Special Paper

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2   A REALIGNMENT OF MARINE BIOGEOGRAPHIC PROVINCES WITH PARTICULAR

3   REFERENCE TO FISH DISTRIBUTIONS

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7   ABSTRACT

8   Marine provinces, founded on contrasting floras or faunas, have been recognized for more than

9   150 years but were not consistently defined by endemism until 1974. At that time, provinces were

10 based on at least a 10% endemism and nested within biogeographic regions that covered large

11 geographic areas with contrasting biotic characteristics. Over time, some minor adjustments were

12 made but the overall arrangement remained essentially unaltered. In many provinces, data on

13 endemism were still not available, or available only for the most widely-studied vertebrates

14 (fishes), an ongoing problem. In this report we propose a realignment for three reasons. First,

15 recent works have provided new information to modify or redefine the various divisions and to

16 describe new ones, including the Mid-Atlantic Ridge, Southern Ocean, Tropical East Pacific, and

17 Northeast Pacific. Second, phylogeographic studies have demonstrated genetic subdivisions

18 within and between species that generally corroborated provinces based on taxonomic partitions,

19 with a notable exception at the Indian-Pacific oceanic boundary. Third, the original separation of

20 the warm-temperate provinces from the adjoining tropical ones has distracted from their close

21 phylogenetic relationships. Here we propose uniting warm-temperate and tropical regions into a

22 single warm region within each ocean basin, while still recognizing provinces within the warm-

23   temperate and tropical zones. These biogeographic subdivisions are based primarily on fish

24   distribution but utilize other marine groups for comparison. They are intended to demonstrate the

25   evolutionary relationships of the living marine biota, and to serve as a framework for the

26   establishment of smaller ecological units in a conservation context.

27   **Keywords**: Endemism, evolution, fishes, marine biogeography, phylogeography, provinces,

28   regions, speciation, zoogeography.

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31   INTRODUCTION

32   Biogeographic patterns are most useful when they identify those parts of the world that host the

33   more unique biotas, i.e., areas of evolutionary innovation or refuges where older biota persists.

34   Edward Forbes, in his posthumous work *The Natural History of European Seas* (Forbes, 1859),

35   made three observations of lasting value: (1) each zoogeographic province is an area where there

36   was a special manifestation of creative power and that the animals originally formed there were

37   apt to become mixed with emigrants from other provinces, (2) each species was created only once

38   and that individuals tended to migrate outward from their centre of origin, and (3) provinces to be

39   understood must be traced back like species to their origins in past time. Sven Ekman undertook

40   the huge task of analyzing all the pertinent literature on marine animal distribution and published

41   his book *Tiergeographie des Meeres* (Ekman, 1935). This was followed by a revised English

42   edition *Zoogeography of the Sea* (Ekman, 1953).

43   Ekman (1953) considered the marine world to be comprised of a series of large regions or

44   subregions. For the continental shelf, he described regions located in warm, temperate, and polar

45   waters; their separation by zoogeographic barriers; and their endemism. Later, Briggs (1974)

46   divided the continental shelf into a series of large biogeographic regions that, in turn, contained

47   smaller provinces. Provinces were defined on the basis of endemism, and it was observed that the

48   greater the proportion of endemic biota, the greater the evolutionary significance. An objective

49   standard was considered to be necessary in order that provinces could be recognized within the

50   larger regions. Various biotic areas had previously been called provinces but there was no

51   agreement as to the qualifications necessary for provincial status. So, after an examination of

52   endemism rates in numerous areas, a value of 10% was chosen for an area to qualify as a distinct

53   province (Briggs, 1974). Notably, this minimum value would admit most of the areas that were

54   previously recognized as provinces, based on less formal criteria.

55   The provinces described herein are in coastal and shallow habitats, and based largely on the

56   distributions of fishes. While both the geographic and taxonomic frameworks are admittedly

57   aligned with the authors' field of study, this limitation also indicates the state of knowledge.

58   Fishes in shallow areas, usually defined as less than 200 m depth (Randall, 2007), often are the

59   only groups with sufficient information for biogeographic inference. We have endeavored to

60   bring in other taxa where information is available and find that, where the fauna is relatively well

61   known, there is a high concordance between levels of endemism in fishes, molluscs, and other

62   biota. For example, the fish fauna of Hawaii is 25% endemic (Randall, 2007), the red algae 25%

63   (Abbott, 1999), and the molluscan fauna 20% (Kay, 1980). In the Caribbean Province, the reef

64   fishes are 33% endemic (Floeter *et al*., 2008), decapod crustaceans 32% (Boschi, 2000), and

65   corals 37% (Veron, 2000). Exceptions to this concordance may become apparent, providing a

66   fascinating foundation for further study, but some of these disparities in endemism may be cases

67   where one or two taxonomic groups are much better known than others. Endemism rates in many

68   areas and many taxa are still poorly known and are likely to change as the marine biota (especially

69   invertebrates, plants, and even microbes) receive greater attention.

70   The definition of provinces by 10% endemism has been generally accepted for the past 35

71 years. Good arguments can be made for a higher criterion (15% or 20% endemism), especially to

72 combine depauperate outposts of larger provinces, which may have little evolutionary

73 significance. However, provinces closely linked to those of Briggs (1995) were recently

74 subdivided into ecoregions to address the appropriate scale for conservation efforts (Spalding *et*

75 *al.*, 2007). Furthermore, the 10% criterion has the advantages of stability and functionality: Areas

76 that possess greater than 10% endemism have proven to be locations of unusual evolutionary

77 interest. The 10% criterion is also conservative, because it is typically based on species lists that

78 include oceanic wanderers such as tunas (Randall, 2007), fishes that are very unlikely candidates

79 for endemism on the scale of provinces. The 10% criterion may often be an underestimate, as

80 phylogeographic studies are revealing unrecognized endemic species (Bowen *et al*., 2006a, 2007;

81 Drew *et al*., 2010). In the absence of compelling reasons to the contrary, we choose to retain the

82 10% criterion, while recognizing that this is not an absolute limit but a guidepost for recognizing

83 unique biotic assemblages.

84   The regions and provinces that were defined in 1974 proved to be useful but discoveries made

85 during the next 20 years required the changes published in Briggs (1995). In order to keep abreast

86 of continuing research, additional modifications are required. In recent years, the upsurge of

87 phylogeography has produced many useful studies with biogeographic connotations. At the same

88 time, palaeontological research has produced discoveries about fossils, earth movements, and sea

89 level changes that are critical to historical biogeography. It is now possible to provide more

90 accurate reconstructions of evolutionary relationships in several of the large oceanic regions.

91 Some of the research advances need to be reflected in the arrangement of regions and provinces,

92 while other advances have improved our concept of how speciation and dispersal operates in the

93 marine environment.

94   MARINE BIOGEOGRAPHY

95   With regard to the continental shelves, the four temperature zones of the world's oceans have

96   usually been identified as tropical, warm-temperate, cold-temperate and cold. Within each zone, a

97   series of biogeographic regions were recognized and provinces were located within the regions

98   (Briggs, 1974). Over time, a primary criticism of this arrangement was the placement of warm-

99   temperate provinces in different regions than the tropical ones. Considering that there is a very

100   close relationship between each warm-temperate province and its adjacent tropical equivalent

101   (Vermeij, 2005a), a separation into different regions eventually proved to be inappropriate. Many

102   families and genera span the tropical and warm-temperate regions within each ocean basin,

103   whereas few extend into the cold-temperate regions (Briggs, 1995; Grant *et al*., 2010**).** Therefore,

104   a realignment is proposed here in which expanded regions (Fig. 1) will encompass provinces in

105   both temperature zones. If new research has indicated that provinces need to be altered, they are

106   illustrated and references are provided. Otherwise, if no change is required provinces will remain

107   as described in Briggs (1995).

108   COMPLETE OUTLINE OF SHELF REGIONS AND PROVINCES

109   **WARM REGIONS** (tropical and warm temperate waters).

