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RHODOLITH BEDS ARE UNDERSTUDIED AND UNDERFUNDED: ANALYSIS OF RESEARCH LINES AND PRIORITIES

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“El océano agita el corazón, inspira la imaginación y trae alegría eterna al alma.”- Robert Wyland

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"The ocean stirs the heart, inspires the imagination and brings eternal joy to the soul." - Robert Wyland

Rhodolith beds are understudied and underfunded: analysis of research lines and priorities.

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ABSTRACT

Rhodoliths are recognized as foundational species because they host a great diversity of organisms. Rhodoliths seabeds have stood out as vital carbonate factories around the world, covering wide sub-tidal environments. Rhodoliths-dominated seabeds provide a wide variety of niches and ecological resources, due to its three-dimensional structure, hosting numerous associated species.

This study compared rhodolith research efforts relative to other coastal habitats, such as seagrass, mangroves, coral reefs and kelp beds, in order to demonstrate whether or not rhodolith science is understudied and underfunded in terms of published papers and funds. I also grouped the number of studies (scientific papers) dealing with rhodolith science according to four major thematic areas: “Basic ecology” (157 scientific articles), “Physiology” (13 scientific articles), “Fauna” (43 scientific articles) and “Effects of stressors” (26 scientific articles), to assess efforts among research lines and, finally, the global distribution of these research efforts. With all the information and research carried out on each of the objectives mentioned above, it can be concluded that rhodolith are the least funded and studied coastal habitat compared to the rest of the habitats studied, despite covering a much larger global area.

Aligning with the mission and scientific challenges of the 2030 Agenda, this study encourages to promote rhodolith science to be on par with the rest of the well-studied coastal habitats.

1. INTRODUCTION

Rhodolith beds are widely distributed worldwide, from the tropics to the poles, and from the lowermost intertidal zone to depths over 200 m (Foster, 2001) and they are among the largest macrophyte-dominated benthic communities in the world, along with kelp beds, seagrass meadows, and coral reefs (Foster, 2001). Since the beginning of the 20th century, rhodoliths are recognized as foundation species, because they support a great diversity of organisms (Weber-Van Bosse et al., 1904). Our understanding of rhodoliths and rhodolith beds has grown from a synergy between geologists and biologists. Geologists were the first to become interested in rhodoliths, albeit as dead nodules, because these corallines are well preserved in the fossil record. At least since Darwin’s (1844) observations of rhodoliths (“nullipores”) in calcareous strata in the Cape Verde Archipelago, rhodolith deposits have been used to interpret geological change and paleoecology (Bassi et al., 2009).

Marine habitats underpinned by 'ecosystem engineers', such as seagrass meadows, coral reefs and kelp beds, provide ecosystem functions and services of paramount importance, which are, however, majorly under a global erosion era (Boström et al., 2011; Nyström et al., 2012; Bulleri et al., 2018). Among these habitats, rhodoliths seabeds (= maerl beds) have been highlighted as vital carbonate factories and supporters of biodiversity, worldwide covering extensive subtidal environments (Teichert, 2014; Schubert et al., 2020) estimated at 4.1 million km2 (Fragkopoulou et al., 2021a). These communities are mainly composed by non-geniculate, free-living, calcareous macroalgae, belonging to the division Rhodophyta, which present a rugged appearance and diverse morphology (Riosmena-Rodriguez, 2017). Rhodolith seabeds provide a wide variety of ecological niches and resources, because of their three-dimensional structure, hosting numerous associated species (Steller et al., 2003; Kamenos et al., 2004; Amado-Filho et al., 2007; Steller and Cáceres-Martínez, 2009; Berlandi et al., 2012; Gondim et al., 2014; Qui-Minet et al., 2018; Otero-Ferrer et al., 2019). Rhodolith beds, or maërl beds, provide a hard habitat for numerous other marine algae that live on their surfaces, and for invertebrates living on and in the rhodoliths and surrounding sediments (Foster, 2001). Rhodoliths provide particulate organic matter for suspensive epifaunal feeders, but also micro-phytobenthos to grazing herbivores (Berlandi et al., 2012; Gagnon et al., 2012). In turn, rhodoliths and attached epiflora facilitate associated epi- and infaunal assemblages by providing food and protection against predators (De Grave, 1999; Hinojosa-Arango & Riosmena-Rodríguez, 2004; Amado-Filho et al., 2010), by creating 'habitat cascades' (Thomsen et al., 2010). For these reasons, rhodolith seabeds are considered 'hot spots' of biodiversity (Sciberras et al., 2009; Riosmena-Rodriguez, 2017). In the north-eastern Atlantic, maerl beds are listed as threatened and/or declining habitats by the OSPAR convention (Hall-Spencer et al. 2010) and included within 'Special Areas of Conservation' by the EU Habitats Directive (EU 92/43, Annex I). Moreover, the two dominant coralline algal species of European maerl beds, Phymatolithon calcareum and Lithothamnion corallioides, are protected by the Annex V.

Even with advances in the last decade, rhodolith beds remain largely unexplored (Hernandez-Kantun et al., 2017; Rindi et al., 2019), including assessments of the ecosystem services they provide, such as their potential Blue Carbon capacity, i.e. the magnitude of Carbon sequestration relative to habitats such as those created by seagrass and mangroves. They are considered major carbonate factories and represent a currently unquantified, long-term, store of carbon, as sequestered carbon is locked away in form of CaCO3 deposits that can reach staggering amounts (Kempf, 1970). In addition, these systems can sequester and store considerable amounts of organic carbon through natural capture during photosynthesis by rhodoliths themselves and their associated flora, and by trapping particulate organic matter and organic debris between the calcareous nodules of rhodoliths (Grall & Hall-Spencer, 2003).

In the north-eastern Atlantic, maerl beds are listed as threatened and/or declining habitats by the OSPAR convention (Hall-Spencer et al., 2010) and included within 'Special Areas of Conservation' by the EU Habitats Directive (EU 92/43, Annex I). Moreover, the two dominant coralline algal species of European maerl beds, Phymatolithon calcareum and Lithothamnion corallioides, are protected by the Annex V.

