Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas

Author(s): MARK D. SPALDING, HELEN E. FOX, GERALD R. ALLEN, NICK DAVIDSON, ZACH A. FERDAÑA, MAX FINLAYSON, BENJAMIN S. HALPERN, MIGUEL A. JORGE, AL LOMBANA, SARA A. LOURIE, KIRSTEN D. MARTIN, EDMUND MCMANUS, JENNIFER MOLNAR, CHERI A. RECCHIA, and JAMES ROBERTSON

Source: BioScience, 57(7):573-583. 2007.
Published By: American Institute of Biological Sciences
DOI: http://dx.doi.org/10.1641/B570707
URL: http://www.bioone.org/doi/full/10.1641/B570707

Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas

MARK D. SPALDING, HELEN E. FOX, GERALD R. ALLEN, NICK DAVIDSON, ZACH A. FERDAÑA, MAX FINLAYSON, BENJAMIN S. HALPERN, MIGUEL A. JORGE, AL LOMBANA, SARA A. LOURIE, KIRSTEN D. MARTIN, EDMUND McMANUS, JENNIFER MOLNAR, CHERI A. RECCHIA, AND JAMES ROBERTSON

The conservation and sustainable use of marine resources is a highlighted goal on a growing number of national and international policy agendas. Unfortunately, efforts to assess progress, as well as to strategically plan and prioritize new marine conservation measures, have been hampered by the lack of a detailed, comprehensive biogeographic system to classify the oceans. Here we report on a new global system for coastal and shelf areas: the Marine Ecoregions of the World, or MEOW, a nested system of 12 realms, 62 provinces, and 232 ecoregions. This system provides considerably better spatial resolution than earlier global systems, yet it preserves many common elements and can be cross-referenced to many regional biogeographic classifications. The designation of terrestrial ecoregions has revolutionized priority setting and planning for terrestrial conservation; we anticipate similar benefits from the use of a coherent and credible marine system.

Keywords: ecoregions, marine biogeography, mapping, marine protected areas, representative conservation

Mapped classifications of patterns in biodiversity have long been an important tool in fields from evolutionary studies to conservation planning (Forbes 1856, Wallace 1876, Spellerberg and Sawyer 1999, Lourie and Vincent 2004). The use of such systems (notably, the widely cited system developed by Olson et al. [2001]) in broadscale conservation, however, has largely been restricted to terrestrial studies (Chape et al. 2003, Hazen and Anthamatten 2004, Hoekstra et al. 2005, Burgess et al. 2006, Lamoreux et al. 2006). In the marine environment, existing global classification systems remain limited in their spatial resolution. Some are inconsistent in their spatial coverage or methodological approach. The few publications that have attempted to use biogeographic regionalization in global marine conservation planning (e.g., Kelleher et al. 1995, Olson and Dinerstein 2002) have been qualitative, and have expressed concern about the lack of an adequate global classification. In the absence of compelling global coverage, numerous regional classifications have been created to meet regional planning needs. This, of course, does not satisfy the need for a global system that is consistent across the many marine realms and coastal zones.

Biogeographic classifications are essential for developing ecologically representative systems of protected areas, as required by international agreements such as the Convention on Biological Diversity's Programme of Work on Protected Areas and the Ramsar Convention on Wetlands. Marine space is still grossly underrepresented in the global protected areas network (only about 0.5% of the surface area of the oceans is currently protected; Chape et al. 2005), a fact that adds urgency to the need for tools to support the scaling up of effective, representative marine conservation. The key idea underlying the term "representative" is the intent to protect a full range of biodiversity worldwide—genes, species, and

Mark D. Spalding (e-mail: mspalding@tnc.org), Zach A. Ferdaña, Jennifer Molnar, and James Robertson are conservation scientists in The Nature Conservancy's Conservation Strategies Group, Arlington, VA 22203. Helen E. Fox and Al Lombana are marine biologists in the Conservation Science Program, World Wildlife Fund–US, Washington, DC 20037. Gerald R. Allen is a research associate at the Western Australian Museum, Perth, Western Australia 6986, Australia. Nick Davidson is the deputy secretary general of the Ramsar Convention Secretariat, CH-1196 Gland, Switzerland. Max Finlayson is a member and former chair of Ramsar's Scientific and Technical Review Panel and principal researcher in wetland ecology at the International Water Management Institute, Colombo, Sri Lanka. Benjamin S. Halpern is project coordinator for ecosystem-based management of coastal marine systems at the National Center for Ecological Analysis and Synthesis, Santa Barbara, CA 93101. Miguel A. Jorge is deputy director of WWF International's Global Marine Programme, CH-1196 Gland, Switzerland. Sara A. Lourie is a research associate at the Redpath Museum, McGill University, Montreal, Quebec H3A 2K6, Canada. Kirsten D. Martin was a marine program officer with IUCN (World Conservation Union) when this article was prepared and is currently working as a freelance consultant for the Census of Marine Life Initiative, 1205 Geneva, Switzerland. Edmund McManus is a senior program officer in the UNEP (United Nations Environment Programme) World Conservation Monitoring Centre, Cambridge CB3 0DL, United Kingdom. Cheri A. Recchia is marine program director at the Wildlife Conservation Society, New York, NY 10461.

higher taxa, along with the communities, evolutionary patterns, and ecological processes that sustain this diversity. Biogeographic classifications provide a crucial foundation for the assessment of representativeness (Olson and Dinerstein 2002, Lourie and Vincent 2004).

The growing commitment by governments and the United Nations (UN; e.g., the UN Law of the Sea, the UN Fish Stocks Agreement) to implement comprehensive arrangements for ocean governance provides an additional arena in which marine biogeographic classifications are needed. Biogeographic regions are natural frameworks for marine zoning, which is a tool increasingly used by regional fisheries management organizations.

In this article, we present a new biogeographic classification for the world's coastal and shelf areas, which draws heavily on the existing global and regional literature. We believe that this classification will be of critical importance in supporting analyses of patterns in marine biodiversity, in understanding processes, and, perhaps most important, in directing future efforts in marine resource management and conservation.

Approaches for defining boundaries

Observations of global biogeographic patterns in the marine environment include early works by Forbes (1856), Ekman (1953, first published in German in 1935), and Hedgpeth (1957a), and more recent publications by Briggs (1974, 1995), Hayden and colleagues (1984), Bailey (1998), and Longhurst (1998). These authors used a variety of definitions and criteria for drawing biogeographic divisions. For example, Briggs (1974, 1995) focused on a system of coastal and shelf provinces defined by their degree of endemism (> 10%). This strong taxonomic focus and clear definition have led to relatively widespread adoption of Briggs's system, including its use by Hayden and colleagues (1984), with minor amendments, as a part of their "classification of the coastal and marine environments." Adey and Steneck (2001) provided independent verification of many of Briggs's subdivisions in a study that modeled "thermogeographic" regions of evolutionary stability.

Another important systematic approach, aimed mainly at pelagic systems, is the two-tier system devised by Longhurst (1998), which focuses on biomes and biogeochemical provinces. These subdivisions were based on a detailed array of oceanographic factors, tested and modified using a large global database of chlorophyll profiles. The results represent one of the most comprehensive partitionings of the pelagic biota, but the scheme is of limited utility in the complex systems of coastal waters, a fact acknowledged by the author, who has recommended combining his open ocean system with others for coastal and shelf waters (Watson et al. 2003; Alan R. Longhurst, Galerie l'Academie, Cajarc, France, personal communication, 2 November 2004).

