

Global connectivity and networks of marine reserves

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15 **Keywords: networks, connectivity, marine, climate change, reserves, marine protected areas**

16 **Abstract**

17 Cooperation between countries in managing and protecting shared marine resources is beneficial both

18 ecologically and economically, but how best to establish the cooperation needed at a global scale is

19 largely unknown. Here, we used hydrodynamic modelling to identify ecologically connected

20 networks of marine reserves (MRs) and evaluated these networks with socio-economic indicators.

21 Most of the networks are homogenous with similar levels of development, shared languages, and

22 other cultural values. However, we found that 17% (11/66) of the largest networks (>20 MRs) span
23 multiple countries. These heterogenous networks are composed of countries with different economic,
24 political, and cultural views. Countries that control more, larger marine reserves also have a more
25 even ratio of source reserves to sinks. We discuss that, while such economic and cultural
26 homogeneity might lead to more efficient ecological management in the short term, heterogeneous
27 networks may prove to be more resilient in the longer term, when climate change will modify marine
28 connectivity.

29 **1 Introduction**

30 Marine ecosystems are highly threatened by anthropogenic pressures such as overfishing, repeated
31 heat waves, and overuse (Hughes et al. 2019, O'Hara 2021). Marine protected areas (MPAs) are an
32 effective way of mitigating some of these pressures (Roberts 2017, Duarte et al. 2020). MPAs restrict
33 human use to protect both living and non-living resources making them useful management tools
34 (Edgar 2014). Especially effective are marine reserves (MR), which are no-take MPAs (Costello &
35 Ballantine 2015) that allow for larger fish and greater population sizes both within their boundaries
36 and in the close vicinity (Edgar 2014, Ohayon 2021). In addition to the well-documented ecological
37 and fisheries benefits, marine reserves can also promote tourism, human wellbeing, and alternative
38 livelihood strategies (Ban et al. 2019). Given the potentially large benefits of marine reserves, it is
39 important to understand which factors contribute the most to reserve success. There is evidence that
40 successful reserves (e.g. those that have greater fish biomass relative to unprotected areas) have high
41 compliance to fishing restrictions, are older, larger, and isolated from humans (Edgar et al. 2014;
42 Cinner et al. 2018). What is less known is the impact of the greater network of reserves on
43 effectiveness.

44 There are many reasons that the connectedness of reserves could be beneficial from a conservation
45 perspective. Connectivity promotes source-sink dynamics, gene flow, demographic and genetic

46 rescue, and also assists in species range shifts (Andrello et al. 2017; Roberts, 2017; Manel et al.
47 2019). Isolated marine reserves are slow to recover after disturbance events; the isolation impeding
48 larval recruitment and significantly slowing recovery time (Olson 2019). Conversely, oceanic
49 currents also mediate the spread of marine pollution, invasive species, and diseases (Jönsson &
50 Watson 2016; Jaspers et al 2018). Therefore, hydrological connectivity among MRs across the
51 seascape is a key process capable of modifying the functioning and the effectiveness of MR
52 networks. Further, understanding how reserves are hydrodynamically connected is necessary to
53 promote long-term ecological and socio-economic resilience under ever increasing disturbances;
54 reserves designed with optimized connectivity in mind greatly improve the benefits of the reserve
55 (Edgar 2014, Sala 2018, Goetze 2020). For these reasons, the Convention for Biological Diversity,
56 through the post-2020 global framework for biodiversity current under discussion, recognizes that
57 connectivity is a necessary component of MR networks and needs to be included in their design
58 (<https://www.cbd.int/conferences/post2020>), and oceanographic connectivity is increasingly
59 considered in spatial conservation planning (Maina 2019).

60
61 So far, this progress in understanding how connectivity impacts marine reserves has mostly been
62 ecological in nature. Understanding how political, economic, and societal collaboration among
63 countries align with the ecological connectivity among their marine reserves at a global scale is
64 largely unknown (Trembl et al 2015). It would be unfair to assume every country is capable of the
65 same level of involvement in implementing new protected areas and reserves due to the high cost,
66 and so managing connected networks will necessitate an understanding of the “burden” that each
67 country is capable of sustaining (Maina 2019). Previous studies have shown that hydrodynamically
68 connected networks of MRs can span Exclusive Economic Zones (EEZ) of multiple countries that
69 have different standards of living with varying levels of governance, environmental performance, and
70 dependency on marine resources (Andrello et al. 2017; Wendling et al 2020). Managing and

71 conserving connected ecosystems requires increasing levels of political and cultural connectedness
72 and collaborations across scales and jurisdictions (Bodin 2016).

