Long-Distance Benefits of Marine Reserves: Myth or Reality?

Stéphanie Manel, Nicolas Loiseau, Marco Andrello, Katharina Fietz, Raquel Goñi, Aitor Forcada, Philippe Lenfant, Stuart Kininmonth, Concepcion Marcos, Virginie Marquès, et al.

1   **Long-distance benefits of marine reserves: myth or reality?**

2   Stéphanie Manel[1], Nicolas Loiseau[2], Marco Andrello[3], Katharina Fietz[4], Raquel Goñi[5], Aitor

3   Forcada[6], Philippe Lenfant[7], Stuart Kininmonth[8,9], Concepción Marcos[10], Virginie Marques[2],

4   Sandra Mallol[5], Angel Pérez-Rufaza[10], Corinna Breusing[4], Oscar Puebla[4], David Mouillot[2,11]

5

6   1-EPHE, PSL Research University, CEFE UMR 5175, CNRS, Université de Montpellier,

7   Université Paul-Valéry Montpellier, Biogéographie et Ecologie des Vertébrés, 1919 route de

8   Mende, Montpellier 34293, France

9   2-UMR 9190 MARBEC, IRD-CNRS-IFREMER-UM, Université de Montpellier, Montpellier

10   34095 France

11   3- Department of Ecology and Evolutionary Biology, University of Toronto, Toronto,

12   Ontario, Canada

13   4- GEOMAR Helmholtz Centre for Ocean Research Kiel, Evolutionary Ecology of Marine

14   Fishes, Düsternbrooker Weg 20, 24105 Kiel, Germany.

15   5- Instituto Español de Oceanografía, Centro Oceanográfico de Baleares, Moll de Ponent s/n,

16   07015 Palma de Mallorca, Spain

17   6- Department of Marine Sciences and Applied Biology, University of Alicante, P.O. Box 99,

18   03080 - Alicante, Spain

19   7- Univ. Perpignan Via Domitia, Centre de Formation et de Recherche sur les

20   Environnements Méditerranéens, UMR 5110, 58 Avenue Paul Alduy, F-66860 Perpignan,

21   France

22   8- School of Marine Studies, University of South Pacific, Suva, Fiji

23   9- Stockholm Resilience Centre, Stockholm University, Stockholm, Sweden

24   10- Departmento de Ecología e Hidrología, Facultad de Biología, Campus de Espinardo,

25   Regional Campus of International Excellence ''Campus Mare Nostrum'', University of

26   Murcia, 30100 Murcia, Spain

27   11-Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook

28   University, Townsville, QLD 4811 Australia.

29   **Correspondence: stephanie.manel@ephe.psl.eu (S. Manel)**

30

1

33

34   **Abstract**

35

36   Long-distance (>40km) dispersal from marine reserves is poorly documented. Yet, it can

37   provide essential benefits such as seedling fished areas or connecting marine reserves into

38   networks. From a meta-analysis, we suggest that the spatial scale of marine connectivity is

39   underestimated due to the limited geographic extent of sampling designs. We also found that

40   the largest marine reserves (>1,000km^2) are the most isolated. These findings have important

41   implications for the assessment of evolutionary, ecological and socio-economic long-distance

42   benefits of marine reserves. We conclude that existing methods to infer dispersal should

43   consider the up-to-date genomic advances and also expand the spatial scale of sampling

44   designs. Incorporating long-distance connectivity in conservation planning will contribute to

45   increase the benefits of marine reserve networks.

46

47

48

49

50

51

52

53

54

55

2

56

57

58

59 **Benefits from marine reserves: where are we?**

60 Marine resources are declining at an alarming rate [1, 2], with more than half of the oceanic

61 area exploited by industrial fishing [3]. In response, marine protected areas (MPAs) have been

62 established in an effort to conserve biodiversity and sustain fisheries [4-7]. Yet, only 3.7 % of

63 the ocean is presently covered by MPAs and less than 2% by no-take MPA**s** (referred to as

64 marine reserves [8]) specifically (mpatlas.org; [9]). Despite the recent establishment of large-

65 scale MPAs (>100,000 km^2) [10], the current trend of protection is not keeping pace with the

66 increasing human footprint on marine resources [11, 12]. In particular, the Aichi Biodiversity

67 Target 11 established by the Convention of Biological Diversity to protect at least 10% of the

68 ocean by 2020 is unlikely to be achieved [9, 13, 14]. In consideration of the ever-growing

69 human population, fishing technological developments and per capita consumption rates, a

70 new target of 30% protected area by 2030 was proposed at the 2016 International Union for

71 Conservation Nature (IUCN) World Conservation Congress in line with scientific advice [6,

72 15]. There is thus an urgent need to better understand the full range of benefits provided by

73 marine reserves to optimize future conservation efforts.

74

75 Theoretical and empirical studies support the positive effects of marine reserves within their

76 boundaries and in their vicinity [16-19]. Indeed, marine reserves unambiguously host more

77 and larger - and thus more fertile - individuals than fished areas (e.g. [5, 20, 21]). They also

78 contribute to preserve genetic diversity [22], increase human wellbeing [23], alleviate poverty

79 [24] and facilitate adaptation to climate change [25]. In addition, when properly designed and

80 enforced, they have the potential to increase catches of commercial species in surrounding

81 fishing grounds [26, 27] due to juvenile or adult **spillover** (see glossary) [28, 29]. However,

82 such direct benefits have been typically documented at short distances from reserve

83 boundaries, i.e. from a few hundred meters to less than 40 km [16, 30 , 31]. In contrast, little

84 is known about the benefits of marine reserves in areas that are 40 to hundreds of kilometers

85 away from their boundaries [32].

86

87 The concept of long-distance (>40 km) **dispersal** is not new in marine ecology and the oceans

88 have been assumed to function as mostly open, well-connected systems until the last two

89 decades [33, 34], when evidence of local recruitment started to accumulate [35, 36]. However,

90 the large-scale impacts of marine reserves resulting from long-distance dispersal of larvae

91 [37], juveniles and adults [38] are still poorly documented. The potential for long-distance

92 dispersal is highest for **pelagic species**, which is consistent with their widespread geographic

93 distributions [39]. Yet, recent findings based on telemetry and genetic tools indicate that

94 **benthic** and **demersal species** (hereafter called benthos), including those in the deep sea, can

95 also disperse up to hundreds of kilometers [32, 40-42]. This recognition of high dispersal

96 capabilities calls for more studies on the effect of dispersal far from reserves and for a better

97 integration of long-distance dispersal in the design of reserve networks.

98

99 Here we review the potential long-distance benefits of marine reserves, including those

100 provided by relatively rare long-distance dispersal events. We focus on the benthos since their

101 adult stages can be more easily assigned to protected versus non-protected areas compared to

102 pelagic species which have large home ranges, often larger than most MPAs [43]. First,

103 through an extensive literature screening, we characterize the spatial scale of dispersal for the

104 benthos. We then discuss how existing methods can be enhanced to expand the scale of

105 connectivity analyses. Finally, we discuss the potential long-distance benefits of marine

106   reserves for both conservation and fisheries and how a well-connected network can enhance

107   those benefits.

