, temperate, and polar waters; their separation by zoogeographic barriers; and their endemism. Later, Briggs (1974) divided the continental shelf into a series of large biogeographic regions that, in turn, contained smaller provinces. Provinces were defined on the basis of endemism, and it was observed that the greater the proportion of endemic biota, the greater the evolutionary

ABSTRACT

Marine provinces, founded on contrasting floras or faunas, have been recognized for more than 150 years but were not consistently defined by endemism until 1974. At that time, provinces were based on at least a 10% endemism and nested within biogeographic regions that covered large geographic areas with contrasting biotic characteristics. Over time, some minor adjustments were made but the overall arrangement remained essentially unaltered. In many provinces, data on endemism were still not available, or were available only for the most widely studied vertebrates (fishes), a problem that is ongoing. In this report we propose a realignment for three reasons. First, recent works have provided new information to modify or redefine the various divisions and to describe new ones, including the Mid-Atlantic Ridge, Southern Ocean, Tropical East Pacific and Northeast Pacific. Second, phylogeographic studies have demonstrated genetic subdivisions within and between species that generally corroborated provinces based on taxonomic partitions, with a notable exception at the Indian–Pacific oceanic boundary. Third, the original separation of the warm-temperate provinces from the adjoining tropical ones has distracted from their close phylogenetic relationships. Here we propose uniting warm-temperate and tropical regions into a single warm region within each ocean basin, while still recognizing provinces within the warm-temperate and tropical zones. These biogeographic subdivisions are based primarily on fish distribution but utilize other marine groups for comparison. They are intended to demonstrate the evolutionary relationships of the living marine biota, and to serve as a framework for the establishment of smaller ecological units in a conservation context.

Keywords

Endemism, evolution, fishes, marine biogeography, phylogeography, provinces, regions, speciation, zoogeography.
significance. An objective standard was considered to be necessary in order that provinces could be recognized within the larger regions. Various biotic areas had previously been called provinces but there was no agreement as to the qualifications necessary for provincial status. So, after an examination of endemism rates in numerous areas, a value of 10% was chosen for an area to qualify as a distinct province (Briggs, 1974). Notably, this minimum value would admit most of the areas that were previously recognized as provinces on the basis of less formal criteria.

The provinces described herein are in coastal and shallow habitats, and based largely on the distributions of fishes. While both the geographic and taxonomic frameworks are admittedly aligned with the authors’ field of study, this limitation also indicates the state of knowledge. Fishes in shallow areas, usually defined as <200 m depth (Randall, 2007), often are the only groups with sufficient information for biogeographic inference. We have endeavoured to bring in other taxa where information is available and find that, where the fauna is relatively well known, there is a high concordance between levels of endemism in fishes, molluscs and other biotas. For example, the fish fauna of Hawaii is 25% endemic (Randall, 2007), the red algae 25% (Abbott, 1999), and the molluscan fauna 20% (Kay, 1980). In the Caribbean Province, the reef fishes are 33% endemic (Floeter et al., 2008), decapod crustaceans 32% (Boscì, 2000) and corals 37% (Veron, 2000). Exceptions to this concordance may become apparent, providing a fascinating foundation for further study, but some of these disparities in endemism may be cases where one or two taxonomic groups are much better known than others. Endemism rates in many areas and many taxa are still poorly known and are likely to change as the marine biota (especially invertebrates, plants and even microbes) receives greater attention.

The definition of provinces by 10% endemism has been generally accepted for the past 35 years. Good arguments can be made for a higher criterion (15% or 20% endemism), especially to combine depauperate outposts of larger provinces, which may have little evolutionary significance. However, provinces closely linked to those of Briggs (1995) were recently subdivided into ecoregions to address the appropriate scale for conservation efforts (Spalding et al., 2007). Furthermore, the 10% criterion has the advantages of stability and functionality: areas that possess >10% endemism have proved to be locations of unusual evolutionary interest. The 10% criterion is also conservative, because it is typically based on species lists that include oceanic wanderers such as tunas (Randall, 2007), fishes that are very unlikely candidates for endemism on the scale of provinces. The 10% criterion may often be an underestimate, as phylogeographic studies are revealing unrecognized endemic species (Bowen et al., 2006a, 2007; Drew et al., 2010). In the absence of compelling reasons to the contrary, we choose to retain the 10% criterion, while recognizing that this is not an absolute limit but a guidepost for recognizing unique biotic assemblages.

The regions and provinces that were defined in 1974 proved to be useful, but discoveries made during the next 20 years required the changes published in Briggs (1995). In order to keep abreast of continuing research, additional modifications are required. In recent years, the upsurge of phylogeography has produced many useful studies with biogeographic connotations. At the same time, palaeontological research has produced discoveries about fossils, earth movements and sea-level changes that are critical to historical biogeography. It is now possible to provide more accurate reconstructions of evolutionary relationships in several of the large oceanic regions. Some of the research advances need to be reflected in the arrangement of regions and provinces, while other advances have improved our concept of how speciation and dispersal operate in the marine environment.

**MARINE BIOGEOGRAPHY**

With regard to the continental shelves, the four temperature zones of the world’s oceans have usually been identified as tropical, warm-temperate, cold-temperate and cold. Within each zone, a series of biogeographic regions was recognized, and provinces were located within the regions (Briggs, 1974). Over time, a primary criticism of this arrangement was the placement of warm-temperate provinces in different regions from tropical ones. Considering that there is a very close relationship between each warm-temperate province and its adjacent tropical equivalent (Vermey, 2005a), a separation into different regions eventually proved to be inappropriate. Many families and genera span the tropical and warm-temperate regions within each ocean basin, whereas few extend into the cold-temperate regions (Briggs, 1995; Grant et al., 2010). Therefore, a realignment is proposed here in which expanded regions (Fig. 1) will encompass provinces in both temperature zones. If new research has indicated that provinces need to be altered, they are illustrated and references are provided. Otherwise, if no change is required, provinces will remain as described in Briggs (1995).

**COMPLETE OUTLINE OF SHELF REGIONS AND PROVINCES**

**WARM REGIONS** (tropical and warm-temperate waters)

1. **Eastern Atlantic Region**
   - **Provinces**: Lusitania, Black Sea, Caspian, Aral, Tropical Eastern Atlantic, Benguela, St Helena, Ascension, Tristan–Gough, Amsterdam–St Paul.

2. **Western Atlantic Region**
   - **Provinces**: Carolina, Caribbean, Brazilian, Argentinian.

3. **Western Pacific Region**

4. **Tropical Indo-West Pacific Region**
   - **Provinces**: Western Indian Ocean, Red Sea, Indo-Polynesian, Hawaiian, Marquesas, Easter Island.

5. **Eastern Pacific Region**
Provinces: California, Cortez, Panamanian, Galapagos, Peru–Chilean, Juan Fernández.

