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# A REALIGNMENT OF MARINE BIOGEOGRAPHIC PROVINCES WITH PARTICULAR REFERENCE TO FISH DISTRIBUTIONS

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## 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 available only for the most widely-studied vertebrates (fishes), an ongoing problem. 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.

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## INTRODUCTION

Biogeographic patterns are most useful when they identify those parts of the world that host the more unique biotas, i.e., areas of evolutionary innovation or refuges where 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 that the animals originally formed there were apt to become mixed with emigrants from other provinces, (2) each species was created only once and that individuals tended to migrate outward from their centre of origin, and (3) provinces to be understood must be traced back like species to their origins in past time. Sven Ekman undertook the huge task of analyzing all the pertinent literature on marine animal distribution and published 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 comprised 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 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, based on 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 less than 200 m depth (Randall, 2007), often are the only groups with sufficient information for biogeographic inference. We have endeavored 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 biota. 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% (Boschi, 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) receive 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 greater than 10% endemism have proven 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 operates 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 were 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 than the tropical ones. Considering that there is a very close relationship between each warm-temperate province and its adjacent tropical equivalent (Vermeij, 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**

*Provinces (warm-temperate***)**: Sino-Japanese, Auckland, Kermadec, Southeastern Australian, Southwestern Australian.

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 Fernandez.

II. **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 southward to the Cape of Good Hope. The Western Atlantic Region extends from Cape Hatteras and the northern Gulf of Mexico southward 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 eastward 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 also 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 phylogeographic 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, Sáo 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 comprised 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. But, 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 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. Phylogeography 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. He regarded the Atlantic section as belonging to a separate "Carolinian" Province but found little more than a 1% 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. Previous 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 was 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 Rocas, 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 southeastern Australia and to Bermagui on the southwestern 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 eastward to East Cape and the offshore Kermadec Islands. The new Eastern Pacific Region begins at Los Angeles on the California coast and extends southward 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 south 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 southward 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). But fish distribution along the coasts of Taiwan has been well studied (Shao *et al*., 1999). The northwestern coast of the island exhibits an affinity with the warm-temperate mainland coast while the southeastern 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 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 3,919 IWP species occupy areas less than 120,000 km². The latter are considered as having restricted distributions and may merit special conservation consideration. But the vast multitude of species that ranged 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 make 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 1,000 fish species and 142 endemics, may be considered distinct with 14.2% endemism. The Red Sea Province is distinguished by 14% endemism in fishes (Randall, 1994; Goren & Dor, 1994), 33% in crustaceans, 15% in echinoderms, and up to 25% in corals (Cox & Moore, 2000). But 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. But there are 22 short-range endemics (3.8%) at Oman. The entrance to the Arabian Gulf (Fig. 2) was previously recognized as a provincial barrier (Briggs, 1974) and there seems to be 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 of them

283 or 25.5% being endemic (Allen, 2008), a separation of the WIO and Red Sea Provinces leaves the
284 remainder of the Indian Ocean with too little endemism to distinguish it from the Western Pacific.
285 The Eastern Indian Ocean, including the Andaman Sea, Christmas Island, Cocos Keeling Islands,
286 Sumatra coast, south India, Sri Lanka, Laccadives, Maldives, and Chagos exhibits only 73
287 endemics. This number when compared to an approximate total of 1,400 species results in 5.2 %
288 endemism. Therefore, one cannot recognize a separate province for the Eastern Indian Ocean. In
289 terms of coral distribution, Veron (1995) regarded the Eastern Indian Ocean as continuous with
290 the IWP. This means that one can distinguish in that area the western extension of a huge
291 biogeographic province that is larger than any of the regions in other parts of the world. The Indo-
292 Polynesian Province (Fig. 2) extends from the Arabian Gulf to the Tuamotu Archipelago
293 (Polynesia). The horizontal measurement of the province extends halfway around the world; its
294 latitudinal reach is from Sandy Cape and Shark Bay on the east and west coasts of Australia to the
295 Amami Islands in southern Japan (Briggs, 1995). Sala y Gomez Island located 3,210 km west of
296 the Chilean mainland possesses a fish fauna with a strong Indo-Polynesian relationship so was
297 considered to be an isolated outpost of this province (Parin, 1994). In fact, the Juan Fernandez
298 Province, which lies only 650 km west of Valparaiso, also has a strong southwest Pacific
299 component in its marine fauna (Pequeño & Sáez, 2000).

300 Genetic surveys of dispersive reef organisms are consistent with the boundaries of the Indo-
301 Polynesian Province. While few studies extend to the Arabian Gulf, phylogeographic studies of
302 the Central and West Pacific show high connectivity in many reef fishes (Bay *et al*., 2004; Craig
303 *et al*., 2007; Schultz *et al*., 2007; Horne *et al*., 2008) and reef echinoderms (Lessios *et al*., 2001;
304 2003). In some cases this Central/West Pacific connectivity extends to the central Indian Ocean
305 (Gaither *et al*., 2010). Schultz *et al*. (2008) use bathymetry profiles to demonstrate that dispersal
306 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 the earlier work (Briggs, 1974) two more tropical provinces were recognized: Lord Howe-Norfolk and Northwestern Australian. But each area is presently known to have less than 10% endemism (Allen, 2008). Springer (1982) identified the Pacific Plate, the tropical area to the east of the Philippines and Australia, as a biogeographical region of major significance. However that vast area did not possess sufficient endemism to qualify for provincial status (Briggs, 1995). The Pacific Plate concept was reexamined by Allen (2008) and 1403 species were documented including 130 endemics. But this number included endemics specific to certain islands and archipelagos on the Pacific Plate as well as those that were widespread yet 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 U.S. Line and Phoenix Islands revealed that 6.3% were restricted to the Pacific Plate (Mundy *et al.*, 2010), not enough to recognize 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 34º-35º N than do those that terminate there. The peaks in the range termini of the molluscs and marine algae occur between 33º and 34º N and between 36º and 37º 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 33º 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) had recognized clusters of geographic endpoints for northern algae species at Monterey Bay and endpoints for southern species near Los Angeles. Horn & Allen (1978) had 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 was 32.9% but that figure may be too large considering that the province now covers less 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 due 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 are not only distinguished by significant endemism but are also separated from the tropics by the 20º C isotherm for the coldest month (Briggs, 1974), i.e., 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, a little more than 10% of the fishes are endemic (D.R. Robertson, 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 16% for decapods (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. Due 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 12º C to 2º 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

403 including the southern tips of Australia and South America. The new cold-temperate biotas were
404 derived ultimately from tropical species that were able to adapt to the new environment (Krug *et*
405 *al*., 2009). Their present global distributions are delineated in Fig. 1. The contrast between the
406 organisms occupying the warm-temperate vs. cold-temperate environments is more extreme than
407 between the other temperature zones. The difference is such that families and genera found in one
408 usually do not appear in the other.

409 NORTHERN HEMISPHERE

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

419 Multiple biogeographic subdivisions were suggested by Golikov *et al*. (1990, see also
420 Kafanov & Kudryashov, 2000). On the world-wide perspective, the various regions were
421 delineated about as they had been for the past 25 years but the northern oceans were more finely
422 divided. The authors recognized a kingdom of temperate and cold waters that was subdivided into
423 regions, subregions, and provinces. Their descriptions and maps indicated, for the most part, that
424 the biotas occupied areas that had been previously outlined (Briggs, 1974) but there were some
425 notable exceptions: (1) in the Eastern North Atlantic, the Arctic/Boreal (A/B) boundary was
426 extended northward 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 special ecological zone rather than 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) closure of the Tethys Sea, (3) collision of Australia with Southeast Asia, and (4) 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 +2º C and -2º 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 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 southward

to the Strait of Belle Isle in the west and to the northeast beyond the Murmansk Peninsula. In the Pacific, Arctic biota extends southward 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 amphiboreal 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 molluscan 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 westward (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 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 (55º N). The northern (Aleutian) province has an endemism rate of about 24% in decapods and 23% in molluscs (Boschi, 2000; Valentine, 1967, respectively). In contrast, the Oregon Province, if considered to terminate at Monterey Bay, has only about 2% endemism in decapods and fishes (Boschi, 2000; Horn & Allen, 1978; Horn *et al*., 2006) respectively. But if 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 -37º N), and a peak in range termination endpoints at about 50º 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 include 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 southward 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 northward 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, Liparididae, 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 & Shroeder, 1953), 53% in all molluscs (Vermeij, 2005c), 21% in opisthobranch gastropods (García & Bertsch, 2009), and only 5% in decapods (Boschi, 2000).