108

109   **Spatial scale of dispersal and connectivity in the marine realm: do we capture the full**

110   **picture?**

111

112   We define marine connectivity as the exchange of individuals among marine populations

113   [44]. This exchange can take place through dispersal of individuals as larvae, juveniles, or

114   adults. When individuals reproduce successfully thereafter, **demographic connectivity**

115   translates into **genetic connectivity**. Determining the spatial scale of marine connectivity is

116   crucial for our understanding of the population dynamics, genetic structure and biogeography

117   of marine organisms, and accordingly for the design of marine reserves.

118

119   To obtain a global estimate of the spatial scale of marine connectivity for the benthos, we

120   conducted an extensive – but non-exhaustive – literature review over the last decade in the ISI

121   Web of Science (supplementary text S1, supplementary file S1). Of the 460 papers identified,

122   130 were included in our meta-analysis as they contain information about maximum sampling

123   geographic range and maximum inferred demographic or genetic connectivity for a total of

124   243 species.

125

126   The different methods used to estimate dispersal distance apply to different spatial and

127   temporal scales (Table I of Box 1). The median potential dispersal distance averaged across

128   all studies based on biophysical models (226 km, interquartile range = 160 - 415 km, number

129   of species = 56) was at least four times higher than the demographic (realized and effective)

130   median dispersal distance (42 km, interquartile range = 27 – 250 km, number of species = 55;

131   Figure 1A; Box 1). These results indicate that studies are either overestimating potential

132   dispersal or underestimating demographic dispersal, with some exceptions where both

133   estimates are congruent (e.g. [45]). However, assessing the full spatial extent of dispersal is

134   challenging due to the inherent difficulty of tracking or recapturing organisms over long

135   distances. With a few exceptions (e.g. [32, 41, 46]), most empirical studies of demographic

136   connectivity were conducted at scales smaller than 40 km [47]. Estimating demographic

137   connectivity at larger spatial scales and over multiple generations would require sampling

138   significantly more individuals and in more distant populations, which would entail high,

139   possibly prohibitive, costs. Genetic assignment approaches at the population level might be

140   scaled-up more easily than mark-recapture or parentage analysis methods and constitute a

141   promising approach when populations are genetically differentiated [48, 49]. For example,

142   putative first-generation migrants between two populations separated by 400 km were

143   detected in the Omani Clownfish (*Amphiprion omanensis*) using assignment tests [40]. If

144   populations are locally adapted, the use of genetic markers that are under divergent selection

145   can contribute to increase the power of such approaches, and can even be used in the absence

146   of neutral genetic structure [50]. Genetic **isolation by distance** at the population or individual

147   level [51] provides dispersal estimates that are consistent with demographic dispersal

148   estimates obtained from parentage analysis (Box 1) [52]. When a reference genome and

149   **haplotype** data are available, the consideration of **admixture tracts** [53] and **blocks of**

150   **identity by descent** [54] constitutes another promising avenue to detect recent dispersal

151   events, that can also apply in isolation by distance contexts [55].

152

153   Our literature review also reveals that genetic connectivity, based on Wright's Fixation Index

154   (F_{ST}), tends to provide higher estimates than any other method (Figure 1A: median = 910 km,

155   interquartile range = 315 - 2346 km, number of species = 126). Yet, genetic connectivity

156   differs from demographic connectivity as it integrates the effects, not just off migration, but

157   also genetic drift, mutation and selection. Translating genetic connectivity into demographic

158   estimates of dispersal is not straightforward [56]. This notably implies estimating effective

159   population sizes [57] or assuming specific population genetic models that are often unrealistic

160   in real-world situations [58]. Furthermore, **gene flow** over large geographic distances might

161   result from **stepping-stone dispersal** over multiple generations without necessarily implying

162   direct long-distance dispersal events [59].

163

164   Globally, the data show a universal positive correlation between the geographic sampling

165   scale of the study and the maximum dispersal or connectivity averaged across all studies and

166   organisms ($R = 0.7$, $p < 0.001$; Figure 1B). The relation holds true when analyzing the data per

167   type of dispersal estimate (potential vs. demographic vs. genetic). In 45 % of the studies, the

168   dispersal distance was equal to the maximum geographic extent of the sampling. This reached

169   48 % when data were restricted to coastal fishes, 41 % for invertebrates and 41 % for deep sea

170   organisms (Figure 1C). These results suggest that estimates are limited by the spatial scale of

171   the sampling, resulting in a global underestimation of the extent of demographic and genetic

172   connectivity.

173

174   For genetic connectivity, an absence of population structure can also result from a lack of

175   statistical power to detect subtle population genetic structure when a small number of genetic

176   markers are used. With the advent of **next-generation sequencing** technologies, this

177   limitation can now be overcome by typing hundreds to millions of **single nucleotide**

178   **polymorphism markers** [60, 61].

179

180   A variety of mechanisms can contribute to long-distance dispersal in marine ecosystems

181   (Figure 2). Foremost, the hydrodynamic forces at play in the marine environment are

182   expected to have a strong influence on the dispersal of **pelagic larvae** [62]. In addition, the

183   conditions encountered in the pelagic environment might influence growth, survival and

184   pelagic larval duration, all of which can in turn induce extreme values in spatial and temporal

185   connectivity patterns. Active larval behavior can also play an important role for the benthos

186   [63, 64]. Extreme events, such as tsunamis [65], and oceanographic eddies and fronts [66] are

187   also important, but overlooked potential dispersal vectors over long distances. They can favor

188   the survival and establishment of individuals beyond their usual dispersal range. Furthermore,

189   marine debris of natural or anthropogenic origin can constitute effective oceanic rafts for

190   dispersal [67, 68]. These debris provide refuges for larvae and adults of **sessile species**,

191   allowing the movement and potential establishment of a variety of species over large

192   distances. For instance, mussels from Japan arrived on the west coast of the US after nearly

193   six years at sea on debris produced by the 2011 East Japan earthquake [65]. Ice blocks also

194   allow invertebrates to disperse across distances of about 20 km per day [69]. Anthropogenic

195   vectors such as international vessel traffic, restocking from aquaculture [70], and species

196   translocation (Box 2) also have the potential to modify the natural spatial and temporal

197   patterns of marine connectivity [71]. Overall, the occurrence of long-distance dispersal

198   events, even if rare, suggest that marine reserves can have an effect far beyond their

199   boundaries, which calls for a re-evaluation of the spatial extent of their potential benefits.

200

201   **Long-distance benefits of marine reserves**

202   We consider a long-distance benefit of marine reserve any change in biomass, biological

203   processes (e.g. recruitment) or biodiversity (including genetic diversity as raw material for

204   adaptation) at distance greater than 40 km from reserve boundaries that contributes to

205 improve ecosystem function or human livelihoods (e.g. fisheries, tourism, culture) (Figure 2).

206 Long-distance benefits from reserves can occur at different spatial and temporal scales

207 depending on the vector of dispersal (Box 1, Figure 2), and this includes both direct and

208 stepping-stone dispersal processes.

209

210 Parentage analyses have demonstrated dispersal from marine reserves at more than 40 km [32,

211 46]. For example, Almany *et al.* [46] revealed connectivity patterns with direct exchanges of

212 larvae over up to 150 km among reefs with varying levels of protection. **Larval dispersal**

213 from reserves towards exploited areas located at more than 100 km has also been suggested

214 by biophysical models [37, 72]. Yet, empirical studies showing an effect of marine reserves

215 on fished areas are largely restricted to spatial scales smaller than 40 km (e.g. [26, 73, 74]).