COOL REGIONS (cold-temperate and polar waters)

A. COLD-TEMPERATE AND POLAR NORTHERN HEMISPHERE

1. Eastern North Pacific Region
   Provinces: Aleutian, Oregon.

2. Western North Pacific Region
   Provinces: Oriental, Kurile, Okhotsk.

3. Western Atlantic Region

4. Eastern Atlantic Region

5. Arctic Region

B. COLD-TEMPERATE AND POLAR SOUTHERN HEMISPHERE

1. South American Region
   Provinces: Southern Chile, Tierra del Fuego, Southern Argentina, Falkland Islands.

2. New Zealand–Australian Region
   Provinces: Tasmania, New Zealand, Antipodes.

3. Sub-Antarctic Region
   Provinces: South Georgia, Bouvet, Crozet, Prince Edward, Kerguelen, Macquarie.

4. Antarctic Region

DISCUSSION

Atlantic Warm Regions

The reconstituted Eastern Atlantic Region (Fig. 1) now extends from the southern entrance to the English Channel southwards to the Cape of Good Hope. The Western Atlantic Region extends from Cape Hatteras and the northern Gulf of Mexico southwards to the Valdes Peninsula on the South American east coast. Included within the two regions are 13 provinces. A comprehensive treatise on tropical Atlantic biogeography and evolution has recently been published by Floeter et al. (2008). Although this work is based on reef fishes, the demonstrated patterns and relationships have significance for many of the other phyla on the continental shelves; it is the source of much of the new information utilized in this section.

Eastern Atlantic Region

From its northern boundary at the southern British Isles, the warm-temperate Lusitania Province extends south to southern Morocco and eastwards through the Mediterranean (Fig. 1). Farther to the east are the Black Sea, Caspian and Aral provinces. There are, to our knowledge, no recent evaluations of endemism in these three provinces; earlier work was reviewed by Briggs (1974). The Lusitania Province includes the offshore islands of the Canaries, Azores and Madeira. The endemism in this province is concentrated within the Mediterranean itself, where 28% of marine species are endemic (IUCN, 2010). The Straits of Gibraltar are often assumed to be a natural barrier between Mediterranean and Atlantic segments of the Lusitania Province. Although phyleogeographic studies of fishes, molluscs, crustaceans and marine mammals show some population genetic separations, there is no consistent pattern of evolutionary partitions at the Straits (reviewed in Paternello et al., 2007).

From southern Morocco, at Cap Juby, the Tropical Eastern Atlantic (TEA) Province extends south to Mossamedes, Angola (Fig. 2). The offshore islands of the Cape Verdes, São Tomé and Principe are included. In the TEA there are about 388
species of reef fishes with some 30% endemism (Floeter et al., 2008); opisthobranch gastropod endemism is about 36% (García & Bertsch, 2009) and tunicate endemism about 31% (Naranjo et al., 1998). To the south, the warm-temperate Southwest Africa Province is now called the Benguela Province (BP).

The two isolated islands on the Mid-Atlantic Ridge, Ascension and St Helena, formerly constituted the St Helena–Ascension Province (Briggs, 1995). The name was changed to the Mid-Atlantic Ridge Province (MAR) by Floeter et al. (2008). Together the two islands harbour 111 fish species with 26% endemism. However, if the islands are considered separately, each has sufficient endemism (St Helena 13% and Ascension 11%) to be considered a distinct province. Although the two islands have many trans-Atlantic species in common, their faunal composition is otherwise quite different, and they lie 1290 km apart. Ascension has a higher affiliation with the Brazilian Province (29% shared species) than with the TEA (6% shared species), while St Helena has nearly equal affiliations (16% Brazilian, 15% TEA; Edwards, 1990). The more southerly St Helena also has molluscan and crustacean fauna shared with the Indian Ocean (Smith, 1890; Chace, 1966), indicating that this island may be a stepping stone for colonization into the wider Atlantic. Phylogeographical studies show genetically distinct populations and perhaps cryptic species at Ascension (Muss et al., 2001; Bowen et al., 2006b) but also corroborate the higher affinities with the Brazilian Province (Rocha et al., 2002; Carlin et al., 2003). Unfortunately, such comparisons are not available for St Helena. Considering that each island demonstrates significant evolutionary innovation, separate St Helena and Ascension provinces (Fig. 2) should be recognized. For the Eastern Atlantic Region as a whole, there are 551 reef fishes with 64% endemism, and 124 genera with 31.5% endemism.

Western Atlantic Region

The warm-temperate Carolina Province exists in two parts (Fig. 1), one in the northern Gulf of Mexico and the other on the Atlantic coast (Briggs, 1995). Within the Gulf, the warm-temperate biota occupies the area north of the tropical boundaries between Cape Romano, Florida and Cape Rojo, Mexico. The Atlantic section is located between Cape Hatteras and Cape Canaveral. Of the two sections, the Gulf is the richer, and, in an earlier work, Briggs (1974) noted that the fishes and invertebrates exhibited about 10% endemism. However, the Atlantic section had very little endemism and was considered a subset of the northern Gulf fauna. Boschi (2000) recognized the northern Gulf as a Texan Province based on decapod crustaceans, but observed only about 5% endemism. In contrast, García & Bertsch (2009) reported 37% endemism for opisthobranch gastropods in the Atlantic section. Phylogeographic studies demonstrate numerous genetic partitions between these areas in co-distributed species, indicating isolation between the two segments of the Carolina Province (Bowen & Avise, 1990; Avise, 1992). Despite the genetic partitions and high endemism in gastropods, we retain the Carolinian Province with two recognized sections.

The Caribbean Province (CA) extends from Bermuda and Cape Canaveral, Florida, to the Amazon River. Formerly, the tropical Western Atlantic was subdivided into three provinces (Briggs, 1974): Caribbean, Brazilian and West Indian.
to that subdivision, the entire region had been considered to be occupied by a homogeneous fauna. A West Indian Province, comprising the islands extending from Bermuda in the north to Grenada in the south, was originally recognized on the basis of considerable endemism in the fishes and several invertebrate groups.

At the time of the original subdivision, about 19% of the West Indian fishes appeared to be endemics (Böhlke & Chaplin, 1968), as well as many of the echinoderms and molluscs. However, as more work was devoted to the fishes, many of the putative island endemics were found along the mainland shores of the Caribbean. The West Indian fauna is not as distinct as it first appeared (Burgess et al., 1994), and this observation is generally supported by phylogeographic studies (Shulman & Bermingham, 1995), but see Baums et al. (2005) and Taylor & Hellberg (2005). Floeter et al. (2008) subsequently recognized a ‘Greater’ Caribbean Province that included all the northern Western Atlantic tropics (Fig. 2). The larger Caribbean Province contains 814 species of reef fishes with about 33% being endemic; the decapod crustaceans include 1058 species with about 32% endemism (Boschi, 2000); and the coral species have about 37% endemism (Veron, 2000). Briggs (2005) suggested that the southern Caribbean had the richer fauna, but it now appears that the fishes of the Greater Caribbean represent a homogeneous assemblage, although this may not be true for some of the invertebrates.

The tropical Brazilian Province was modified by Floeter et al. (2008) and now extends from the mouth of the Amazon River south to Santa Catarina, Brazil (Fig. 2). Included are the offshore islands of Atol das Rocos, Fernando de Noronha, St Paul’s Rocks and Trindade. There are about 471 fish species with 25% endemism. For the decapods, Boschi (2000), who recognized a southern boundary at Cape Frio, found 572 species with 11% endemism. Coelho et al. (2008) also examined decapod distributions, reporting 12.5% endemism in the Brazilian Province. About 25% of the coral species are endemic (Veron, 2000). The warm-temperate Argentinian Province extends from Santa Catarina, Brazil, to the Valdez Peninsula, Argentina. In total, the Western Atlantic Region has about 1023 reef fish species with 86% endemism, and 158 genera with about 35% endemism.