73

74 A broad coalition of environmental organizations are campaigning to protect at least 30% of the
75 amount of land and sea by 2030 (Dinerstein 2019), but this effort could be hindered by our limited
76 understanding of how countries interact within ecologically connected networks of MRs on a global
77 scale. Countries that have a desired outcome in common, be it increased wealth, better environmental
78 protections, or another goal should have an easier time creating policies that can be agreed upon by
79 all parties involved. By contrast, countries with different ideas or with different dependencies upon
80 marine areas for subsistence are less likely to reach common agreements regarding the levels of
81 protection and management of marine areas (Tremblay 2015).

82

83 Here, we aim to document the large-scale connectivity between marine reserves and their degree of
84 isolation while also characterizing the social configuration of reserve networks. We first identify all
85 the hydrodynamically connected networks of marine reserves in the world, as well as the highly
86 isolated reserves. We then identify the most well-connected countries, as well as countries that have
87 significantly higher ratios of incoming or outgoing connections. We last describe the shared cultural,
88 political, and economic characteristics of the countries which control the largest networks, in an
89 attempt to understand why they are so successful in creating highly connected, multi-country
90 networks.

91

92 **2 Materials and Methods**

93 **2.1 Marine protected areas and marine reserves**

94 The MPA database was downloaded from the World Database on Protected Areas and filtered to only
95 keep protected areas known as ‘marine’ (WDPA, downloaded January 2019). From there we retained
96 only the MRs that are either in IUCN category Ia or Ib or designated as at least partially no-take,
97 since only marine reserves provide widely recognized ecological benefits (Turnbull 2021). The final
98 database includes 2,203 marine protected areas that we refer to as marine reserves (MRs) in the
99 following sections.

100 **2.2 Hydrodynamic connectivity between marine reserves**

101 We evaluated hydrodynamic connectivity using Lagrangian models of dispersal. We used sea surface
102 current velocities from Copernicus Marine Environment Monitoring Service from January 2008 to
103 March 2017. The horizontal resolution of the current velocity datasets was 1/12th degree, and the
104 temporal resolution was one day. We released 10,000 virtual particles from the centroid of each
105 marine reserve and tracked their trajectories using Ichthyop 3.3 (Lett et al. 2008). This was designed
106 to show the trans-boundary dispersal, and not capture local retention and higher variability that could
107 been seen with a higher resolution.

108 We calculated the probability of connection between all pairs of MRs. The spatial position of
109 particles relative to MR polygons was assessed using the function ‘gContains’ in the R package rgeos
110 0.3–19 (Bivand & Rundel, 2017) on the latitude and longitude of each particle. Connection
111 probabilities were used to construct a connectivity matrix among all MRs. Each value is the
112 probability that particles released in one marine reserve are recruited in another, thereby giving the
113 probability of inputs and outputs of each marine reserve to and from all others. Networks are a set of
114 connected MRs, and were determined using the ‘clusters’ function of the R package igraph 1.0.1
115 (Csardi 2006). However, direction of the connection was disregarded to create the networks.

116

117 Networks were initially found for multiple pelagic particle durations, including 20, 40, and 60 days
118 (Appendix 2, 3). Ultimately, we chose to analyze based on a 40-day particle duration because it is
119 closest to the mean pelagic duration of fish larvae (Booth and Parkinson 2011, Graham et al. 2008,
120 Jones et al. 2009).

121 We performed analyses at the network and at the country level. At the network level, we analyzed the
122 indicators for countries involved in each individual network. At the country level, we analyzed the
123 connections that the MRs controlled by each country have to other countries. More detailed methods
124 are available in Appendix 1.