216 Scaling-up these studies is challenging for a variety of logistic reasons, including the

217 difficulty to sample and monitor individuals over large spatial scales.

218

219 Even if long-distance dispersal events from marine reserves are rare, a few successful

220 migrants can be sufficient to re-colonize areas where local populations have been extirpated

221 or to expand species distributions in response to global change [75]. Long-distance dispersal

222 between populations that are genetically differentiated or locally adapted can moreover

223 contribute to limit inbreeding, increase genetic diversity and facilitate adaptation to a

224 changing environment [25, 76]. However, in case of local adaptation, long-distance dispersal

225 can also reduce fitness of recipient populations through immigration of locally maladapted

226 alleles [77].

227

228 Active translocations from marine reserves can also contribute to restore locally depleted or

229 extinct populations [78]. For example, the Bumphead Parrotfish (*Bolbometopon muricatum*)

230 is highly targeted by spear fishers due to its large size and therefore population densities tend

231 to be low in areas close to human populations [79]. This species is only abundant in reserves

232 and on the most protected reefs such as in Palau where it aggregates to spawn. These

233 populations have been used as a source of eggs and larvae for active translocations (Box 2).

234 Nearly 500 translocation projects of 242 marine species have been recorded [78]. However,

235 still few projects take advantage of large stocks in marine reserves. It should also be

236 emphasized that translocations entail a number of risks (e.g. disease, invasion, gene pool

237 mixing). Overall, marine reserves could support a wide variety of long-distance benefits that

238 are potentially underestimated and that should be considered for the design of reserve

239 networks.

240

241 **Implications of long-distance dispersal for marine reserve design**

242 An underestimate of dispersal ability can profoundly influence the design of marine reserve

243 networks. Long-distance dispersal can potentially connect distant and isolated reserves, and

244 sustain biodiversity and biomass in exploited areas located at more than 40 km from their

245 boundaries. In this respect, long-distance dispersal provides a fresh perspective on two long-

246 lasting and active debates in the marine reserve literature.

247

248 First, long-distance dispersal has implications for the unresolved single-large-or-several-

249 small (SLOSS) marine reserve debate. Simulations suggest that a network of well-connected

250 reserves on a scale of 10-100 km can meet both conservation and fisheries goals [7, 80].

251 However, the idea that a network constituted of many small reserves spaced within species

252 maximum dispersal distance [4] maximizes reserve benefits to fisheries has been recently

253 revisited and challenged. Based on a spatially explicit model of population dynamics, De Leo

254 & Micheli [81] show that for larval dispersal >10 km, one or two large reserves are more

255 efficient in terms of fisheries gains than 10 or 20 small reserves covering the same area. This

256 is notably due to the fact that large (>100 km^2), old (>10 years, [5]) and well-managed

257 reserves tend to increase fish density and biomass [5, 82], and that large females over-

258 contribute to reproduction since the relation between female body mass and reproductive

259 output is hyperallometric for the vast majority of fishes (i.e. a 2-kg female has a higher

260 reproductive output in terms of egg number, volume and energy, than two 1-kg females [83]).

261 We can therefore expect large, old and well-managed reserves to disproportionately

262 contribute to larval seedling within a network when dispersal distances are greater than ten

263 kilometers. Using a rigorously calibrated metapopulation model with empirical data from the

264 Great Barrier Reef, Hopf et al. [84] also show that reserves are unable to compensate for the

265 increased mortality outside reserve boundaries when they are small or at the periphery of the

266 metapopulation [84]. In contrast, the establishment of a single large reserve, that is able to

267 seed overexploited areas through dispersal, is expected to result in higher population growth

268 within reserve boundaries and shorter recovery times after overexploitation outside the

269 reserve. Finally, a global analysis indicates that when larval dispersal distances are long (>40

270 km), the magnitude of biomass increase within large reserves is expected to be sufficient to

271 compensate for the redistributed fishing pressure associated with reserve establishment [85].

272

273 The median nearest-neighbor distance between marine reserves is estimated at 12 km globally

274 (interquartile distance: 4 to 40 km) (Supplementary text S2). This geographical pattern is

275 highly variable, with some reserves being very isolated (e.g. the Parque Natural Obô do

276 Príncipe in São Tomé and Príncipe at 4130 km from the nearest reserve, the Monumento

277 Natural do Arquipelago de Sao Pedro e Sao Paulo at 940 km off the coast of Brazil) (Figure

278 3A, supplementary text S2). Fortunately, 76 % of reserves are found closer to the nearest

279 reserve than the median demographic dispersal distance estimated in our literature review (42

280   km) (Figure 3B). It implies that three-quarters of marine reserves are potentially

281   demographically embedded in a connected network providing spatial insurance. The median

282   nearest-neighbor distance in the 24 % remaining reserves is estimated to be 129 km, with a

283   very skewed distribution (Figure 3B). Notably, 83% of large reserves (> 1000 km^2) are

284   isolated (>42km) (Figure 3C). The mean nearest neighbor of this subset of large marine

285   reserves is 359 km away, decreasing their potential contribution to the global network.

286   Therefore, the largest marine reserves, allowing large spillover of individuals and providing

287   benefits for both biodiversity and human population, are the least connected. However, we did

288   not consider how sea surface currents could modify our assessment of connectivity among

289   isolated reserves.

290

291   Second, long-distance dispersal has also implications for prioritizing the conservation of

292   human-impacted versus non-impacted areas. Intuitively, one can see little benefit in placing

293   reserves in isolated areas which are difficult to access and therefore *de facto* protected [86].

294   On the other hand, reserves close to dense human populations can mitigate but not eliminate

295   the high anthropogenic pressure outside but also inside their boundaries [87]. It has therefore

296   been suggested that reserves located at an intermediate level of human pressure might offer

297   the maximum benefits in terms of fish biomass within their boundaries [87]. For top predators

298   like sharks, only isolated marine reserves with low human pressure can be effective [87]. The

299   realization of long-distance dispersal would also make a case for the protection of such areas

300   isolated from human pressure. More generally, it would suggest to reconsider the design of

301   marine reserve networks with fewer but larger reserves, including isolated ones, to sustain

302   large populations of large individuals, even of top predators, that can massively seed larvae

303   towards fishing grounds. Tools that integrate species dispersal in conservation planning are

304   now available to reach both conservation and fisheries management objectives in a

305   multispecies framework [88]. The consideration of long-distance dispersal would certainly

306   modify the outputs of conservation plans.

307

308   **Concluding remarks**

309   Marine dispersal has been extensively documented at short distance (mostly <40 km). We

310   suggest that this has been due, at least in part, to logistic constraints and a restricted

311   geographic extend of the sampling design (e.g. the median sampling distance in parentage

312   analyses is only 33 km, interquartile range = 29 – 60 km, number of species = 22). While a

313   significant fraction of dispersal indeed occurs at small spatial scales, the fraction of the

314   **dispersal kernel** that we are missing is largely unknown (see Outstanding Questions). A few

315   recent empirical studies have demonstrated dispersal of fish at larger spatial scales (up to 400

316   km), but even these estimates were limited by the maximum sampling distance [40]. Dispersal

317   estimates from biophysical modelling studies at larger spatial scales suggest even longer

318   dispersal distances (median sampling distances = 600 km, interquartile range: 237-1400,

319   Figure 1A). Such long-distance connectivity patterns remain challenging to validate

320   empirically, but have potentially important consequences in terms of reserve design and

321   benefits. The more isolated reserves are, the more critical long-distance dispersal becomes to

322   maintain source-sink dynamics between protected and exploited populations. Thus, long-

323   distance benefits imply a more regional and network-based perspective, which entails specific

324   challenges. Long-distance dispersal will often cross countries as well in-shore-offshore

325   boundaries. The designation of marines reserves is largely carried out by individual countries

326   and they rarely able coordinate efforts with other countries and high-seas authorities [89].