**Indo-Pacific Warm Regions**

The newly expanded Western Pacific Region begins in the north at Cape Inubo on the Pacific coast of Japan (Fig. 1). Along the mainland shores, the regional fauna begins at the Korean Peninsula and the south entrance to the Sea of Japan. It may also be found along the Chinese coast and Taiwan as far as Hong Kong (Briggs, 1974). To the south of these boundaries, the region extends to Robe in south-eastern Australia and to Bermagui on the south-western coast. The northern Indian Ocean is included and so is the East African coast to the Cape of Good Hope. The region also reaches northern New Zealand, including the Auckland Peninsula eastwards to East Cape and the offshore Kermadec Islands. The new Eastern Pacific Region begins at Los Angeles on the California coast and extends southwards to southern Chile, ending at the Taitao Peninsula (Fig. 1).

**Western Pacific Region**

The warm-temperate Sino-Japanese Province extends, on the oceanic side, from Cape Inubo southwards to, but not including, the Amami Islands. On the mainland side, it begins at the tip of the Korean Peninsula and at Hamada on the lower part of the Sea of Japan. On the Chinese coast, it begins at about Wenchou and extends southwards to Hong Kong (Fig. 1). The latter two boundaries are suggested primarily on the basis of sea surface temperature, because distribution patterns along the Chinese coast are not well known (at least in the Western literature). However, fish distribution along the coasts of Taiwan has been well studied (Shao et al., 1999). The north-western coast of the island exhibits an affinity with the warm-temperate mainland coast, while the south-eastern coast is purely tropical, being under the influence of the Kuroshio Current. The Southern Hemisphere warm-temperate provinces are discussed separately.

**Tropical Indo-West Pacific Region**

In contrast to the case in the Atlantic, Indo-West Pacific (IWP) tropical marine provinces are characterized by prodigious numbers of wide-ranging species. Allen (2008) documented an average range of 9,357,070 km² for reef fishes, or an area roughly the size of China. In general, even limited-range endemics occupy much larger areas than their terrestrial counterparts, with the exception of those occupying the shallows around tiny oceanic islands. Only about 10.8% of the 3919 IWP species occupy areas smaller than 120,000 km². The latter are considered as having restricted distributions and may merit special conservation consideration. However, the vast multitude of species that range from the Central Indian Ocean to the eastern limits of the Western Pacific give the impression of one homogeneous fauna.

Information on the reef fishes of the IWP, as the result of recent surveys (Allen, 2008 and updated information from him), now makes it possible to define biogeographic subdivisions with increased confidence. However, we caution that some boundaries have not been tested or supported with data from invertebrates (see Veron, 2000). The Western Indian Ocean (WIO) Province (Fig. 2), including Madagascar, the Mascarenes, the Seychelles and the Comoros, with about 1000 fish species and 142 endemics, may be considered distinct, with 14.2% endemism. The Red Sea Province is distinguished by 14% endemism in fishes (Goren & Dor, 1994; Randall, 1994), 33% in crustaceans, 15% in echinoderms, and up to 25% in corals (Cox & Moore, 2000). However, many Red Sea fishes (and possibly other fauna) extend into the Gulf of Aden, so that area needs to be added to the Red Sea Province (Fig. 2).
The area between the Horn of Africa and the Arabian Gulf has been described as a major biogeographic barrier (Kemp, 1998). The barrier effect is demonstrated by the composition of the fish fauna of Oman (Randall, 1995). Almost half are widespread Indo-Pacific species, and most of the others belong to the WIO Province. There are, however, 22 short-range endemics (3.8%) off Oman. The entrance to the Arabian Gulf (Fig. 2) was previously recognized as a provincial barrier (Briggs, 1974), and there seems no reason for a change. The presence of short-range endemics has been noted in conjunction with other barriers.

Although the Indian Ocean, in its entirety, includes about 2086 fish species with 532 or 25.5% of them being endemic (Allen, 2008), a separation of the WIO and Red Sea provinces leaves the remainder of the Indian Ocean with too little endemism to distinguish it from the Western Pacific. The Eastern Indian Ocean, including the Andaman Sea, Christmas Island, Cocos Keeling Islands, Sumatra coast, south India, Sri Lanka, Laccadives, the Maldives and Chagos exhibits only 73 endemics. This number, when compared with an approximate total of 1400 species results in 5.2% endemism. Therefore, one cannot recognize a separate province for the Eastern Indian Ocean. In terms of coral distribution, Veron (1995) regarded the Eastern Indian Ocean as continuous with the IWP. This means that one can distinguish in that area the western extension of a huge biogeographic province that is larger than any of the regions in other parts of the world. The Indo-Polynesian Province (Fig. 2) extends from the Arabian Gulf to the Tuamotu Archipelago (Polynesia). The horizontal measurement of the province extends halfway around the world: its latitudinal reach is from Sandy Cape and Shark Bay on the east and west coasts of Australia to the Amami Islands in southern Japan (Briggs, 1995). Sala y Gomez Island, located 3210 km west of the Chilean mainland, possesses a fish fauna with a strong Indo-Polynesian relationship so was considered to be an isolated outpost of this province (Parin, 1994). In fact, the Juan Fernández Province, which lies only 650 km west of Valparaíso, also has a strong south-west Pacific component in its marine fauna (Pequeño & Sáez, 2000).

Genetic surveys of dispersive reef organisms are consistent with the boundaries of the Indo-Polynesian Province. While few studies extend to the Arabian Gulf, phylogeographic studies of the Central and West Pacific show high connectivity in many reef fishes (Bay et al., 2004; Craig et al., 2007; Schultz et al., 2007; Horne et al., 2008) and reef echinoderms (Lessios et al., 2001, 2003). In some cases, this Central/West Pacific connectivity extends to the central Indian Ocean (Gaither et al., 2010). Schultz et al. (2008) use bathymetry profiles to demonstrate that dispersal between Australia and the Tuamotus (Polynesia) requires no deep-water traverse longer than 800 km. This continuity of shallow habitat is doubtless a primary factor in shaping the cohesiveness of the Indo-Polynesian Province.

Adjacent to the enormous Indo-Polynesian Province are three isolated locations whose relatively high endemism in reef fishes requires provincial status: (1) the Hawaiian Islands, with 612 species and 25% endemics (Randall, 2007); (2) Easter Island, with 169 species and 21.7% endemism (Randall & Cea, 2010); and (3) the Marquesas, with 415 species and 11.6% endemism (Randall & Earle, 2000) (Fig. 2).

In earlier work (Briggs, 1974), two more tropical provinces were recognized: Lord Howe–Norfolk and Northwestern Australian. However, each area is now known to have < 10% endemism (Allen, 2008). Springer (1982) identified the Pacific Plate, the tropical area to the east of the Philippines and Australia, as a biogeographic region of major significance. That vast area did not, however, possess sufficient endemism to qualify for provincial status (Briggs, 1995). The Pacific Plate concept was re-examined by Allen (2008), and 1403 species were documented, including 130 endemics. This number, though, included endemics specific to certain islands and archipelagos on the Pacific Plate as well as those that were widespread but confined to that area. Species endemic to a given island group are so characterized because they occur at that particular location and nowhere else. They are not, at the same time, Pacific Plate endemics. The latter, by definition, need to be characteristic of and confined to the Pacific Plate. A study of the inshore fishes of the US Line and Phoenix Islands revealed that 6.3% were restricted to the Pacific Plate (Mundy et al., 2010), which is not enough to define a biogeographic province.