Since habitats underpinned by rhodoliths are a conservation priority for the EU, i.e., they are included in the Habitat Directive (EU 92/43), these habitats should be a research priority in the EU agenda. The development of coastal activities, such as construction of infrastructures, dredging, aquaculture facilities, implementation of marine wind parks, certain fishing modalities (trawling), etc., requires information about these habitats and their sensibility and resilience to environmental alterations caused by these human actions. This information may help policymakers to implement conservation programs to ensure their persistence. This is particularly pertinent in an era dominated by concomitant, global, human-mediated impacts, such as ocean acidification, which decreases the diversity of coralline algae (Peña et al., 2021b), and ocean warming, which may cause distribution shifts in rhodolith species (Fragkopoulou et al., 2021a).The slow growth rates of rhodoliths (1-2 mm per year) make them particularly vulnerable to human actions (Rindi et al., 2019; Schubert et al., 2020; Neves et al., 2021; Fragkopoulou et al., 2021a).

In temperate waters of the north-eastern Atlantic Ocean, the main species of rhodoliths are those within the genus Lithothamnion and Phymatolithon (Pardo et al., 2014; Hernandez-Kantun et al., 2017; Peña et al., 2021a). In Macaronesia (eastern Atlantic Ocean), rhodoliths beds occupy extensive areas across a wide bathymetric gradient, from 15 m to 100 m depth (Otero-Ferrer et al., 2020; Neves et al., 2021) (Fig 1a). Despite the relevance of rhodoliths as contributors to sandy beaches having been highlighted elsewhere (Harvey et al., 2018), their contribution to the magnificence of the 'Popcorn' beaches, created by these deposits (Fig. 1b) remains unknown. So-called

Figure 1. Case study habitat, including (left) a rhodolith-dominated bottom in the study region and (right) 'Popcorn' beach in the north coast of Fuerteventura Island.

‘Popcorn’ beaches attract thousands of visitors to Fuerteventura Island with a ban on collection of dead rhodoliths.

The objectives of this work were to compare the research effort, by considering production of papers and financing funds, relative to other coastal habitats (such as seagrass, coral reefs, mangroves and kelp beds), and secondly, to look for what has been the distribution, at the global level, of the research effort between four major thematic areas, "Basic ecology", "Physiology", "Fauna" and "Effects of stressors”.

2. MATERIAL AND METHODS

The present study is based on bibliographical searches in order to know the variation over the last 30 years in the research effort on different coastal habitats, including the number of publications (considering both the "title" and "topic") of rhodoliths in relation to other habitats, such as seagrass, mangroves, coral reefs and kelp beds.

We searched for articles with keywords such as: "Rhodoliths", "Seagrass", "Mangroves", "Coral reefs", "Kelp bed"; And in the case of the topic: "Rhodolith*", "Seagrass*", "Coral*" y "Kelp*". The total funding and number of funded projects by three funding agencies (2017-2022) were carried out by considering three webpages: the European Union (EU, https://cordis.europa.eu), the National Science Foundation (NSF, https://nsf.gov), and the Australian Research Council (ARC, https://dataportal.arc.gov.au). These are three of the main funding bodies worldwide.

The data were obtained from websites and search engines, such as Web of Science (https://www.webofscience.com), Google Scholar (https://scholar.google.es) and Scopus (https://www.scopus.com). Then, all papers dealing with rhodolith science were classified in 4 thematic areas: "Basic ecology", "Physiology", "Fauna" and "Effects of stressors", all of which were subdivided into different fields. In the case of "Basic ecology", it was subdivided into "Distribution", "Structure", "Paleoecology" and "Primary taxonomic descriptions". For "Physiology", it was subdivided into "Photosynthesis", "Calcification", "Growth" and "Nutrients". For "Fauna", it was divided into "Macrofauna", "Worms", "Molluscs", "Fishes", "Crustaceans", "Echinoderms", "Briozoa", "Sponges" and "Cnidarios". In the latter case, the "Stressors of effects", were subdivided into "Temperature" "Light", "Acidification", "Physical alterations", "Erosion" and "Fertilization".

Each article was also classified according to the marine ecoregion, province and realm, following Spalding et al. (2007) (Figure 2).

These biogeographical systems include:

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." (Spalding et al., 2007).

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. (Spalding et al., 2007).

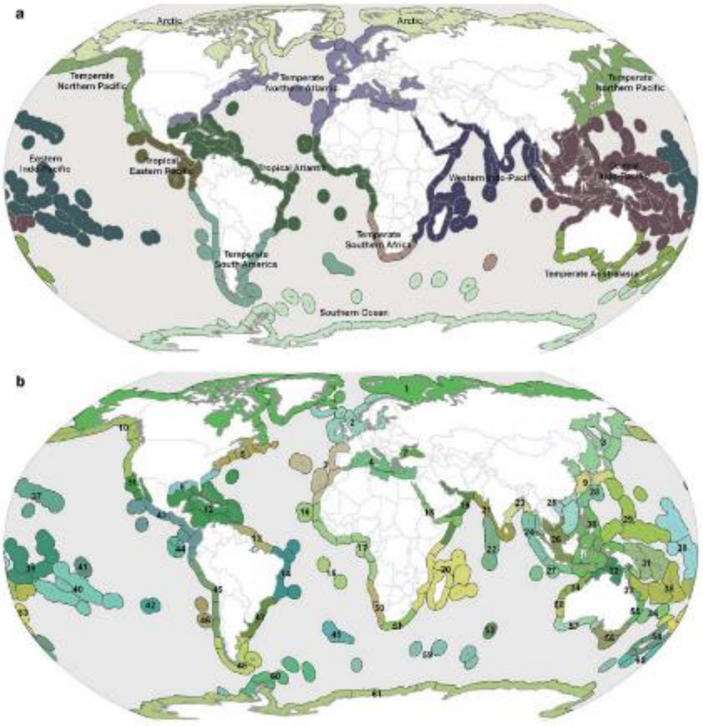

Figure 2. Final biogeographic framework: Realms and provinces. (a) Biogeographic realms with ecoregion boundaries outlined. (b) Provinces with ecoregions outlined. Provinces are numbered and listed in box 1.

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 (Spalding et al., 2007).

Then, different graphs were made comparing the number of studies through years, the total number of projects, the number of papers (according to keywords in "titles" and "topics) and, finally, to standardize research efforts among habitats per area, it was necessary to look for that area (km2) covered each of the different coastal habitats. Thus, mangroves cover 152.000 km2 (Stoddard and Smith, 2007), coral reefs 284.300 km2 (Spalding et al., 2001), seagrasses 266.562 km2 (McKenzie et al., 2020), seaweed beds 1.469.900 km2 (Jayathilake and Costello, 2020) and rhodoliths 4.100.000 km2 (Fragkopoulou et al., 2021a).