125 **2.3 Social, economic, and political indicators**

126 We used the fisheries dependency index and the human development index to characterize the
127 socioeconomic dimensions of MR networks. The fisheries dependency index assesses the importance
128 of a coastal country's fisheries in terms of their contributions to a national economy, employment,
129 and food security (Andrello et al. 2017). The fisheries dependency index is bounded between 0 and
130 100, with higher values indicating higher dependency. We used the 2018 Human Development Index
131 (HDI) (United Nations Development Program, downloaded 2019) as an indicator of human
132 development. The HDI is based on national statistics of life expectancy, education level, and gross
133 national income per capita, ranges from 0 to 1, with higher values indicating higher development.

134
135 We used the 2018 Environmental Performance Index (EPI) as an indicator of the importance each
136 country places on the environment (Wendling et al 2020). The EPI ranks 180 countries on two dozen
137 indicators spanning ten categories across environmental health and ecosystem vitality, including air
138 pollution, climate and energy, and fisheries. The EPI is produced jointly by Yale University and
139 Columbia University in collaboration with the world economic forum, ranges from 0 to 100, with
140 higher values indicating higher importance placed on environmental issues.

141

142 Data on languages were taken from the Ethnologue Global Dataset compiled by SIL International, a
143 comprehensive database of all languages present in each country (Eberhard 2019). It also documents
144 the number of speakers, literacy rate, and characteristics of each language. In this study, we used the
145 official language of the country, either *de facto* or *de jure*, in which language governmental and cross
146 border issues would be discussed. If a country has two official languages, both were included in the
147 analysis.

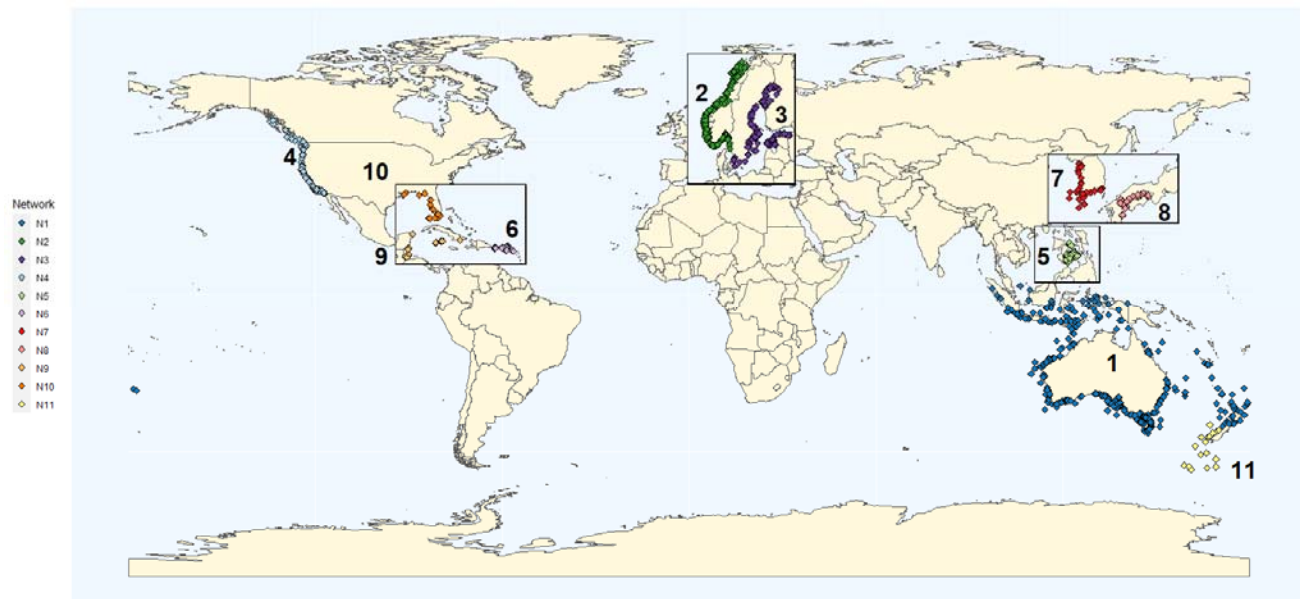
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149 **3 Results**

150 **3.1 The global structure of marine reserve networks**

151 We identified a total of 65 networks of marine reserves based on a cluster analysis. Out of 2,203
152 marine reserves described at the time of the study, 1,618 (73.4%) are included in a network of more
153 than one reserve. Of the 65 total networks, we further focused on the largest 11 networks that each
154 are composed of 20 or more marine reserves (Fig. 1). These 11 networks contain 60.7% (1339) of
155 marine reserves as well as 42.1% of the total surface area of all marine reserves.