**Eastern Atlantic Boreal Region**

This region is now considered to extend from Svalbard and the southern end of Novaya Zemlya to the southern entrance of the English Channel (Golikov *et al*., 1990) (Fig. 1). Previously, 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 García & 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 toward 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 in the eastern side (69% endemic) and 262 in 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 for 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

Due to the presence of many tropical eurythermic species, and to endemics with nearby tropical ancestors, the faunal relationship of most northern warm-temperate provinces is closest to their adjoining tropical province. But, in the Southern Hemisphere (Fig.1), 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 southward through the Eastern Pacific to Tierra del Fuego. From this point, they reached, apparently via the WWD, the

595 Falkland Islands, Tristan da Cunha, and the tip of southern Africa (Rocha-Olivares *et al.*, 1999).

596 A number of taxa originating in Australia-New Zealand were able to achieve circumglobal
597 ranges via the WWD. Such a dispersal history had been proposed for the fish families
598 Cheilodactylidae and Latridae (Briggs, 1974). Recently, this suggestion has been reinforced by
599 genetic evidence (Burridge & Smolenski, 2004). The spiny lobster genus *Jasus* provides another
600 example (Pollock, 1990). Genetic and morphological evidence has indicated that two species of
601 chironemid fishes (Chironemidae) found on Juan Fernandez Island represent colonizations from
602 Australia-New Zealand (Burridge *et al*., 2006). Other recent phylogeographic studies have
603 produced strong evidence for WWD dispersal in the Southern Hemisphere (Waters & Burridge,
604 1999; Waters, 2008).

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

612 The Southwestern (Flindersian) and Southeastern (Peronian) Provinces of Australia (Briggs,
613 1995), based on the work of Bennett & Pope (1953, 1960), are still recognized in the recent
614 literature (Waters *et al*., 2010), although the provincial names have varied. For New Zealand, the
615 Auckland and Kermadec provinces are recognized. The Auckland Province shares many species
616 and has a historic relationship with southern Australia (Waters *et al.*, 2007); there may be a
617 considerable endemic component although there are no published estimates. The Kermadec
618 Province invertebrates revealed a large number of species, 296 gastropods, 77 bivalves, and 203

619 cheilostome bryozoans in this small area, with endemism rates of 71%, 69%, and 69%
620 respectively (Griffiths *et al*., 2009). However, there are few endemic fishes.

621 The warm-temperate Peru-Chilean Province (Fig. 1) includes the major part of the western
622 coast of South America extending from the Gulf of Guayaquil to about the Taitao Peninsula. Lee
623 *et al.*, (2006) referred to a Peruvian/Chilean Province extending to around 40º S, an intermediate
624 zone from 40º to 43º S, and the beginning of the cold-temperate waters at 43º S. Marine fishes of
625 southern Chile also show three latitudinal fish zones but they are located farther south (Sielfeld &
626 Vargas, 1999). Those authors indicated that species belonging to typical warm-temperate families
627 (Blenniidae, Clinidae, Normanichthyidae) extended as far as 45º-46º S, concordant with the faunal
628 barrier for sea anemonies (Haussermann & Forsterra, 2005). Briggs (1995) designated Chiloe
629 Island (41.5º S) as the southern limit of the province, but the Taitao Peninsula now seems to be
630 more appropriate. An endemism rate of 13% was noted for the decapod fauna (Boschi, 2000).

631 The Juan Fernandez Province consists of three islands 650 km west of Valparaiso, Chile. The
632 early literature on fishes, invertebrates, and algae indicated considerable endemism, corroborated
633 by a recent survey of the littoral fish fauna that revealed 25.5% endemism (Pequeño & Sáez,
634 2000). The external relationship proved to be stronger to the southwest Pacific than to the Chilean
635 coast, for both the fishes and decapod fauna (Boschi, 2000).

636 The Argentinian Province lies between Santa Catarina, Brazil and the Valdes Peninsula,
637 Argentina (Fig. 1). Previously labeled the Eastern South America Region (Briggs, 1974), it
638 extended from Cape Frio, Brazil to the Rio de la Plata. Later the southern boundary was extended
639 to the Valdes Peninsula, Argentina (Briggs, 1995) and the northern boundary was set at Santa
640 Catarina, Brazil (Floeter *et al*., 2008). Boschi (2000), who accepted the Cape Frio boundary,
641 reported 13% endemism in the decapod crustaceans; García & Bertsch (2009) reported 24%
642 endemism in opisthobranch gastropods in the same area. A new assessment of the reef fish fauna

643 by Galvan *et al*. (2009) illustrates a sharp change from a warm-temperate to cold-temperate fauna
644 near Valdes Peninsula (42º S). Five cold-temperate fish families (Bovichtidae, Eleginopidae,
645 Nototheniidae, Congiopodidae, Moridae) do not extend north of this region, illustrating the
646 dramatic faunal transition in this boundary area.

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

662 COLD-TEMPERATE REGIONS

663 Cold-temperate waters are found around the tip of South America and the Falkland Islands,
664 Tasmania and Victoria in Australia, southern New Zealand and nearby islands, and the Sub-
665 Antarctic (Fig. 1). These areas had been apportioned into four regions and seven provinces
666 (Briggs, 1995): South America (Magellan), Tasmanian, New Zealand, and Sub-Antarctic regions

667 with two provinces in the New Zealand Region and five provinces in the Sub–Antarctic. However,
668 because of much recent work on the cold-temperate invertebrate fauna, especially by Linse *et al*.
669 (2006), Clarke *et al*. (2007), and Griffiths *et al*. (2009), the southern cold-temperate and cold
670 regions and provinces can now be more confidently defined.

671 Endemism in four classes of benthic invertebrates (Bivalvia, Gastropoda, Cyclostomata, and
672 Cheilostomata) was determined by Griffiths *et al*. (2009) based on more than 7,000 specimens
673 collected from all parts of the Antarctic and Sub-Antarctic. Although the endemism percentages
674 varied among the classes, we recognize the following geographic areas as provinces if at least two
675 classes have endemism rates of more than 10%. This procedure resulted in the designation of 12
676 provinces and four regions within the Southern Ocean area. Three of the collection localities were
677 in South Africa, Tristan da Cunha, and the Kermadec Islands, all located in warm-temperate
678 provinces, so they were not included in the following cold-temperate arrangement. All three
679 showed exceedingly high endemism. Macquarie Island was not surveyed by Griffiths *et al*.
680 (2009), but was designated as a province by Briggs (1974), based on a 66% molluscan endemism
681 (Dell 1964). The inclusion of Macquarie brings the total number of cold-temperate provinces to
682 13.

683 **South American Region**

684 Previously the cold-temperate waters of South America were united in a Magellan Province
685 spanning from Chiloe Island in the Pacific side to Rio de La Plata (Argentina/Uruguay border) on
686 the Atlantic side (Briggs 1974). However, the very high endemism rates for invertebrates in
687 southern Chile, Tierra del Fuego, southern Argentina, and the Falkland Islands (Griffiths *et al*.,
688 2009) indicate that all four areas should be designated as provinces within a South American
689 Region (Fig. 4). This represents a significant change from the previous scheme that assumed an
690 undivided fauna for the entire region. In contrast, the shore fish fauna of the region shows no

691 indications of provincial endemism (Sielfeld & Vargas, 1999).

692 Notably, the molluscs of the Chilean coast do not demonstrate a reduction in species
693 diversity at higher latitudes, but rather a sharp increase in diversity above 42º S (Valdovinos *et al*.,
694 2003). In their review of invertebrate zoogeographic patterns in the Magellan Province,
695 Haussermann & Forsterra (2005) noted that the polychaetes and anemonies indicated a barrier
696 between the Pacific and Atlantic sections because those faunas showed very little overlap.
697 Although Boschi & Gavio (2005) recognized a single Magellan Province for the decapod
698 crustaceans, their data indicate about 35% endemism for the Pacific side and about 18% for the
699 Atlantic. These references provide additional justification for a separation between Southern Chile
700 and Southern Argentina provinces.