Eastern Pacific Region

A phylogenetic analysis involving the genetic structure of 40 taxa in coastal California (Dawson, 2001), data on all California fishes (Allen et al., 2006), and the phylogeography of the rockfishes (genus Sebastes) (Sivasundar & Palumbi, 2010) leads to a reconsideration of the limits of the warm-temperate California Province (formerly the San Diego Province). Although transition zones within provinces have not previously been recognized (Briggs, 1995), it appears that there is good reason for doing so in this case. Many more species extend past Pt Conception at 34°–35° N than terminate there. The peaks in the range termini of the molluscs and marine algae occur between 33° and 34° N and between 36° and 37° N. Furthermore, a high incidence of short-range ‘edge-effect’ species occurs at the same two latitudes, which approximate the vicinities of Los Angeles and Monterey Bay. A peak in the southern range termini of cold-temperate fishes occurs at 33° N (Horn et al., 2006), but genetic breaks in some rockfish species were found at Cape Mendocino (Sivasundar & Palumbi, 2010). Previously, Murray et al. (1980) recognized clusters of geographic endpoints for northern algae species at Monterey Bay and endpoints for southern species near Los Angeles. Horn & Allen (1978) recognized a similar boundary for fishes at Monterey Bay. In view of such information, a California Transition Zone (CTZ), within the Oregon Province, is now recognized between Monterey Bay and Los Angeles, with the California Province extending from the latter to Magdalena Bay, Mexico (Fig. 1).
The California Province as reconstituted still contains large numbers of northern fishes, about 163 out of 271 species (Horn et al., 2006). Hubbs (1960) determined provincial endemism at 32.9%, but that figure may be too large considering that the province now covers a smaller area. Many of the northern species are usually found in relatively deep water (Eschmeyer et al., 1983) but also tend to be concentrated in cool, upwelling zones along the Baja coast. The molluscan data from Valentine (1967) indicated a provincial endemism of about 21%, but that figure also may be too high owing to the smaller province. The California Channel Islands have several fishes that demonstrate some genetic differentiation, but only one endemic species (*Rimicola cabrilloi*) (Dawson et al., 2006). Robertson & Cramer (2009) recognized a tropical Cortez Province extending from Magdalena Bay south around the tip of the Baja California Peninsula to include all of the Gulf of California. We suggest that this province should still be confined to the Gulf and be considered warm-temperate. Around the rest of the world, warm-temperate provinces not only are distinguished by significant endemism but also are separated from the tropics by the 20 °C isotherm for the coldest month (Briggs, 1974); that is, this temperature barrier prevents the passage of many tropical species and allows speciation to take place in the adjoining warm-temperate provinces. In this case, the barrier extends across the southern end of the Gulf of California approximately between La Paz and Topolobampo. Within the Gulf, slightly more than 10% of the fishes are endemic (D.R. Robertson, Smithsonian Research Institute, Panama, pers. comm.). Boschi (2000) found 265 species of decapods in the northern part of the Gulf, with 9% endemism. The great majority of species in the Gulf range well into tropical waters, but the northern Gulf also contains about 20 California Province species with disjunct distributions (Dawson et al., 2006). Provincial recognition is given according to endemism, without regard to the origin of other species. Therefore, the Cortez Province is retained as a warm-temperate unit within the Gulf of California.

The tropical fauna of the Panamanian (Panamic) Province extends from the mouth of the Gulf of California south to the Gulf of Guayaquil, on the border between Ecuador and Peru (Fig. 2). In the northern part of this range, a Mexican Province was previously recognized (Briggs, 1974; Hastings, 2009), but the more recent information from Robertson & Cramer (2009) indicates that the section from the mouth of the Gulf of California to the Gulf of Tehuantepec does not demonstrate sufficient endemism. In the extended Panamanian Province about 49% of the fish species are endemics. Boschi (2000) found 38% endemism in the decapods.

Robertson & Cramer (2009) placed all of the tropical offshore islands in a single Ocean Island Province, but only one archipelago, the Galapagos, has sufficient endemism to be considered a biogeographic province. The other groups that retain strong faunal affinities with the Panamanian Province include the Revillagigedos, with 8.0% endemism among the shore fishes, Clipperton, with 5.8%, Malpelo, with 2.5%, and Cocos, with 4.6%. As noted previously for the Pacific Plate, species endemic to a particular island cannot, at the same time, be considered endemic to a larger area. The Galapagos Archipelago has 13.6% endemism for shore fishes (McCosker & Rosenblatt, 2010) and has been continuously recognized as a separate province (Briggs, 1974). Several invertebrate groups have higher endemism, including decapods at 16% (Boschi, 2000). A significant number of species, in some groups more than 10%, are trans-Pacific migrants. A few species shared with the Caribbean, either exclusively or also with the Panamanian Province, are examples of taxa that apparently have not changed since the formation of the Panamanian Isthmus. Owing to the high level of endemism, provincial status for the Galapagos should be retained, and the other offshore islands should be regarded as outposts of the Panamanian Province.

**Cold-temperate regions**

A global cooling episode took place across the Eocene–Oligocene boundary c. 35 Ma (Zachos et al., 2001). This episode and subsequent cool periods resulted in cold-temperate sea surface conditions in the Arctic Ocean, North Pacific, North Atlantic and the waters surrounding the Antarctic continent. Warm-temperate waters were displaced into lower latitudes, resulting in a latitudinal restriction of the tropical seas, and the formation of a new cold-temperate zone in each hemisphere.

Cold-temperate surface temperatures for the coldest month generally range from 12 to 2 °C. The colder waters absorb more atmospheric oxygen, and their increased density stimulates thermohaline circulation. This results in an increased upwelling, which brings more nutrients to the surface and enhances primary production. In the Northern Hemisphere, cold-temperate waters occupied the Arctic–North Atlantic and the North Pacific oceans at a time when the two areas were separated by the Bering land bridge. In the south, they occupied the circum-Antarctic region, including the southern tips of Australia and South America. The new cold-temperate biotas were derived ultimately from tropical species that were able to adapt to the new environment (Krug et al., 2009). Their present global distributions are delineated in Fig. 1. The contrast between the organisms occupying the warm-temperate versus cold-temperate environments is more extreme than that between the other temperature zones. The difference is such that families and genera found in one usually do not appear in the other.

**Northern Hemisphere**

Most of the early work on the history and biogeography of the cold-temperate and cold waters of the north was carried out by Russian scientists (reviewed in Briggs, 1974). A recent Russian summary on marine biogeography (Golikov et al., 1990) paid particular attention to the Northern Hemisphere and reviewed the climatic history as well as the biogeographic subdivisions. The authors concluded that the initial formation of the cold-temperate faunas in the North Pacific took place coincident
with a significant temperature fall about 14 Ma. Sediment cores in the polar North Atlantic detected ice-rafted debris 14–12 Ma (Thiéde et al., 1998). More recently, Stickley et al. (2009) presented evidence for ice formation in the Arctic Ocean in the middle Eocene (47 Ma). So, the northern cold-temperate biota may be much older than originally thought.