The system of large marine ecosystems (LMEs) was developed over many years by a number of regional experts, with considerable input from fisheries scientist Ken Sherman (e.g., Sherman and Alexander 1989, Hempel and Sherman 2003, Sherman et al. 2005). Unlike the systems of Briggs and Longhurst, LMEs represent an expert-derived system without a rigorous, replicable core definition. LMEs are "relatively large regions on the order of 200,000 km^2 or greater, characterized by distinct: (1) bathymetry, (2) hydrography, (3) productivity, and (4) trophically dependent populations" (*www.lme.noaa.gov/Portal/*). LMEs are largely conceived as units for the practical application of transboundary management issues (fish and fisheries, pollution, habitat restoration, productivity, socioeconomics, and governance). The LME system focuses on productivity and oceanographic processes, and in its present form omits substantial areas of islands in the Pacific and the Indian oceans.

These and other global systems continue to play an important role in developing our understanding of marine biogeography and in practical issues of natural resource management. However, improvements are clearly possible and desirable. An ideal system would be hierarchical and nested, and would allow for multiscale analyses. Each level of the hierarchy would be relevant for conservation planning or management interventions, from the global to the local, although it is beyond the scope of the present effort to classify individual habitats or smaller features, such as individual estuaries or seagrass meadows.

We focus here on coastal and shelf waters, combining benthic and shelf pelagic (neritic) biotas. These waters represent the areas in which most marine biodiversity is confined, where human interest and attention are greatest, and where there is often a complex synergy of threats far greater than in offshore waters (UNEP 2006). From a biodiversity perspective, it is not simply that coastal and shelf waters have greater species numbers and higher productivity, but also that they are biogeographically distinct from the adjacent high seas and deep benthic environments (Ekman 1953, Hedgpeth 1957a, Briggs 1974).

Our intention was to develop a hierarchical system based on taxonomic configurations, influenced by evolutionary history, patterns of dispersal, and isolation. We drew up initial guidelines on definitions and nomenclature to guide the first data-gathering phase, then reviewed and refined them iteratively on the basis of the available data.

We reviewed over 230 works in journals, NGO (nongovernmental organization) reports, government publications, and other sources. For each of these, we looked at the underlying data and at the process of identification and definition of biogeographic units; we also considered the objectives of the classifications. To facilitate comparisons, we used digital mapped versions of many of the existing biogeographic units. More than 40 independent experts provided further advice (see the acknowledgments section). We refined a draft classification scheme through an assessment and review process that involved a three-day workshop. In arriving at our classification scheme, we adhered to three principles for our classification: that it should have a strong biogeographic basis, offer practical utility, and be characterized by parsimony.

A strong biogeographic basis. All spatial units were defined on a broadly comparable biogeographic basis. Existing systems rely on a broad array of source information—range discontinuities, dominant habitats, geomorphological features, currents, and temperatures, for example—to identify areas and boundaries. In many cases these divergent approaches are compatible, given the close links between biodiversity and the underlying abiotic drivers (see the comparisons below). We preferred to be informed by composite studies that combined multiple divergent taxa or multiple oceanographic drivers in the derivation of boundaries, as these were more likely to capture robust or recurring patterns in overall biodiversity.

A number of systems we reviewed were broadly biogeographic, but with some adjustments to fit political boundaries. Where it was possible to discern the biogeographic elements from the political, these systems were still used to inform the process.

Practical utility. We sought to develop a nested system, operating globally at broadly consistent spatial scales and incorporating the full spectrum of habitats found across shelves. We thus avoided very fine-resolution systems that separated coastal and shelf waters into constituent habitats. We chose not to try to define minimum or maximum spatial areas for our bioregions, but in some cases we did seek out systems that subdivided very large spatial units (such as Briggs's Indo-Polynesian Province, which covers more than 20% of the world's shallow shelf areas) or that amalgamated fine-scale units such as single large estuaries or sounds.

Parsimony. There are a number of respected and widely utilized global and regional systems, and lack of agreement between such systems can be problematic. In developing a new system, we sought to minimize further divergence from existing systems, yet still to obtain a truly global classification system. We did this by adopting a nested hierarchy that (a) utilized systems that are already widely adopted (e.g., the Nature Conservancy's system in much of the Americas and the Interim Marine and Coastal Regionalisation for Australia) and (b) fitted closely within broader-scale systems or alongside other regional systems.

Definitions

After the review process, we arrived at a set of critical working definitions.

Realms. The system's largest spatial units are based on the terrestrial concept of realms, described by Udvardy (1975) as "continent or subcontinent-sized areas with unifying features of geography and fauna/flora/vegetation." From our marine perspective, realms are defined as follows:

> Very large regions of coastal, benthic, or pelagic ocean across which biotas are internally coherent at higher taxonomic levels, as a result of a shared and unique evolutionary history. Realms have high levels of endemism, including unique taxa at generic and family levels in some groups. Driving factors behind the development of such unique biotas include water temperature, historical and broadscale isolation, and the proximity of the benthos.

This article, with its focus on coastal and shelf areas, does not consider realms in pelagic or deep benthic environments. This is an area requiring further analysis and development.

Provinces. Nested within the realms are provinces:

> Large areas defined by the presence of distinct biotas that have at least some cohesion over evolutionary time frames. Provinces will hold some level of endemism, principally at the level of species. Although historical isolation will play a role, many of these distinct biotas have arisen as a result of distinctive abiotic features that circumscribe their boundaries. These may include geomorphological features (isolated island and shelf systems, semienclosed seas); hydrographic features (currents, upwellings, ice dynamics); or geochemical influences (broadest-scale elements of nutrient supply and salinity).

In ecological terms, provinces are cohesive units likely, for example, to encompass the broader life history of many constituent taxa, including mobile and dispersive species. In many areas, the scale at which provinces may be conceived is similar to that of the detailed spatial units used in global systems such as Briggs's provinces, Longhurst's biogeochemical provinces, and LMEs.

Ecoregions. Ecoregions are the smallest-scale units in the Marine Ecoregions of the World (MEOW) system and are defined as follows:

> Areas of relatively homogeneous species composition, clearly distinct from adjacent systems. The species composition is likely to be determined by the predominance of a small number of ecosystems and/or a distinct suite of oceanographic or topographic features. The dominant biogeographic forcing agents defining the ecoregions vary from location to location but may include isolation, upwelling, nutrient inputs, freshwater influx, temperature regimes, ice regimes, exposure, sediments, currents, and bathymetric or coastal complexity.

In ecological terms, these are strongly cohesive units, sufficiently large to encompass ecological or life history processes for most sedentary species. Although some marine ecoregions may have important levels of endemism, this is not a key determinant in ecoregion identification, as it has been in terrestrial ecoregions.

We suggest that the most appropriate outer boundary for these coastal and shelf realms, provinces, and ecoregions is the 200-meter (m) isobath, which is a widely used proxy for the shelf edge and often corresponds to a dramatic ecotone (Forbes 1856, Hedgpeth 1957b, Briggs 1974). Such a sharp boundary can only be indicative: Shelf breaks are not always clear; the bathymetric location of an "equivalent" biotic transition is highly variable; and there is considerable overlap and influence between shelf, slope, and adjacent pelagic biotas. At the same time, most of the classifications that we reviewed have been heavily influenced by data from nearshore and intertidal biotas, and data from deeper water typically had decreasing influence on boundary definitions. We believe that beyond 200 m, other biogeographic patterns will increasingly predominate, altering or hiding the patterns represented by the system proposed here.