110   1**. Eastern Atlantic Region**

111   *Provinces*: Lusitania, Black Sea, Caspian, Aral, Tropical Eastern Atlantic, Benguela, St.

112   Helena, Ascension, Tristan-Gough, Amsterdam-St. Paul.

113   2. **Western Atlantic Region**

114   *Provinces*: Carolina, Caribbean, Brazilian, Argentinian.

115   3. **Western Pacific Region**

116   *Provinces (warm-temperate*): Sino-Japanese, Auckland, Kermadec, Southeastern

117   Australian, Southwestern Australian.

118   4. **Tropical Indo-West Pacific Region**

119   *Provinces*: Western Indian Ocean, Red Sea, Indo-Polynesian, Hawaiian, Marquesas,

120   Easter Island.

121   5. **Eastern Pacific Region**

122   *Provinces*: California, Cortez, Panamanian, Galapagos, Peru-Chilean, Juan

123   Fernandez.   II.

124   **COOL REGIONS** (cold-temperate and polar waters)

125   A. COLD-TEMPERATE AND POLAR NORTHERN HEMISPHERE.

126   1**. Eastern North Pacific Region**

127   *Provinces*: Aleutian, Oregon.

128   2. **Western North Pacific Region**

129   *Provinces*: Oriental, Kurile, Okhotsk.

130   3. **Western Atlantic Region**.

131   4**. Eastern Atlantic Region**.

132   5. **Arctic Region**.

133   B. COLD-TEMPERATE AND POLAR SOUTHERN HEMISPHERE.

134   1**. South American Region**

135   *Provinces*: Southern Chile, Tierra del Fuego, Southern Argentina, Falkland Islands.

136   2**. New Zealand-Australian Region**

137   *Provinces*: Tasmania, New Zealand, Antipodes.

138   3. **Sub-Antarctic Region**

139   *Provinces*: South Georgia, Bouvet, Crozet, Prince Edward, Kerguelen, Macquarie.

140   4. **Antarctic Region**.

141   **DISCUSSION**

142   ATLANTIC WARM REGIONS

143   The reconstituted Eastern Atlantic Region (Fig. 1) now extends from the southern entrance to the

144   English Channel southward to the Cape of Good Hope. The Western Atlantic Region extends

145   from Cape Hatteras and the northern Gulf of Mexico southward to the Valdes Peninsula on the

146   South American east coast. Included within the two regions are 13 provinces. A comprehensive

147   treatise on tropical Atlantic biogeography and evolution has recently been published by Floeter *et*

148   *al.* (2008). Although this work is based on reef fishes, the demonstrated patterns and relationships

149   have significance for many of the other phyla on the continental shelves; it is the source of much

150   of the new information utilized in this section.

151   **Eastern Atlantic Region**

152   From its northern boundary at the southern British Isles, the warm-temperate Lusitania Province

153   extends south to southern Morocco and eastward through the Mediterranean (Fig. 1). Farther to

154   the east are the Black Sea, Caspian, and Aral Provinces. There are, to our knowledge, no recent

155   evaluations of endemism in these three provinces; earlier work was reviewed by Briggs (1974).

156   The Lusitania Province also includes the offshore islands of the Canaries, Azores, and Madeira.

157   The endemism in this province is concentrated within the Mediterranean itself where 28% of

158   marine species are endemic (IUCN, 2010). The Straits of Gibraltar are often assumed to be a

159   natural barrier between Mediterranean and Atlantic segments of the Lusitania Province. Although

160   phylogeographic studies of fishes, molluscs, crustaceans, and marine mammals show some

161   population genetic separations, there is no consistent pattern of evolutionary partitions at the

162   Straits (reviewed in Paternello *et al.*, 2007).

163   From southern Morocco, at Cap Juby, the Tropical Eastern Atlantic (TEA) Province extends

164   south to Mossamedes, Angola (Fig. 2). The offshore islands of the Cape Verdes, Sáo Tomé, and

165   Principe are included. In the TEA there are about 388 species of reef fishes with some 30%

166   endemism (Floeter *et al*., 2008), opisthobranch gastropod endemism is about 36% (García &

167   Bertsch, 2009) and tunicate endemism about 31% (Naranjo *et al*., 1998). To the south, the warm-

168   temperate Southwest Africa Province is now called the Benguela Province (BP).

169   The two isolated islands on the Mid-Atlantic Ridge, Ascension and St. Helena, formerly

170   comprised the St. Helena-Ascension Province (Briggs, 1995). The name was changed to the Mid-

171   Atlantic Ridge Province (MAR) by Floeter *et al*. (2008). Together the two islands harbour 111

172   fish species with 26% endemism. But, if the islands are considered separately, each has sufficient

173   endemism (St. Helena 13% and Ascension 11%) to be considered a distinct province. Although

174   the two islands have many trans-Atlantic species in common, their faunal composition is

175   otherwise quite different, and they lie 1290 km apart. Ascension has higher affiliation with the

176   Brazilian Province (29% shared species), than with the TEA (6% shared species), while St. Helena

177   has nearly equal affiliations (16% Brazilian, 15% TEA; Edwards, 1990). The more southerly St.

178   Helena also has molluscan and crustacean fauna shared with the Indian Ocean (Smith, 1890;

179   Chace, 1966), indicating that this island may be a stepping stone for colonization into the wider

180   Atlantic. Phylogeography studies show genetically distinct populations and perhaps cryptic

181   species at Ascension (Muss *et al.*, 2001; Bowen *et al.*, 2006b) but also corroborate the higher

182   affinities with the Brazilian Province (Rocha *et al.*, 2002; Carlin *et al*., 2003). Unfortunately such

183   comparisons are not available for St. Helena. Considering that each island demonstrates

184   significant evolutionary innovation, separate St. Helena and Ascension provinces (Fig. 2) should

185   be recognized. For the Eastern Atlantic Region as a whole, there are 551 reef fishes with 64%

186   endemism, and 124 genera with 31.5% endemism.

187   **Western Atlantic Region**

188   The warm-temperate Carolina Province exists in two parts (Fig. 1), one in the northern Gulf of

189   Mexico and the other on the Atlantic coast (Briggs, 1995). Within the Gulf, the warm-temperate

190   biota occupies the area north of the tropical boundaries between Cape Romano, Florida and Cape

191   Rojo, Mexico. The Atlantic section is located between Cape Hatteras and Cape Canaveral. Of the

192   two sections, the Gulf is the richer and, in an earlier work, Briggs (1974) noted that the fishes and

193   invertebrates exhibited about 10% endemism. However, the Atlantic section had very little

194   endemism and was considered a subset of the northern Gulf fauna. Boschi (2000) recognized the

195   northern Gulf as a Texan Province based on decapod crustaceans, but observed only about 5%

196   endemism. He regarded the Atlantic section as belonging to a separate "Carolinian" Province but

197   found little more than a 1% endemism. In contrast, García & Bertsch (2009) reported 37%

198   endemism for opisthobranch gastropods in the Atlantic section. Phylogeographic studies

199   demonstrate numerous genetic partitions between these areas in co-distributed species, indicating

200   isolation between the two segments of the Carolina Province (Bowen & Avise, 1990, Avise,

201   1992). Despite the genetic partitions and high endemism in gastropods, we retain the Carolinian

202   Province with two recognized sections.

203   The Caribbean Province (CA) extends from Bermuda and Cape Canaveral, Florida to the

204   Amazon River. Formerly, the tropical Western Atlantic was subdivided into three provinces

205   (Briggs, 1974): Caribbean, Brazilian and West Indian. Previous to that subdivision, the entire

206   region had been considered to be occupied by a homogeneous fauna. A West Indian Province,

207   comprising the islands extending from Bermuda in the north to Grenada in the south, was

208   originally recognized on the basis of considerable endemism in the fishes and several invertebrate

209   groups.