Multiple biogeographic subdivisions were suggested by Golikov et al. (1990, see also Kafanov & Kudryashov, 2000). From a world-wide perspective, the various regions were delineated about as they had been for the past 25 years, but the northern oceans were more finely divided. The authors recognized a kingdom of temperate and cold waters that was subdivided into regions, subregions and provinces. Their descriptions and maps indicated that, for the most part, the biotas occupied areas that had been previously outlined (Briggs, 1974), but there were some notable exceptions: (1) in the Eastern North Atlantic, the Arctic/Boreal (A/B) boundary was extended northwards to Svalbard and the south end of Novaya Zemlya, (2) in the North Pacific, the A/B boundary was placed at the Bering Strait, and (3) an Estuary–Arctic Interzonal Province was noted to occur along the shores of the Arctic Ocean. The North Atlantic change is adopted here (Fig. 1) but the justification for the Bering Strait boundary does not appear strong. The Estuary–Arctic Interzonal area is probably best defined as a special ecological zone rather than as a biogeographic province.

In the North Pacific and Arctic–North Atlantic, the new cold-temperate, often-called ‘boreal’, biotas evolved separately until the late Miocene when marine connections across the Bering land bridge began to develop. Previously, it was generally thought that the land bridge remained intact until c. 3.5 Ma. However, recent fossil studies indicate that the first opening may have occurred as early as 5.3 Ma (Gladenkov et al., 2002). When the Bering Strait first opened it may have been shallow with limited passage, but by c. 3.5 Ma it allowed an unrestricted mingling of biotas that had been separated for more than 30 Myr (Vermeij, 1991a, 2004), an event subsequently called the Great Trans-Arctic Interchange. At the time of the Great Interchange, the Arctic Ocean had little ice, and cold-temperate conditions prevailed. Global cooling during this (mid-Pliocene) interval was probably caused by four key tectonic events: (1) the isolation of Antarctica, (2) the closure of the Tethys Sea, (3) the collision of Australia with Southeast Asia, and (4) the uplift of the Panamanian isthmus (Crame, 2004). The final event apparently produced a major intensification of Northern Hemisphere glaciations between 2.9 and 2.4 Ma (Mudelsee & Raymo, 2005). As a result, the Arctic sea surface temperature for the coldest month dropped to between +2 and −2 °C, most of the boreal species were eliminated, and the modern Arctic marine fauna began to develop. The mid-Pliocene cooling of the northern oceans resulted in the resumed isolation of Atlantic and Pacific boreal biotas.

An important effect of the mid-Pliocene cooling of the northern oceans was the separation of boreal biotas (Briggs, 1995). In the Atlantic, the cold-water Arctic Region now extends southwards to the Strait of Belle Isle in the west and to the north-east beyond the Murmansk Peninsula. In the Pacific, the Arctic biota extends southwards to Cape Olyutorsky in the west and Nunivak Island to the east. In each ocean, these southern extensions of Arctic water divided the original Pliocene boreal assemblage into eastern and western components. Typical boreal species were no longer able to maintain amphi-Atlantic and amphi-Pacific distributions, and in both oceans the eastern and western faunas developed independent evolutionary trajectories. The contemporary result is a distinct boreal region on each side of each ocean, defined in terms of endemic species. This separation is also apparent in phylogeographic studies both within and between species, including faunas as diverse as seagrass (Zostera marina; Olsen et al., 2004), fish (Merluccius spp.; Grant & Leslie, 2001) and several invertebrate groups (Wares & Cunningham, 2001; Addison & Hart, 2005).

With regard to longitudinal relationships, it is apparent that, in each ocean, the east and west boreal faunas are closely related. In the North Pacific, the relationship is primarily due to the presence of a group of Arctic-boreal species common to both sides of the ocean. In addition, some Pliocene amphi-boreal species have apparently not yet developed specific differences. In the North Atlantic, there are also Arctic-boreal species, but a good part of the relationship between the two regions is caused by the large number of Pacific species that invaded in the mid-Pliocene. Approximately half of the mollusc invaders have speciated and many of them are now endemic to one boreal region or the other (Vermeij, 1991b). Much of the native North Atlantic molluscan fauna originated in European waters and then spread westwards (Wares & Cunningham, 2001; Vermeij, 2005b).

**Eastern North Pacific Region**

Cold-temperate conditions extend from Nunivak Island in the north to about Los Angeles on the California coast, the southern limit of the Oregon Province, including the California Transition Zone (CTZ). The northern boundary is concordant with the mean southern limit of the pack ice in January–February. This region may be divided into Aleutian and Oregon provinces, with a boundary previously described at the Dixon Entrance (55° N). The northern (Aleutian) province has an endemism rate of about 24% in decapods and 23% in molluscs (Valentine, 1967; Boschi, 2000, respectively). In contrast, the Oregon Province, if considered to terminate at Monterey Bay, has only about 2% endemism in decapods and fishes (Horn & Allen, 1978; Boschi, 2000; Horn et al., 2006), respectively. If, however, the cold-temperate biota of the CTZ is included, the endemism level would probably rise to more than 10%. Horn et al. (2006) reported many California fish range terminations at the latitude of Monterey Bay (36°–37° N), and a peak in range termination endpoints at about 50° N, near the northern tip of Vancouver Island. This coincides with a similar peak reported by Peden & Wilson (1976) based on fish distributions in British Columbia and Alaska. Based on these findings, the boundary between the
Aleutian and the Oregon provinces should be shifted south from the Dixon Entrance to the northern tip of Vancouver Island, and the CTZ included within the Oregon Province.

**Western North Pacific Region**

Cold-temperate conditions in the Northwest Pacific apply to three provinces, defined in part by the complex geological history of the Sea of Japan and adjacent regions (Wang, 1999). An Oriental Province exists in three segments (Fig. 3). The first extends north from the warm-temperate boundary at Wenchou and continues through the Yellow Sea. Its continuity is broken by the tip of the Korean Peninsula, but it then continues up the north side of the peninsula to about Chongjin. On the eastern side of the Sea of Japan, the Oriental Province extends from about Hamada to the Tsugaru Strait. From that point, it continues southwards on the outer coast of Honshu Island to Cape Inubo, Japan.

A faunal break exists at about the location of the Tsugaru Strait between the islands of Honshu and Hokkaido. To the north of this point, both along the outer coast and within the Sea of Japan, one may find a different species assemblage, of the Kurile Province (Fig. 3). This province extends northwards along the Kurile chain of islands and the east coast of the Kamchatka Peninsula to about Cape Olyutorsky. The Okhotsk Province is confined to the Sea of Okhotsk. Although this sea is now confluent with the North Pacific through the Kurile Islands and with the Sea of Japan around Sakhalin Island, it was probably isolated during the glacial stages and perhaps earlier. Indeed, phylogeographic analyses indicate that the Northwest Pacific marginal seas were isolated during glacial maxima (Liu et al., 2007). Although there are no recent taxonomic evaluations (known to us), the older literature demonstrated considerable endemism in ascidians, pycnogonids, and fishes (Briggs, 1974).

As noted, some of the Russian biologists preferred to recognize more provinces than those just described. For example, in the Sea of Japan the fish fauna was separated into four provinces by Kafanov et al. (2000). The divisions were made on the basis of breaks in the species diversity gradient and their relationship to temperature and prevailing currents. The provinces that were identified reflected interesting ecological differences but did not exhibit sufficient endemism to qualify as provinces according to the 10% rule. In contrast, the currently used scheme indicates only two provinces in the Sea of Japan, one penetrating from the north and the other from the south.

**East–west relationships.** The Bering Sea is essentially a broad, shallow basin almost completely enclosed to the north and bordered by the Alaskan 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), recognized significant differences. 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. The fish families Cottidae, Zoarcidae, Liparidae, as well as the genera Oncorhynchus and Sebastes (Hyde & Vetter, 2007), probably underwent major radiations in that area. In contrast, the fish family Embiotocidae and the gastropod genera Nucella and Littorina may have originated on the eastern side (Ilves & Taylor, 2007).