156



157

158 **Figure 1:** The 11 largest networks of marine reserves (with 20 or more connected reserves) based on
159 a 40-day pelagic larval duration. See appendix 4 for detailed information on the country and language
160 composition of each network.

161

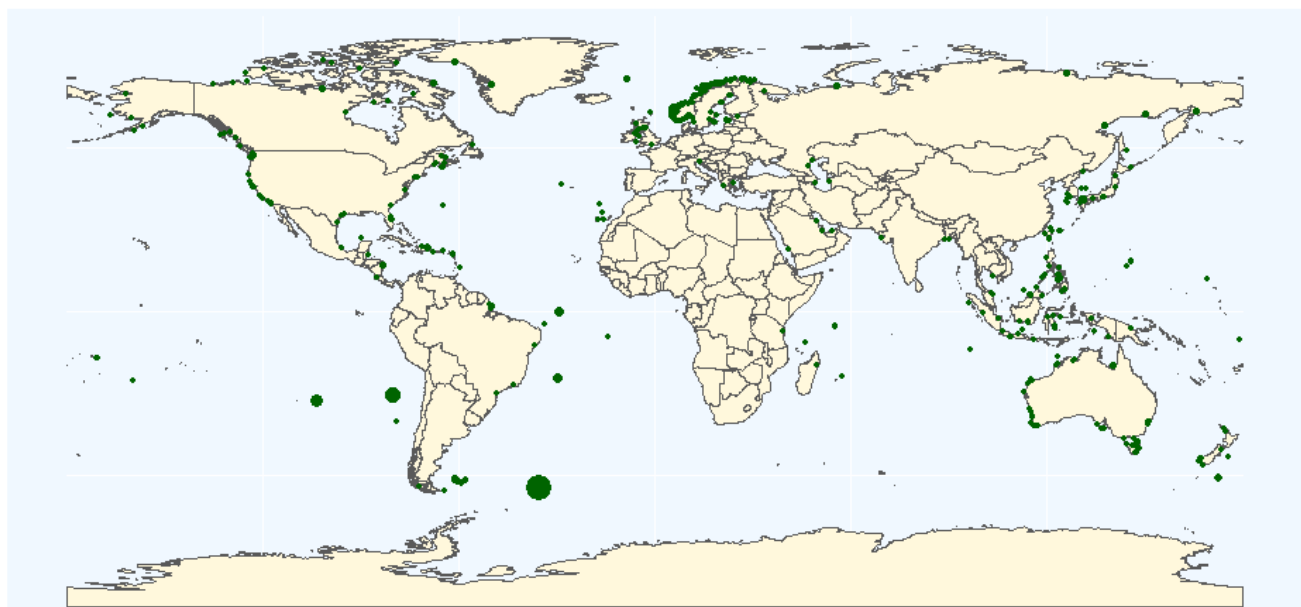
162 The largest network in terms of the number and size of reserves links the Indian and Pacific oceans
163 (N1, Fig. 1, Appendix 4). N1 has 475 reserves, spans five countries, and covers more than twice the
164 area of the next largest reserve network. The second largest network in terms of the number of
165 reserves is in the Norwegian Sea with 374 reserves, composed primarily of Norwegian reserves with
166 a few Swedish reserves (N2, Fig. 1). Despite its high quantity of reserves, N2 is much smaller than
167 N1 in terms of size, ranking 43rd by area covered out of all 66 networks. The other nine top networks
168 range in size from 20 to 200 reserves. The third largest network is located in the Baltic region and
169 three large networks are located in the Caribbean—one in the eastern Caribbean (N6), one in the
170 western Caribbean (N9) and one in the Gulf of Mexico (N10). By contrast, Africa, South America,
171 and Eastern Indian Ocean have no networks that rank in the top 11, despite each having multiple
172 marine reserves. Similar to the number and size of reserves in each network, the number of involved

173 countries is also variable ranging from multi-national networks spanning five countries (N1 in and
174 around Australia and N6 in the easter Caribbean) to networks completely within the domain of a
175 single country. Of the total 66 networks identified, 51 of them are single nation networks.