A global, nested system

We propose a nested system of 12 realms, 62 provinces, and 232 ecoregions covering all coastal and shelf waters of the world.

As the MEOW system is based on existing classifications, variation and mismatch among systems led to challenges and compromises. The global coastal classifications of Briggs and Hayden, for example, do not show great congruence with the LMEs. The Briggs and related Hayden systems appeared to be more closely allied to our need for a system with a stronger biogeographic basis than the current LME delineations. Both the Briggs and Hayden systems and the LMEs show considerable variation in the size of their spatial units; the Briggs approach of using 10% endemism distinguishes many isolated communities around oceanic islands, but fails to disaggregate vast areas with gradual faunal changes, even where the incremental effects of such changes are very large indeed (e.g., the Indo-Pacific). The large spatial units in all of these systems clearly encompass significant levels of internal biogeographic heterogeneity, which we were keen to disaggregate through a more detailed system of ecoregions.

We found regional systems for almost all coastal and shelf waters, although many are described only in the gray literature. Notable exceptions were the Russian Arctic and the continental coasts of much of South, Southeast, and East Asia. For these areas, we relied heavily on global data sets and unpublished expert opinion, using more focused biogeographic publications (where available) for refining individual boundaries.

Figure 1 depicts the review process, showing four biogeographic schemes: Briggs's system of provinces (1974, 1995); an expert-derived system combining biotic and abiotic features for South America (Sullivan Sealey and Bustamante 1999); the current LMEs; and a regional classification based on a single taxonomic grouping (decapod crustaceans; Boschi 2000). Despite their different origins, these systems show a re-

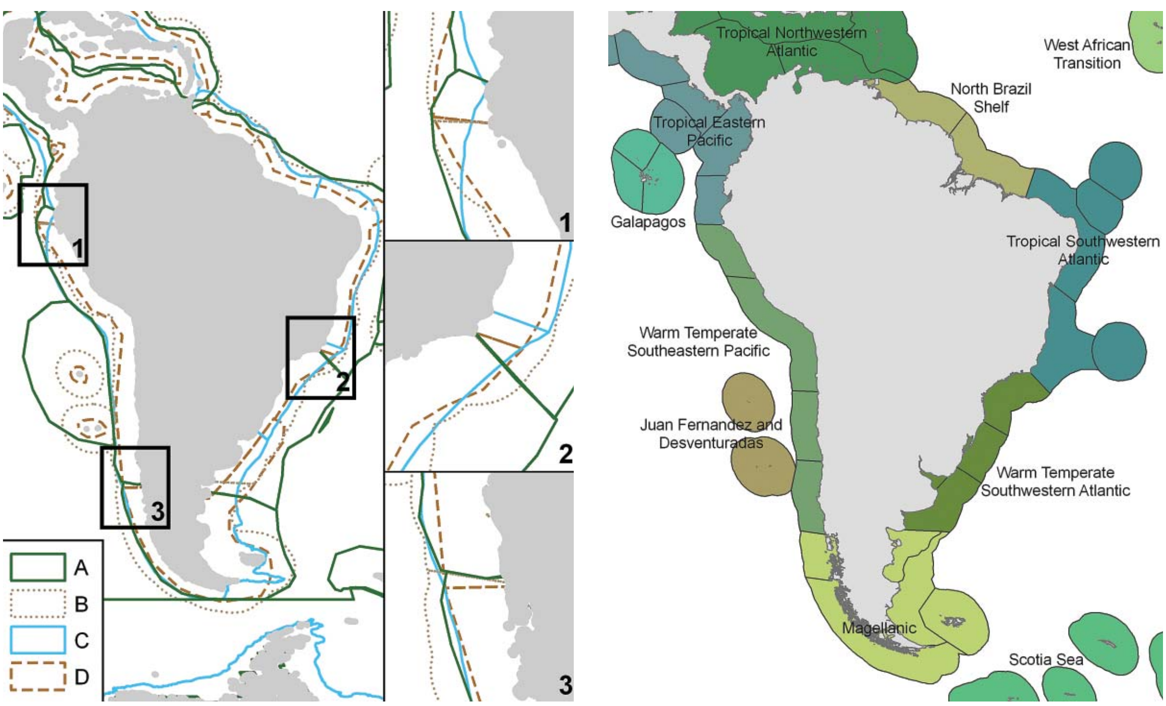

Figure 1. Reconciliation of differing boundary systems for South America. The map on the left illustrates four biogeographic systems: (A) Briggs's provinces, (B) Sullivan Sealey and Bustamante's provinces, (C) large marine ecosystems, and (D) Boschi's provinces. System similarities are exemplified in three inset maps: northern Peru (inset 1), Cabo Frio (inset 2), and Chiloé Island (inset 3). The map on the right shows the Marine Ecoregions of the World provinces (labeled) and their ecoregion subdivision boundaries.

markable congruence at a number of key biogeographic boundaries.

Thus, it was possible to adopt a single system as a primary source, and the MEOW provinces (figure 1, right) were based almost entirely on Sullivan Sealey and Bustamante (1999), while remaining well aligned with the other systems. At a finer resolution, the ecoregions for South America are derived almost entirely from the same publication (Sullivan Sealey and Bustamante 1999), this being the only comprehensive system for these coasts. Even at this scale, however, efforts were made to locate independent verification of boundaries, and it is reassuring to note that these more detailed subdivisions were often supported by data from other oceanographic and ecological literature (see, e.g., Strub et al. [1998], Fernandez et al. [2000], Ojeda et al. [2000], and Camus [2001] for data concerning the Chilean coast).

Although the boundaries in other regions were not as simple to resolve as those along the South American coast, we applied the same approaches. The section that follows gives some information on the key sources used in drawing boundaries.

Marine Ecoregions of the World

Box 1 and figures 2 and 3 give a summary of the entire MEOW system, which covers all coastal and shelf waters shallower than 200 m. The shaded area of each map (figures 2, 3) extends 370 kilometers (200 nautical miles) offshore (or to the 200-m isobath, where this lies further offshore),