701 **New Zealand-Australia Region**

702 The Tasmania (Maugean) Province has an exceedingly high endemism for both molluscan classes
703 (Griffiths *et al*., 2009). However this province may extend to the Victoria coast of Australia
704 (Briggs, 1995), an area not reported on by Griffiths *et al*. (2009), so the endemism figures
705 probably will be adjusted downward in the future. Even so, the province is very distinct. New
706 Zealand has very high endemism for all four invertebrate classes; and the endemism figures
707 provided by MacDairmid & Patuawa (2010) for the bivalves (85.5%) and the gastropods (86.6%)
708 are considerably higher than those listed by Griffiths *et al*. (2009). The coastal fish fauna of 270
709 species has 25% endemism (Walrond, 2009). High endemism for other New Zealand marine
710 groups are indicated in the online summary edited by MacDairmid (2010). It should be noted that
711 the north coast between Auckland and East Cape is in the warm-temperate zone. Is there sufficient
712 endemism to recognize a separate province? The Antipodes Province, consisting of the Auckland,
713 Antipodes, Campbell, and Bounty Islands, demonstrates elevated endemism for the two molluscan
714 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) persistence of a small ancestral group of Mesozoic and early Cenozoic taxa, (2) 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 to that of the Arctic Region. By late Oligocene time, *c*. 24 Ma, there was evidence of a major ice sheet (Ivany *et al*., 2006) indicating

739 close to modern conditions. In contrast, the Arctic Ocean did not decline to similar temperatures
740 until about 2.9 -- 2.4 Ma (Mudelsee & Raymo, 2005, but see Stickley *et al*., 2009). The Antarctic
741 Continent and the South Orkney, South Sandwich, and South Shetland Islands are all below the
742 February one degree C isotherm (Dietrick 1981). The Region includes all of the waters
743 surrounding the continent and the noted island groups (Fig. 6). This agrees with the conclusion of
744 Griffiths *et al*. (2009) who recognized a single Antarctic "Province", in contrast to many earlier
745 workers who divided the continent into various segments. They also determined a general
746 endemism level between 42% and 56% for the four invertebrate classes surveyed in Griffiths *et al*.
747 (2009). Other invertebrate classes recently investigated, the ascidians (Primo & Vázquez, 2007)
748 and the anemones (Rodriguez *et al*., 2007), indicate similar levels of endemism. Estimates for
749 other invertebrate groups are also high: 51% for sponges, 57% for polychaetes, and 75% for
750 molluscs (Arntz *et al*., 1997). Previously, Knox (1994) had observed that more than half the
751 invertebrate species were endemics. Phylogeographic studies are consistent with a single Antarctic
752 Province, showing little (or no) population structure across this vast region for two decapods
753 (Raupach *et al*., 2010), one nemertean (Thornhill *et al*., 2008), and four notothenioids (ice fishes;
754 Janko *et al*., 2007). The fast-moving Antarctic Circumpolar Current must facilitate the high
755 dispersal observed in this region.

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

763 families represent invasions from the North Pacific, and the unique notothenioids probably arose
764 in the Antarctic.

765 CONCLUSIONS AND CONSERVATION IMPLICATIONS

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

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

787 provinces but, nested within the latter, a new series of 232 ecoregions.

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

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

Abbott, I.A. (1999) *Marine red algae of the Hawaiian Islands*. Bishop Museum Press, Honolulu.

Addison, J.A., & Hart, M.W. (2005) Colonization, dispersal, and hybridization influence the phylogeography of North Atlantic sea urchins (*Strongylocentrotus droebachiensis*) *Evolution*, **59**, 532 – 543.

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, L.G., Pondella, D.J. & Horn, M.H. (2006) *The ecology of marine fishes: California and adjacent waters.* University of California Press, Berkeley.

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

Arntz, W.E., Gutt, J., & Klages, M. (1997) Antarctic marine biodiversity: an overview. *Antarctic*

834 *communities: species, structure and survival* (ed. by B. Battaglia, J. Valencia, & D.W.H.
835 Walton), pp. 3-13, Cambridge University Press, Cambridge.

836 Avise, J.C. 1992. Molecular population structure and the biogeographic history of a regional
837 fauna: a case history with lessons for conservation biology. *Oikos*, **63**, 62-76.

838 Baums, I.B., Miller, M.W. & Hellberg, M.E. (2005) Regionally isolated populations of an
839 imperiled Caribbean coral, *Acropora palmata*. Molecular Ecology, 14, 1377 – 1390.

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

843 Bennett, I. & Pope, E.C. (1953) Intertidal zonation of the exposed rocky shores of Victoria,
844 together with a rearrangement of the biogeographical provinces of temperate Australian shores.
845 *Australian Journal of Marine and Freshwater Research*, **4**, 105-159.

846 Bennett, I. & Pope, E.C. (1960) Intertidal zonation of the exposed rocky shores of Tasmania and
847 its relationship with the rest of Australia. *Australian Journal of Marine and Freshwater Research*,
848 **11**, 182-221.

849 Bigelow, H.B. & Schroeder, W.C. (1953) *Fishes of the Gulf of Maine*. U.S. Fish and Wildlife
850 Service, Fishery Bulletin 74, Washington, D.C.

851 Böhlke, J.E. & Chaplin, C.C.G. (1968) *Fishes of the Bahamas and adjacent tropical waters*.
852 Livingston, Wynnewood, PA.

853 Boschi, E.E. (2000) Species of decapod crustaceans and their distribution in the American marine
854 zoogeographic provinces. *Revista de Investigacion y Desarrollo Pesquero*, **13**, 7-64.

855 Boschi, E.E. & Gavio, M.A. (2005) On the distribution of decapod crustaceans from the Magellan
856 Biogeographic Province and the Antarctic region. *Scientia Marina*, **69**, 195-200.

857 Bowen, B.W. & Avise, J.C. (1990) The genetic structure of Atlantic and Gulf of Mexico
858 populations of sea bass, menhaden, and sturgeon: the influence of zoogeographic factors and life
859 history patterns. *Marine Biology*, **107**, 371-381.

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

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

866 Bowen, B.W., Karl, S.A. & Pfeiler, E. (2007) Resolving evolutionary lineages and taxonomy of
867 bonefishes (*Albula* spp.). *Biology and Management of the World Tarpon and Bonefish Fisheries*
868 (ed. by J.S. Ault), pp. 147-154. CRC Press, Boca Raton, FL.

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

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

871 Briggs, J.C. (2003) Marine centres of origin as evolutionary engines. *Journal of Biogeography*,
872 **30**, 1–18.

873 Briggs, J.C. (2005) The marine East Indies: diversity and speciation. *Journal of Biogeography*, **32**,
874 1517-1522.

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

877 Brunner, P.C., Douglas, M.R., Osinov, A., Wilson, C.C. & Bernatchez, L. (2001) Holarctic
878 phylogeography of the Arctic charr (*Salvelinus alpinus*) inferred from mitochondrial DNA
879 sequences. *Evolution*, **55**, 573 – 586.

880 Burgess, G.H., Smith, S.H. & Lane, E.D. (1994) Fishes of the Cayman Islands. *The Cayman*
881 *Islands: natural history and biogeography* (ed. by M.A. Brunt and J.E. Davies), pp. 199-228.
882 Kluwer Academic Publishers, Dordrecht.

883 Burridge, C.P. & Smolenski, A.J. (2004) Molecular phylogeny of the Cheilodactylidae and
884 Latridae (Perciformes: Cirrhitoidea) with notes on taxonomy and biogeography. *Molecular*
885 *Phylogenetics and Evolution*, **30**, 118-127.

886 Burridge, C.P., Melendez, R. & Dyer, B.S. (2006) Multiple origins of the Juan Fernandez kelpfish
887 fauna and evidence for frequent and unidirectional dispersal of cirrhitoid fishes across the South
888 Pacific. *Systematic Biology*, **55**, 566-578.

889 Carlin, J.L., Robertson, D.R., & Bowen, B.W. (2003) Ancient divergences and recent connections
890 in two tropical Atlantic reef fishes *Epinephelus adscensionis* and *Rypticus saponaceous*
891 (Percoidei: Serranidae). *Marine Biology*, **143**, 1057–1069.