**Western Atlantic Boreal Region**

This region extends from the Strait of Belle Isle to Cape Hatteras (Fig. 1). In considering the geographic extent of this cold-temperate region, one is confronted with a good deal of conflicting opinion. Most of the disagreement is concerned with the relationship of the fauna that occupies the area between Cape Hatteras and Cape Cod, often called the ‘Middle Atlantic Seaboard’. The area is penetrated during the summer months by large numbers of tropical and warm-temperate organisms. This has often resulted in its being allied with the Carolina Province to the south. However, the presence of large numbers of boreal species, together with very little endemism, shows that it clearly belongs to the Boreal Region (Briggs, 1974). There is about 19% regional endemism in shore fishes (Bigelow & Schroeder, 1953), 53% in all molluscs (Vermeij, 2005c), 21% in opisthobranch gastropods (Garcia & Bertsch, 2009), and only 5% in decapods (Boschi, 2000).
the northern boundary was located at the base of the Murmansk Peninsula. Iceland possesses an interesting biotic mixture. The older literature (Briggs, 1974) suggested a purely boreal component, pure Arctic, Arctic-boreal, and some eurythermic temperate forms. The relationships are almost entirely with the Eastern Atlantic. The absence of any special American relationship and the almost complete absence of endemics (except for a few subspecies) indicate that Iceland, or at least the south and east shores, should be included in the Eastern Atlantic Boreal Region. For the entire region, an early estimate was 20–25% endemism for both fishes and invertebrates (Briggs, 1974). New data from Vermeij (2005c) indicate that about 69% of the molluscs are endemic, and Garcia & Bertsch (2009) estimate 25% for the opisthobranch gastropods alone.

The Faroes, a group of 21 volcanic islands located between Iceland and the Shetlands, host species that are either boreal or Arctic-boreal. The demersal fish fauna is closely related to that of the North Sea, with no endemics or any indication of relationship to the Western Atlantic (Magnussen, 2002). The Baltic Sea is the world’s largest estuarine area. The salinity is relatively stable and decreases gradually towards the inner end of the long, narrow basin. Although Golikov et al. (1990) recognized a Baltic Province, this designation does not appear to be justified on the basis of endemism.

East–west relationships. The richest boreal fauna occurs on the eastern side of the North Atlantic, as demonstrated by the superior species diversity in fishes (Wheeler, 1969). This, when considered with the strong European relationship of Iceland, indicated that the principal evolutionary centre for the recent Atlantic boreal fauna was on the eastern side of that ocean (Briggs, 1974). This suggestion has been verified by Vermeij (2005c), who examined mollusc distribution in the North Atlantic. He found 402 extant species on the eastern side (69% endemic) and 262 on the west (54% endemic); 124 species had transatlantic ranges. Furthermore, Vermeij (2005c) determined that all of the transatlantic species had apparently dispersed from Europe to America within the past 3.5 Myr. More than 50% of those species had their ultimate origins in the North Pacific.

Cold Arctic Region

Although sea ice has been detected in the Arctic as far back as 47 Ma (Stickley et al., 2009), the present glacial regime probably began about 2.9–2.4 Ma (Mudelsee & Raymo, 2005), so the polar biota of the Arctic Region is much younger than that of the Antarctic. Consequently, although there are significant numbers of endemic species, there are very few endemics at the higher taxonomic levels. An exception is the narwhal, Monodon monoceros, with a relict distribution (Jefferson et al., 1993). The Arctic seas have traditionally been divided into a number of separate zones and provinces, but recent works indicate an essentially homogeneous biota so that a single region is now recognized. Endemism in Arctic fishes has been estimated at about 25% (Eastman, 1997), and the earlier literature indicates high endemism in sponges, amphipods and echinoderms (Briggs, 1974). Phylogeographic analyses of the Arctic charr (Salvelinus alpinus) demonstrate that most of this region was recolonized after the last glacial retreat (10,000–20,000 years ago), indicating a lack of substantial biogeographic barriers (Brunner et al., 2001). The polar cod (Boreogadus saida) may be considered an indicator species because it extends to all parts of the region but no farther (Cohen et al., 1990). The Arctic Region occupies all of the area north of the cold-temperate boundaries previously identified.

Southern Hemisphere

Warm-temperate provinces

Owing to the presence of many tropical eurythermic species, and of endemics with nearby tropical ancestors, the faunal relationship of most northern warm-temperate provinces is closest to their adjoining tropical province. In the Southern Hemisphere (Fig. 1), however, there is considerable longitudinal relationship due to the influence of the West Wind Drift (WWD). Three species of the fish genus Sebastes (Scorpaenidae) dispersed from the North Pacific southwards through the Eastern Pacific to Tierra del Fuego. From this point, they reached, apparently via the WWD, the Falkland Islands, Tristan da Cunha and the tip of southern Africa (Rocha-Olivares et al., 1999).

A number of taxa originating in Australia–New Zealand were able to achieve circum-global ranges via the WWD. Such a dispersal history had been proposed for the fish families Cheilodactyliidae and Latridae (Briggs, 1974). Recently, this suggestion has been reinforced by genetic evidence (Burridge & Smolenski, 2004). The spiny lobster genus Jasus provides another example (Pollock, 1990). Genetic and morphological evidence has indicated that two species of chironomid fishes (Chironomidae) found on Juan Fernández Island represent colonizations from Australia–New Zealand (Burridge et al., 2006). Other recent phylogeographic studies have produced strong evidence for WWD dispersal in the Southern Hemisphere (Waters & Burridge, 1999; Waters, 2008).

The Agulhas Province extends from the Cape of Good Hope north-eastwards to about the mouth of the Kei River. It was apparently the ancestral habitat for the seastar Patiriella exigua, which was subsequently transported by the WWD across the Indian, Pacific and Atlantic oceans (Waters & Roy, 2004). This province has been reported to possess high levels of invertebrate endemism (Griffiths et al., 2009) but it is not known how many of the suspected endemics actually extend northwards into the tropics of the south-eastern African coast. The Agulhas Province contains large numbers of eurythermic species shared with the tropical WIO Province.

The Southwestern (Flindersian) and Southeastern (Peronian) provinces of Australia (Briggs, 1995), based on the work of Bennett & Pope (1953, 1960), are still recognized in the recent literature (Waters et al., 2010), although the provincial
names have varied. For New Zealand, the Auckland and Kermadec provinces are recognized. The Auckland Province shares many species and has a historical relationship with southern Australia (Waters et al., 2007); there may be a considerable endemic component although there are no published estimates. The Kermadec Province invertebrates revealed a large number of species, 296 gastropods, 77 bivalves and 203 chelostome bryozaos in this small area, with endemism rates of 71%, 69% and 69%, respectively (Griffiths et al., 2009). However, there are few endemic fishes.