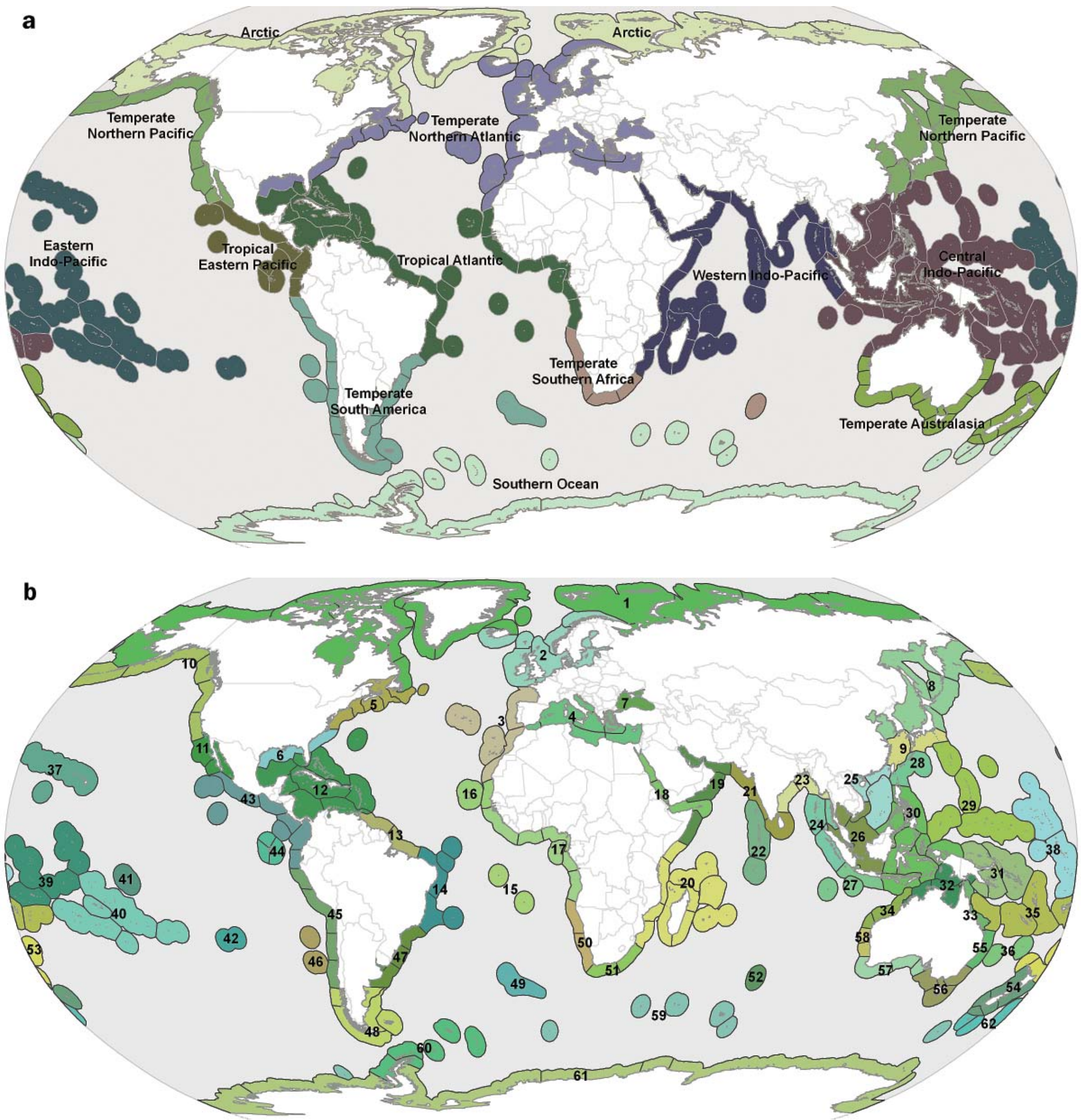

Figure 2. Final biogeographic framework: Realms and provinces. (a) Biogeographic realms with ecoregion boundaries outlined. (b) Provinces with ecoregions outlined. Provinces are numbered and listed in box 1.

Box 1. Marine Ecoregions of the World.

Numbers for the provinces and ecoregions match those shown on the maps in figures 2b and 3. Realms are indicated in boldface, provinces (1–62) in italics, and ecoregions (1–232) in roman type.

Arctic

1. Arctic (no provinces identified)
1. North Greenland
2. North and East Iceland
3. East Greenland Shelf
4. West Greenland Shelf
5. Northern Grand Banks–Southern Labrador
6. Northern Labrador
7. Baffin Bay–Davis Strait
8. Hudson Complex
9. Lancaster Sound
10. High Arctic Archipelago
11. Beaufort–Amundsen–Viscount Melville–Queen Maud
12. Beaufort Sea—continental coast and shelf
13. Chukchi Sea
14. Eastern Bering Sea
15. East Siberian Sea
16. Laptev Sea
17. Kara Sea
18. North and East Barents Sea
19. White Sea

Temperate Northern Atlantic

2. Northern European Seas
20. South and West Iceland
21. Faroe Plateau
22. Southern Norway
23. Northern Norway and Finnmark
24. Baltic Sea
25. North Sea
26. Celtic Seas

3. Lusitanian
27. South European Atlantic Shelf
28. Saharan Upwelling
29. Azores Canaries Madeira

4. Mediterranean Sea
30. Adriatic Sea
31. Aegean Sea
32. Levantine Sea
33. Tunisian Plateau/Gulf of Sidra
34. Ionian Sea
35. Western Mediterranean
36. Alboran Sea

5. Cold Temperate Northwest Atlantic
37. Gulf of St. Lawrence–Eastern Scotian Shelf
38. Southern Grand Banks–South Newfoundland
39. Scotian Shelf
40. Gulf of Maine/Bay of Fundy
41. Virginian

6. Warm Temperate Northwest Atlantic
42. Carolinian
43. Northern Gulf of Mexico

7. Black Sea
44. Black Sea

Temperate Northern Pacific

8. Cold Temperate Northwest Pacific
45. Sea of Okhotsk
46. Kamchatka Shelf and Coast
47. Oyashio Current
48. Northeastern Honshu
49. Sea of Japan
50. Yellow Sea

9. Warm Temperate Northwest Pacific
51. Central Kuroshio Current
52. East China Sea

10. Cold Temperate Northeast Pacific
53. Aleutian Islands
54. Gulf of Alaska
55. North American Pacific Fijordland
56. Puget Trough/Georgia Basin
57. Oregon, Washington, Vancouver Coast and Shelf
58. Northern California

11. Warm Temperate Northeast Pacific
59. Southern California Bight
60. Cortezian
61. Magdalena Transition

Tropical Atlantic

12. Tropical Northwestern Atlantic
62. Bermuda
63. Bahamian
64. Eastern Caribbean
65. Greater Antilles
66. Southern Caribbean
67. Southwestern Caribbean
68. Western Caribbean
69. Southern Gulf of Mexico
70. Floridian

13. North Brazil Shelf
71. Guianan
72. Amazonia

14. Tropical Southwestern Atlantic
73. Sao Pedro and Sao Paulo Islands
74. Fernando de Naronha and Atoll das Rocas
75. Northeastern Brazil
76. Eastern Brazil
77. Trindade and Martin Vaz Islands

15. St. Helena and Ascension Islands
78. St. Helena and Ascension Islands

16. West African Transition
79. Cape Verde
80. Sahelian Upwelling

17. Gulf of Guinea
81. Gulf of Guinea West
82. Gulf of Guinea Upwelling
83. Gulf of Guinea Central
84. Gulf of Guinea Islands
85. Gulf of Guinea South
86. Angolan

Western Indo-Pacific

18. Red Sea and Gulf of Aden
87. Northern and Central Red Sea
88. Southern Red Sea
89. Gulf of Aden

19. Somali/Arabian
90. Arabian (Persian) Gulf
91. Gulf of Oman
92. Western Arabian Sea
93. Central Somali Coast

20. Western Indian Ocean
94. Northern Monsoon Current Coast
95. East African Coral Coast
96. Seychelles
97. Cargados Carajos/Tromelin Island
98. Mascarene Islands
99. Southeast Madagascar
100. Western and Northern Madagascar
101. Bight of Sofala/Swamp Coast
102. Delagoa