210   At the time of the original subdivision, about 19% of the West Indian fishes appeared to be

211   endemics (Böhlke & Chaplin, 1968), as well as many of the echinoderms and molluscs. However,

212   as more work was devoted to the fishes, many of the putative island endemics were found along

213   the mainland shores of the Caribbean. The West Indian fauna was not as distinct as it first

214   appeared (Burgess *et al.*, 1994), and this observation is generally supported by phylogeographic

215   studies (Shulman & Bermingham, 1995), but see Baums *et al.* (2005) and Taylor & Hellberg

216   (2005). Floeter *et al.* (2008) subsequently recognized a "Greater" Caribbean Province that

217   included all the northern Western Atlantic tropics (Fig. 2). The larger Caribbean Province contains

218   814 species of reef fishes with about 33% being endemic, the decapod crustaceans include 1058

219   species with about 32% endemism (Boschi 2000), and the coral species have about 37%

220   endemism (Veron, 2000). Briggs (2005) suggested that the southern Caribbean had the richer

221   fauna but it now appears that the fishes of the Greater Caribbean represent a homogeneous

222   assemblage, although this may not be true for some of the invertebrates.

223   The tropical Brazilian Province was modified by Floeter *et al.* (2008) and now extends from

224   the mouth of the Amazon River south to Santa Catarina, Brazil (Fig. 2). Included are the offshore

225   islands of Atol das Rocas, Fernando de Noronha, St. Paul's Rocks, and Trindade. There are about

226   471 fish species with 25% endemism. For the decapods, Boschi (2000), who recognized a

227   southern boundary at Cape Frio, found 572 species with 11% endemism. Coelho *et al.* (2008) also

228   examined decapod distributions, reporting 12.5% endemism in the Brazilian Province. About 25%

229   of the coral species are endemic (Veron, 2000). The warm-temperate Argentinian Province

230   extends from Santa Catarina, Brazil, to the Valdez Peninsula, Argentina. In total, the Western

231   Atlantic Region has about 1023 reef fish species with 86% endemism; and 158 genera with about

232   35% endemism.

233   INDO-PACIFIC WARM REGIONS

234   The newly expanded Western Pacific Region begins in the north at Cape Inubo on the Pacific

235 coast of Japan (Fig. 1). Along the mainland shores, the regional fauna begins at the Korean

236 Peninsula and the south entrance to the Sea of Japan. It may also be found along the Chinese coast

237 and Taiwan as far as Hong Kong (Briggs, 1974). To the south of these boundaries, the region

238 extends to Robe in southeastern Australia and to Bermagui on the southwestern coast. The

239 northern Indian Ocean is included and so is the East African coast to the Cape of Good Hope. The

240 region also reaches northern New Zealand including the Auckland Peninsula eastward to East

241 Cape and the offshore Kermadec Islands. The new Eastern Pacific Region begins at Los Angeles

242 on the California coast and extends southward to southern Chile ending at the Taitao Peninsula

243 (Fig. 1).

244 **Western Pacific Region**

245 The warm-temperate Sino-Japanese Province extends, on the oceanic side, from Cape Inubo south

246 to, but not including, the Amami Islands. On the mainland side, it begins at the tip of the Korean

247 Peninsula and at Hamada on the lower part of the Sea of Japan. On the Chinese coast, it begins at

248 about Wenchou and extends southward to Hong Kong (Fig. 1). The latter two boundaries are

249 suggested primarily on the basis of sea surface temperature because distribution patterns along the

250 Chinese coast are not well known (at least in the western literature). But fish distribution along the

251 coasts of Taiwan has been well studied (Shao *et al*., 1999). The northwestern coast of the island

252 exhibits an affinity with the warm-temperate mainland coast while the southeastern coast is purely

253 tropical, being under the influence of the Kuroshio Current. The southern hemisphere warm-

254 temperate provinces are discussed separately.

255 **Tropical Indo-West Pacific Region**

256 In contrast to the Atlantic, Indo-West Pacific (IWP) tropical marine provinces are characterized by

257 prodigious numbers of wide-ranging species. Allen (2008) documented an average range of

258 9,357,070 km² for reef fishes, or an area roughly the size of China. In general, even limited-range

259 endemics occupy much larger areas than their terrestrial counterparts, with the exception of those

260 occupying the shallows around tiny oceanic islands. Only about 10.8 % of the 3,919 IWP species

261 occupy areas less than 120,000 km². The latter are considered as having restricted distributions

262 and may merit special conservation consideration. But the vast multitude of species that ranged

263 from the Central Indian Ocean to the eastern limits of the Western Pacific give the impression of

264 one homogeneous fauna.

265 Information on the reef fishes of the IWP, as the result of recent surveys (Allen, 2008 and

266 updated information from him), now make it possible to define biogeographic subdivisions with

267 increased confidence. However, we caution that some boundaries have not been tested or

268 supported with data from invertebrates (see Veron, 2000). The Western Indian Ocean (WIO)

269 Province (Fig. 2), including Madagascar, the Mascarenes, the Seychelles, and the Comoros, with

270 about 1,000 fish species and 142 endemics, may be considered distinct with 14.2% endemism.

271 The Red Sea Province is distinguished by 14% endemism in fishes (Randall, 1994; Goren & Dor,

272 1994), 33% in crustaceans, 15% in echinoderms, and up to 25% in corals (Cox & Moore, 2000).

273 But many Red Sea fishes (and possibly other fauna) extend into the Gulf of Aden so that area

274 needs to be added to the Red Sea Province (Fig. 2).

275 The area between the Horn of Africa and the Arabian Gulf has been described as a major

276 biogeographic barrier (Kemp, 1998). The barrier effect is demonstrated by the composition of the

277 fish fauna of Oman (Randall, 1995). Almost half are widespread Indo-Pacific species and most of

278 the others belong to the WIO Province. But there are 22 short-range endemics (3.8%) at Oman.

279 The entrance to the Arabian Gulf (Fig. 2) was previously recognized as a provincial barrier

280 (Briggs, 1974) and there seems to be no reason for a change. The presence of short-range

281 endemics has been noted in conjunction with other barriers.

282 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

307   km. This continuity of shallow habitat is doubtless a primary factor in shaping the cohesiveness

308   of the Indo-Polynesian Province.

309   Adjacent to the enormous Indo-Polynesian Province are three isolated locations whose

310   relatively high endemism in reef fishes requires provincial status: (1) the Hawaiian Islands with

311   612 species and 25% endemics (Randall, 2007), (2) Easter Island with 169 species and 21.7%

312   endemism (Randall & Cea, 2010), and (3) the Marquesas with 415 species and 11.6% endemism

313   (Randall & Earle, 2000) (Fig. 2).

314   In the earlier work (Briggs, 1974) two more tropical provinces were recognized: Lord Howe-

315   Norfolk and Northwestern Australian. But each area is presently known to have less than 10%

316   endemism (Allen, 2008). Springer (1982) identified the Pacific Plate, the tropical area to the east

317   of the Philippines and Australia, as a biogeographical region of major significance. However that

318   vast area did not possess sufficient endemism to qualify for provincial status (Briggs, 1995). The

319   Pacific Plate concept was reexamined by Allen (2008) and 1403 species were documented

320   including 130 endemics. But this number included endemics specific to certain islands and

321   archipelagos on the Pacific Plate as well as those that were widespread yet confined to that area.

322   Species endemic to a given island group are so characterized because they occur at that particular

323   location and nowhere else. They are not, at the same time, Pacific Plate endemics. The latter, by

324   definition, need to be characteristic of and confined to the Pacific Plate. A study of the inshore

325   fishes of the U.S. Line and Phoenix Islands revealed that 6.3% were restricted to the Pacific Plate

326   (Mundy *et al.*, 2010), not enough to recognize a biogeographic province.