3. RESULTS

Our results shown that, overall, "Rhodoliths" are the less studied habitat, with a total of 835 articles, followed by "Kelp beds" (8.036), "Seagrass" (16.554), "Mangroves" (30791) and "Coral reefs" (79.395), considering each habitat as a “topic” (Figure 3).

Given the “title” as a search, 224 papers were found for "Rhodoliths", 2,178 for "Kelp beds", 4,710 for "Seagrass", 10,570 for "Mangroves" and 25,036 for "Coral reefs". The habitat with the highest number of articles and projects corresponds to coral reefs, being also the one that obtains the most financing (Fig. 4). Again, rhodoliths are in the last position, in terms of funding research efforts (Fig 4).

Most studies focusing on rhodoliths have included themes related to their basic ecology (157 papers), followed by studies focusing on associated fauna (43 papers), the effect of stressors on rhodolith physiology and ecology (26) and rhodolith physiology (13) (Table 1).

Category	Number of studies
Basic Ecology	157
Physiology	13
Associated fauna (invertebrates and fish)	43
Effect of stressors on physiology and ecology	26

Table 1. Classification of studies into four thematic areas.

These four major thematic areas have been subdivided into varying sub-fields (Table 2). The number of studies found, for basic ecology, on the distribution of rhodoliths were 57, on its structure, 55, its paleoecology 63 (being the subcategory with the highest number of studies in general) and its taxonomy 43. Regarding their physiology, 4 studies were found about its photosynthesis, 9 about its calcification, one about its growth, and 3 about nutrients. With regard to associated fauna, a total of 16 studies focused on general macrofauna, 7 focused on worms, 4 on molluscs, 4 on fishes, 2 on crustaceans, 4 on echinoderms, 1 on bryozoans, 3 on sponges and 1 on cnidarians. Finally, regarding stressors, 7 papers have focused on temperature, 3 on light, 5 on acidification, 16 on physical disturbances and erosion 16, and 6 on fertilization (pollution).

	Distribution	**Structure**	**Paleoecology**	**Taxonomy**					
Basic Ecology	57	55	63	43					
	Photosynthesis	**Calcification**	**Growth**	**Nutrients**					
Physiology	4	9	1	3					
	Macrofauna	**Worms**	**Molluscs**	**Fish**	**Crustaceans**	**Echinoderms**	**Bryozoans**	**Sponges**	**Cnidarians**
Fauna	16	7	4	4	2	4	1	3	1
	Temperature	**Light**	**Acidification**	**Physical disturbance Erosion**	**Fertilization Pollution**				
Stressors	7	3	5	16	6				

Table 2. Subclassification of the four thematic areas.

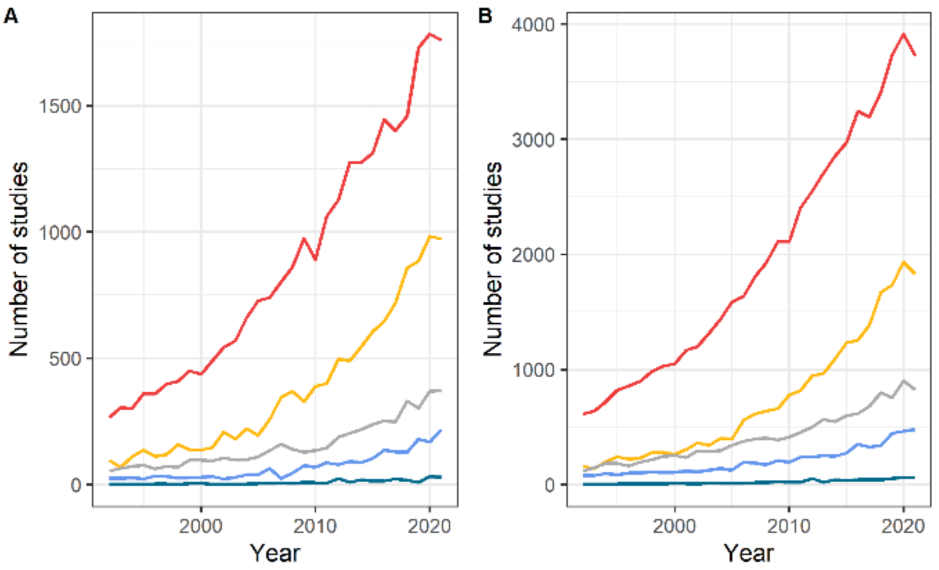

Figure 3. Cumulated number of scientific papers including each habitat as a keyword in either (a) the title and (b) as a topic through the last 30 years.

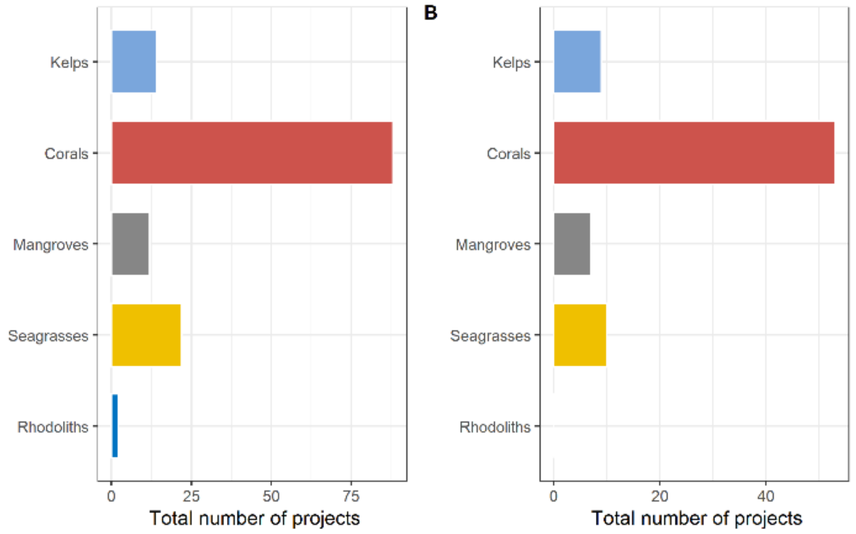

Figure 4. Total number of funded projects with habitat keywords appearing either in (a) titles or as topics (b).

When the total area of each habitat is considered, it can be seen that mangroves are the most studied (i.e., on an area-based), followed by coral reefs, seagrasses, kelps beds and rhodoliths. It should be noted that the rhodoliths cover a large part of the planet, specifically, 4.1 million km2 (Fragkopoulou et al., 2021a), but are still understudied with respect to the rest of habitats. (Fig 5).