21. West and South Indian Shelf
103. Western India
104. South India and Sri Lanka

22. Central Indian Ocean Islands
105. Maldives
106. Chagos

23. Bay of Bengal
107. Eastern India
108. Northern Bay of Bengal

24. Andaman
109. Andaman and Nicobar Islands
110. Andaman Sea Coral Coast
111. Western Sumatra

Central Indo-Pacific

25. South China Sea
112. Gulf of Tonkin
113. Southern China
114. South China Sea Oceanic Islands

26. Sunda Shelf
115. Gulf of Thailand
116. Southern Vietnam
117. Sunda Shelf/Java Sea
118. Malacca Strait

27. Java Transitional
119. Southern Java
120. Cocos-Keeling/Christmas Island

28. South Kuroshio
121. South Kuroshio

29. Tropical Northwestern Pacific
122. Ogasawara Islands
123. Mariana Islands
124. East Caroline Islands
125. West Caroline Islands

30. Western Coral Triangle
126. Palawan/North Borneo
127. Eastern Philippines
128. Sulawesi Sea/Makassar Strait
129. Halmahera
130. Papua
131. Banda Sea
132. Lesser Sunda
133. Northeast Sulawesi

31. Eastern Coral Triangle
134. Bismarck Sea
135. Solomon Archipelago
136. Solomon Sea
137. Southeast Papua New Guinea

32. Sahul Shelf
138. Gulf of Papua
139. Arafura Sea
140. Arnhem Coast to Gulf of Carpenteria
141. Bonaparte Coast

33. Northeast Australian Shelf
142. Torres Strait Northern Great Barrier Reef
143. Central and Southern Great Barrier Reef

34. Northwest Australian Shelf
144. Exmouth to Broome
145. Ningaloo

35. Tropical Southwestern Pacific
146. Tonga Islands
147. Fiji Islands
148. Vanuatu
149. New Caledonia
150. Coral Sea

36. Lord Howe and Norfolk Islands
151. Lord Howe and Norfolk Islands

Eastern Indo-Pacific

37. Hawaii
152. Hawaii

38. Marshall, Gilbert, and Ellis Islands
153. Marshall Islands
154. Gilbert/Ellis Island

Box 1. *(continued)*

Numbers for the provinces and ecoregions match those shown on the maps in figures 2b and 3. Realms are indicated in boldface, provinces (1–62) in italics, and ecoregions (1–232) in roman type.

39. Central Polynesia
- 155. Line Islands
- 156. Phoenix/Tokelau/Northern Cook Islands
- 157. Samoa Islands

40. Southeast Polynesia
- 158. Tuamotus
- 159. Rapa-Pitcairn
- 160. Southern Cook/Austral Islands
- 161. Society Islands

41. Marquesas
- 162. Marquesas

42. Easter Island
- 163. Easter Island

Tropical Eastern Pacific

43. Tropical East Pacific
- 164. Revillagigedos
- 165. Clipperton
- 166. Mexican Tropical Pacific
- 167. Chiapas–Nicaragua
- 168. Nicoya
- 169. Cocos Islands
- 170. Panama Bight
- 171. Guayaquil

44. Galapagos
- 172. Northern Galapagos Islands
- 173. Eastern Galapagos Islands
- 174. Western Galapagos Islands

Temperate South America

45. Warm Temperate Southeastern Pacific
- 175. Central Peru
- 176. Humboldtian
- 177. Central Chile
- 178. Araucanian

46. Juan Fernández and Desventuradas
- 179. Juan Fernández and Desventuradas

47. Warm Temperate Southwestern Atlantic
- 180. Southeastern Brazil
- 181. Rio Grande
- 182. Rio de la Plata
- 183. Uruguay–Buenos Aires Shelf

48. Magellanic
- 184. North Patagonian Gulfs
- 185. Patagonian Shelf
- 186. Malvinas/Falklands
- 187. Channels and Fjords of Southern Chile
- 188. Chiloense

49. Tristan Gough
- 189. Tristan Gough

Temperate Southern Africa

50. Benguela
- 190. Namib
- 191. Namaqua

51. Agulhas
- 192. Agulhas Bank
- 193. Natal

52. Amsterdam–St Paul
- 194. Amsterdam–St Paul

Temperate Australasia

53. Northern New Zealand
- 195. Kermadec Island
- 196. Northeastern New Zealand
- 197. Three Kings–North Cape

54. Southern New Zealand
- 198. Chatham Island
- 199. Central New Zealand
- 200. South New Zealand
- 201. Snares Island

55. East Central Australian Shelf
- 202. Tweed-Moreton
- 203. Manning-Hawkesbury

56. Southeast Australian Shelf
- 204. Cape Howe
- 205. Bassian
- 206. Western Bassian

57. Southwest Australian Shelf
- 207. South Australian Gulfs
- 208. Great Australian Bight
- 209. Leeuwin

58. West Central Australian Shelf
- 210. Shark Bay
- 211. Houtman

Southern Ocean

59. Subantarctic Islands
- 212. Macquarie Island
- 213. Heard and Macdonald Islands
- 214. Kerguelen Islands
- 215. Crozet Islands
- 216. Prince Edward Islands
- 217. Bouvet Island
- 218. Peter the First Island

60. Scotia Sea
- 219. South Sandwich Islands
- 220. South Georgia
- 221. South Orkney Islands
- 222. South Shetland Islands
- 223. Antarctic Peninsula

61. Continental High Antarctic
- 224. East Antarctic Wilkes Land
- 225. East Antarctic Enderby Land
- 226. East Antarctic Dronning Maud Land
- 227. Weddell Sea
- 228. Amundsen/Bellingshausen Sea
- 229. Ross Sea

62. Subantarctic New Zealand
- 230. Bounty and Antipodes Islands
- 231. Campbell Island
- 232. Auckland Island

but, as already noted, we consider the principal focus of this classification to be the benthos above 200 m and the overlying water column.

Key sources included the following:

- Biogeographic assessments in the peer-reviewed literature, including the global studies already mentioned and many regional publications (e.g., Bustamante and Branch [1996] and Turpie et al. [2000] for temperate southern Africa, Linse et al. [2006] for the Southern Ocean)
- Ecoregional assessments conducted by NGOs (e.g., Sullivan Sealey and Bustamante [1999] for Latin America, WWF [2004 and unpublished reports] for much of Africa, Green and Mous [2006] for the Coral Triangle provinces)
- Government-derived or supported systems (e.g., Thackway and Cresswell [1998] for Australia, Powles et al. [2004] for Canada)
- Input from several of the authors of this article and assessments commissioned explicitly for the MEOW process (e.g., unpublished reports by Jerry M. Kemp in 2005 for the Middle Eastern seas and by S. A. L. in 2006 for the Andaman to Java coasts); the system for the Indo-Pacific oceanic islands was developed by one of us (G. R. A.) on the basis of many years of field experience, expert review, and networking with other scientists across the region

These schemes were assessed alongside other biogeographic literature, and in some cases alterations were made to better represent the arguments of biogeography, utility, and parsimony outlined above. A full listing of the sources referenced can be found at *www.nature.org/MEOW* or *www.worldwildlife.org/MEOW.*

The proposed realms adopt the broad latitudinal divisions of polar, temperate, and tropical, with subdivisions based on ocean basin (broadly following the oceanic biomes of Longhurst [1998]). In the temperate waters of the Southern Hemisphere, we diverge from this approach. We consider the differences across the oceans too substantial, and the connections around the continental margins too great, to support either ocean basin subdivisions or a single circumglobal realm (equivalent to Longhurst's Antarctic Westerly Winds Biome), and hence we have adopted continental