The warm-temperate Peru–Chilean Province (Fig. 1) includes the major part of the western coast of South America, extending from the Gulf of Guayaquil to about the Taitao Peninsula. Lee et al. (2008) referred to a Peruvian/Chilean Province extending to around 40° S, an intermediate zone from 40° to 43° S, and the beginning of the cold-temperate waters at 43° S. Marine fishes of southern Chile also show three latitudinal fish zones but they are located farther south by Siefeld & Vargas (1999). These authors indicated that species belonging to typical warm-temperate families (Blenniidae, Clinidae, Normanichthyidae) extended as far as 45°–46° S, concordant with the faunal barrier for sea anemones (Haussermann & Forsterra, 2005). Briggs (1995) designated Chiloe Island (41.5° S) as the southern limit of the province, but the Taitao Peninsula now seems to be more appropriate. An endemism rate of 13% was noted for the decapod fauna (Boschi, 2000).

The Juan Fernández Province consists of three islands 650 km west of Valparaiso, Chile. The early literature on fishes, invertebrates and algae indicated considerable endemism, corroborated by a recent survey of the littoral fish fauna that revealed 25.5% endemism (Pequenó & Sáez, 2000). The external relationship proved to be stronger to the south-west Pacific than to the Chilean coast, for both the fishes and the decapod fauna (Boschi, 2000).

The Argentinian Province lies between Santa Catarina, Brazil and the Valdes Peninsula, Argentina (Fig. 1). Previously labelled the Eastern South America Region (Briggs, 1974), it extended from Cape Frio, Brazil to the Rio de la Plata. Later, the southern boundary was extended to the Valdes Peninsula, Argentina (Briggs, 1995) and the northern boundary was set at Santa Catarina, Brazil (Floeter et al., 2008). Boschi (2000), who accepted the Cape Frio boundary, reported 13% endemism in the decapod crustaceans; García & Bertsh (2009) reported 24% endemism in opisthobranch gastropods in the same area. A new assessment of the reef fish fauna by Galvan et al. (2009) illustrates a sharp change from a warm-temperate to cold-temperate fauna near the Valdes Peninsula (42° S). Five cold-temperate fish families (Bovichtidae, Eleginopidae, Nototheniidae, Congiopodidae, Moridae) do not extend north of this region, illustrating the dramatic faunal transition in this boundary area.

In the south-eastern Atlantic, the warm-temperate Benguela Province is located between Mossamedes and the Cape of Good Hope (Floeter et al., 2008). The Cape is the dividing line between the Benguela and Agulhas provinces, the former exhibiting an Atlantic relationship and the latter linked to the Indo-Pacific. The endemic rate in the Benguela Province is about 12% for fishes and 53% for opisthobranch gastropods (García & Bertsh, 2009). Two sets of widely separated offshore islands, Tristan–Gough and Amsterdam–St Paul, formerly comprised the warm-temperate West Wind Drift Province (Collette & Parin, 1991; Briggs, 1995). The provincial status was based on a 30–40% endemism rate for the shore fishes. However for Tristan da Cunha, by itself, endemic rates of 60% for bivalves, 100% for gastropods (Griffiths et al., 2009) and 31% for ascidians (Primo & Vázquez, 2007) indicate a highly distinct invertebrate fauna. Nearby Gough Island probably should be included so we can recognize a Tristan–Gough Province. Amsterdam–St Paul, originally considered to be a distinct province (Briggs, 1974), should retain that status; 31% of the ascidians are endemic (Primo & Vázquez, 2007). Although the fish fauna indicates a relationship between the two island groups, the invertebrates so far as known appear to be unrelated.

Cold-temperate regions

Cold-temperate waters are found around the tip of South America and the Falkland Islands, Tasmania and Victoria in Australia, southern New Zealand and nearby islands, and the Sub-Antarctic (Fig. 1). These areas had been apportioned into four regions and seven provinces (Briggs, 1995): South America (Magellan), Tasmanian, New Zealand, and Sub-Antarctic regions, with two provinces in the New Zealand Region and five provinces in the Sub-Antarctic. However, because of much recent work on the cold-temperate invertebrate fauna, especially by Linse et al. (2006), Clarke et al. (2007) and Griffiths et al. (2009), the southern cold-temperate and cold regions and provinces can now be more confidently defined.

Endemism in four classes of benthic invertebrates (Bivalvia, Gastropoda, Cyclostomata and Cheilostomata) was determined by Griffiths et al. (2009) based on more than 7000 specimens collected from all parts of the Antarctic and Sub-Antarctic. Although the endemism percentages varied among the classes, we recognize the following geographic areas as provinces if at least two classes have endemism rates of more than 10%. This procedure resulted in the designation of 12 provinces and four regions within the Southern Ocean area. Three of the collection localities were in South Africa, Tristan da Cunha and the Kermadec Islands, all located in warm-temperate provinces, so they were not included in the following cold-temperate arrangement. All three showed exceedingly high endemism. Macquarie Island was not surveyed by Griffiths et al. (2009), but was designated as a province by Briggs (1974), based on a 66% molluscan endemism (Dell, 1964). The inclusion of Macquarie brings the total number of cold-temperate provinces to 13.

South American Region. Previously the cold-temperate waters of South America were united in a Magellan Province spanning from Chiloe Island on the Pacific side to Rio de la Plata.
(Argentina/Uruguay border) on the Atlantic side (Briggs, 1974). However, the very high endemism rates for invertebrates in southern Chile, Tierra del Fuego, southern Argentina and the Falkland Islands (Griffiths et al., 2009) indicate that all four areas should be designated as provinces within a South American Region (Fig. 4). This represents a significant change from the previous scheme that assumed an undivided fauna for the entire region. In contrast, the shore fish fauna of the region shows no indications of provincial endemism (Sielfeld & Vargas, 1999).

Notably, the molluscs of the Chilean coast do not demonstrate a reduction in species diversity at higher latitudes, but rather a sharp increase in diversity above 42° S (Valdovinos et al., 2003). In their review of invertebrate zoogeographic patterns in the Magellan Province, Haussermann & Forsterra (2005) noted that the polychaetes and anemones indicated a barrier between the Pacific and Atlantic sections because those faunas showed very little overlap. Although Boschi & Gavio (2005) recognized a single Magellan Province for the decapod crustaceans, their data indicate about 35% endemism for the Pacific side and about 18% for the Atlantic. These references provide additional justification for a separation between Southern Chile and Southern Argentina provinces.

New Zealand–Australia Region. The Tasmania (Maugean) Province (Fig. 5) has an exceedingly high endemism for both molluscan classes (Griffiths et al., 2009). However, this province may extend to the Victoria coast of Australia (Briggs, 1995), an area not reported on by Griffiths et al. (2009), so the endemism figures probably will be adjusted downwards in the future. Even so, the province is very distinct. New Zealand has very high endemism for all four invertebrate classes, and the endemism figures provided by MacDiarmid & Patuawa (2010) for the bivalves (85.5%) and the gastropods (86.6%) are considerably higher than those listed by Griffiths et al. (2009). The coastal fish fauna of 270 species has 25% endemism (Walrond, 2009). High endemism for other New Zealand marine groups are indicated in the online summary edited by MacDiarmid (2010). It should be noted that the north coast between Auckland and East Cape is in the warm-temperate zone. Is there sufficient endemism to recognize a separate province? The Antipodes Province (Fig. 5), consisting of the Auckland, Antipodes, Campbell and Bounty Islands, demonstrates elevated endemism for the two molluscan classes (Griffiths et al., 2009). However, Dell (1962) had found molluscan endemism rates of 16% for the Aucklands, 23% for the Bounties, and 23% for the Snares, and asked if all these island groups should be provinces. Almost 50 years later, the answer still eludes us.