892 Chace, F.A. (1966) Decapod crustaceans from St. Helena Island, South Atlantic. *Proceedings of*
893 *the U.S. National Museum*, **118**, 622 – 662.

894 Clarke, A., Griffiths, H.J., Linse, K., Barnes, D.K.A. & Crame, J.A. (2007) How well do we know
895 the Antarctic marine fauna? A preliminary study of macroecological and biogeographic patterns in
896 Southern Ocean gastropod and bivalve molluscs. *Diversity and Distributions*, **13**, 620-632.

897 Coelho, P.A., De Almeida, A.O. & Bezerra, L.E.A. (2008) Checklist of the marine and estuarine
898 Brachyura (Crustacea: Decapoda) of northern and northeastern Brazil. *Zootaxa*, **1956**, 1-58.

899 Cohen, D.M., Inada, T., Iwamoto, T. & Scialabba, N. (1990) *Gadiform fishes of the world*. FAO
900 Species Catalog, Vol. 10, FAO, Rome.

901 Collette, B.B. & Parin N. V. (1991) Shallow-water fishes of Walters Shoals, Madagascar Ridge.
902 *Bulletin of Marine Science*, **48,** 1-22.

903 Cox, C.B. & Moore, P.D. (2000) *Biogeography: An ecological and evolutionary Approach*, 6th
904 edn. Blackwell Science, Oxford.

905 Craig, M.T., Eble, J.A., Bowen, B.W. & Robertson, D.R. (2007) High genetic connectivity across
906 the Indian and Pacific Oceans in the reef fish *Myripristis berndti* (Holocentridae). *Marine Ecology*
907 *Progress Series*, **334**, 245–254.

908 Crame, J. A. (2004) Pattern and process in marine biogeography. *Frontiers of biogeography* (ed.
909 by M.V. Lomolino and L.R. Heaney), pp. 271-291. Sinauer Associates, Sunderland, MA.

910 Dawson, M.N. (2001) Phylogeography in coastal marine animals: a solution from California?
911 *Journal of Biogeography*, **28**, 723-736.

912 Dawson, M.N., Waples, R.S. & Bernardi, G. (2006) Phylogeography. In *The ecology of marine*
913 *fishes: California and adjacent waters* (ed. by L.G. Allen, D.J. Pondella, and M.H. Horn), pp. 26-
914 54. University of California Press, Berkeley.

915 Dell, R.K. (1962) New Zealand marine provinces- do they exist? *Tuatara*, **10**, 44-51.

916 Dell, R.K. (1964) Marine Mollusca from Macquarie and Heard Islands. *Records Dominion*
917 *Museum, Wellington*, **4**, 267-301.

918 Dietrick, G. (1981) *General oceanography: an introduction*, 2nd edn. John Wiley & Sons,
919 Hoboken, NJ.

920 Drew, J.A., Allen, G.R. & Erdmann, M.V. (2010) Congruence between genes and color morphs in
921 a coral reef fish: Population variability in the Indo-Pacific damselfish *Chrysiptera rex* (Snyder,
922 1909). *Coral Reefs*, **29**, 439-444.

923 Eastman, J.T. (1997) Comparison of the Antarctic and Arctic fish faunas. *Cybium*, **21**, 335-352.

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

925 Edwards, A. J. (1990) *Fish and fisheries of Saint Helena Island.* Centre for Tropical Coastal
926 Managemet Studies, Newcastle-upon-Tyne, UK.

927 Ekman, S. (1935) *Tiergeographie des Meeres*. Akademische Verlagsgesellschaft M.B.H., Leipzig.

928 Ekman, S. (1953) *Zoogeography of the sea*. Sidgwick and Jackson, London.

929 Eschmeyer, W.N., Herald, E.S. & Hammann, H. (1983) *A field guide to Pacific coast fishes*.
930 Houghton Mifflin, Boston, MA.

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

935 Forbes, E. (1859) *The natural history of European seas*….(edited and continued by Robert
936 Goodwin-Austin). John Van Voorst, London.

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

940 Gaither, M.R., Bowen, B.W., Bordenave, T.-R., Rocha, L.A., Newman, S.J., Gomez, J.A., van
941 Herwerden, L. & Craig, M.T. (2011) Phylogeography of the reef fish *Cephalopholis argus*
942 (Epinephelidae) indicates Pleistocene isolation across the Indo-Pacific Barrier with contemporary
943 overlap in the Coral Triangle. BMC Evolutionary Biology, **11**, 189. doi: 10.1186/1471-2148-11-
944 189.

945 Galvan, D.E., Veneris, L.A. & Irigoyen, A.J. (2009) Reef-fish fauna of the northern Patagonian
946 gulfs, Argentina, southwestern Atlantic. *The Open Fish Science Journal*, **2**, 90-98.

947 García, F.J. & Bertsch, H. (2009) Diversity and distribution of the Gastropoda Opisthobranchia

948 from the Atlantic Ocean: a global biogeographic approach. *Scientia Marina*, **73**, 153-160.

949 Gladenkov, A.Y., Oleinik, A., Marinkovitch, L. & Baranov, K.B. (2002) A refined age for the
950 earliest opening of Bering Strait. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **183,** 321-
951 328.

952 Golikov, A. N., Dolgolenko, M.A., Maximovitch, N.V. & Scarlato, O.A. (1990) Theoretical
953 approaches to marine biogeography. *Marine Ecology Progress Series*, **63**, 289-301.

954 Goren, M. & Dor, M. (1994) *An updated checklist of the fishes of the Red Sea (CLOFRES II)*.
955 Israel Academy of Sciences and Humanities, Jerusalem.

956 Grant, W.S., & Leslie, R.W. (2001) Inter-ocean dispersal is an important mechanism in the
957 zoogeography of hakes (Pisces: *Merluccius* spp.). *Journal of Biogeography*, **28**, 699-721.

958 Grant, W.S., Lecomte, F., & Bowen, B.W. (2010) Biogeographical contingency and the evolution
959 of tropical anchovies *Cetengraulis* from temperate *Engraulis*. *Journal of Biogeography*, **37**, 1352-
960 1362.

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

963 Hastings, P.A. (2009) Biogeography of New World Blennies. *The biology of blennies* (eds. R.A.
964 Patzner, E.J. Goncalves, P.A. Hastings, and B.G. Kapoor), pp. 95-118. Science Publishers,
965 Enfield, NH.

966 Haussermann, V. & Forsterra, G. (2005) Distribution patterns of Chilean shallow-water sea
967 anemonies (Cnidaria: Anthozoa: Actiniaria, Corralimorpharia), with a discussion of the taxonomic
968 and zoogeographic relationships between the actinofauna of the south east Pacific, the south west
969 Atlantic and Antarctic. *Scientia Marina*, **69** (Suppl. 2), 91-102.

970 Horn, M.H. & Allen, L.G. (1978) A distributional analyses of California coastal marine fishes.

971 *Journal of Biogeography*, **5**, 23-42.

972 Horn, M.H., Allen, L.G. & Lea, R.N. (2006) Biogeography. *The ecology of marine fishes:*
973 *California and adjacent waters* (ed. by L.G. Allen, D.J. Pondella, and M.H. Horn), pp. 3-25.
974 University of California Press, Berkeley, CA

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

978 Hubbs, C.L. (1960) The marine vertebrates of the outer coast. Part 2. The biogeography of Baja
979 California and adjacent seas. *Systematic Zoology*, **9**, 134-147.

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

982 Ivany, L.C., Van Simaeys, S., Domack, E.W. & Samson, S.D. (2006) Evidence for the earliest
983 Oligocene ice sheet on the Antarctic Peninsula. *Geology*, **34**, 377-380.

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

986 IUCN (2010) *Med News*. International Union for Conservation of Nature (IUCN), Center for
987 Marine Cooperation, Rome, Italy.

988 Janko, K., Lecointre, G., DeVries, A., Couloux, A., Cruaud, C. & Marshall, C. (2007) Did glacial
989 advances during the Pleistocene influence differently the demographic histories of benthic and
990 pelagic Antarctic shelf fishes? – Inferences from intraspecific mitochondrial and nuclear DNA
991 sequence diversity. *BMC Evolutionary Biology*, **7**, 220. doi:10.1186/1471-2148-7-220.