327   Furthermore, the focus on marine reserves is strongly constrained by the perspective of local

328   stakeholders [15], which is perfectly justified but should nonetheless not obliterate a broader

329   perspective.

330   We suggest scaling-up dispersal studies at regional instead of local scale. We can now

331   genotype a large number of genetic markers, which provides the opportunity to apply

332   population-level assignment tests at large spatial scales and in a context of low spatial

333   structure [90]. Such studies can be guided by high-resolution biophysical models to target the

334   specific populations among which long-distance distance dispersal occurs. A large number of

335   single nucleotide polymorphism markers will also provide the statistical power to detect very

336   subtle population structure, which will allow refining genetic connectivity estimates [90, 91].

337   Finally, approaches based on admixture tracts [53] and blocks of identity by descent [54] are

338   largely untapped. The combination of genetic, chemical and biophysical approaches within an

339   integrative statistical framework also appears to be a promising approach to estimate long-

340   distance dispersal [92] and guide the design of new reserve networks to keep pace with ever

341   increasing threats on marine ecosystems.

342

350

351   **References**

352 1. McCauley, D.J. et al. (2015) Marine defaunation: Animal loss in the global ocean. *Science*

353 DOI: 10.1126/science.1255641.

354 2. Worm, B. (2016) Averting a global fisheries disaster. *Proc. Natl. Acad. Sci. U.S.A.*
355   113, 4895-4897.

356 3. Kroodsma, D.A. et al. (2018) Tracking the global footprint of fisheries. *Science* 359, 904-

357 907.

358 4. Gaines, S.D. et al. (2010) Designing marine reserve networks for both conservation and

359 fisheries management. *Proc. Natl. Acad. Sci. U.S.A.* 107, 18286-18293.

360 5. Edgar, G.J. et al. (2014) Global conservation outcomes depend on marine protected areas

361 with five key features. *Nature* 506, 216-220.

362 6. Krueck, N.C. et al. (2017) Marine reserve targets to sustain and rebuild unregulated

363 Fisheries. *Plos Biol.* 15, 1-20.

364 7. Lubchenco, J. and Grorud-Colvert, K. (2015) Making waves: The science and politics of

365 ocean protection. *Science* 350, 382-383.

366 8. Costello, M.J. and Ballantine, B. (2015) Biodiversity conservation should focus on no-take

367 Marine Reserves. *Trends Ecol. Evol.* 30, 507-509.

368 9. Sala, E. et al. (2018) Assessing real progress towards effective ocean protection. *Mar.*

369 *Policy* 91, 11-13.

370 10. O'Leary, B.C. et al. (2018) Addressing criticisms of large-scale Marine Protected Areas.

371 *BioSci.* 68, 359-370.

372 11. Watson, R.A. et al. (2015) Marine foods sourced from farther as their use of global ocean

373 primary production increases. *Nat. Commun.* 6, DOI: 10.1038/ncomms8365.

374 12. Halpern, B.S. et al. (2015) Spatial and temporal changes in cumulative human impacts on

375 the world's ocean. *Nat. Commun.* 6, DOI: 10.1038/ncomms861.

376 13. Tittensor, D.P. et al. (2014) A mid-term analysis of progress toward international

377 biodiversity targets. *Science* 346, 241-244.

378   14. Di Marco, M. et al. (2016) Global biodiversity targets require both sufficiency and

379   efficiency. *Conserv. Lett.* 9, 395-397.

380   15. O'Leary, B.C. et al. (2016) Effective coverage targets for ocean protection. *Conserv. Lett.*

381   9, 398-404.

382   16. Gell, F.R. and Roberts, C.M. (2003) Benefits beyond boundaries: the fishery effects of

383   marine reserves. *Trends Ecol. Evol.* 18, 448-455.

384   17. Lester, S.E. et al. (2009) Biological effects within no-take marine reserves: a global

385   synthesis. *Mar. Ecol. Prog. Ser.* 384, 33-46.

386   18. Stobart, B. et al. (2009) Long-term and spillover effects of a marine protected area on an

387   exploited fish community. *Mar. Ecol. Prog. Ser.* 384, 47-60.

388   19. Sciberras, M. et al. (2015) Evaluating the relative conservation value of fully and partially

389   protected marine areas. *Fish Fish.* 16, 58-77.

390   20. Diaz, D. et al. (2016) A 25-year marine reserve as proxy for the unfished condition of an

391   exploited species. *Biol. Conserv.* 203, 97-107.

392   21. MacNeil, M.A. et al. (2015) Recovery potential of the world's coral reef fishes. *Nature*

393   520, 341-344.

394   22. Perez-Ruzafa, A. et al. (2006) Effects of fishing protection on the genetic structure of fish

395   populations. *Biol. Conserv.* 129, 244-255.

396   23. Coulthard, S. et al. (2017) Exploring 'islandness' and the impacts of nature conservation

397   through the lens of wellbeing. *Environ. Conserv.* 44, 298-309.

398   24. Gurney, G.G. et al. (2014) Poverty and protected areas: An evaluation of a marine

399   integrated conservation and development project in Indonesia. *Glob. Environ. Change* 26,

400   98-107.

401   25. Roberts, C.M. et al. (2017) Marine reserves can mitigate and promote adaptation to

402   climate change. *Proc. Natl. Acad. Sci. U.S.A.* 114, 6167-6175.

403   26. Kerwath, S.E. et al. (2013) Marine protected area improves yield without disadvantaging

404   fishers. *Nat. Commun.* 4, DOI: 10.1126/science.

405   27. Di Franco, A. et al. (2016) Five key attributes can increase marine protected areas

406   performance for small-scale fisheries management. *Sci. Rep.* 6, DOI: 10.1038/srep38135.

407   28. Abesamis, R.A. and Russ, G.R. (2005) Density-dependent spillover from a marine

408   reserve: Long-term evidence. *Ecol. Appl.* 15, 1798-1812.

409   29. Goni, R. et al. (2010) Net contribution of spillover from a marine reserve to fishery

410   catches. *Mar. Ecol. Prog. Ser.* 400, 233-243.

411   30. Russ, G.R. and Alcala, A.C. (2011) Enhanced biodiversity beyond marine reserve

412   boundaries: The cup spillith over. *Ecol. Appl.* 21, 241-250.

413   31. Goni, R. et al. (2006) Spillover of spiny lobsters Palinurus elephas from a marine reserve

414   to an adjoining fishery. *Mar. Ecol. Prog. Ser.* 308, 207-219.

415   32. Williamson, D.H. et al. (2016) Large-scale, multidirectional larval connectivity among

416   coral reef fish populations in the Great Barrier Reef Marine Park. *Mol. Ecol.* 25, 6039-6054.

417   33. Roberts, C.M. (1997) Connectivity and management of Caribbean coral reefs. *Science*

418   278, 1454-1457.

419   34. Mora, C. and Sale, P.F. (2002) Are populations of coral reef fish open or closed? *Trends*

420   *Ecol. Evol.* 17, 422-428.