Sub-Antarctic Region. The shelf waters of the Antarctic and Sub-Antarctic are occupied by a highly distinctive fauna that owes its origin to four historical factors: (1) the persistence of a small ancestral group of Mesozoic and early Cenozoic taxa, (2) the extinction of many early Tertiary warm-temperate species, (3) geographical isolation produced by the opening of Drake Passage, and (4) invasions by cold-temperate species from the North Pacific. Five provinces in the Sub-Antarctic Region were previously recognized (Briggs, 1995), but now we recognize six (Griffiths et al., 2009; Fig. 6). The fauna of South Georgia is highly endemic for three out of the four invertebrate classes, and about 34% of the shore fishes may be endemic (Briggs, 1974). The Bouvet Province is now known to have a very distinct fauna with 50% endemism in gastropods. The Crozet Islands were previously considered part of the Kerguelen Province, but now must be assigned to a separate province based on two of the four invertebrate classes (Griffiths et al., 2009). Likewise, Prince Edward Island is a separate province and probably should include the Marion Islands based on proximity. Kerguelen Island has a distinctive molluscan fauna,
and about 73% of its ascidian species are endemic (Primo & Vázquez, 2007); this province probably should include the nearby Heard and McDonald islands. Early literature (Briggs, 1974) indicates that about 66% of the Kerguelen shore fishes may be endemic species. As noted, Macquarie Island was not reported on by Griffiths et al. (2009), but four of nine ascidian species are endemic (Primo & Vázquez, 2007) and older references indicate a 64% molluscan endemism (Dell, 1964).

Cold Antarctic Region. The fauna of the Antarctic Region is relatively old compared with that of the Arctic Region. There is evidence of a major ice sheet by late Oligocene times, c. 24 Ma (Ivany et al., 2006), indicating close to modern conditions. In contrast, the Arctic Ocean did not decline to similar temperatures until about 2.9–2.4 Ma (Mudelsee & Raymo, 2005; but see Stickley et al., 2009). The Antarctic Continent and the South Orkney, South Sandwich and South Shetland islands are all below the February 1 °C isotherm (Dietrick, 1981). The Region includes all of the waters surrounding the continent and the noted island groups (Fig. 6). This agrees with the conclusion of Griffiths et al. (2009), who recognized a single Antarctic ‘Province’, in contrast to many earlier workers who divided the continent into various segments. They also determined a general endemism level between 42% and 56% for the four invertebrate classes surveyed in Griffiths et al. (2009). Other invertebrate classes recently investigated, the ascidians (Primo & Vázquez, 2007) and the anemones (Rodríguez et al., 2007), indicate similar levels of endemism. Estimates for other invertebrate groups are also high: 51% for sponges, 57% for polychaetes and 75% for molluscs (Arntz et al., 1997). Previously, Knox (1994) had observed that more than half the invertebrate species were endemics. Phylogeographic studies are consistent with a single Antarctic Province, showing little (or no) population structure across this vast region for two decapods (Raupach et al., 2010), one nemertean (Thornhill et al., 2008), and four notothenioids (ice fishes; Janko et al., 2007). The fast-moving Antarctic Circumpolar Current must facilitate the high dispersal observed in this region.

The fishes have restricted taxonomic diversity but an endemism rate of 88% on the continental shelf and upper slope (including depths to 1200 m; Eastman, 2005). Considering the 20+ Myr of isolation, this degree of species endemism is not unexpected, but there are also exceedingly large numbers of endemic genera (76%; Eastman, 2005). The shelf and upper slope support about 222 fish species, including 96 notothenioids (five families), 67 liparidids (Liparididae) and 23 zoarcids (Zoarcidae). Together, these three groups account for more than 85% of the fish fauna, which for the most part is not related to cold-temperate faunas in adjacent regions. The latter two families represent invasions from the North Pacific, and the unique notothenioids probably arose in the Antarctic.

CONCLUSIONS AND CONSERVATION IMPLICATIONS

The vast reservoir of new biogeographical information emerging since Briggs (1995) has revealed several trends. First, underexplored regions of the planet have revealed high diversity, endemism and new biogeographic provinces, most notably in the Southern Ocean. Second, sufficient phylogeographic information now exists to conclude that genetic architecture (primarily within species) and the biogeographic structures defined by endemism are largely concordant, with the notable exception of the ephemeral Indo-Pacific barrier. Third, the phylogenetic and taxonomic affinities of warm-temperate and adjacent tropical provinces (relative to cold-temperate provinces) indicate that they should be united in a single warm region. This does not affect the status of individual provinces in the tropics and warm-temperate zones, but more accurately reflects the alignment of provinces into warm (temperate and tropical) and cool (temperate and cold) regions. We anticipate that the combination of warm (temperate and tropical) regions should more closely align marine biogeography with the evolutionary relationships discovered in the oceans. Many temperate marine biota originated in the tropics, and the alignment of tropical and warm-temperate regions is intended to accommodate this relationship. This
new arrangement may also serve as a framework for designing phylogenetic and phylogeographic studies.

In recent years, marine conservation has become focused on the value of certain habitats. In order that generally small habitats or ecological communities can be recognized for management purposes, a new publication entitled Marine Ecoregions of the World is now available (Spalding et al., 2007). The 15 authors of this comprehensive map utilized the global biogeographic arrangement of Briggs (1974, 1995) together with many additional sources. The result was a classification that generally recognized the traditional biogeographic regions (realms) and provinces but, nested within the latter, a new series of 232 ecoregions.

In order to establish a conservation priority system for the continental shelves of the world, it would seem reasonable to first consider the centres of origin, that is, those locations that are actively contributing species to and maintaining diversity in large portions of the marine environment (Briggs, 2003). From these centres, new lineages spread out, bringing to outlying environments the increases in productivity and regulation that already existed in the centres (Vermeij, 2005a). This means that priority should be given to the Coral Triangle in the Indo-Pacific, the Caribbean Province in the Western Atlantic, the North Pacific Ocean, and the waters surrounding the Antarctic. It has become customary to refer to areas of exceptionally high biodiversity or endemism as ‘hotspots’ in need of special conservation attention. These criteria have drawn considerable attention to the tropics (Krug et al., 2009), but it is not the tropics as a whole that produces invasions into higher latitudes but primarily the two centres of origin in the Coral Triangle and Caribbean.

Endemism in the cold-temperate and cold Southern Ocean provinces tends to be greater than that of similar-size provinces in the equivalent temperature zones of the Northern Hemisphere. According to the analysis of the four invertebrate classes by Griffiths et al. (2009), the hotspot of the Southern Ocean is New Zealand. However, Tasmania, with its much smaller area, was the second richest, and if the Tasmanian fauna were to be combined with that of the Victoria coast of Australia, as indicated by the provincial boundaries, the total fauna would be more diverse. Both the Chatham and the Kermadec islands have very rich faunas and demonstrate a New Zealand influence. Other areas that should merit conservation attention are the newly recognized provinces in southern South America, and several Sub-Antarctic islands such as Prince Edward, Crozet, Kerguelen and Macquarie. Such lesser-known places, isolated for extensive periods of time, offer rich biological rewards.

Finally, as dominant species continue to invade from high-diversity centres to occupy communities that are less diverse, the invaders constitute branches of a dynamic dispersal tree that extends to all parts of the shallow oceans. Invader species that are continually being accommodated by the natives at the community levels (Briggs, 2010) are ultimately responsible for the global dispersal system that operates on a contemporary (as well as a historical) time-scale.

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