992 Jefferson T. A., Leatherwood, S. & Webber, M.A. (1993) *Marine mammals of the world*. FAO
993 United Nations, Rome.

994 Kafanov, A.I. & Kudryashov, V.A. (2000) *Marine biogeography: a text-book.* Nauka, Moscow.

995 Kafanov, A.I., Volvenko, I.V., Fedorov, V.V. & Pitruk, D.L. (2000) Ichthyofaunistic
996 biogeography of the Japan (East) Sea. *Journal of Biogeography*, **27**, 915-933.

997 Kay, E.A. (1980) Little worlds of the Pacific: an essay on Pacific Basin biogeography. Lyon
998 Aboretum, University of Hawaii.

999 Kemp, J.M. (1998) Zoogeography of the coral reef fishes of the Socotra Archipelago. *Journal of*
1000 *Biogeography,* **25**, 919-933.

1001 Krug, A.Z., Jablonski, D., Valentine, J.W. & Roy, K. (2009) Generation of Earth's first-order
1002 biodiversity pattern. *Astrobiology*, **9**, 113-124.

1003 Lee, M.R., Castilla, J.C., Fernandez, M., Clarke, M., Gonzales, C., Prado, L., Rosbaczylo, N. &
1004 Valdovinos, C. (2008) Free-living benthic marine invertebrates in Chile. *Revista Chilena de*
1005 *Historia Natural*, **81,** 51-67**.**

1006 Lessios, H.A., Kessing, B.D. & Pearse, J.S. (2001) Population structure and speciation in tropical
1007 seas: global phylogeography of the sea urchin *Diadema*. *Evolution*, **55**, 955 – 975.

1008 Lessios, H.A., Kane, J. & Robertson, D.R. (2003) Phylogeography of the pantropical sea urchin
1009 Tripneustes: contrasting patterns of population structure between oceans. *Evolution*, **57**, 2026 –
1010 2036.

1011 Linse, K., Griffiths, H.J., Barnes, D.K.A. & Clarke, A. (2006) Biodiversity and biogeography of
1012 Antarctic and sub-Antarctic mollusca. *Deep-Sea Research II*, **53**, 985-1008.

1013 Liu, J.-X., Gao, T.-X., Wu, S.-F. & Zhang, Y.-P. (2007) Pleistocene isolation in the Northwestern
1014 Pacific marginal seas and limited dispersal in a marine fish, *Chelon haematocheilus* (Temminck &
1015 Schlegal, 1845) *Molecular Ecology*, **16**, 275 – 288.

1016 MacDiarmid, A. (2010) (ed.), *The treasures of the sea*: *a summary of marine life biodiversity in*

1017 *the New Zealand marine ecoregion*. Available at: http://www.treasuresofthesea.org.nz/. 5/15/10.

1018 MacDiarmid, A. & Patuawa, T. (2010) Bivalves and gastropods. In A. MacDiarmid (ed.) *The*
1019 *treasures of the sea, a summary of marine life biodiversity in the New Zealand marine ecoregion*,
1020 (ed. by A. MacDiarmid). Available at: http://www. treasurersofmarinelife.org.nz/. 5/15/10.

1021 Magnussen, E. (2002) Demersal fish assemblages of Faroe Bank: species composition,
1022 distribution, biomass spectrum and diversity. *Marine Ecology Progress Series*, **238**, 211-225.

1023 McCosker, J.E. & Rosenblatt, R.H. (2010) The fishes of the Galapagos Archipelago: an update.
1024 *Proceedings of the California Academy of Sciences*, **61**, 167-195.

1025 Mudelsee, M. & Raymo, M.E. (2005) Slow dynamics of the Northern Hemisphere glaciation.
1026 *Paleoceanography*, **20**, 1-14.

1027 Mundy, B.G., Wass, R., Demartini, E., Green , B., Zgliczynski, B., Schroeder, R.E. & Musberger,
1028 C. (2010) *Inshore fishes of Howland Island, Baker Island, Jarvis Island, Palmyra Atoll, and*
1029 *Kingman Reef.* Atoll Research Bulletin 585. National Museum of Natural History, Washington,
1030 D.C.

1031 Murray, S.N., Littler, M.M. & Abbott, I.A. (1980) Biogeography of the California marine algae
1032 with emphasis on the southern California islands. *The California islands* (ed. by D.M. Power), pp.
1033 325-339. Santa Barbara Museum of Natural History, Santa Barbara, CA.

1034 Muss, A., Robertson, D.R., Stepien, C.A., Wirtz, P., & Bowen, B.W. (2001) Phylogeography of
1035 the genus *Ophioblennius*: the role of ocean currents and geography in reef fish evolution.
1036 *Evolution*, **55**, 561-572.

1037 Naranjo, S., Carballo, J.L. & García-Gómez, J.C. (1998) Towards a knowledge of marine
1038 boundaries using ascidians as indicators: characterising transition zones for species distribution
1039 along Atlantic-Mediterranean shores. *Biological Journal of the Linnean Society*, **64**, 151-177.

1040 Olsen, J.L., Stam, W.T, Coyer, J.A., Reusch, T.B.H., Billingham, M., Bostrom, C., Calvert, E.,
1041 Christie, H., Granger, S., LaLumiere, R., Milchakova, N., Oudet-Le Secq, M.-P., Procaccini, G.,
1042 Sanjabi, B., Serrao, E., Veldsink, J., Widdicombe, S., & Wyllie-Echeverria, S. (2004) North
1043 Atlantic phylogeography and large-scale population differentiation of the seagrass *Zostera marina*
1044 L. *Molecular Ecology*, **13**, 1923-1941.

1045 Parin, N.V. (1994) Fish fauna of the Nasca and Sala y Gomez submarine ridges, the easternmost
1046 outpost of the Indo-West Pacific Zoogeographic Region. *Bulletin of Marine Science*, **49**, 671-683.

1047 Paternello, T., Volckaert, A.M.J., & Castilho, R. (2007) Pillars of Hercules: Is the Atlantic-
1048 Mediterranean transition a phylogeographic break? *Molecular Ecology*, **16**, 4426 – 4444.

1049 Peden, A.E. & Wilson, D.E. (1976) Distribution of intertidal and subtidal fishes of northern
1050 British Columbia and southeastern Alaska. *Syesis*, **9**, 221-248.

1051 Pequeño, G. & Sáez, S. (2000) Los peces litorales del archipielago de Juan Fernandez (Chile):
1052 endesmismo y relaciones ictiogeograficas. *Investigaciones Marinas, Valparaiso*, **28**, 27-37.

1053 Pollock, D.E. (1990) Palaeoceanography and speciation in the spiny lobster genus *Jasus*. *Bulletin*
1054 *of Marine Science*, **46**, 387-405.

1055 Primo, C. & Vázquez, E. (2007) Zoogeography of the Antarctic ascidian fauna in relation to the
1056 sub-Antarctic and South America. *Antarctic Science,* **19**, 321-336.

1057 Randall, J.E. (1994) Twenty two new records of fishes from the Red Sea. Fauna of Saudi Arabia
1058 14:259 – 275.

1059 Randall, J.E. (1995) *Coastal fishes of Oman*. Crawford House Publishing, Bathurst, NSW,
1060 Australia.

1061 Randall, J.E. (2007) *Reef and Shore Fishes of the Hawaiian Islands*. Sea Grant College Program,
1062 University of Hawaii, Honolulu.

1063 Randall, J.E. & Cea, A. (2010) *Shore fishes of Easter Island*. University of Hawaii Press,
1064 Honolulu.

1065 Randall, J.E. & Earle, J.L. (2000) Annotated checklist of the shore fishes of the Marquesaqs
1066 Islands. *Occasional Papers Bishop Museum*, **66**, 1 – 39.

1067 Raupach, M.J., Thatje, S., Dambach, J., Rehm, P., Misof, B. & Leese, F. (2010) Genetic
1068 homogeneity and circum-Antarctic distribution of two benthic shrimp species of the Southern
1069 Ocean, *Chorismus antarcticus* and *Nematocarcinus lanceopes*. *Marine Biology*, **157**, 1783-1797.

1070 Robertson, D.R. & Cramer, K.L. (2009) Shore fishes and biogeographic subdivisions of the
1071 tropical Eastern Pacific. *Marine Ecology Progress Series*, **380**, 1-17.