176

177 While most marine reserves are connected to at least one other reserve, 585 (26.6%) out of the
178 analyzed reserves are not connected to any single other reserve. These isolated reserves are
179 widespread (Figure 2), even in areas that are regionally dominated by large networks. For example,
180 Australia, Norway, and Sweden are all surrounded by isolated marine reserves while at the same time
181 being the locations of the top three largest networks. These isolated reserves are not always small;
182 isolated reserves are some of the largest by area with eight of them each covering 10,000 square
183 kilometers. For example, the South Georgia and South Sandwich Island marine reserve is over 1.24
184 million square kilometers, yet has no probability of connectivity to other sources. However, most
185 isolated reserves (394, or 57.9%) are less than 1 square kilometer and 490 (78.0%) are under 10
186 square kilometers. Many of the smallest marine reserves are located in Norway and Sweden, an area
187 of generally high connectivity.

188



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190

191 **Figure 2:** Isolated marine reserves that are not connected to any others with a PLD of 40 days. Dots
192 show the relative surface area of each reserve.

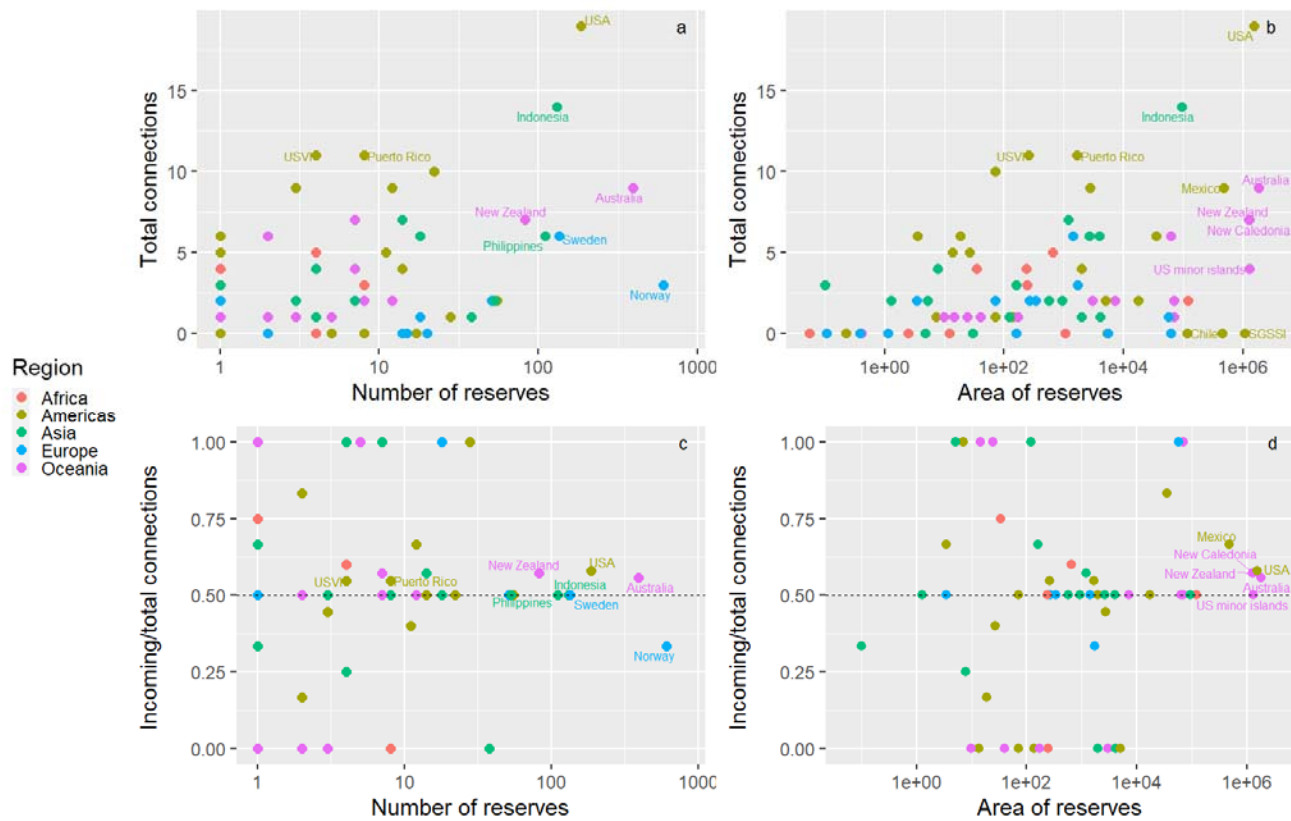
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194 **3.2 Relationship between country protection coverage and connectedness**