327   **Eastern Pacific Region**

328   A phylogenetic analysis involving the genetic structure of 40 taxa in coastal California (Dawson,

329   2001), data on all California fishes (Allen *et al.*, 2006), and the phylogeography of the rockfishes

330   (genus *Sebastes*) (Sivasundar & Palumbi, 2010) leads to a reconsideration of the limits of the

331   warm-temperate California Province (formerly the San Diego Province). Although transition

332   zones within provinces have not previously been recognized (Briggs, 1995), it appears that there is

333   good reason for doing so in this case. Many more species extend past Pt. Conception at 34º-35º N

334   than do those that terminate there. The peaks in the range termini of the molluscs and marine algae

335   occur between 33º and 34º N and between 36º and 37º N. Furthermore, a high incidence of short-

336   range "edge-effect" species occurs at the same two latitudes which approximate the vicinities of

337   Los Angeles and Monterey Bay. A peak in the southern range termini of cold-temperate fishes

338   occurs at 33º N (Horn *et al.*, 2006). But genetic breaks in some rockfish species were found at

339   Cape Mendocino (Sivasundar & Palumbi, 2010). Previously, Murray *et al*. (1980) had recognized

340   clusters of geographic endpoints for northern algae species at Monterey Bay and endpoints for

341   southern species near Los Angeles. Horn & Allen (1978) had recognized a similar boundary for

342   fishes at Monterey Bay. In view of such information, a California Transition Zone (CTZ), within

343   the Oregon Province, is now recognized between Monterey Bay and Los Angeles, with the

344   California Province extending from the latter to Magdalena Bay, Mexico (Fig. 1).

345   The California Province as reconstituted still contains large numbers of northern fishes, about

346   163 out of 271 species (Horn *et al.*, 2006). Hubbs (1960) determined provincial endemism was

347   32.9% but that figure may be too large considering that the province now covers less area. Many

348   of the northern species are usually found in relatively deep water (Eschmeyer *et al*., 1983) but also

349   tend to be concentrated in cool, upwelling zones along the Baja coast. The molluscan data from

350   Valentine (1967) indicated a provincial endemism of about 21%, but that figure also may be too

351   high due to the smaller province. The California Channel Islands have several fishes that

352   demonstrate some genetic differentiation but only one endemic species (*Rimicola cabrilloi*)

353   (Dawson *et al.*, 2006). Robertson & Cramer (2009) recognized a tropical Cortez Province

354   extending from Magdalena Bay south around the tip of the Baja California Peninsula to include all

355 of the Gulf of California. We suggest that this province should still be confined to the Gulf and be

356 considered warm-temperate. Around the rest of the world, warm-temperate provinces are not only

357 distinguished by significant endemism but are also separated from the tropics by the 20º C

358 isotherm for the coldest month (Briggs, 1974), i.e., this temperature barrier prevents the passage of

359 many tropical species and allows speciation to take place in the adjoining warm-temperate

360 provinces. In this case, the barrier extends across the southern end of the Gulf of California

361 approximately between La Paz and Topolobampo. Within the Gulf, a little more than 10% of the

362 fishes are endemic (D.R. Robertson, pers. comm.). Boschi (2000) found 265 species of decapods

363 in the northern part of the Gulf, with 9% endemism. The great majority of species in the Gulf

364 range well into tropical waters but the northern Gulf also contains about 20 California Province

365 species with disjunct distributions (Dawson *et al*., 2006). Provincial recognition is given

366 according to endemism, without regard to the origin of other species. Therefore, the Cortez

367 Province is retained as a warm-temperate unit within the Gulf of California.

368   The tropical fauna of the Panamanian (Panamic) Province extends from the mouth of the

369 Gulf of California south to the Gulf of Guayaquil, on the border between Ecuador and Peru (Fig.

370 2). In the northern part of this range, a Mexican Province was previously recognized (Briggs,

371 1974; Hastings, 2009), but the more recent information from Robertson & Cramer (2009)

372 indicates that the section from the mouth of the Gulf of California to the Gulf of Tehuantepec does

373 not demonstrate sufficient endemism. In the extended Panamanian Province about 49% of the fish

374 species are endemics. Boschi (2000) found 38% endemism in the decapods.

375   Robertson & Cramer (2009) placed all of the tropical offshore islands in a single Ocean

376 Island Province, but only one archipelago, the Galapagos, has sufficient endemism to be

377 considered a biogeographic province. The other groups that retain strong faunal affinities with the

378 Panamanian Province, include the Revillagigedos with 8.0% endemism among the shore fishes,

379   Clipperton with 5.8%, Malpelo with 2.5%, and Cocos with 4.6%. As noted previously for the

380   Pacific plate, species endemic to a particular island cannot, at the same time, be considered

381   endemic to a larger area. The Galapagos Archipelago has 13.6% endemism for shore fishes

382   (McCosker & Rosenblatt, 2010) and has been continuously recognized as a separate province

383   (Briggs, 1974). Several invertebrate groups have higher endemism, including 16% for decapods

384   (Boschi, 2000). A significant number of species, in some groups more than 10%, are trans-Pacific

385   migrants. A few species shared with the Caribbean, either exclusively or also with the Panamanian

386   Province, are examples of taxa that apparently have not changed since the formation of the

387   Panamanian Isthmus. Due to the high level of endemism, provincial status for the Galapagos

388   should be retained and the other offshore islands should be regarded as outposts of the

389   Panamanian Province.

390   COLD-TEMPERATE REGIONS

391   A global cooling episode took place across the Eocene-Oligocene boundary *c.* 35 Ma (Zachos *et*

392   *al.*, 2001). This episode and subsequent cool periods resulted in cold-temperate sea surface

393   conditions in the Arctic Ocean, North Pacific, North Atlantic, and the waters surrounding the

394   Antarctic continent. Warm-temperate waters were displaced into lower latitudes, resulting in a

395   latitudinal restriction of the tropical seas, and the formation of a new cold-temperate zone in each

396   hemisphere.

397   Cold-temperate surface temperatures for the coldest month generally range from 12° C to 2°

398   C. The colder waters absorb more atmospheric oxygen and their increased density stimulates

399   thermohaline circulation. This results in an increased upwelling which brings more nutrients to the

400   surface and enhances primary production. In the Northern Hemisphere, cold-temperate waters

401   occupied the Arctic-North Atlantic and the North Pacific oceans at a time when the two areas

402   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

427   A/B boundary was placed at the Bering Strait, and (3) an Estuary-Arctic Interzonal Province was

428   noted to occur along the shores of the Arctic Ocean. The North Atlantic change is adopted here

429   (Fig. 1) but the justification for the Bering Strait boundary does not appear strong. The Estuary-

430   Arctic Interzonal area is probably best defined as special ecological zone rather than a

431   biogeographic province.

432   In the North Pacific and Arctic-North Atlantic, the new cold-temperate, often called "boreal",

433   biotas evolved separately until the late Miocene when marine connections across the Bering land

434   bridge began to develop. Previously, it was generally thought that the land bridge remained intact

435   until *c.* 3.5 Ma. However recent fossil studies indicate that the first opening may have occurred as

436   early as 5.3 Ma (Gladenkov *et al.*, 2002). When the Bering Strait first opened it may have been

437   shallow with limited passage, but by *c.* 3.5 Ma it allowed an unrestricted mingling of biotas that

438   had been separated for more than 30 Myr (Vermeij, 1991a; 2004), an event subsequently called

439   the Great Trans-Arctic Interchange.

440   At the time of the great interchange, the Arctic Ocean had little ice and cold-temperate

441   conditions prevailed. Global cooling during this (mid-Pliocene) interval was probably caused by

442   four key tectonic events: (1) the isolation of Antarctica, (2) closure of the Tethys Sea, (3) collision

443   of Australia with Southeast Asia, and (4) uplift of the Panamanian isthmus (Crame, 2004). The

444   final event apparently produced a major intensification of Northern Hemisphere glaciations

445   between 2.9 and 2.4 Ma (Mudelsee & Raymo, 2005). As a result, the Arctic sea surface

446   temperature for the coldest month dropped to between +2º C and -2º C, most of the boreal species

447   were eliminated, and the modern Arctic marine fauna began to develop. The mid-Pliocene cooling

448   of the northern oceans resulted in resumed isolation of Atlantic and Pacific boreal biotas.