1072 Rocha, L.A., Bass, A.L., Robertson, D.R., & Bowen, B.W. (2002) Adult habitat preferences,
1073 larval dispersal, and the comparative phylogeography of three Atlantic surgeonfishes (Teleostei:
1074 Acanthuridae). *Molecular Ecology*, **11**, 243-252.

1075 Rocha-Olivares, A., Rosenblatt, R.H. & Vetter, R.D. (1999) Cryptic species of rockfishes
1076 (*Sebastes*: Scorpaenidae) in the Southern Hemisphere inferred from mitochondrial lineages.
1077 *Journal of Heredity*, **90**, 404-411.

1078 Rodríguez, E., López-González, P.J. & Gili, J.M. (2007) Biogeography of Antarctic sea anemones
1079 (Anthozoa, Actinaria): what do they tell us about the origin of the Antarctic benthic fauna? *Deep-*
1080 *Sea Research II*, **54**, 1876-1904.

1081 Schultz, J.K., Pyle, R.L., DeMartini, E. & Bowen, B.W. (2007) Genetic connectivity among color
1082 morphs and Pacific archipelagos for the flame angelfish, *Centropyge loricula*. *Marine Biology*,
1083 **151**, 167 – 175.

1084 Schultz, J.K., Feldheim, K.A., Gruber, S.H., Ashley, M.V., McGovern, T.M. & Bowen, B.W.
1085 (2008) Global phylogeography and seascape genetics of the lemon sharks (genus *Negaprion*).

1086 *Molecular Ecology*, **17**, 5336–5348.

1087 Shao, K.-T., Chen, J.-P., & Wang, S.-C. (1999) Biogeography and data base of marine fishes in
1088 Taiwan waters. *Proceedings 5th Indo-Pacific Fish Conference, Noumea, 1997* (eds. by B. Seret
1089 and J.-Y. Sire), pp. 673-680. Societe Francaise Ichthyologique, Paris.

1090 Shulman, M.J., & Bermingham, E. (1995) Early life histories, ocean currents, and the population
1091 genetics of Caribbean reef fishes. *Evolution*, **49**, 897 – 910.

1092 Sielfeld, W. & Vargas, M. (1999) Review of marine fish zoogeography of Chilean Patagonia (42-
1093 57 S). *Scientia Marina*, **63**, 451-463.

1094 Sivasundar, A. & Palumbi, S.R. (2010) Life history, ecology and biogeography of strong genetic
1095 breaks among 15 species of Pacific rockfish *Sebastes*. *Marine Biology*, **157**, 1433-1452.

1096 Smith, E.A. (1890) Report on the marine molluscan fauna of the island of St. Helena. *Proceedings*
1097 *of the Zoological Society of London*, **1890**, 246 – 317.

1098 Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdana, Z.A., Finlayson, M., Halpern,
1099 B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia,
1100 C.A. & Robertson, J. (2007) Marine ecoregions of the world: a bioregionalization of coastal and
1101 shelf areas. *BioScience*, **57**, 573-583.

1102 Springer, V.G. (1982) Pacific plate biogeography, with special reference to shore fishes.
1103 *Smithsonian Contributions to Zoology*, **465**, 1-182.

1104 Stickley, C.E., St. John, K., Koc, N., Jordan, R.W., Passchier, S., Pearce, R.B. & Kearns L.E.
1105 (2009) Evidence for middle Eocene Arctic Sea ice from diatoms and ice-rafted debris. *Nature*,
1106 **460**, 376-379.

1107 Taylor, M.S., & Hellberg, M.E (2005) Marine radiations at small geographic scales: speciation in
1108 small neotropical reef gobies (*Elactinus*). *Evolution*, **59**, 374 – 385.

1109 Thiede, J., Winkler, A., Wolf-Welling, T., Eldholm, O., Myhre, A.M., Baumann, K.L., Henrich,R.
1110 & Stein, R. (1998) Late Cenozoic history of the polar North Atlantic. *Quaternary Science*
1111 *Reviews*, **17**, 185-208.

1112 Thornhill, D.J., Mahon, A.R., Norenburg, J.L. & Halanych, K.M. (2008) Open-ocean barriers to
1113 dispersal: a test case with the Antarctic Polar Front and the ribbon worm *Parborlasia corrugatus*
1114 (Nemertia: Lineidae). *Molecular Ecology*, **17**, 5104 – 5117.

1115 Valdovinos, C., Navarrete, S.A. & Marquet , P.A. (2003) Mollusk species diversity in the
1116 Southeastern Pacific: why are there more species towards the pole? *Ecography*, **26**, 139-144.

1117 Valentine, J.W. (1967) The influence of climatic fluctuation on species diversity within the
1118 Tethyan provincial system. *Systematic Association Publication*, **7**, 153-166.

1119 Vermeij, G.J. (1991a) Anatomy of an invasion: the trans-Arctic interchange. *Paleobiology*, **17**,
1120 281-307.

1121 Vermeij, G.J. (1991b) When biotas meet: understanding biotic interchange. *Science*, **253**, 1099-
1122 1100.

1123 Vermeij, G.J. (2004) *Nature: an economic history*. Princeton University Press, Princeton, NJ.

1124 Vermeij, G.J. (2005a) Invasion as expectation. *Species invasions: insights into ecology, evolution,*
1125 *and biogeography* (ed. by D.F. Sax, J.J. Stachowicz and S.D. Gaines), pp. 315-339. Sinauer
1126 Associates, Sunderland, MA.

1127 Vermeij, G.J. (2005b) One-way traffic in the western Atlantic: causes and consequences of
1128 Miocene to early Pleistocene molluscan invasions into Florida and the Caribbean. *Paleobiology*,
1129 **34**, 624-632.

1130 Vermeij, G.J. (2005c) From Europe to America: Pliocene to Recent trans-Atlantic expansion of
1131 cold-water North American mollusks. *Proceedings of the Royal Society B, Biological Sciences*,

**272,** 2545-2550.

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

Veron, J.E.N. (2000) *Corals of the world*, 3 vols. Australian Institute of Marine Science, Townsville, QLD.

Walrond, C. (2009) New Zealand's coastal fishes. *Te Ara, The Encylopedia of New Zealand*. Available at: http://www.teara.govt.nz/. 5/12/10.

Wang, P.X. (1999) Response of Western Pacific marginal seas to glacial cycles: paleoceanographic and sedimentological features. *Marine Geology*, **156**, 5–39.

Wares, J.P., & Cunningham, C.W. (2001) Phylogeography and historical ecology of the North Atlantic intertidal. *Evolution*, **55**, 2455 – 2469.

Waters, J.M. (2008) Driven by the West Wind Drift? A synthesis of southern temperate marine biogeography, with new directions for dispersalism. *Journal of Biogeography*, **35**, 417-427.

Waters, J.M. & Burridge, C.P. (1999) Extreme intraspecific mitochondrial DNA sequence divergence in *Galaxias maculatus* (Osteichthys: Galaxidae), one of the world's most widespread freshwater fish. *Molecular Phylogenetics and Evolution*, **11**, 1-12.

Waters, J.M. & Roy, M. (2004) Out of Africa: the slow train to Australasia. *Systematic Biology*, **53,** 18-24.

Waters, J.M., McCulloch, G.A. & Eason, J.A. (2007) Marine biogeographical structure in two highly dispersive gastropods: implications for trans-Tasman dispersal. *Journal of Biogeography*, **34**, 678-687.

Waters, J.M., Wernberg, T., Connell, S.D., Thomsen, M.S., Zuccarello, G.C., Kraft, G.T., Sanderson, J.C., West, J.A., & Gurgel, C.F.D. (2010) Australia's marine biogeography revisited:

back to the future? *Austral Ecology*, **35**, 988-992.

Wheeler, A. (1969) The fishes of the British Isles and North-West Europe. Macmillan, London.

Winterbottom, R. & Anderson, R.C. (1997) A revised checklist of the epipelagic and shore fishes of the Chagos Archipelago, Central Indian Ocean. J.L.B. Smith Institute of Ichthyology Ichthyological Bulletin 66:1-28.

Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) Trends, rhythms and aberrations in global climate 65 Ma to present. *Science*, **292**, 686-693.