195 While networks were designated without directionality, the probability matrix does show which
196 reserves act as sources and sinks. Combining reserves by country provides an overview of the
197 hydrodynamics that connect countries, as opposed to individual reserves. This explains the flow of
198 resources and shows which countries most benefit from incoming larval dispersal, and which
199 countries can primarily serve as a source of larvae. Countries that act only as sources or sinks tend to
200 control few marine reserves and, therefore, have few overall connections. For example, the
201 Seychelles (8 reserves in total) have 3 outgoing connections but no incoming connections, while the
202 Dominican Republic (2 reserves total) has 5 incoming connections but only 1 outgoing. Countries
203 with more reserves show better connectivity and have a more equal ratio of incoming to outgoing
204 connections. The USA is a good model for high connectivity with a good incoming to outgoing ratio:
205 it manages both a large area of reserves and a high number of reserves, in total it has 186 reserves
206 with 19 external connections, 11 of which are incoming and 8 are outgoing. Norway is also an
207 extreme case, with many more reserves than any other country, but low surface coverage. Norway is
208 also not highly connected to other countries, with external connections to only three countries despite
209 controlling 610 reserves.

210

211



212

213 **Figure 3:** How the MRs of each country relate to that country's hydrological connections to other

214 countries, including how the number (a) and area (b) of MRs of one country relate to the total

215 connections to all other countries within the same ecological network. The percent of connections in

216 each country that are incoming only is show vs the number of reserves in (c) and vs the area of

217 reserves in (d). Points are countries and point colors are geographic regions.

218

219 Overall, countries with more and larger marine reserves tend to be more connected to other countries

220 (Figure 3). Both the number and size of reserves relate to the external connectivity a country has, but

221 the size of reserves has a slightly stronger but still not significant relationship to the external