421   35. Jones, G.P. et al. (1999) Self-recruitment in a coral reef fish population. *Nature* 402, 802-

422   804.

423   36. Swearer, S.E. et al. (1999) Larval retention and recruitment in an island population of a

424   coral-reef fish. *Nature* 402, 799-802.

425   37. Andrello, M. et al. (2017) Global mismatch between fishing dependency and larval supply

426   from marine reserves. *Nat. Commun.* 8, DOI: 10.1038/ncomms16039.

427   38. Christie, M.R. (2010) Parentage in natural populations: novel methods to detect parent-

428   offspring pairs in large data sets. Molecular Ecolog *Mol. Ecol. Resour.* 10, 115-128.

429   39. Costello, M.J. et al. (2017) Marine biogeographic realms and species endemicity. *Nat.*

430   *Commun.* 8, https://doi.org/10.1038/s41467-017-01121-2.

431   40. Simpson, S.D. et al. (2014) Long-distance dispersal via ocean currents connects omani

432   clownfish populations throughout entire species range. *PLoS ONE* 9, DOI:

433   10.1371/journal.pone.0107610.

434   41. Christie, M.R. et al. (2010) Larval connectivity in an effective network of Marine

435   Protected Areas. *PLoS ONE* 5, DOI: 10.1371/journal.pone.0015715.

436   42. Espinoza, M. et al. (2015) Contrasting movements and connectivity of reef-associated

437   sharks using acoustic telemetry: implications for management. *Ecol. Appl.* 25, 2101-2118.

438   43. Daly, R. et al. (2018) Refuges and risks: Evaluating the benefits of an expanded Marine

439   Protecte Area network for mobile apex predators. *Divers. Distrib.* 24, 1217-1230.

440   44. Cowen, R.K. et al. (2006) Scaling of connectivity in marine populations. *Science* 311,

441   522-527.

442   45. Costello, M.J. (2009) How sea lice from salmon farms may cause wild salmonid declines

443   in Europe and North America and be a threat to fishes elsewhere. *Proc. Royal. Soc. Lond. B*

444   *Biol. Sci.* 276, 3385-3394.

445   46. Almany, G.R. et al. (2017) Larval fish dispersal in a coral-reef seascape. *Nat. Ecol. Evol.*

446   1, DOI: 10.1038/s41559-017-0148.

447   47. Hameed, S.O. et al. (2016) Inverse approach to estimating larval dispersal reveals limited

448   population connectivity along 700 km of wave-swept open coast. *Proc. Royal. Soc. Lond. B*

449   *Biol. Sci.* 283, doi: 10.1098/rspb.2016.0370.

450   48. Paetkau, D. et al. (1995) Microsatellite analysis of population-structure in Canadian polar

451   bears. *Mol. Ecol.* 4, 347-354.

452   49. Manel, S. et al. (2005) Assignment methods: matching biological questions with

453   appropriate techniques. *Trends Ecol. Evol.* 20, 136-142.

454   50. Gagnaire, P.-A. et al. (2015) Using neutral, selected, and hitchhiker loci to assess

455   connectivity of marine populations in the genomic era. *Evol. Appl.* 8, 769-786.

456   51. Puebla, O. et al. (2012) On the spatial scale of dispersal in coral reef fishes. *Mol. Ecol.*

457   21, 5675-5688.

458   52. Pinsky, M. et al. (2017) Marine dispersal scales are congruent over evolutionary and

459   ecological time. *Curr. Biol.* 27, 1-6.

460   53. Liang, M. and Nielsen, R. (2014) The lengths of admixture tracts. *Genet.* 197,

461   https://doi.org/10.1534/genetics.114.162362.

462   54. Browning, S.R. and Browning, B.L. (2012) Identity by descent between distant relatives:

463   detection and applications. *Annu. Rev. Genet.* 46, 617-633.

464   55. Ringbauer, H. et al. (2017) Inferring recent demography from isolation by distance of long

465   shared sequence blocks. *Genet.* 205, https://doi.org/10.1534/genetics.116.196220.

466   56. Lowe, W.H. and Allendorf, F.W. (2010) What can genetics tell us about population

467   connectivity? *Mol. Ecol.* 19, 3038-3051.

468   57. Beerli, P. and Felsenstein, J. (2001) Maximum likelihood estimation of a migration matrix

469   and effective population sizes in n subpopulations by using a coalescent approach. *Proc. Natl.*

470   *Acad. Sci. U.S.A.* 98, 4563-4568.

471   58. Whitlock, M.C. and McCauley, D.E. (1999) Indirect measures of gene flow and

472   migration: F_{ST} not equal 1/(4Nm+1). *Heredity* 82, 117-125.

473   59. Saura, S. et al. (2014) Stepping stones are crucial for species' long-distance dispersal and

474   range expansion through habitat networks. *J. Appl. Ecol.* 51, 171-182.

475   60. Fischer, M.C. et al. (2017) Estimating genomic diversity and population differentiation –

476   an empirical comparison of microsatellite and SNP variation in *Arabidopsis halleri*. *BMC*

477   *Genomics* 18, https://doi.org/10.1186/s12864-016-3459-7.

478   61. Hodel, R.G.J. et al. (2017) Adding loci improves phylogeographic resolution in red

479   mangroves despite increased missing data: comparing microsatellites and RAD-Seq and

480   investigating loci filtering. *Sci. Rep.* 7, https://doi.org/10.1038/s41598-017-16810-7.

481   62. Gillespie, R.G. et al. (2012) Long-distance dispersal: a framework for hypothesis testing.

482   *Trends Ecol. Evol.* 27, 47-56.

483   63. Faillettaz, R. et al. (2018) Larval fish swimming behavior alters dispersal patterns from

484   Marine Protected Areas in the North-Western Mediterranean Sea. *Front. Mar. Sci.* 5,

485   https://doi.org/10.3389/fmars.2018.00097.

486   64. Nanninga, G.B. and Manica, A. (2018) Larval swimming capacities affect genetic

487   differentiation and range size in demersal marine fishes. *Mar. Ecol. Prog. Ser.* 589, 1-12.

488   65. Carlton, J.T. et al. (2017) Tsunami-driven rafting: Transoceanic species dispersal and

489   implications for marine biogeography. *Science* 357, 1402.

490   66. Shulzitski, K. et al. (2016) Encounter with mesoscale eddies enhances survival to

491   settlement in larval coral reef fishes. *Proc. Natl. Acad. Sci. U.S.A.* 113, 6928-6933.

492   67. Mora, C. et al. (2001) Dispersal of juvenile and adult reef fishes associated with floating

493   objects and their recruitment into Gorgona Island Reefs, Colombia. *Bull. Mar. Sci.* 68, 557-

494   561.

495   68. Castro, J.J. et al. (2001) A general theory on fish aggregation to floating objects: An

496   alternative to the meeting point hypothesis. *Rev. Fish Biol. Fish.* 11, 255-277.

497   69. Macfarlane, C.B.A. et al. (2013) Dispersal of marine benthic invertebrates through ice

498   rafting. *Ecol.* 94, 250-256.

499   70. Waters, C.G. et al. (2013) A methodology for recruiting a giant clam, *Tridacna maxima*,

500   directly to natural substrata: A first step in reversing functional extinctions? *Biol.Cons.* 160,

501   19-24.