449   An important effect of the mid-Pliocene cooling of the northern oceans was the separation of

450   boreal biotas (Briggs, 1995). In the Atlantic, the cold-water Arctic Region now extends southward

451   to the Strait of Belle Isle in the west and to the northeast beyond the Murmansk Peninsula. In the

452   Pacific, Arctic biota extends southward to Cape Olyutorsky in the west and Nunivak Island to the

453   east. In each ocean, these southern extensions of Arctic water divided the original Pliocene boreal

454   assemblage into eastern and western components. Typical boreal species were no longer able to

455   maintain amphi-atlantic and amphi-pacific distributions and in both oceans the eastern and

456   western faunas developed independent evolutionary trajectories. The contemporary result is a

457   distinct boreal region on each side of each ocean, defined in terms of endemic species. This

458   separation is also apparent in phylogeographic studies both within and between species, including

459   faunas as diverse as seagrass (*Zostera marina*; Olsen *et al*., 2004), fish (*Merluccius* spp.; Grant &

460   Leslie, 2001), and several invertebrate groups (Wares & Cunningham, 2001; Addison & Hart,

461   2005).

462   With regard to longitudinal relationships, it is apparent that, in each ocean, the east and west

463   boreal faunas are closely related. In the North Pacific, the relationship is primarily due to the

464   presence of a group of Arctic-boreal species common to both sides of the ocean. In addition, some

465   Pliocene amphiboreal species have apparently not yet developed specific differences. In the North

466   Atlantic, there are also Arctic-boreal species but a good part of the relationship between the two

467   regions is caused by the large number of Pacific species that invaded in the mid-Pliocene.

468   Approximately half of the molluscan invaders have speciated and many of them are now endemic

469   to one boreal region or the other (Vermeij, 1991b). Much of the native North Atlantic molluscan

470   fauna originated in European waters and then spread westward (Wares & Cunningham, 2001;

471   Vermeij, 2005b).

472   **Eastern North Pacific Region**

473   Cold-temperate conditions extend from Nunivak Island in the north to about Los Angeles on the

474   California coast, the southern limit of the Oregon Province, including the California Transition

475 Zone (CTZ). The northern boundary is concordant with mean southern limit of the pack ice in

476 January-February. This region may be divided into Aleutian and Oregon provinces, with a

477 boundary previously described at the Dixon Entrance (55º N). The northern (Aleutian) province

478 has an endemism rate of about 24% in decapods and 23% in molluscs (Boschi, 2000; Valentine,

479 1967, respectively). In contrast, the Oregon Province, if considered to terminate at Monterey Bay,

480 has only about 2% endemism in decapods and fishes (Boschi, 2000; Horn & Allen, 1978; Horn *et*

481 *al.*, 2006) respectively. But if the cold–temperate biota of the CTZ is included, the endemism level

482 would probably rise to more than 10%. Horn *et al.*, (2006) reported many California fish range

483 terminations at the latitude of Monterey Bay (36 -37º N), and a peak in range termination

484 endpoints at about 50º N, near the northern tip of Vancouver Island. This coincides with a similar

485 peak reported by Peden & Wilson (1976) based on fish distributions in British Columbia and

486 Alaska. Based on these findings, the boundary between the Aleutian and the Oregon provinces

487 should be shifted south from the Dixon Entrance to the northern tip of Vancouver Island, and the

488 CTZ included within the Oregon Province.

489 **Western North Pacific Region**

490 Cold temperate conditions in the Northwest Pacific include three provinces, defined in part by the

491 complex geological history of the Sea of Japan and adjacent regions (Wang 1999). An Oriental

492 Province exists in three segments (Fig. 3). The first extends north from the warm-temperate

493 boundary at Wenchou and continues through the Yellow Sea. Its continuity is broken by the tip of

494 the Korean Peninsula, but it then continues up the north side of the peninsula to about Chongjin.

495 On the eastern side of the Sea of Japan, the Oriental Province extends from about Hamada to the

496 Tsugaru Strait. From that point, it continues southward on the outer coast of Honshu Island to

497 Cape Inubo, Japan.

498 A faunal break exists at about the location of the Tsugaru Strait between the islands of

499   Honshu and Hokkaido. To the north of this point, both along the outer coast and within the Sea of

500   Japan, one may find a different species assemblage of the Kurile Province (Fig. 3). This province

501   extends northward along the Kurile chain of islands and the east coast of the Kamchatka Peninsula

502   to about Cape Olyutorsky. The Okhotsk Province is confined to the Sea of Okhotsk. Although

503   this sea is now confluent with the North Pacific through the Kurile Islands and with the Sea of

504   Japan around Sakhalin Island, it was probably isolated during the glacial stages and perhaps

505   earlier. Indeed, phylogeographic analyses indicate that the Northwest Pacific marginal seas were

506   isolated during glacial maxima (Liu *et al*., 2007). Although there are no recent taxonomic

507   evaluations (known to us), the older literature demonstrated considerable endemism in ascidians,

508   pycnogonids, and fishes (Briggs, 1974).

509   As noted, some of the Russian biologists preferred to recognize more provinces than those

510   just described. For example, in the Sea of Japan the fish fauna was separated into four provinces

511   by Kafanov *et al*. (2000). The divisions were made on the basis of breaks in the species diversity

512   gradient and their relationship to temperature and prevailing currents. The provinces that were

513   identified reflected interesting ecological differences but did not exhibit sufficient endemism to

514   qualify as provinces according to the 10% rule. In contrast, the currently used scheme indicates

515   only two provinces in the Sea of Japan, one penetrating from the north and the other from the

516   south.

517   *East-West Relationships*

518   The Bering Sea is essentially a broad, shallow basin almost completely enclosed to the north and

519   bordered by the Alaskan Peninsula and the Aleutian islands to the south. The absence of obvious

520   barriers might lead one to expect a homogeneous marine fauna, but several investigators

521   beginning with Andriashev (1939) recognized significant differences. Numerous species,

522   considered to be endemic to one side or the other, are documented among the anomuran crabs,

523   polychaetes, ascidians, and fishes (Briggs, 1974). The more recent literature pertaining to amphi-

524   Pacific relationships has been reviewed by Ilves & Taylor (2007). On the western side, the

525   complex geological history with periodic isolations of the Sea of Japan and the Okhotsk Sea was

526   probably important in generating diversity. The fish families Cottidae, Zoarcidae, Liparididae, as

527   well as the genera *Oncorhynchus* and *Sebastes* (Hyde & Vetter, 2007) probably underwent major

528   radiations in that area. In contrast, the fish family Embiotocidae and the gastropod genera *Nucella*

529   and *Littorina* may have originated on the eastern side (Ilves & Taylor, 2007).

530   **Western Atlantic Boreal Region**

531   This region extends from the Strait of Belle Isle to Cape Hatteras (Fig. 1). In considering the

532   geographic extent of this cold-temperate region, one is confronted with a good deal of conflicting

533   opinion. Most of the disagreement is concerned with the relationship of the fauna that occupies

534   the area between Cape Hatteras and Cape Cod, often called the "Middle Atlantic Seaboard." The

535   area is penetrated during the summer months by large numbers of tropical and warm-temperate

536   organisms. This has often resulted in its being allied with the Carolina Province to the south.

537   However, the presence of large numbers of boreal species, together with very little endemism,

538   shows that it clearly belongs to the Boreal Region (Briggs, 1974). There is about 19% regional

539   endemism in shore fishes (Bigelow & Shroeder, 1953), 53% in all molluscs (Vermeij, 2005c),

540   21% in opisthobranch gastropods (García & Bertsch, 2009), and only 5% in decapods (Boschi,

541   2000).