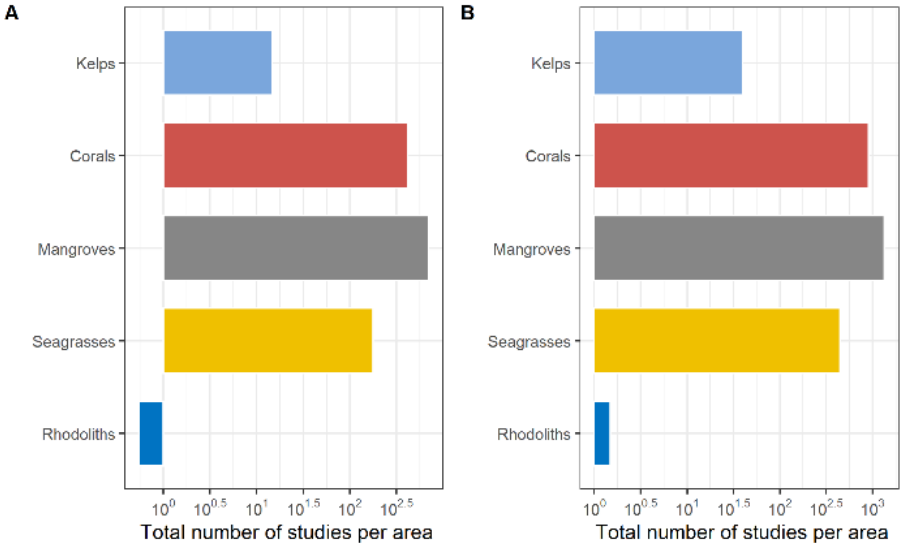

Figure 5. Total number of studies (scientific papers), on an area-basis with habitat keywords appearing either in (a) titles and (b) as topics.

In terms of the distribution of research efforts across the planet’s oceans, the province most studied for the categories: “Basic Ecology” and “Fauna” is the "Tropical Southwestern Atlantic". Several provinces have hardly been studied, as for example, the "Central Indo-Pacific" and "Temperate Australassia" (Fig. 6 and 8).

For the “Physiology” category, it may seem that the most studied provinces are "Artic" and "Warm Temperate Northeast Pacific", with hardly studied provinces such as the "Temperate northern Pacific" and the "Artic" (Fig 7).

Finally, in the case of the “Stressors” category, the province most studied is the "Artic", followed by the "Tropical Atlantic", "Temperate South America", "Temperate Northern Pacific", "Temperate Northern Atlantic" (Fig 9).

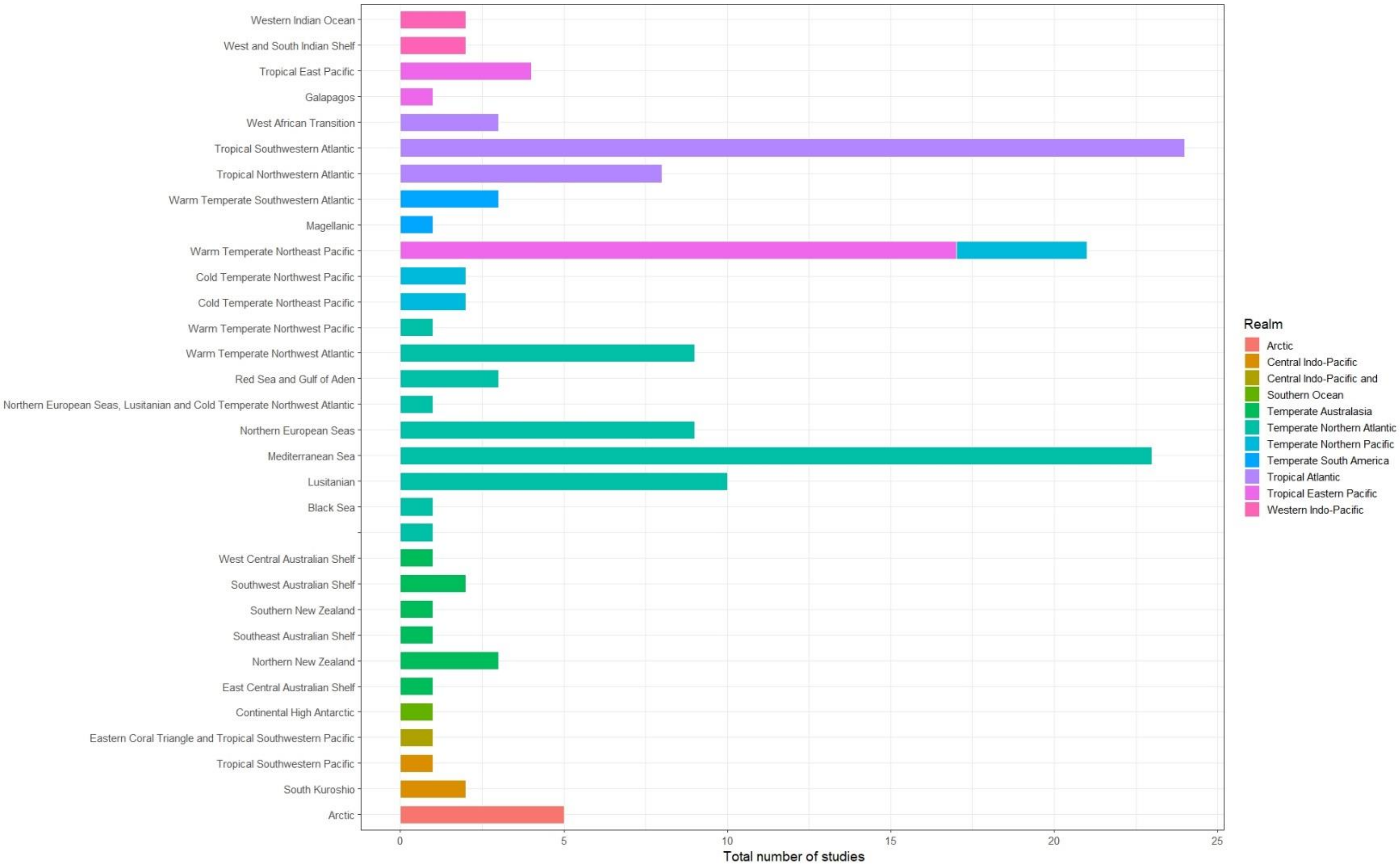

Figure 6. Distribution of the global number of studies for “Basic ecology”.