502   71. Clarke Murray, C. et al. (2011) Recreational boating: a large unregulated vector

503   transporting marine invasive species. *Divers. Distrib.* 17, 1161-1172.

504   72. Andrello, M. et al. (2013) Low Connectivity between Mediterranean Marine Protected

505   Areas: A biophysical modeling approach for the Dusky Grouper *Epinephelus marginatus*.

506   *PLoS ONE* 8, DOI: 10.1371/journal.pone.0068564.

507   73. Harrison, H.B. et al. (2012) Larval export from marine reserves and the recruitment

508   benefit for fish and fisheries. *Curr. Biol.* 22, 1023-1028.

509   74. Le Port, A. et al. (2017) Temperate marine protected area provides recruitment subsidies

510   to local fisheries. *Proc. Royal. Soc. Lond. B Biol. Sci.* 284, DOI: 10.1098/rspb.2017.1300.

511   75. Stuart-Smith, R.D. et al. (2015) Thermal biases and vulnerability to warming in the

512   world's marine fauna. *Nature* 528, 88-92.

513   76. Kremer, A. et al. (2012) Long-distance gene flow and adaptation of forest trees to rapid

514   climate change. *Ecol. Lett.* 15, 378-392.

515   77. Bolnick, D.I. and Nosil, P. (2007) Natural selectin in populations subject to a migration

516   load. *Evol.* 61, 2229-2243.

517   78. Swan, K.D. et al. (2016) Managing marine biodiversity: The rising diversity and

518   prevalence of marine conservation translocations. *Conserv. Lett.* 9, 239-251.

519   79. Bellwood, D.R. et al. (2012) Human activity selectively impacts the ecosystem roles of

520   parrotfishes on coral reefs. *Proc. Natl. Acad. Sci. U.S.A* 279, DOI: 10.1098/rspb.2011.1906.

521   80. Pelc, R.A. et al. (2010) Detecting larval export from marine reserves. *Proc. Natl. Acad.*

522   *Sci. U.S.A.* 107, 18266-18271.

523   81. De Leo, G.A. and Micheli, F. (2015) The good, the bad and the ugly of marine reserves

524   for fishery yields. *Philos. Trans. R. Soc. B Biol. Sci.* 370, DOI: 10.1098/rstb.2014.0276.

525   82. Claudet, J. et al. (2008) Marine reserves: size and age do matter. *Ecol. Lett.* 11, 481-489.

526   83. Barneche, D.R. et al. (2018) Fish reproductive-energy output increases disproportionately

527   with body size. *Science* 360, 642-644.

528   84. Hopf, J.K. et al. (2016) Fishery consequences of marine reserves: short-term pain for

529   longer-term gain. *Ecol. Appl.* 26, 818-829.

530   85. Halpern, B.S. et al. (2010) Placing marine protected areas onto the ecosystem-based

531   management seascape. *Proc. Natl. Acad. Sci. U.S.A.* 107, 18312-18317.

532   86. Devillers, R. et al. (2014) Reinventing residual reserves in the sea: are we favouring ease

533   of establishment over need for protection? *Aquat. Conserv.: Mar. Freshwat. Ecosyst.* 25,

534   480-504.

535   87. Cinner, J.E. et al. (2018) Gravity of human impacts mediates coral reef conservation

536   gains. *Proc. Natl. Acad. Sci. U.S.A.* 115, DOI: 10.1073/pnas.1708001115.

537   88. Magris, R.A. et al. Biologically representative and well-connected marine reserves

538   enhance biodiversity persistence in conservation planning. *Cons.   Lett.*   11

539   https://doi.org/10.1111/conl.12439.

540   89. Treml, E.A. et al. (2015) Analyzing the (mis)fit between the institutional and ecological

541   networks of the Indo-West Pacific. *Glob. Environ. Change* 31, 263-271.

542   90. Benestan, L. et al. (2015) RAD genotyping reveals fine-scale genetic structuring and

543   provides powerful population assignment in a widely distributed marine species, the

544   American lobster (*Homarus americanus*). *Mol. Ecol.* 24, 3299-3315.

545   91. Nielsen, E.E. et al. (2012) Gene-associated markers provide tools for tackling illegal

546   fishing and false eco-certification. *Nat. Commun.* 3, DOI: 10.1038/ncomms1845.

547   92. Gaggiotti, O.E. (2017) Metapopulations of marine species with larval dispersal: A

548   counterpoint to Ilkka's Glanville fritillary metapopulations. *Ann. Zool. Fennici* 54, 97-112.

549   93. Bryan-Brown, D.N. et al. (2017) Patterns and trends in marine population connectivity

550   research. *Mar. Ecol. Prog. Ser.* 585, 243-256.

551   94. Kool, J.T. et al. (2013) Population connectivity: recent advances and new perspectives.

552   *Lands. Ecol.* 28, 165-185.

553   95. Calò, A. et al. (2013) A review of methods to assess connectivity and dispersal between

554   fish populations in the Mediterranean Sea. *Adv. Oceano. Limn.* 4, 150-175.

555   96. Gallego, A. et al. (2017) Bio-physical connectivity patterns of benthic marine species used

556   in the designation of Scottish nature conservation marine protected areas. *Ices J. Mar. Sci.* 74,

557   1797-1811.

558   97. Treml, E.A. et al. (2008) Modeling population connectivity by ocean currents, a graph-

559   theoretic approach for marine conservation. *Lands. Ecol.* 23, 19-36.

560   98. Treml, E.A. et al. (2015) Identifying the key biophysical drivers, connectivity outcomes,

561   and metapopulation consequences of larval dispersal in the sea. *Mov. Ecol.* 3, DOI:

562   10.1186/s40462-015-0045-6.

563   99. Planes, S. et al. (2009) Larval dispersal connects fish populations in a network of marine

564   protected areas. *Proc. Natl. Acad. Sci. U.S.A.* 106, 5693-5697.

565   100. Saenz-Agudelo, P. et al. (2011) Connectivity dominates larval replenishment in a coastal

566   reef fish metapopulation. *Proc. Royal. Soc. Lond. B Biol. Sci.* 278, 2954-2961.

567   101. Gandra, M. et al. (2018) Diel and seasonal changes in the spatial behaviour of a soft-

568   sediment fish (*Solea senegalensis*) inside a marine reserve. *Mar. Environ. Res.* 135, 82-92.

569   102. Starrs, D. et al. (2016) All in the ears: unlocking the early life history biology and spatial

570   ecology of fishes. *Biol. Rev.* 91, 86-105.

571   103. Calò, A. et al. (2013) A review of methods to assess connectivity and dispersal between

572   fish populations in the Mediterranean Sea. *Adv. Oceano. Limn*. 4, 150 - 175.

573   104. Jones, G. (2015) Mission impossible: Unlocking the secrets of coral reef fish dispersal.

574   In *Ecology of Fishes on Coral Reefs*. (Mora, C) Cambridge University Press, pp. 16-27.

575   Cambridge, UK,.

576   105. Rousset, F. (2000) Genetic differentiation between individuals. *J. Evol. Biol*. 13, 58-62.

577   106. Leblois, R. et al. (2004) Influence of spatial and temporal heterogeneities on the

578   estimation of demographic parameters in a continuous population using individual

579   microsatellite data. *Genet.* 166, 1081-1092.