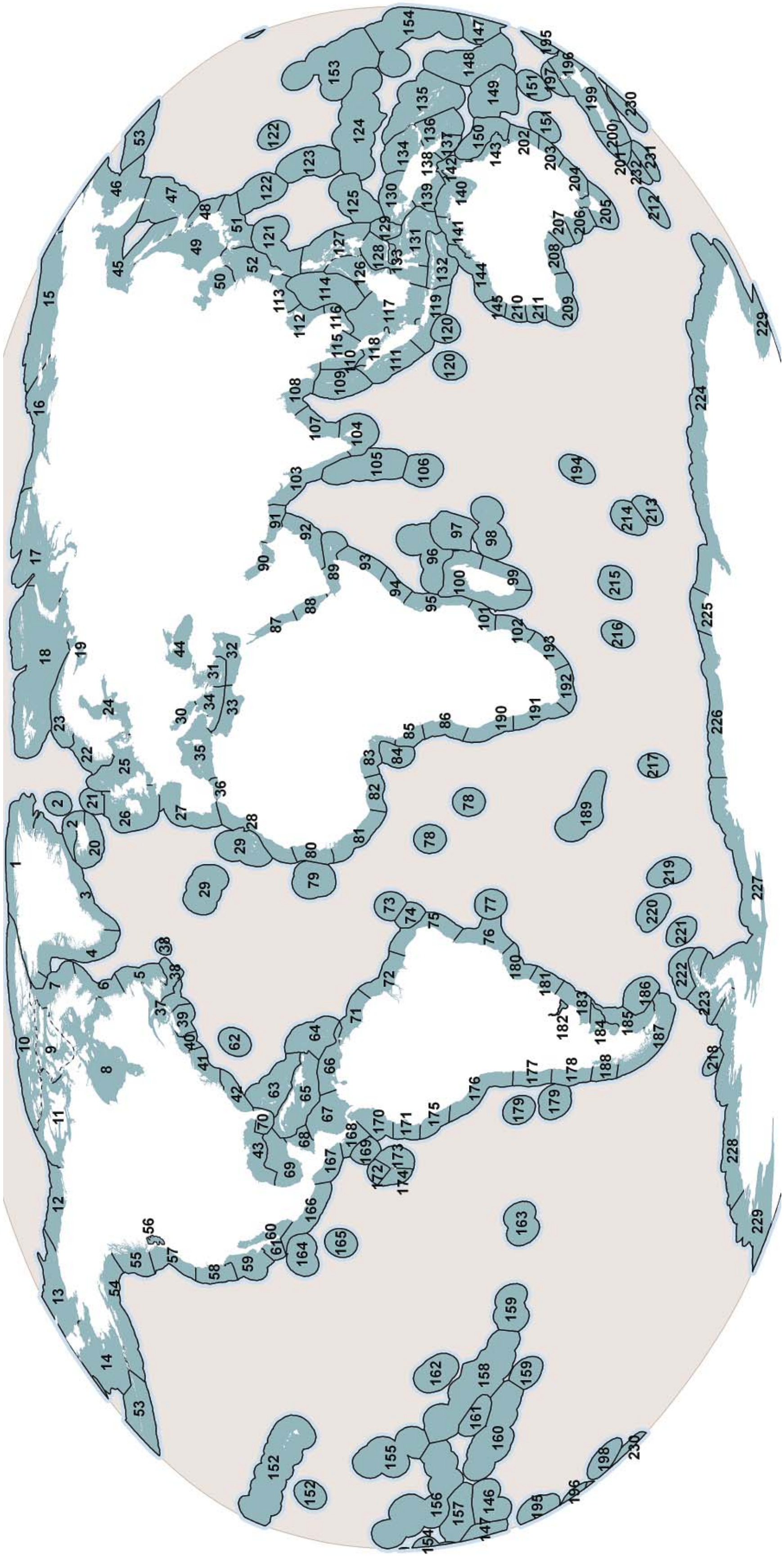

Figure 3. Final biogeographic framework, showing ecoregions. Ecoregions are numbered and listed in box 1.

margin realms for temperate Australasia, southern Africa, and South America. The paucity of existing literature discussing these broadest-scale biogeographic units from a global perspective presents a stark contrast to the terrestrial biogeographic literature.

The level of internal heterogeneity of biotas within different realms is quite varied. For some realms, the differences in biota at the provincial level are substantial, including the warm temperate faunas on either side of the Temperate South America realm and the tropical faunas on either side of the Tropical Atlantic realm. By contrast, we have subdivided the widely used Indo-Pacific "realm" into three units. This is the region of greatest diversity, and it covers a vast area. Across this region are clinal changes in taxa that lack clear breaks, but are sufficiently large that faunas at either end bear little resemblance to each other. Our Indo-Pacific subdivisions (which it might be appropriate to consider as subrealms) follow less clearly defined biogeographic boundaries than other realms, but these divisions produce spatial units that are more comparable to other realms in overall biodiversity, levels of endemism, and spatial area.

At broader scales, we undertook a simple spatial analysis to explore the links or possible crossovers between the MEOW system, LMEs, and Briggs's provinces. The incomplete coverage of the LME system is clearly limiting for global conservation planning: 78 of our 232 ecoregions include a substantive area (greater than 10% of their total area) that is not covered by any LME. Of the remainder, some 49% of LMEs show good congruence (> 90% of shelf area) with either single ecoregions or ecoregion combinations. (The boundary of the Arctic LME has not been mapped, and so was ignored in these calculations.) In comparison, 30 of Briggs's 53 provinces (57%) show good congruence (> 90% of shelf area) with single ecoregions or ecoregion combinations. This figure rises to 39 (74%) if we include congruence at 85% of the shelf area.

We also used the MEOW system to look at the coverage of the marine and coastal network of Ramsar sites. Contracting parties to the Ramsar Convention have committed to achieve a "coherent and comprehensive national and international network" (Ramsar Convention 1999), although until now it has not been possible to assess the biogeographic coverage of marine and coastal Ramsar sites at the global level. The results of this overlay are presented in table 1.

One value of biogeographic classifications is their use in uncovering inequities and dramatic gaps in conservation coverage. Although a more thorough analysis would be required to determine more clearly the degree of representation provided by the existing selection of Ramsar sites, some basic observations are immediately apparent. The Ramsar network is extensive, but it is dominated by sites in the temperate North Atlantic and shows a striking paucity of sites in, for example, the eastern Indo-Pacific and the Southern Ocean. At finer hierarchical resolution, further gaps can be identified: While 92% of realms are represented, this translates to only 73% of provinces and 52% of ecoregions, leaving some 112 ecoregions with no Ramsar representation. These gaps are widespread, including four ecoregions in the temperate North Atlantic.

Conclusions

The MEOW classification provides a critical tool for marine conservation planning. It will enable gap analyses and assessments of representativeness in a global framework. It provides a level of detail that will support linkage to practical conservation interventions at the field level. For example, two major international conservation organizations (the Nature Conservancy and WWF) use ecoregions as planning units. From a global standpoint, the MEOW system offers similar opportunities for the marine environment. It also provides a rational framework in which to analyze patterns and processes in coastal and shelf biodiversity.

The global and hierarchical nature of the MEOW can support analytical approaches that move between scales. Using MEOW, global information can also be used to target action on the ground, while field-level information can be placed alongside information on adjacent or remote locations,

Table 1. The geographic spread of marine and coastal Ramsar sites within the Marine Ecoregions of the World classification.