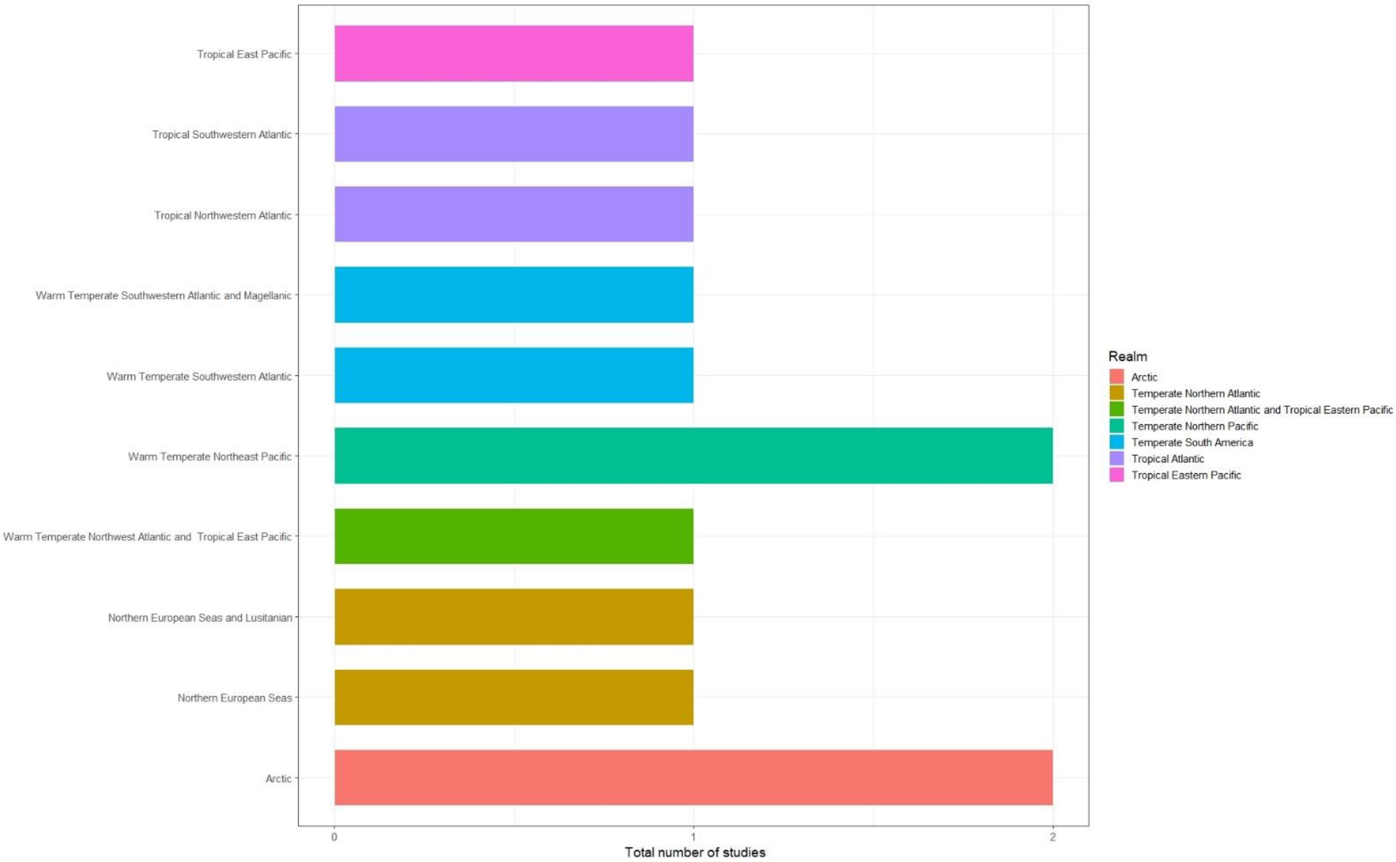

Figure 7. Distribution of the global number of studies for "Physiology".