BIOSKETCHES

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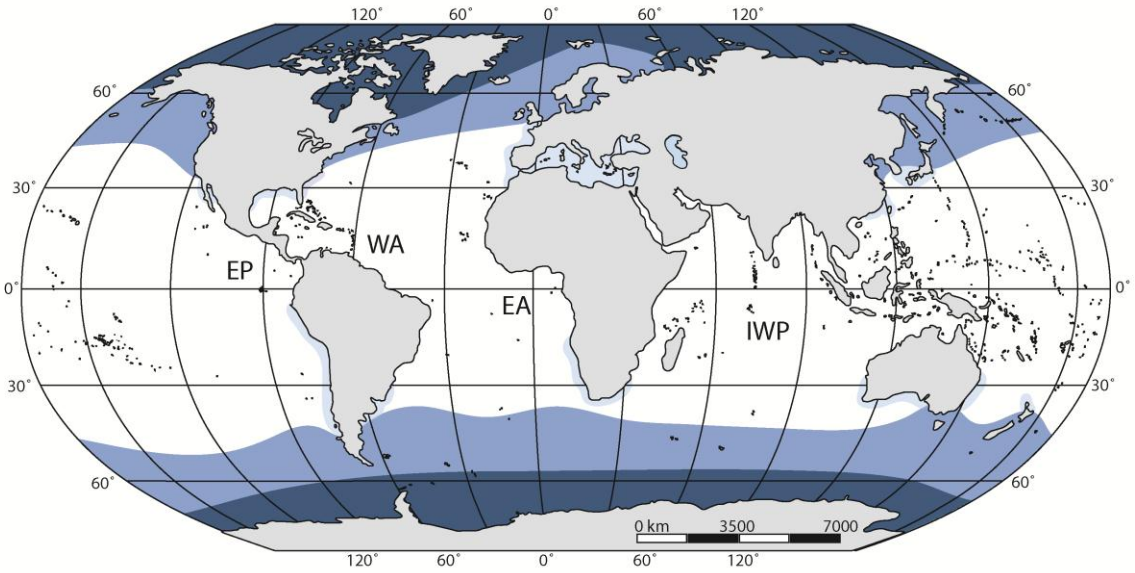
1178 FIGURES

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1180 **Figure. 1**. The realignment of marine biogeographic provinces eliminates the distinction between
1181 tropical and warm-temperate regions, and between cold and cold-temperate regions. Cold regions
1182 (Arctic and Antarctic) are depicted in white, and cold-temperate regions are depicted in dark blue.
1183 Warm-temperate provinces are depicted along the shore lines in medium blue, including Carolina
1184 and Argentinian Provinces in the West Atlantic (WA); Lusitania, Black Sea, Caspian, Aral, and
1185 Benguela Provinces in the East Atlantic (EA) and Mediterranean; Sino-Japanese, Auckland,
1186 Kermadec, Southeastern Australian, and Southwestern Australian Provinces in the Indo-West
1187 Pacific (IWP); California and Peru-Chilean Provinces in the East Pacific (EP). See text for precise
1188 geographic boundaries and additional warm-temperate provinces at oceanic islands.

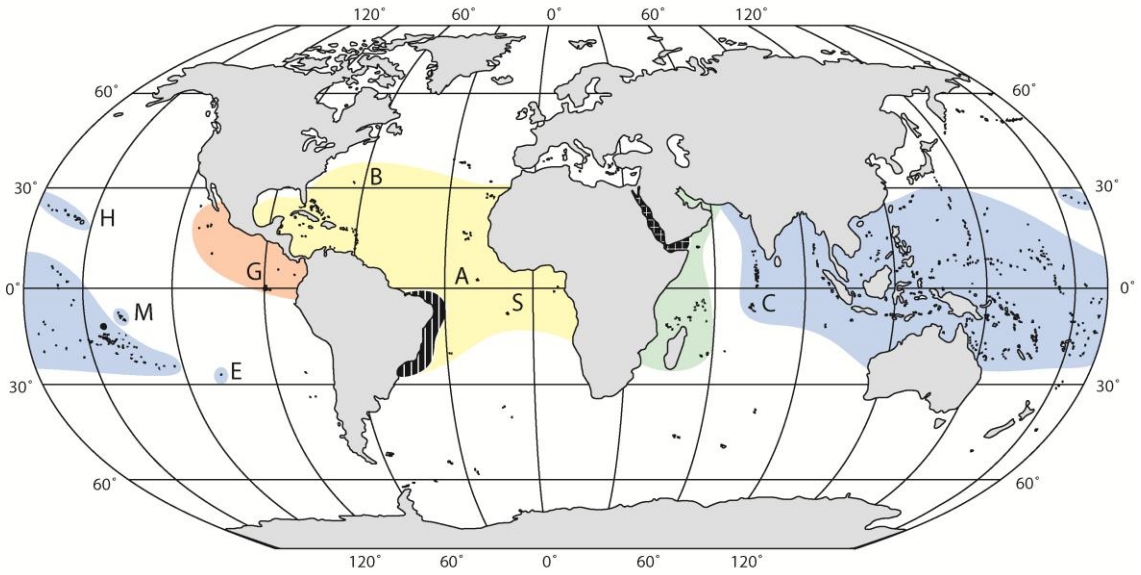


**Figure. 2.** Tropical Regions and Provinces, including the Indo-Polynesian, Hawaiian, Marquesas, and Easter Island Provinces (blue), the East Pacific Region (orange), East and West Atlantic Regions (yellow), and Western Indian Ocean Province (green). Vertical bars indicate Brazilian Province, and crosshatching indicates the Red Sea Province. Selected islands and archipelagos are indicated with the following abbreviations: H = Hawaii, M = Marquesas, E = Easter, G = Galapagos, B = Bermuda, A = Ascension, S = St. Helena, C = Chagos. The Chagos is depicted here as part of the Indo-Polynesian Province, but has faunal affinities with both the Indo-Polynesian Province and the Western Indian Ocean Province (Winterbottom & Anderson, 1997; Gaither et al. 2011)

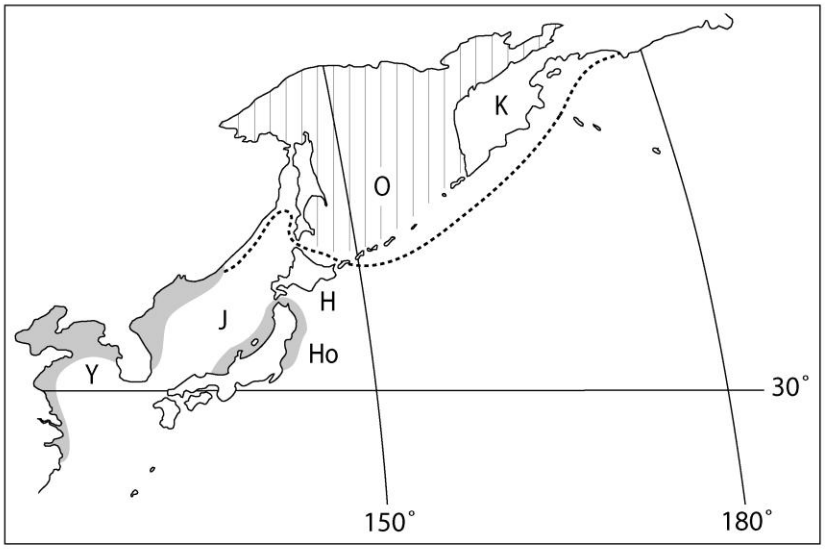


**Figure. 3**. Three Northwest Pacific provinces: The Okhotsk Province (hatched) is confined to the Sea of Okhotsk (O). The Kurile Province (dots) extends across the Pacific side of the Kamchatka Peninsula (K) to the southern tip of Hokkaido (H) and the Sea of Japan (J). The Oriental Province includes three parts, the Yellow Sea (Y), southwestern Sea of Japan, and northern Honshu Island (Ho). See text for precise boundaries.