		Ecoregions			Provinces		
Realm	Total Ramsar sites	Number with Ramsar sites	Total number	Percentage with Ramsar sites	Number with Ramsar sites	Total number	Percentage with Ramsar sites
Arctic	26	10	19	53	1	1	100
Temperate Northern Atlantic	374	21	25	84	6	6	100
Temperate Northern Pacific	38	12	17	71	4	4	100
Tropical Atlantic	117	17	25	68	4	6	67
Western Indo-Pacific	41	14	25	56	7	7	100
Central Indo-Pacific	35	16	40	40	10	12	83
Eastern Indo-Pacific	1	1	12	8	1	6	17
Tropical Eastern Pacific	29	8	11	73	2	2	100
Temperate South America	14	9	15	60	3	5	60
Temperate Southern Africa	9	3	5	60	2	3	67
Temperate Australasia	25	9	17	53	5	6	83
Southern Ocean	0	0	21	0	0	4	0
Total	709	120	232	52	45	62	73

providing a wider spatial perspective. Rooted in existing regional systems, the base units of the MEOW already underpin conservation efforts at regional levels, and a strong body of marine ecoregional planning literature illustrates how global or regional concerns can be converted into field-based conservation action (Banks et al. 2000, Beck and Odaya 2001, Larsen et al. 2001, Kramer and Kramer 2002, Ferdaña 2005).

The value of the MEOW system extends beyond conservation planning. Looking afresh at the broader-scale classes and taking advantage of the improved resolution offered by the MEOW system, it is possible to review wider issues of biodiversity distribution and evolution. At the broadest scales, the most important elements of biogeographic subdivision are the barriers that have separated substantial areas over evolutionary timescales (Adey and Steneck 2001). In the MEOW realms (noting the special case of the Indo-Pacific described above), these barriers consist of landmasses, wide ocean basins, and temperature gradients.

Although there is variation in degree, the provinces can be seen as finer-scale units of evolutionary isolation. They align with many of the more important factors driving recent and contemporary evolutionary processes. Temperature, or latitude, continues to play an important role (separating warm and cold temperate provinces), but so does the further isolation provided by deep water, narrow straits, or rapid changes in shelf conditions. Elsewhere, the connectivity provided by ocean currents, such as the Antarctic Coastal Current and the Canaries Current, can be seen in the classifications, and the importance of biological stepping-stones through various island chains is clearly illustrated. Finally, the ecoregions, which distinguish the MEOW system, reflect unique ecological patterns that extend beyond the broad drivers of evolutionary processes.

Of course, as Wallace (1876) noted, "nothing like a perfect zoological division of the earth is possible. The causes that have led to the present distribution of animal life are so varied, their action and reaction have been so complex, that anomalies and irregularities are sure to exist which will mar the symmetry of any rigid system" (p. 53). Consequently, the use of biogeographic data in a global classification is inevitably a process of accommodation and pragmatism. The lines we have drawn should be regarded as indicative, marking approximate locations of relatively rapid change in dominant habitats or community composition. Ocean boundaries shift continuously with weather patterns, with seasons, and with longer or more random fluctuations in oceanographic conditions. In the future, the impacts of climate change will add to the instability of many boundaries in the ocean (Sagarin et al. 1999, Beaugrand et al. 2002, Hiscock et al. 2004).

The need for a comprehensive, detailed, and globally consistent marine biogeography has been recognized for many years in marine conservation. The requirements for representative approaches to marine protected area designation in various national, regional, and global planning commitments and legal frameworks have given added urgency to this need. The MEOW system provides a basis for planning for coastal and shelf areas, and the links between this system and other global and regional systems make it possible to adopt and use it with minimal disruption to existing data sets or analytical approaches. The unique collaboration of conservation organizations in developing this system adds further value, and may reduce the duplication of effort that so often undermines global conservation approaches (Mace et al. 2000). In short, the system proposed here is powerful and robust, and should prove to be of great value in conservation planning and broader biogeographic discussion. Two international conservation agencies (the Nature Conservancy and WWF) have already begun to use this system and expect to use it more widely in the future. Similarly, members of the Scientific and Technical Review Panel of the Ramsar Convention who participated in developing this system are undertaking more detailed analyses to explore its utility to support the future identification and designation of coastal and marine Wetlands of International Importance.

Acknowledgments

The Marine Ecosystems of the World system draws heavily on the work of others, including the hundreds of contributors to the publications, gray literature, and workshops that created the many regional classifications. In addition, we would especially like to thank the following people, who have provided advice or commentary: Asa Andersson, Jeff Ardron, Allison Arnold, Paul Barber, Mike Beck, Carlo Nike Bianchi, John Bolton, George Branch, John Briggs, Georgina Bustamante, Rodrigo Bustamante, Jose Farina, Sergio Floeter, Angus Gascoigne, Serge Gofas, Charlie Griffiths, Huw Griffiths, Randy Hagenstein, Jon Hoekstra, David John, Peter Kareiva, Ken Kassem, Jerry Kemp, Phil Kramer, Katrin Linse, Gilly Llewellyn, Stephan Lutter, Kasim Moosa, Alexis Morgan, Dag Nagoda, Sergio Navarete, Kate Newman, (Bina) Maya Paul, Sian Pullen, Callum Roberts, Rod Salm, Andrew Smith, Jennifer Smith, Vassily Spiridonov, Victor Springer, Juan Luis Suárez de Vivero, Marco Taviani, Charlie Veron, Eleni Voultsiadou, Mohideen Wafar, Carden Wallace, Kathy Walls, and David Woodland.

References cited

Adey WH, Steneck RS. 2001. Thermogeography over time creates biogeographic regions: A temperature/space/time-integrated model and an abundance-weighted test for benthic marine algae. Journal of Phycology 37: 677–698.

Bailey RG. 1998. Ecoregions: The Ecosystem Geography of the Oceans and Continents. New York: Springer.

Banks D, Williams M, Pearce J, Springer A, Hagenstein R, Olson D, eds. 2000. Ecoregion-based Conservation in the Bering Sea: Identifying Important Areas for Biodiversity Conservation. Washington (DC): World Wildlife Fund, The Nature Conservancy of Alaska.

Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296: 1692–1694.

Beck MW, Odaya M. 2001. Ecoregional planning in marine environments: Identifying priority sites for conservation in the northern Gulf of Mexico. Aquatic Conservation: Marine and Freshwater Ecosystems 11: 235–242.

Boschi E. 2000. Species of decapod crustaceans and their distribution in the American marine zoogeographic provinces. Revista de Investigación y Desarrollo Pesquero 13: 7–136.

Briggs JC. 1974. Marine Zoogeography. New York: McGraw-Hill.

———. 1995. Global Biogeography. Amsterdam: Elsevier.

Burgess ND, Hales JDA, Ricketts TH, Dinerstein E. 2006. Factoring species, non-species values and threats into biodiversity prioritisation across the ecoregions of Africa and its islands. Biological Conservation 127: 383–401.

Bustamante RH, Branch GM. 1996. Large scale patterns and trophic structure of Southern African rocky shores: The roles of geographic variation and wave exposure. Journal of Biogeography 23: 339–351.

Camus PA. 2001. Biogeografía marina de Chile continental. Revista Chilena de Historia Natural 74: 587–617.

Chape S, Blyth S, Fish L, Fox P, Spalding M. 2003. 2003 United Nations List of Protected Areas. Gland (Switzerland): IUCN—World Conservation Union; Cambridge (United Kingdom): UNEP World Conservation Monitoring Centre.

Chape S, Harrison J, Spalding M, Lysenko I. 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Proceedings of the Royal Society B 360: 443–455.