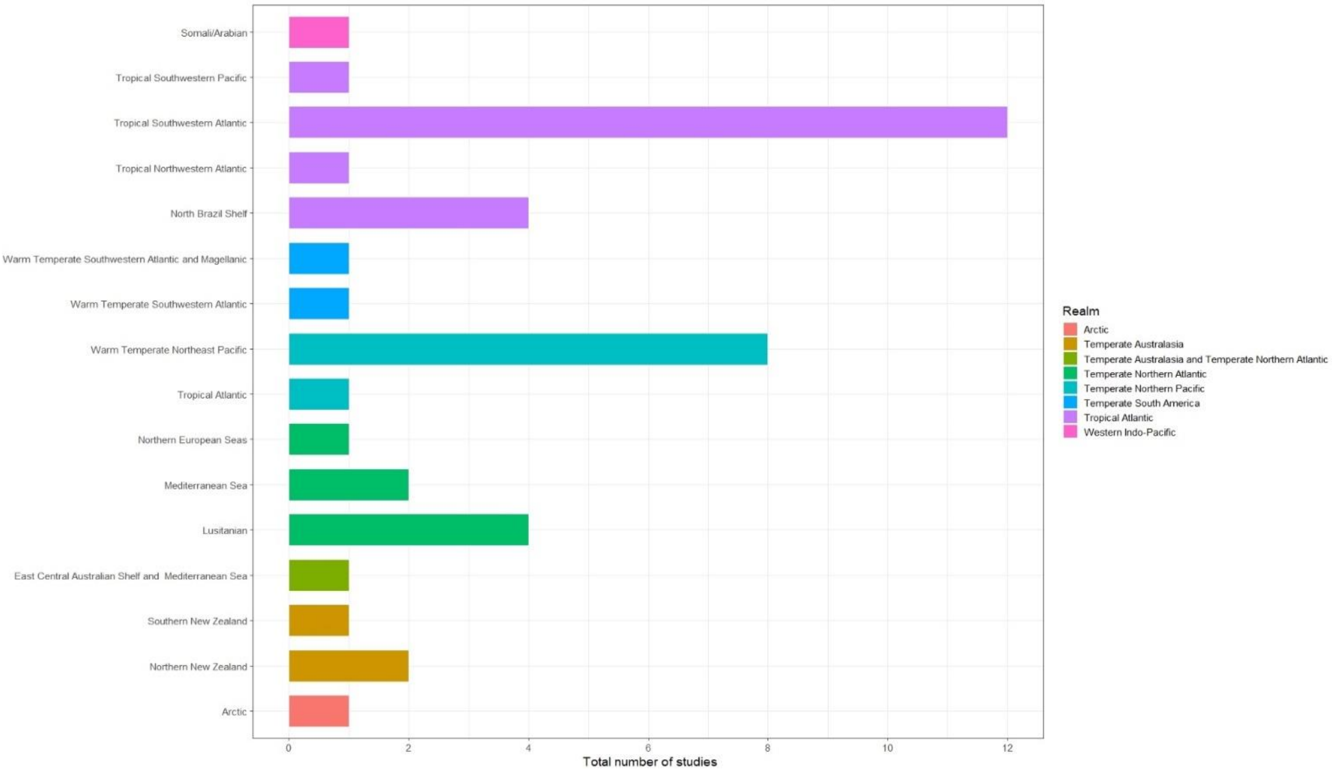

Figure 8. Distribution of the global number of studies for "Fauna".

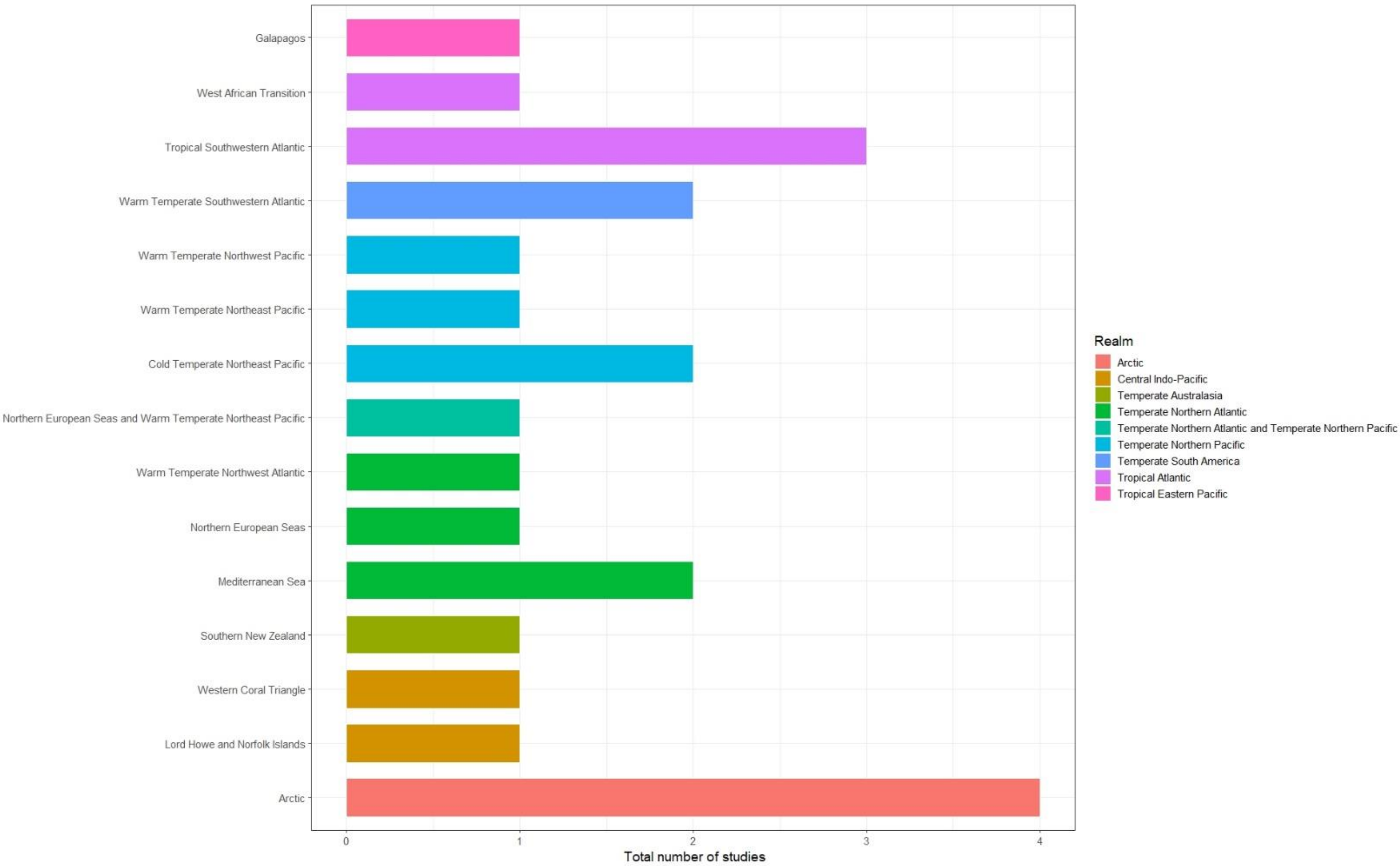

Figure 9. Distribution of the global number of studies for Stressors.

4. DISCUSSION

In this study, our objectives were mainly to demonstrate that rhodoliths are understudied and underfunded compared to other coastal habitats, such as seagrass, coral reefs and mangroves.

The results have shown that rhodoliths beds are the least financed habitat and, therefore, the less studied habitat, this may be due to certain reasons such as the comparison with coral reefs or mangroves, either because they are more iconic habitats or because they are visually more spectacular, that is, the influence of their aspect; another reason may be because rhodoliths are in deeper areas.

Factors such as the size and shape of rhodoliths are highly affected by the local environment, particularly water motion, light availability and sedimentation (Bassi et al., 2012; Dutertre et al., 2015; Queiroz et al., 2016; Cabanellas-Reboredo et al., 2018; Melbourne et al., 2018). These environmental drivers typically co-vary with depth, modifying the morphology of rhodolith nodules (Steller et al., 2003; Hinojosa-Arango et al., 2009; Riul et al., 2009; San et al., 2016).

Water motion is, in turn, the most important environmental driver of rhodolith attributes (Wilson et al., 2004; Pereira-Filho et al., 2012; Queiroz et al., 2016; Melbourne et al., 2018). On shallow waters, high water motion induced by waves can reduce rhodolith bed cover, with the breakage of nodules (Marrack, 1999); (Pascelli et al., 2013). On deeper layers, decreased water motion, however, negatively affect rhodoliths through increased sedimentation (Villas-Boas et al., 2014; Melbourne et al., 2018), affecting rhodolith survival and growth (Wilson et al., 2004; Figueiredo et al., 2015). Light avail ability is also important, although rhodoliths have the ability to adapt their photo-metabolism to a large spectrum of irradiance conditions, from shallow to deeper layers. But later we will see how there is research that shows that rhodolites are of great importance and therefore, that it should be a more studied habitat.