542   **Eastern Atlantic Boreal Region**

543   This region is now considered to extend from Svalbard and the southern end of Novaya Zemlya to

544   the southern entrance of the English Channel (Golikov *et al*., 1990) (Fig. 1). Previously, the

545   northern boundary was located at the base of the Murmansk Peninsula. Iceland possesses an

546   interesting biotic mixture. The older literature (Briggs, 1974) suggested a purely boreal

547   component, pure Arctic, Arctic-boreal, and some eurythermic temperate forms. The relationships

548   are almost entirely with the Eastern Atlantic. The absence of any special American relationship

549   and the almost complete absence of endemics (except for a few subspecies) indicate that Iceland,

550   or at least the south and east shores, should be included in the Eastern Atlantic Boreal Region. For

551   the entire region, an early estimate was 20-25% endemism for both fishes and invertebrates

552   (Briggs, 1974). New data from Vermeij (2005c) indicate that about 69% of the molluscs are

553   endemic, and García & Bertsch (2009) estimate 25% for the opisthobranch gastropods alone.

554   The Faroes, a group of 21 volcanic islands located between Iceland and the Shetlands, host

555   species that are either boreal or Arctic-boreal. The demersal fish fauna is closely related to that of

556   the North Sea with no endemics or any indication of relationship to the Western Atlantic

557   (Magnussen, 2002). The Baltic Sea is the world's largest estuarine area. The salinity is relatively

558   stable and decreases gradually toward the inner end of the long, narrow basin. Although Golikov

559   *et al*. (1990) recognized a Baltic Province, this designation does not appear to be justified on the

560   basis of endemism.

561   *East-West Relationships*

562   The richest boreal fauna occurs on the eastern side of the North Atlantic as demonstrated by the

563   superior species diversity in fishes (Wheeler, 1969). This, when considered with the strong

564   European relationship of Iceland, indicated that the principal evolutionary centre for the recent

565   Atlantic boreal fauna was on the eastern side of that ocean (Briggs, 1974). This suggestion has

566   been verified by Vermeij (2005c) who examined mollusc distribution in the North Atlantic. He

567   found 402 extant species in the eastern side (69% endemic) and 262 in the west (54% endemic);

568   124 species had transatlantic ranges. Furthermore, Vermeij (2005c) determined that all of the

569   transatlantic species had apparently dispersed from Europe to America within the past 3.5 Myr.

570   More than 50% of those species had their ultimate origins in the North Pacific.

571 **Cold Arctic Region**

572 Although sea ice has been detected in the Arctic as far back as 47 Ma (Stickley *et al*., 2009), the

573 present glacial regime probably began about 2.9-2.4 Ma (Mudelsee & Raymo, 2005), so the polar

574 biota of the Arctic Region is much younger than that of the Antarctic. Consequently, although

575 there are significant numbers of endemic species, there are very few endemics at the higher

576 taxonomic levels. An exception is the narwhal, *Monodon monoceros*, with a relict distribution

577 (Jefferson *et al*., 1993). The Arctic seas have traditionally been divided into a number of separate

578 zones and provinces; but recent works indicate an essentially homogeneous biota so that a single

579 region is now recognized. Endemism in Arctic fishes has been estimated at about 25% (Eastman,

580 1997), and the earlier literature indicates high endemism in sponges, amphipods, and echinoderms

581 (Briggs, 1974). Phylogeographic analyses of the Arctic charr (*Salvelinus alpinus*) demonstrate

582 that most of this region was recolonized after the last glacial retreat (10,000 – 20,000 years ago),

583 indicating a lack of substantial biogeographic barriers (Brunner *et al*., 2001). The polar cod

584 (*Boreogadus saida*) may be considered an indicator species for it extends to all parts of the region

585 but no farther (Cohen *et al*., 1990). The Arctic Region occupies all of the area north of the cold-

586 temperate boundaries previously identified.

587 SOUTHERN HEMISPHERE

588 WARM-TEMPERATE PROVINCES

589 Due to the presence of many tropical eurythermic species, and to endemics with nearby tropical

590 ancestors, the faunal relationship of most northern warm-temperate provinces is closest to their

591 adjoining tropical province. But, in the Southern Hemisphere (Fig.1), there is considerable

592 longitudinal relationship due to the influence of the West Wind Drift (WWD). Three species of

593 the fish genus *Sebastes* (Scorpaenidae) dispersed from the North Pacific southward through the

594 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 (42° 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%

715   for the Aucklands, 23% for the Bounties, and 23% for the Snares, and asked if all these island

716   groups should be provinces. Almost 50 years later, the answer still eludes us.

717   **Sub-Antarctic Region**

718   The shelf waters of the Antarctic and Sub-Antarctic are occupied by a highly distinctive fauna that

719   owes its origin to four historical factors: (1) persistence of a small ancestral group of Mesozoic

720   and early Cenozoic taxa, (2) extinction of many early Tertiary warm-temperate species, (3)

721   geographical isolation produced by the opening of Drake Passage, and (4) invasions by cold-

722   temperate species from the North Pacific. Five provinces in the Sub-Antarctic Region were

723   previously recognized (Briggs, 1995), but now we recognize six (Griffiths et al., 2009; Fig. 6).

724   The fauna of South Georgia is highly endemic for three out of the four invertebrate classes, and

725   about 34% of the shore fishes may be endemic (Briggs, 1974). The Bouvet Province is now

726   known to have a very distinct fauna with 50% endemism in gastropods. The Crozet Islands were

727   previously considered part of the Kerguelen Province, but now must be assigned to a separate

728   province based on two of the four invertebrate classes (Griffiths *et al.*, 2009). Likewise, Prince

729   Edward Island is a separate province and probably should include the Marion Islands based on

730   proximity. Kerguelen Island has a distinctive molluscan fauna and about 73% of its ascidian

731   species are endemic (Primo & Vázquez, 2007); this province probably should include the nearby

732   Heard and McDonald islands. Early literature (Briggs, 1974) indicates that about 66% of the

733   Kerguelen shore fishes may be endemic species. As noted, Macquarie Island was not reported on

734   by Griffiths *et al*. (2009) but four of nine ascidian species are endemic (Primo & Vázquez, 2007)

735   and older references indicate a 64% molluscan endemism (Dell, 1964).

736   **Cold Antarctic Region**

737   The fauna of the Antarctic Region is relatively old compared to that of the Arctic Region. By late

738   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.

811   Finally, as dominant species continue to invade from high diversity centres to occupy

812   communities that are less diverse, the invaders constitute branches of a dynamic dispersal tree that

813   extends to all parts of the shallow oceans. Invader species that are continually being

814   accommodated by the natives at the community levels (Briggs, 2010) are ultimately responsible

815   for the global dispersal system that operates on a contemporary (as well as a historical) time scale.

816   ACKNOWLEDGEMENTS

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1161

1162   BIOSKETCHES

1163   **John C. Briggs** is a Professor Emeritus from the University of South Florida and is now affiliated

1164   with Oregon State University. His research deals primarily with the origin and distribution of

1165   contemporary groups of organisms. His biogeographical books include *Marine Zoogeography*

1166   (McGraw-Hill, 1974), *Biogeography and Plate Tectonics* (Elsevier, 1987) and *Global*

1167   *Biogeography* (Elsevier, 1995). In 2005, Professor Briggs received the Alfred Russel Wallace

1168   Award from the International Biogeography Society for his lifetime contributions to

1169   biogeography.