580   107. Gutenkunst, R.N. et al. (2009) Inferring the joint demographic history of multiple

581   populations   from   multidimensional   SNP   frequency   data.   *PLoS   Genet*.   5,

582   https://doi.org/10.1371/journal.pgen.1000695.

583

584   **Figure Legends**
585
586   **Figure 1: The spatial scale of sampling constraints dispersal estimates**

587   (A) Boxplot representing the maximum dispersal distance and the sampling geographic extent

588   across all studies. Central lines represent median values and whiskers first and third quartiles.

589   (B) Mean maximum dispersal distance increases with the maximal sampling geographic

590   extent and (C) the pattern remains consistent among groups: fish, invertebrates and deep-sea

591   organisms (>200 m).   In (B) and (C), the color gradient displays the difference between

592   maximal dispersal estimate and sampling geographic extent, with warmer colors (red)

593   indicating that the maximum dispersal distance is closer to the maximal sampling geographic

594   extent. The methods used to estimate connectivity include tracking, parentage analysis,

595   assignment tests and isolation by distance (= demographic dispersal) described in Box 1 (see

596   B and C), biophysical models (potential dispersal), and genetic connectivity estimated from

597   Fixation Index (F_{ST}). See supplementary method S1 and supplementary file S1 for details on

598   the data used to generate the figure.

599

600   **Figure 2**: **Potential long-distance dispersal processes and marine reserve benefits from**

601   The main processes that contribute to long-dispersal distance are indicated with numbers and

602   the main benefits due to long-dispersal distance are indicated with letters. The marine reserve

603   is represented by a circle. (1) Active dispersal can drive larvae or adults far from the reserve

604   boundaries, independently of the sea currents. (2) Larvae are pelagic and disperse passively

605   due to currents. (3) They can associate with floating and drifting debris. (4) Translocation

606   involves deliberately moving organisms from one site ("productive" reserves) to another (e.g.

607   overexploited population). Thus, long distance dispersal can (A) increase biomass in fished

608   areas far from the reserve, (B) potentially maintain species and genetic diversity across

609   reserves, (C) maintain commercially and culturally important species that were the target of

610   protection in the reserve.

611

612   **Figure 3: Connectivity patterns in the global network of marine reserves.**

613   (A) Map showing the neighbor distance for each marine reserve, i.e. the distance to the

614   nearest marine reserves. To improve the visibility of the figure, we used both size and color of

615   the circles to indicate the nearest-neighbor distance of each marine reserve. Small yellow

616   circles indicate the most connected marine reserves (e.g. Scandinavian region or Australia)

617   while large blue circles indicate the most isolated reserves (e.g. Western African coast). (B)

618   Distribution of nearest-neighbor distances between marine reserves. The median and mean

619   nearest-neighbor distances are 12 km and 65 km, respectively. The dashed red line indicates

620   the demographic median dispersal distance estimated for all organisms from the meta-analysis

621   (42 km). (C) The nearest-neighbor distance increases with the no-take surface area of marine

622   reserves (from 752 no-take marine reserves).

623　**Box**

624　**Box 1: Methods for estimating long-distance dispersal in marine ecosystems**

625　Methods to estimate marine dispersal [93-95] can be partitioned into three categories:

626　**A. Potential dispersal** (inferred from biophysical models)

627　Biophysical models can be used to simulate larval dispersal trajectories over large spatial and

628　temporal scales (Table I) [96]. These models usually incorporate three elements: a physical

629　model that simulates the ocean hydrodynamics, a particle tracking model that simulates the

630　passive movement of virtual larvae, and optionally a coupled model that simulates the activity

631　of the larvae when information on their ecology, behavior and physiology is available [97].

632　This third element is often lacking and it is therefore important to better understand the

633　biology of marine larvae. Biophysical models are becoming increasingly complex and

634　realistic, yet they always need to be validated with empirical data [98].

635

636　**B. Realized dispersal** (dispersal took place, but dispersers can or cannot successfully

637　　　reproduce)

638　Specific dispersal events can be inferred using genetics. Parentage analyses identify dispersal

639　events by using individual genotypes to assign juveniles to their parents [99]. This approach

640　provides a snapshot of dispersal events over one generation. It requires considerable effort to

641　sample and genotype a large number of juveniles and potential parents. Similarly, population

642　genetic assignment tests use individual genotypes to assign individuals to their population of

643　origin [48]. This approach relies on the occurrence of genetic structure among populations

644　[100], but can also be applied in the absence of population genetic structure if populations are

645　locally adapted [50]. Various tracking methods can also identify dispersal events. Acoustic

646　telemetry can be used to observe the movement of individuals, often adults, providing the

647　opportunity to directly observe dispersal [101]. Electronic and physical tags can provide

648 information on the movement of individuals. Some, however, have the drawback that

649 individuals need to be recaptured to retrieve the data. Otolith analyses can also provide

650 evidence of dispersal when the microchemistry or stable isotope composition of populations

651 differ [102, 103]. When these approaches are applied to many individuals, it is possible to

652 derive empirical distributions of dispersal kernel [104]. Yet the fact that individuals disperse

653 does not necessary imply that they will successfully reproduce.

654

655 **C. Effective dispersal** (dispersal took place and dispersers successfully reproduced)
656
657 In the presence of **genetic isolation by distance** [105], it is possible to estimate dispersal at

658 ecological timescales (tens of generations, [106]). This approach can be applied at the

659 individual or population level. Another interesting avenue to infer dispersal is **cline analysis**

660 [50]. Additional approaches based on **coalescent theory** [57] or the **site frequency spectrum**

661 [107] go deeper back in time (tens to thousands of generations) and are therefore less relevant

662 at ecological timescales.

663

664 **Table I**: Spatial extent and temporal resolution of the various methods used to estimate

665 individual dispersal and connectivity in marine organisms.

		Spatial extent			Temporal resolution	
Dispersal category	**Method**	Low (1-40 km)	Medium (40-100 km)	Large (=>100 km)	Within generation	trans-generational
Potential	Biophysical		x	x	x	
Realized	Parentage	x	x	x		x
	Assignment	x	x	x	x	x
	Tracking	x	x	x	x	
	Otolith	x	x	x	x	x
Effective	Isolation by distance	x	x			x
	Cline analysis	x	x	x		x

666

667

668

669   **Box 2**

670   Translocation is the process by which living organisms are deliberately removed from one site

671   for release in another. This definition excludes captive or cultivated organisms, sometimes

672   genetically modified, that are massively released into the wild to support agriculture,

673   fisheries, aquarium trade or pest control. The translocation process begins with the capture of

674   wild organisms in a donor site and ends with post-release monitoring in the receiving site.

675   Translocation has only recently become prominent in the oceans, particularly in coastal

676   environments, where human impacts are the highest [67]. Translocations are equivalent to

677   long-dispersal events.

678

679   Translocation in terrestrial environments is historically more common from non-protected to

680   protected areas in order to prevent vulnerable organisms from being killed (e.g. African

681   megafauna). In this scenario, protected areas are considered a sink, so the benefit is limited to

682   individuals that are more likely to survive under protection. However, following the IUCN

683   recommendations, conservation translocation must yield a measurable conservation benefit at

684   the level of the population, species or ecosystem. Protected areas thus need to shift their role

685   to become a source of translocated organisms and to provide long-distance benefits through

686   human assistance. Marine reserves host more abundant and larger individuals, thus producing

687   more larvae and juveniles than exploited areas [6, 19]. The challenge is now to capture these

688   small larvae and juveniles, which are under high predation risk, to seed locally depleted or

689   extinct populations elsewhere. This recently burgeoning strategy seems extremely promising.