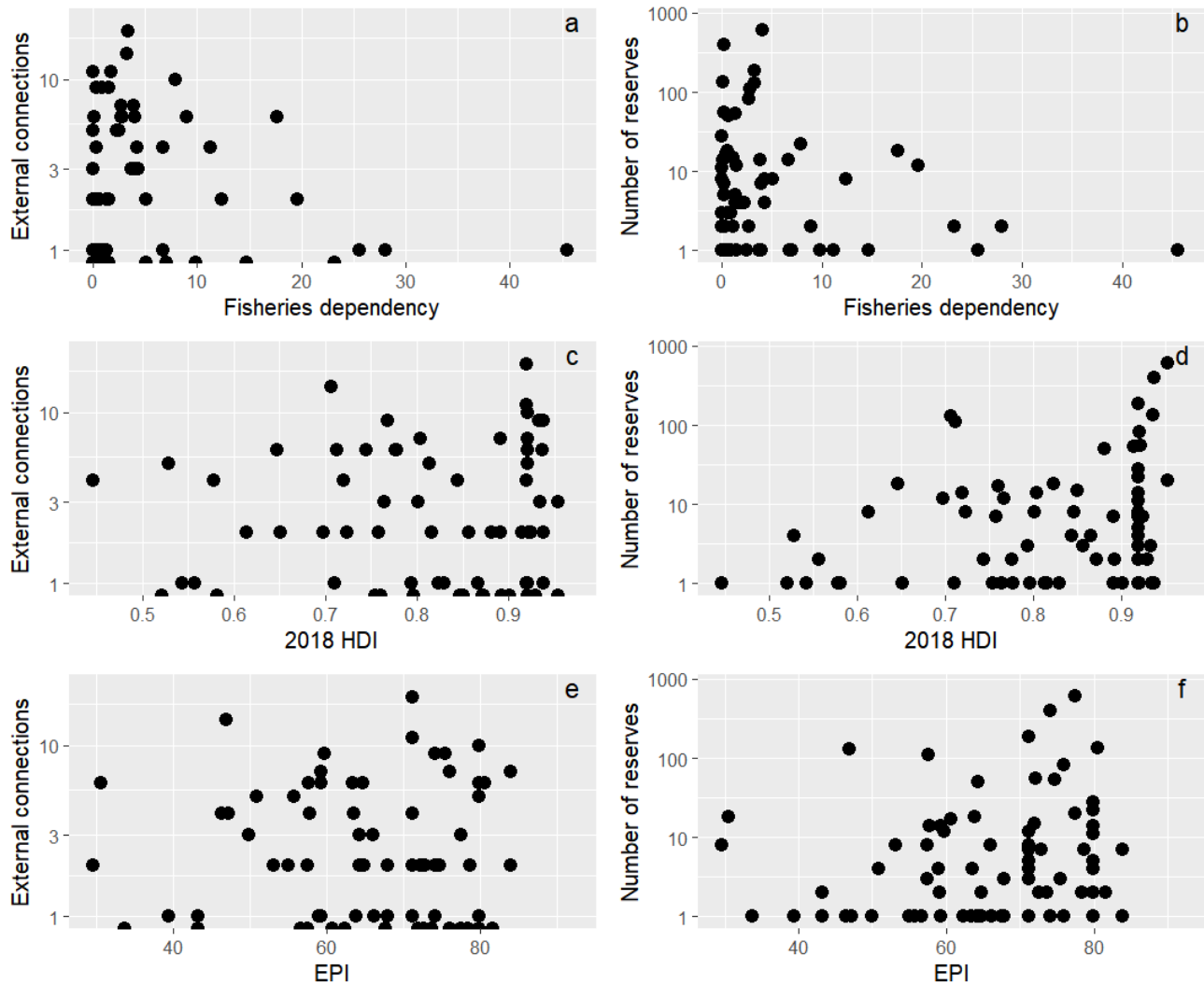
222 connectivity than number of reserves has. Some countries have an unexpectedly high number of

223 connections given their number and size of reserves, such as the US Virgin Islands, which has few

224 reserves but many connections and overall a relatively even distribution of incoming to outgoing

225 connections.

226



227

228 **Figure 4:** the number of external connections and the number of reserves controlled relate to the

229 social, economic, and cultural characteristics of the countries that manage the reserves. External

230 connections as a function of a) fisheries dependency, c) human development index and e)

231 environmental performance index. Total number of reserves controlled by a country as a function of

232 b) fisheries dependency, d) human development index, and f) environmental performance index.

233

234

235 The number of connections to other countries' marine reserves is more dependent on the total area of

236 reserves each country controls, rather than the number of reserves (Figure 3). However, countries

237 with a high number of reserves, as well as a high number of external connections are more likely to
238 have a high human development index, have a low fisheries dependency score, and have a high
239 environmental performance index (Figure 4).

240

241 **4 Discussion**

242 Overall, we found that the majority of marine reserves (73.4%) are connected to at least one other
243 reserve, and of these networks more are very well connected in a large (>20 MR) network (60.7%).
244 Of the seven largest networks that span multiple countries, few have diverse social and political
245 indicators, and tend to be managed by countries with similar economic indicators. Our main results
246 show that: 1) while most marine reserves across the globe are connected to other reserves, many are
247 connected in large networks of more than 20 separate reserves that span multiple diverse countries, 2)
248 isolated reserves make up a significant portion of total reserves (26.6%) and are present across the
249 world, 3) and connections between marine reserves are directional, implying that some of them, and
250 countries that control them, are likely to act more as sources or as sinks.