1170   **Brian W. Bowen** is a research professor for University of Hawaii at the Hawaii Institute of

1171   Marine Biology (http://www.hawaii.edu/HIMB). He studies the phylogeography of marine

1172   vertebrates, with a focus on the origin and maintenance of marine biodiversity, and ecosystem

1173   connectivity in the Papahanaumokuakea Marine National Monument in the Northwest Hawaiian
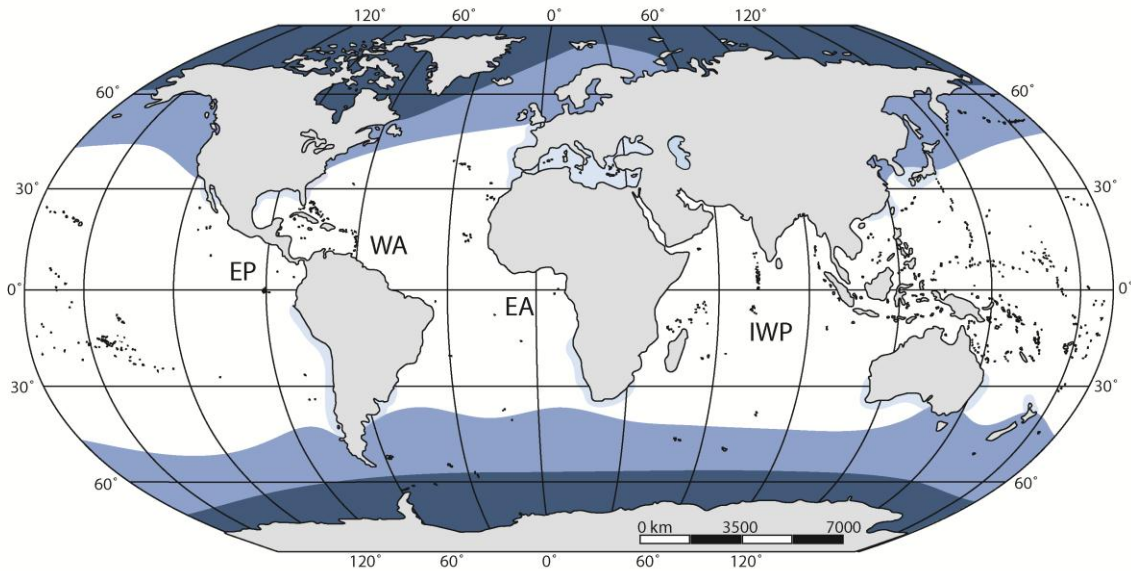
1174   Islands.

1175   Editor: Alistair Crame

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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.
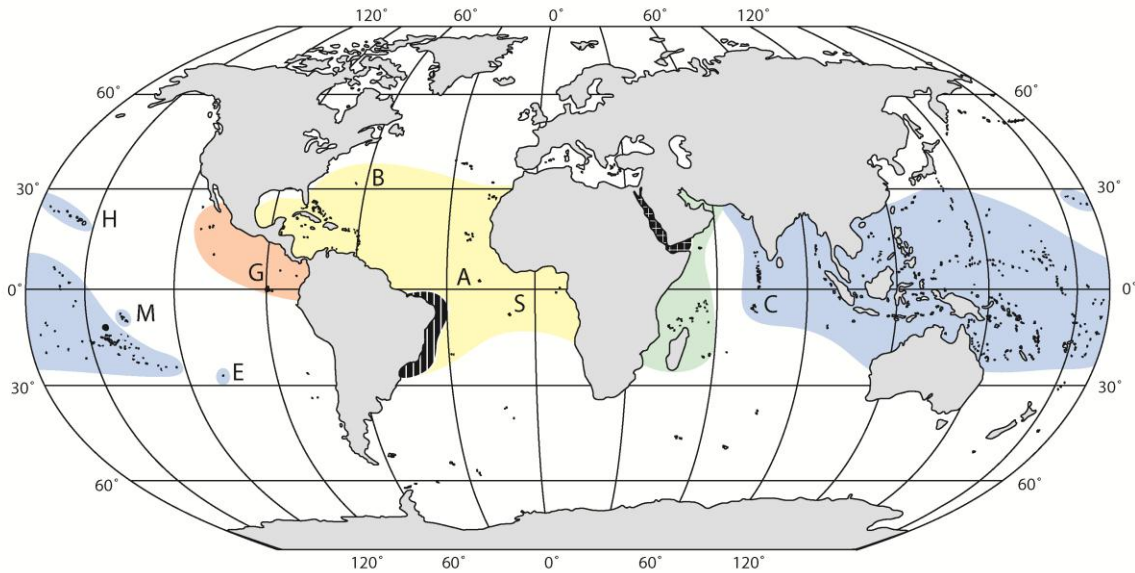
1189

1190 **Figure. 2.** Tropical Regions and Provinces, including the Indo-Polynesian, Hawaiian, Marquesas,

1191 and Easter Island Provinces (blue), the East Pacific Region (orange), East and West Atlantic

1192 Regions (yellow), and Western Indian Ocean Province (green). Vertical bars indicate Brazilian

1193 Province, and crosshatching indicates the Red Sea Province. Selected islands and archipelagos are

1194 indicated with the following abbreviations: H = Hawaii, M = Marquesas, E = Easter, G =

1195 Galapagos, B = Bermuda, A = Ascension, S = St. Helena, C = Chagos. The Chagos is depicted

1196 here as part of the Indo-Polynesian Province, but has faunal affinities with both the Indo-

1197 Polynesian Province and the Western Indian Ocean Province (Winterbottom & Anderson, 1997;

1198 Gaither et al. 2011)

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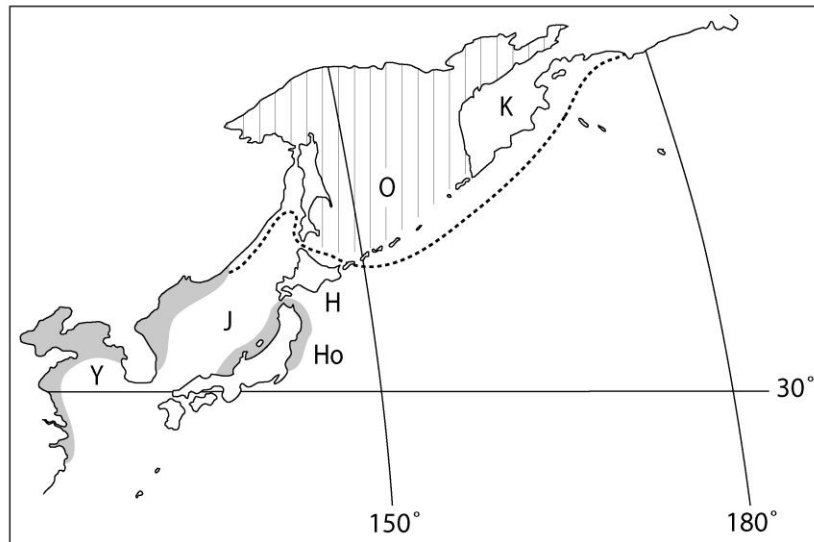
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Figure. 3. Three Northwest Pacific provinces: The Okhotsk Province (hatched) is confined to the

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.