Rhodoliths are a type of marine algae with a coral-like appearance; in their cell walls they store calcium carbonate to form solid structures resembling coral reefs. Unlike corals, rhodoliths are not attached to the seabed but drift and cover large areas of the seabed (Fernández, 2015). But rhodoliths have also been shown to be of great importance. The studies carried out by (Riosmena-Rodriguez, 2001), like many others on biodiversity, determined that there is a high richness and abundance of associated organisms, mainly macroalgae, invertebrates and fish. Rhodolith mantles provide an alternative habitat for species of both rocky and sandy habitats and, on numerous occasions, recruitment and development of species is carried out, because they are a refuge and food for the juvenile life stages of many species of ecological and commercial importance (Kamenos et al., 2004).

In this study, however, the habitat of the rhodoliths is not given much value, knowing the great importance of the characteristics of the rhodoliths (coverage, density of branches, living versus dead mantles, etc.) for their infancy (Figueiredo et al., 2007). This is due to the great ecological and commercial importance of both coral reefs and mangroves, but these also suffer threats. These observations partially match with previous literature.

As for the thematic areas ("Basic ecology", "Physiology", "Fauna" and "Effects of stressors"), some have been addressed more than others, that is, there are certain areas that suffer from knowledge vacuum. Basic ecology is the area with the highest number of studies since it is the part that is used to describe, list or distribute the different species or habitats. As is the case with "The effect of stressors on rhodolith physiology and ecology", since it is both an explanatory and experimental area, whose purpose is to know the factors that threaten the marine environment. As for the associated fauna, it could be said that it is the easiest topic to study since, you count the different species that can be found in a specific place. And finally, physiology, which is the most complex as it is an experimental area where sampling or experiments are performed, requiring sampling tools and materials such as laboratory slides, spatula, microscope, flask among others.

In addition, the distribution of rhodoliths is mainly determined by the availability of light (above a minimum threshold), the maximum and minimum temperature and pH (above a minimum threshold); environmental predictors that are directly related to the physiology of photosynthetic calcifying organisms (Carvalho et al., 2020). Rhodolith communities, known as rhodolith beds, are found in tropical to polar seas at depths near the surface to the photic limit (Teed et al., 2020).

According to the results obtained in this study, the distribution of effort is located in some areas such as "Tropical Southwestern Atlantic", followed by "Tropical Atlantic", "Temperate South America" but we focus on the province of "Tropical Southwestern Atlantic", because the rhodolite mantles are from the largest benthic communities on the Brazilian continental shelf (Amado-Filho et al., 2007b), thanks to the necessary resources it was possible to carry out studies on the abundance and density of this type of funds of rodolites, as well as the impact they produce. Although there are studies that indicate that in certain areas of Brazil rodolite beds are less abundant or even absent (due to factors such as light and temperature). To carry out these studies, it is necessary from an experiment to manipulate, acquire data, compare production estimates, analyse the studied area to use the appropriate research material. The results also indicated provinces where research is scarcer, as is the case of the "Arctic" in the Physiology, this may be due to several reasons such as funding or resources for that area is less, biodiversity is not impactful or can lead to risk factors. Rhodolith beds are currently ‘at risk’, around the world, from anthropogenic disturbances such as ocean acidification, coastal degradation and sedimentation (Harvey et al., 2017).

Finally, future climate change could substantially affect the extent and geographical distribution of rhodoliths (Fragkopoulou et al., 2021b). This could imply a serious disadvantage to the studies of the rhodoliths. The global distribution of rhodolith beds is highly discontinuous (Foster, 2001); these tend to live in relatively flat or slightly inclined areas where non-adhesive algae can remain and grow for long periods of time (Riosmena-Rodriguez et al., 2009).

For all these reasons, the present study can conclude that the habitat of the rhodoliths is of great importance in the marine world, but is not recognized as such, Likewise, the distribution of these is determined by certain factors that allow or hinder the investigation of rhodolith beds.

5. CONCLUSSIONS

The conclusions of the present work about rhodoliths beds are:

- It was shown that rhodolith beds is the least studied habitat and the least funded coastal habitat compared to habitats of great ecological importance (e.g., coral reefs and mangroves).
- Rhodoliths occupy a large area worldwide but remain the least studied and least funded nearshore habitat.
- Studies on Basic ecology contain the largest number of studies, while there is considerably less efforts on associated fauna and physiology.
- Studies on the effect of stress on rhodoliths are more localized in certain areas (such as Brazil) due to its extensive presence of rhodoliths.