Ekman S. 1953. Zoogeography of the Sea. London: Sidgwick and Jackson.

Ferdaña Z. 2005. Nearshore marine conservation planning in the Pacific Northwest: Exploring the utility of a siting algorithm for representing marine biodiversity. Pages 150–172 in Wright DJ, Scholz AJ, eds. Place Matters: Geospatial Tools for Marine Science, Conservation, and Management in the Pacific Northwest. Corvallis: Oregon State University.

Fernandez M, Jaramillo E, Marquet PA, Moreno CA, Navarrete SA, Ojeda FP, Valdovinos CR, Vasquez JA. 2000. Diversity, dynamics and biogeography of Chilean benthic nearshore ecosystems: An overview and guidelines for conservation. Revista Chilena de Historia Natural 73: 797–830.

Forbes E. 1856. Map of the distribution of marine life. Pages 99–102 and plate 131 in Johnston AK, ed. The Physical Atlas of Natural Phenomena. Edinburgh (Scotland): William Blackwood and Sons.

Green A, Mous P. 2006. Delineating the Coral Triangle, Its Ecoregions and Functional Seascapes. Report Based on an Expert Workshop Held at the TNC Coral Triangle Center, Bali, Indonesia (April–May 2003), and on Expert Consultations Held in June and August 2005. Version 3.1 (February 2006). Bali (Indonesia): The Nature Conservancy, Coral Triangle Center; Brisbane (Australia): Global Marine Initiative, Indo-Pacific Resource Centre.

Hayden BP, Ray GC, Dolan R. 1984. Classification of coastal and marine environments. Environmental Conservation 11: 199–207.

Hazen HD, Anthamatten PJ. 2004. Representation of ecological regions by protected areas at the global scale. Physical Geography 25: 499–512.

Hedgpeth JW. 1957a. Marine biogeography. Geological Society of America Memoirs 67: 359–382.

———. 1957b. Classification of marine environments. Geological Society of America Memoirs 67: 17–28.

Hempel G, Sherman K, eds. 2003. Large Marine Ecosystems of the World: Trends in Exploitation, Protection, and Research. Amsterdam: Elsevier.

Hiscock K, Southward A, Tittley I, Hawkins S. 2004. Effects of changing temperature on benthic marine life in Britain and Ireland. Aquatic Conservation: Marine and Freshwater Ecosystems 14: 333–362.

Hoekstra JM, Boucher TM, Ricketts TH, Roberts C. 2005. Confronting a biome crisis: Global disparities of habitat loss and protection. Ecology Letters 8: 23–29.

Kelleher G, Bleakley C, Wells S, eds. 1995. A Global Representative System of Marine Protected Areas, vols. 2–4. Washington (DC): Great Barrier Reef Marine Park Authority, World Bank, IUCN (World Conservation Union).

Kramer PA, Kramer PR. 2002. Ecoregional Conservation Planning for the Mesoamerican Caribbean Reef. Washington (DC): World Wildlife Fund.

Lamoreux JF, Morrison JC, Ricketts TH, Olson DM, Dinerstein E, McKnight MW, Shugart HH. 2006. Global tests of biodiversity concordance and the importance of endemism. Nature 440: 212–214.

Larsen T, Nagoda D, Anderson JR, eds. 2001. The Barents Sea Ecoregion: A Biodiversity Assessment. Oslo (Norway): World Wildlife Fund.

Linse K, Griffiths HJ, Barnes DKA, Clarke A. 2006. Biodiversity and biogeography of Antarctic and sub-Antarctic mollusca. Deep Sea Research II 53: 985–1008.

Longhurst A. 1998. Ecological Geography of the Sea. San Diego: Academic Press.

Lourie SA, Vincent ACJ. 2004. Using biogeography to help set priorities in marine conservation. Conservation Biology 18: 1004–1020.

Mace GM, et al. 2000. It's time to work together and stop duplicating conservation efforts. Nature 405: 393.

Ojeda FP, Labra FA, Muñoz AA. 2000. Biogeographic patterns of Chilean littoral fishes. Revista Chilena de Historia Natural 73: 625–641.

Olson DM, Dinerstein E. 2002. The Global 200: Priority ecoregions for conservation. Annals of the Missouri Botanical Garden 89: 199–224.

Olson DM, et al. 2001. Terrestrial ecoregions of the world: A new map of life on Earth. BioScience 51: 933–938.

Powles H, Vendette V, Siron R, O'Boyle B. 2004. Proceedings of the Canadian Marine Ecoregions Workshop. Ottawa (Canada): Fisheries and Oceans Canada.

Ramsar Convention. 1999. Strategic Framework and guidelines for the future development of the List of Wetlands of International Importance. Resolution VII.11 of the 7th Conference of the Contracting Parties. (1 June 2007; *www.ramsar.org/res/key_res_vii_index.htm*)

Sagarin RD, Barry JP, Gilman SE, Baxter CH. 1999. Climate related changes in an intertidal community over short and long time scales. Ecological Monographs 69: 465–490.

Sherman K, Alexander LM. 1989. Biomass Yields and Geography of Large Marine Ecosystems. Boulder (CO): Westview Press.

Sherman K, et al. 2005. A global movement toward an ecosystem approach to management of marine resources. Marine Ecology Progress Series 300: 275–279.

Spellerberg IF, Sawyer JWD. 1999. An Introduction to Applied Biogeography. Cambridge (United Kingdom): Cambridge University Press.

Strub PT, Mesías JM, Montecino V, Rutllant J, Salinas S. 1998. Coastal ocean circulation off western South America. Pages 273–313 in Robinson A, Brink K, eds. The Sea, vol. 14A: The Global Coastal Ocean: Interdisciplinary Regional Studies and Syntheses. New York: John Wiley and Sons.

Sullivan Sealey K, Bustamante G. 1999. Setting Geographic Priorities for Marine Conservation in Latin America and the Caribbean. Arlington (VA): The Nature Conservancy.

Thackway R, Cresswell ID. 1998. Interim Marine and Coastal Regionalisation for Australia: An Ecosystem-based Classification for Marine and Coastal Environments. Version 3.3. Canberra (Australia): Environment Australia, Commonwealth Department of the Environment.

Turpie JK, Beckley LE, Katua SM. 2000. Biogeography and the selection of priority areas for conservation of South African coastal fishes. Biological Conservation 92: 59–72.

Udvardy MDF. 1975. A Classification of the Biogeographic Provinces of the World. Morges (Switzerland): International Union for Conservation of Nature and Natural Resources.

[UNEP] United Nations Environment Programme. 2006. Marine and Coastal Ecosystems and Human Well-being: A Synthesis Report Based on the Findings of the Millennium Ecosystem Assessment. Nairobi: UNEP.

Wallace AR. 1876. The Geographical Distribution of Animals: With a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface. London: Macmillan.

Watson R, Pauly D, Christensen V, Froese R, Longhurst A, Platt T, Sathyendranath S, Sherman K, O'Reilly J, Celone P. 2003. Mapping fisheries onto marine ecosystems for regional, oceanic and global integrations. Pages 365–396 in Hempel G, Sherman K, eds. Large Marine Ecosystems of the World: Trends in Exploitation, Protection, and Research. Amsterdam: Elsevier.

[WWF] World Wide Fund for Nature. 2004. The Eastern African Marine Ecoregion Vision: A Large Scale Conservation Approach to the Management of Biodiversity. Dar es Salaam (Tanzania): WWF.

doi:10.1641/B570707
Include this information when citing this material.