251

252 Here, we find that the majority of the highly connected networks are managed by multiple countries,
253 meaning successful management of most of the world's largest ecological networks will require
254 coordination between countries. Countries with a high human development index have the most
255 connections because they have the most reserves, as previously recognized (Marinesque et al. 2012).
256 Countries with similar sociopolitical characteristics have fewer barriers to coordination; for example,
257 Network 2 is split between Norway and Sweden, which both have a high human development index,
258 a strong focus on the environment, and low fisheries dependency, as well as sharing a border. Canada
259 and the United States also share a large network, as do Australia and New Zealand. These networks
260 are likely to have an immediate advantage over networks with divergent cultural or socioeconomic

261 attributes in terms of management and communication (Cámara-Leret 2019, Wang 2015, Putnam
262 2008). Over time however, higher levels of diversity have been shown to create better societies, as
263 long as there is a common goal (Page 2008), so while diverse decision maker groups may prove to
264 have lower levels of social trust in the first stages of cooperation, over the longer-term diverse
265 networks could prove to be more ecologically efficient (Wang 2015). In addition, networks with a
266 diverse range of EPIs might bolster the protection efforts of the included countries with lower EPIs
267 with an overall positive effect.

268

269 Though connected networks are more prevalent, isolated reserves are well represented around the
270 world, both in places with large networks and without. Isolated reserves near large networks are
271 likely to be smaller, but make for good candidates to connect to the nearby large networks in the
272 future. Many isolated large reserves in the open ocean are in highly diverse areas such as the
273 Southern Atlantic. Isolated reserves are in danger of slower recovery after catastrophic events, and in
274 having lower gene diversity. Identifying sites that are highly connected to, but not currently part of, a
275 marine reserve or protected area is another good way to find new sites to extent existing networks of
276 protected areas to achieve the ambitious goals of the post-2020 biodiversity framework (Magris et al
277 2018).

278

279 Many countries have asymmetric connectivity, and act primarily as either sources or sinks. As the
280 number of reserves managed by a country increases, so does the symmetry. This is probably a
281 sampling effect, caused by the fact that increasing the number of reserves will also increase the
282 chances of including both source and sink reserves. Not only is the level of connectivity important,
283 but the direction of the connectivity is also. Effectively connected networks can only be created if the
284 importance of the direction of connection is taken into consideration by the managing body of the
285 network.

286 Larval dispersal has the potential to reach up to hundreds of kilometers outside of reserves based on
287 biophysical models, and recruitment from external sources can be a valuable component of recovery
288 and persistence of coral reefs, with some reefs acting as sources for larvae and other more connected
289 reserves acting as stepping-stones aiding in dispersal (Roberts 2017, Alvarez-Romero 2018). Larval
290 dispersal is however mediated by larval behavior such as active swimming and orientation, and can
291 result in different patterns of marine reserve connectivity compared to those identified using
292 hydrodynamic connectivity (Faillettaz et al 2018). The identity and size of the marine reserve
293 networks identified here might therefore be different when considered under the lens of marine larval
294 dispersal.

295
296 These results demonstrate the need for more research into how different countries that share an
297 ecological network interact regarding management measures. While this work gives a snapshot of
298 similarities between countries, it does not delve into the actual interactions between the countries
299 with regards to marine management and how external connectivity is managed. Identifying key areas
300 of connectivity and ensuring convergent management styles to protect these areas would help
301 countries better protect their marine resources, help vulnerable populations that depend on the sea for
302 their livelihoods, and help mitigate some of the impacts of anthropogenic climate change.

303 **5 Conflict of Interest**

304 *The authors declare that the research was conducted in the absence of any commercial or financial*
305 *relationships that could be construed as a potential conflict of interest.*

306 **6 Author Contributions**

307 JM, DM, and MA conceived of the study, LV and NB contributed to analysis, JM wrote the first draft, and all
308 authors commented on the manuscript.

309 7 Funding

310 Funding was provided by the French governments “Make our planet great again” PhD scholarship

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444 **9 Data Availability Statement**

445 The datasets analyzed for this study can be found in the Protected Planet database
446 [<https://www.protectedplanet.net/en/thematic-areas/marine-protected-areas>].