6. ACKNOWLEDGEMENTS

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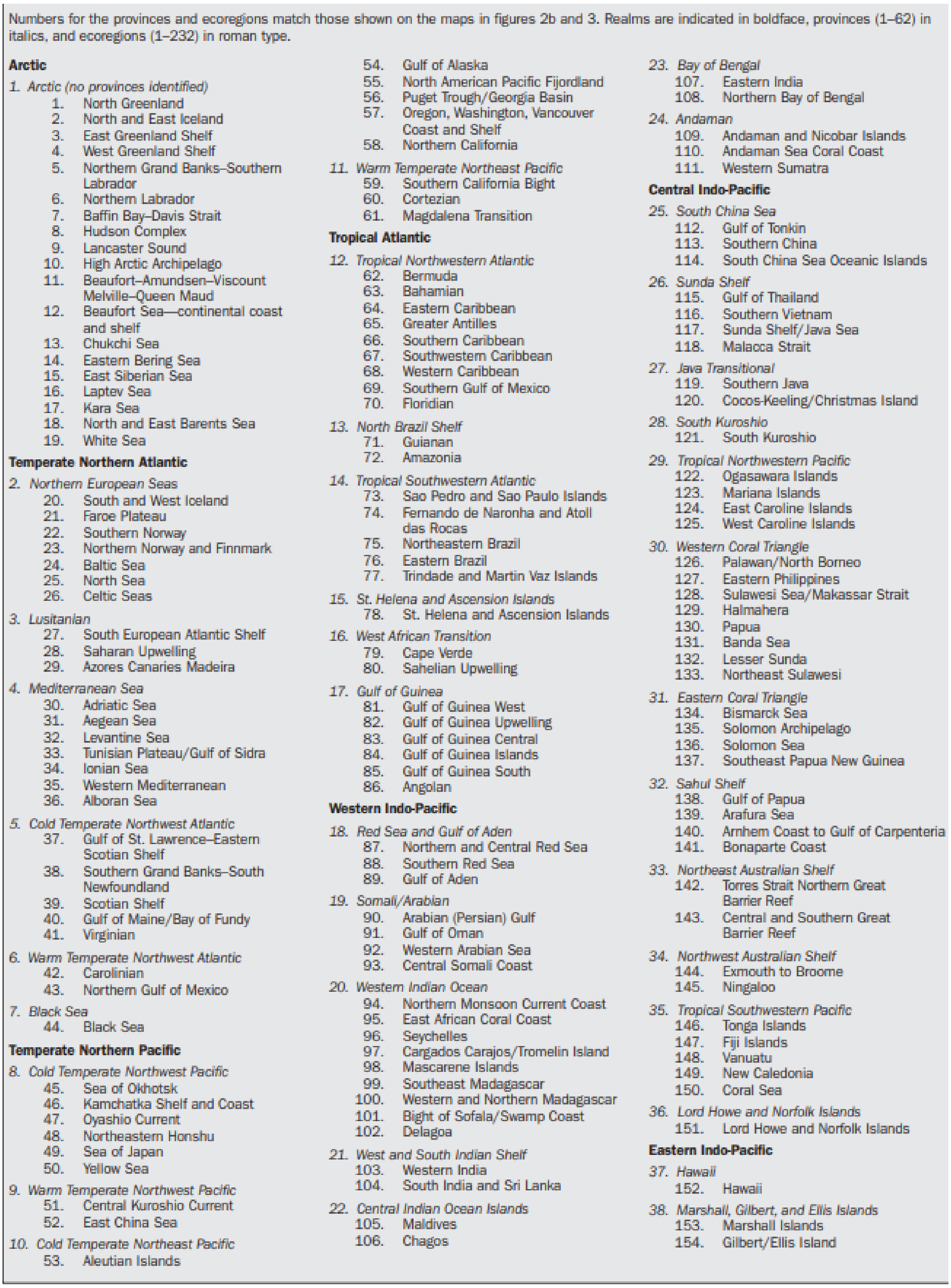
7. APPENDIX



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

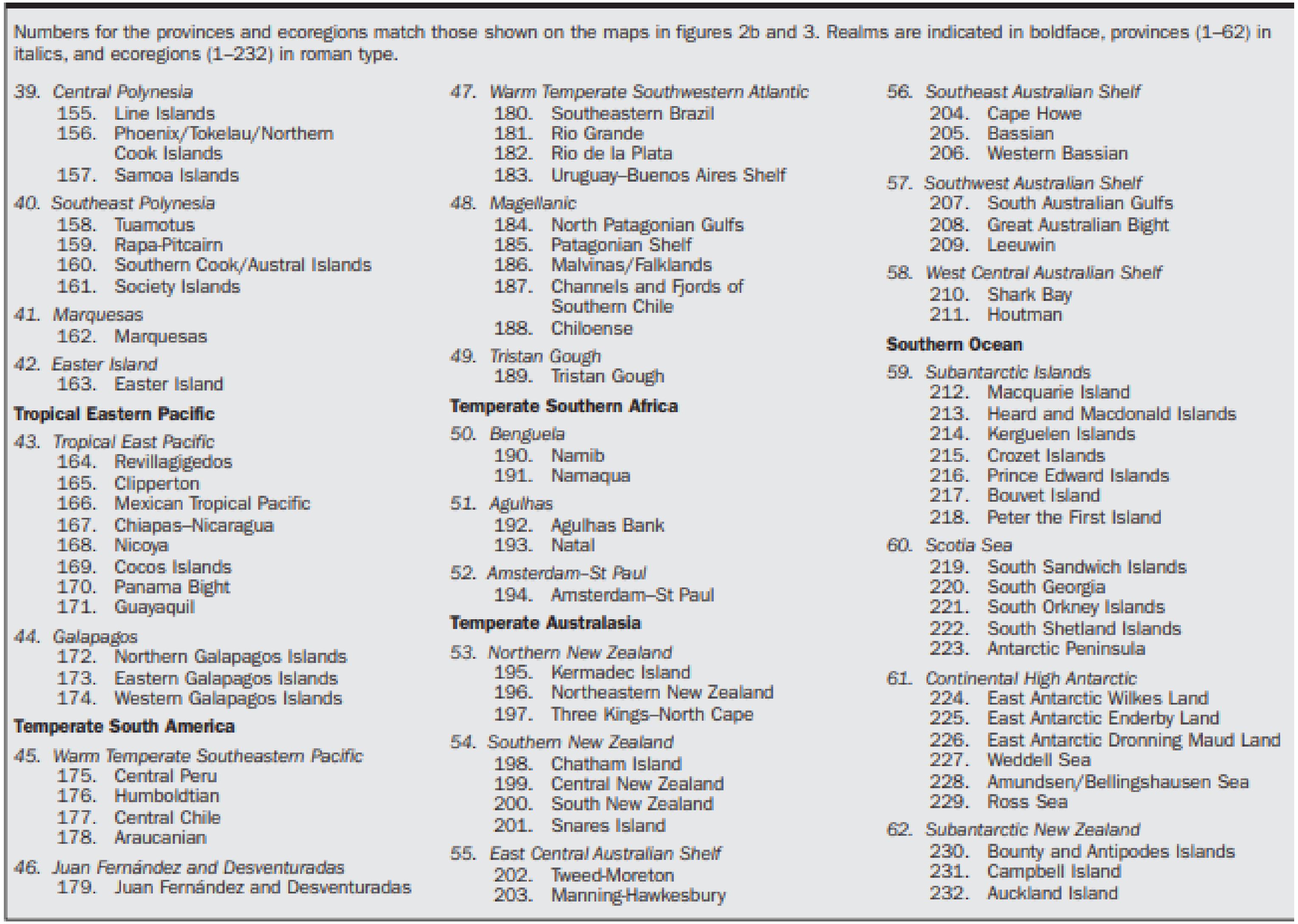
37. Hawaii

152. Hawaii

38. Marshall, Gilbert, and Ellis Islands

153. Marshall Islands
154. Gilbert/Ellis Island

Box 1. The world's marine ecoregions



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

Box 1. (Continued)

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