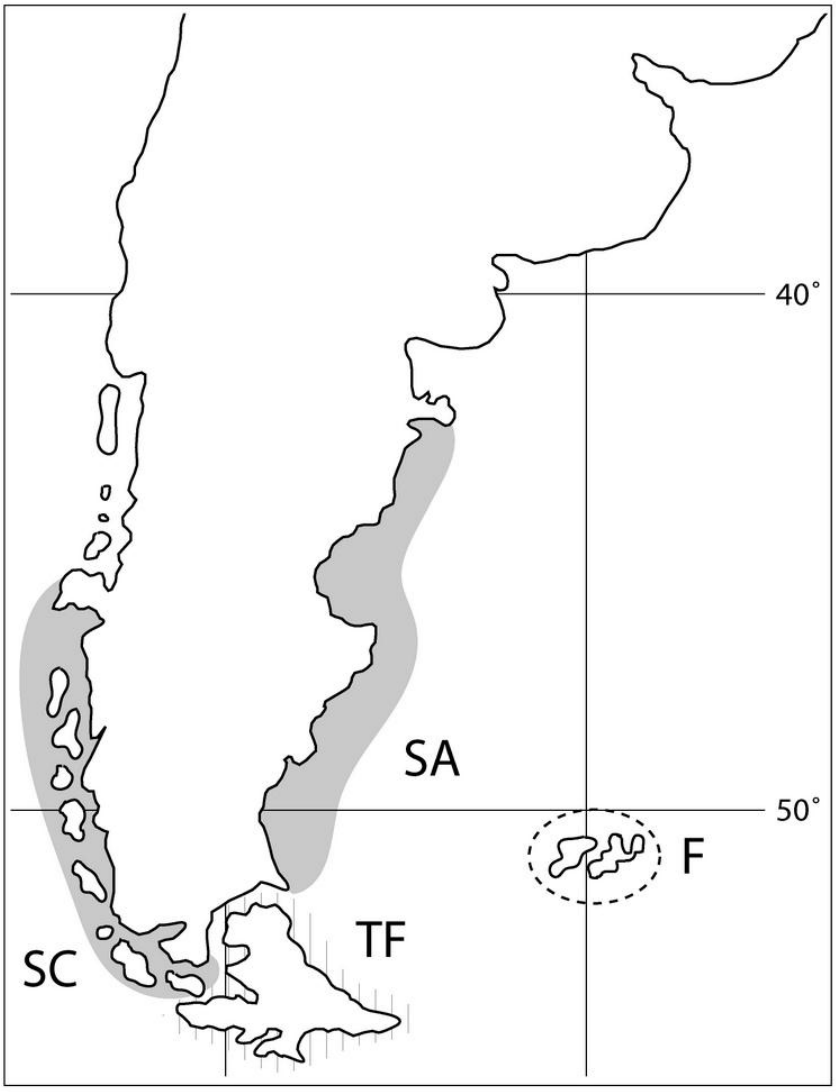


**Figure. 4**. The cold-temperate South American Region (northern boundaries are Valdez Peninsula on the east coast and Taitao Peninsula on the west coast). New provinces are Southern Chile (SC), Tierra del Fuego (TF), Southern Argentina (SA), and Falkland Islands (F).

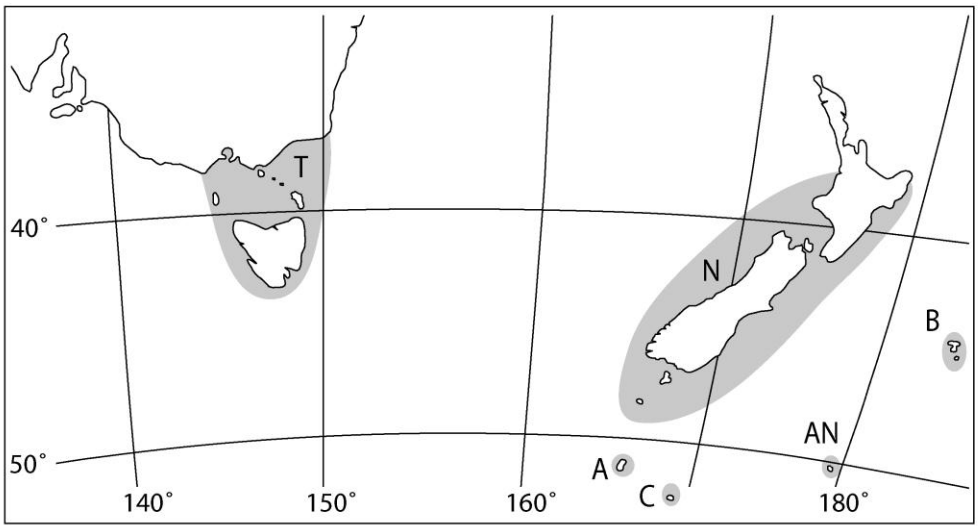


**Figure. 5**. Cold Temperate Provinces of the Southwest Pacific, including the Tasmanian Province (T), the New Zealand Province (N), and the Antipodes Province, consisting of the Aucklands (A), Campbell (C), Antipodes (AN), and Bounty Islands (B).

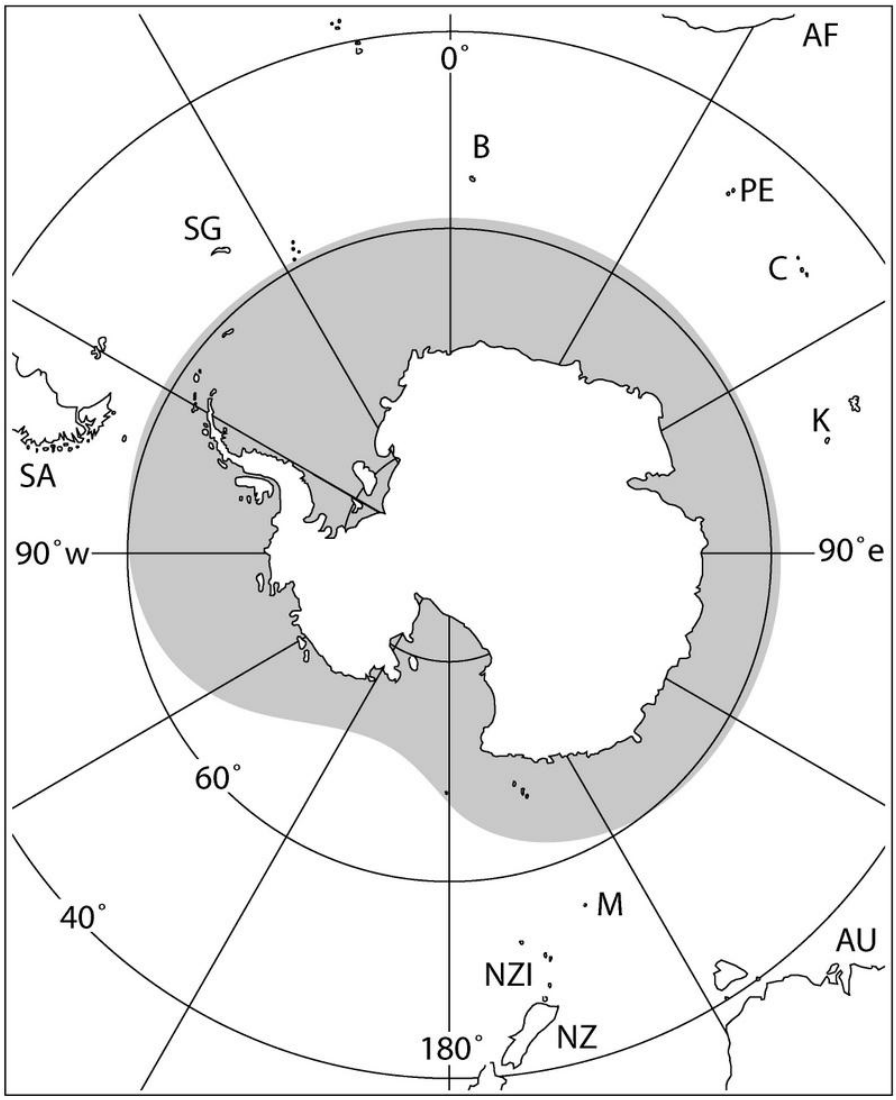


**Figure. 6**. Antarctic and Sub-Antarctic regions. The cold Antarctic Region is indicated by shading. The Sub-Antarctic Provinces include South Georgia (SG), Bouvet Island (B), Prince Edward Islands (PE), Crozet Islands (C), Kerguelen (K), and Macquarie Island (M). Also indicated are the southern tips of South America (SA), Africa (AF), Australia (AU), New Zealand (NZ) and New Zealand Islands (Antipodes, NZI).

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