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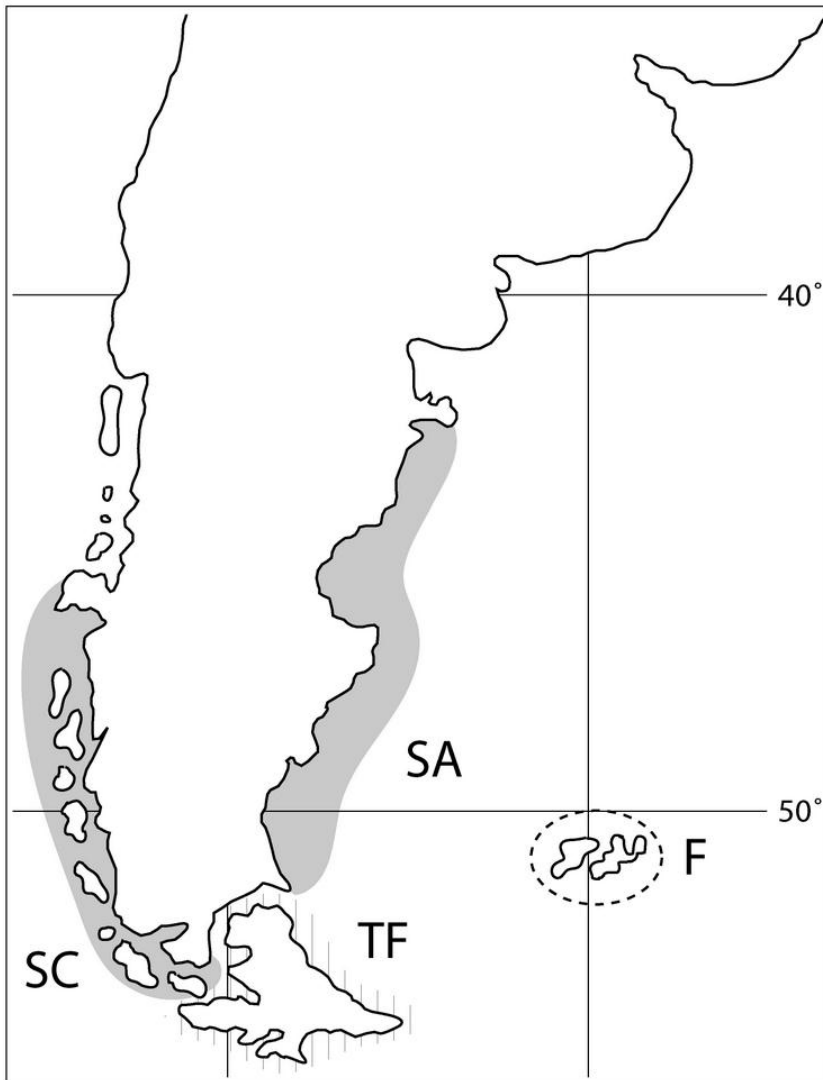
Figure. 4. The cold-temperate South American Region (northern boundaries are Valdez Peninsula on the east coast and Taitao Peninsula on the west coast). New provinces are Southern Chile (SC), Tierra del Fuego (TF), Southern Argentina (SA), and Falkland Islands (F).
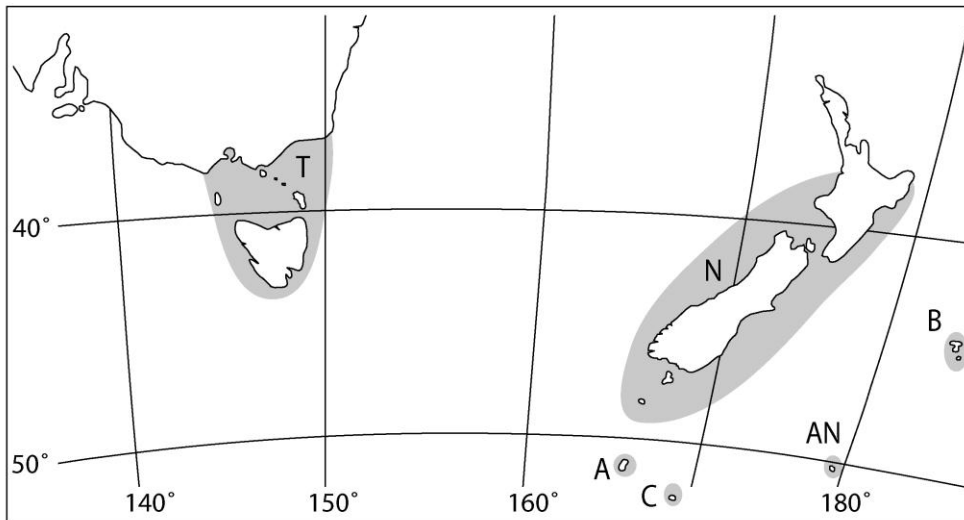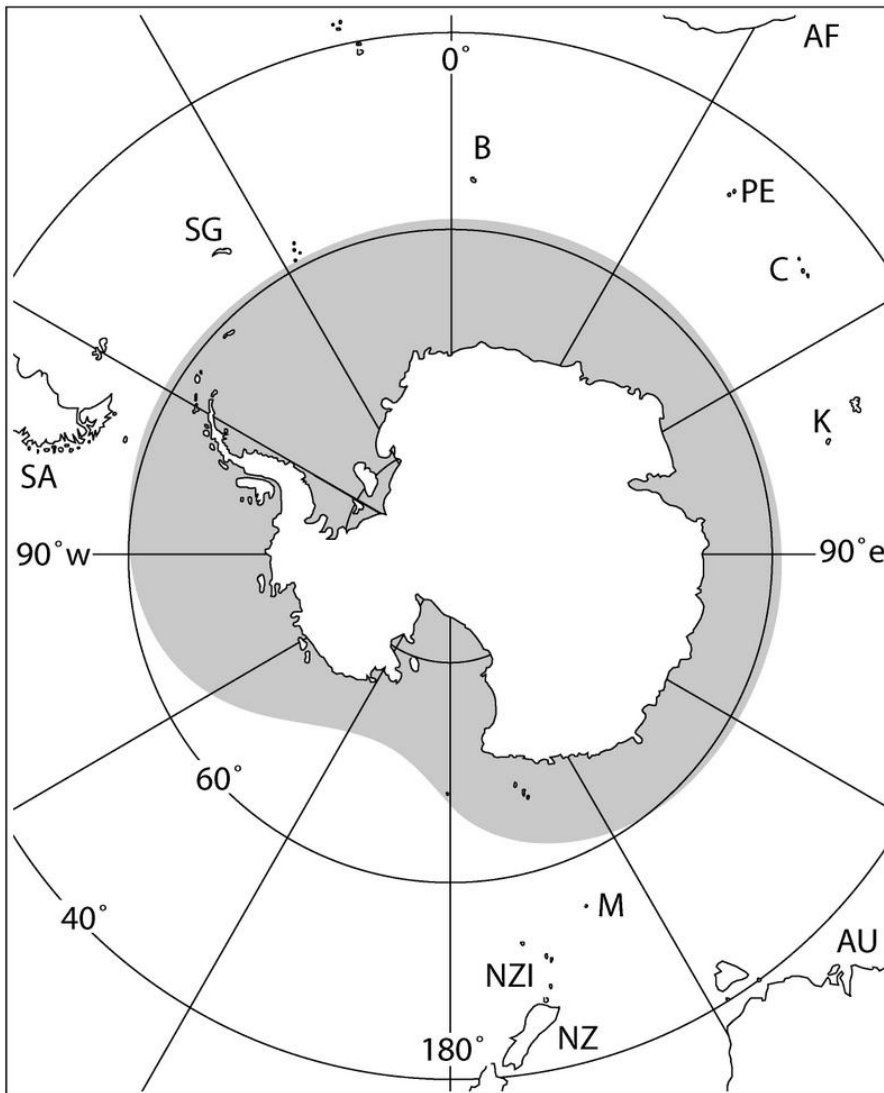
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1223 **Figure. 5**. Cold Temperate Provinces of the Southwest Pacific, including the Tasmanian Province

1224 (T), the New Zealand Province (N), and the Antipodes Province, consisting of the Aucklands (A),

1225 Campbell (C), Antipodes (AN), and Bounty Islands (B).

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1227 **Figure. 6**. Antarctic and Sub-Antarctic regions. The cold Antarctic Region is indicated by

1228 shading. The Sub-Antarctic Provinces include South Georgia (SG), Bouvet Island (B), Prince

1229 Edward Islands (PE), Crozet Islands (C), Kerguelen (K), and Macquarie Island (M). Also

1230 indicated are the southern tips of South America (SA), Africa (AF), Australia (AU), New Zealand

1231 (NZ) and New Zealand Islands (Antipodes, NZI).

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