690   For instance, Palau, a small island nation created one of the largest marine reserves on the

691   planet in 2015. Palau is now a sanctuary for marine animals that are globally endangered or

692   under severe threats like the Bumphead Parrotfish (*Bolbometopon muricatum*) which has

693   critical and unique ecological functions in coral reef ecosystems [68]. The extremely high

694   density of Bumphead Parrotfish in Palau induces massive spawning aggregations from which

695   eggs can be collected and juveniles can be grown in tanks and then released at other sites

696   where this species has been depleted (Figure I). Humans protect individuals through the

697   period of high mortality and then release sub-adults in other reserves where populations have

698   been exploited or are still being exploited to restore a certain density. This example highlights

699   how marine reserves can play a pivotal role in long-distance translocations and broaden the

700   geographic extent of their benefits in the near future.

701

702   Figure I. The translocation process for the threatened Bumphead Parrotfish (*Bolbometopon*

703   *muricatum*) species from Palau. This island nation hosts the highest density of Bumphead

704   Parrotfish worldwide (A) due to severe fishing restrictions. Massive spawning aggregations

705   produce eggs (B) that can be caught without damage using nets (C). Larvae are then grown in

706   optimal conditions to avoid mortality and juveniles (D) can be released to restore depleted or

707   extinct local populations on overexploited reefs (E) but also revitalize a key functional role on

708   coral reefs by bio-eroding dead corals (F). Photos from Tom Bowling (Biota Palau).

709

710

711

712

713 **Glossary**

714 **Admixture tracts:** Continuous blocks of the genome inherited from an admixed population.

715 **Benthic species:** Species that live and feed in or on the seabed.

716

717 **Blocks of identity by descent:** Continuous blocks of the genome that share the same alleles

718 inherited from a common ancestor**.**

719

720 **Cline analysis:** A framework that uses the relation between the genetic variation and the

721 geography or environment to estimate dispersal and selection.

722

723 **Coalescent theory: A** model that traces back gene variants from populations to their common

724 ancestor.

725

726 **Demersal species:** Species that live and feed near the bottom of the sea floor.

727

728 **Dispersal**: In this context, any movement of individuals or propagules from a source location

729 followed by successful immigration into a novel location with potential for gene flow.

730

731 **Demographic connectivity:** The process by which the dispersal of propagules, juveniles or

732 adults affects population growth and vital rates.

733

734 **Dispersal kernel**: Probability function describing the distribution of dispersal distances.

735

736 **Genetic connectivity:** A measure of gene flow and other evolutionary processes among

737 populations.

738

739 **Gene flow:** The exchange of genetic information among (sub)populations.

740

741 **Haplotype**:   A combination of physically linked genetic variants on a single chromosome.
742

743 **Isolation by distance**: A pattern whereby genetic distance increases with geographic

744 distance. It can be used to estimate dispersal distance from population or individual genotype

745 data and regression analysis.

746

747 **Larval dispersal**: The dispersal of larvae from a spawning site to a settlement site.

748

749 **Next-generation sequencing**: Sequencing technologies that allows millions of DNA-

750 fragments to be sequenced in a single run.

751

752 **Pelagic larvae:** Larvae that spend time in the water column after hatching.

753

754 **Pelagic species**: Species living mainly in the water column.

755

756 **Sessile species:** Species that are fixed to a substratum for most of their life. Many sessile

757 species, however, have other stages in their life cycle, usually as eggs or larvae, that allow for

758 active or passive dispersal.

759

760   **Spillover**: The net movement of (adult and juvenile) organisms across the boundary of a

761   reserve into a fished area.

762

763   **Stepping-stone dispersal:** A dispersal process involving intermediate steps across several

764   generations.

765

766   **Single nucleotide polymorphism markers:** Molecular markers used to detect genetic

767   variation among individuals that correspond to a difference in a single DNA building block,

768   called a nucleotide.

769

770

771   Highlights and Outstanding questions inserted here for purposes of editorial markup.

772   **Highlights**

773   ▪ Marine dispersal estimates are limited by the spatial scale of sampling

774   design and therefore biased downwards;

775   ▪ Active larval behavior, oceanographic eddies and fronts, tsunamis,

776   marine debris and translocations are potentially important, but

777   overlooked, dispersal vectors over long distances;

778   ▪ The largest marine reserves have the highest potential for massive and

779   long-distance benefits, but are the most isolated ones;

780

781   • Long-distance dispersal has important consequences for the design of
782   marine reserve networks;

783   Box 3: Outstanding questions Box

784   • What proportion of the dispersal kernel of marine species are we
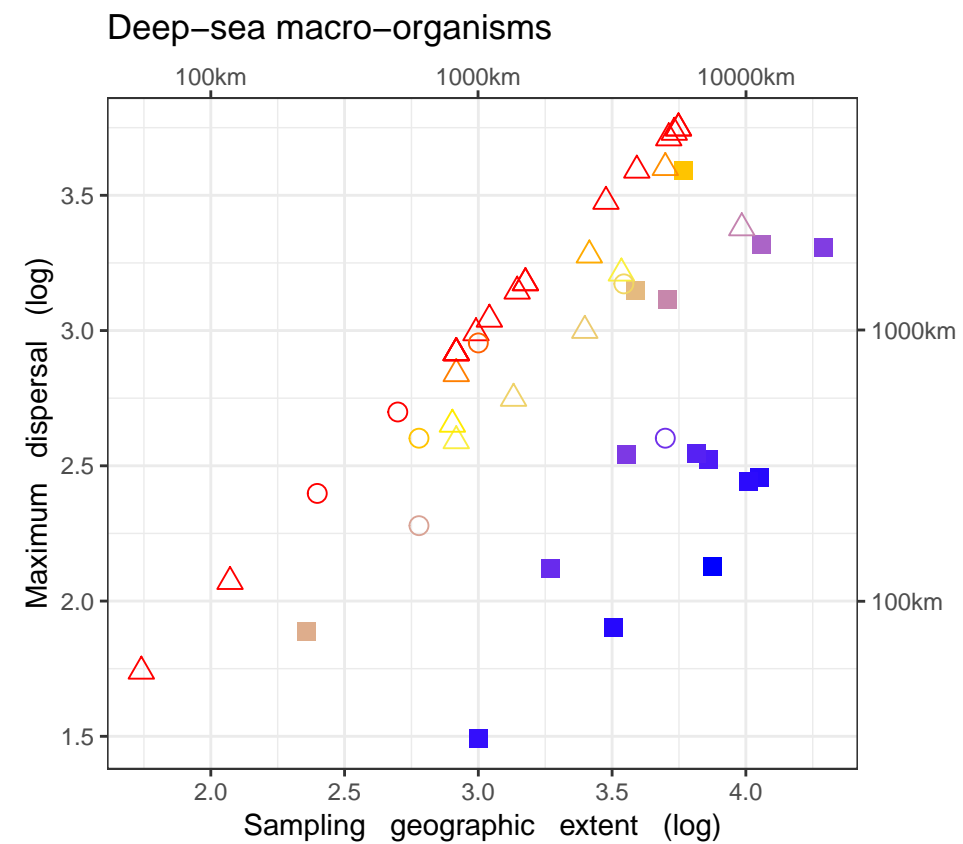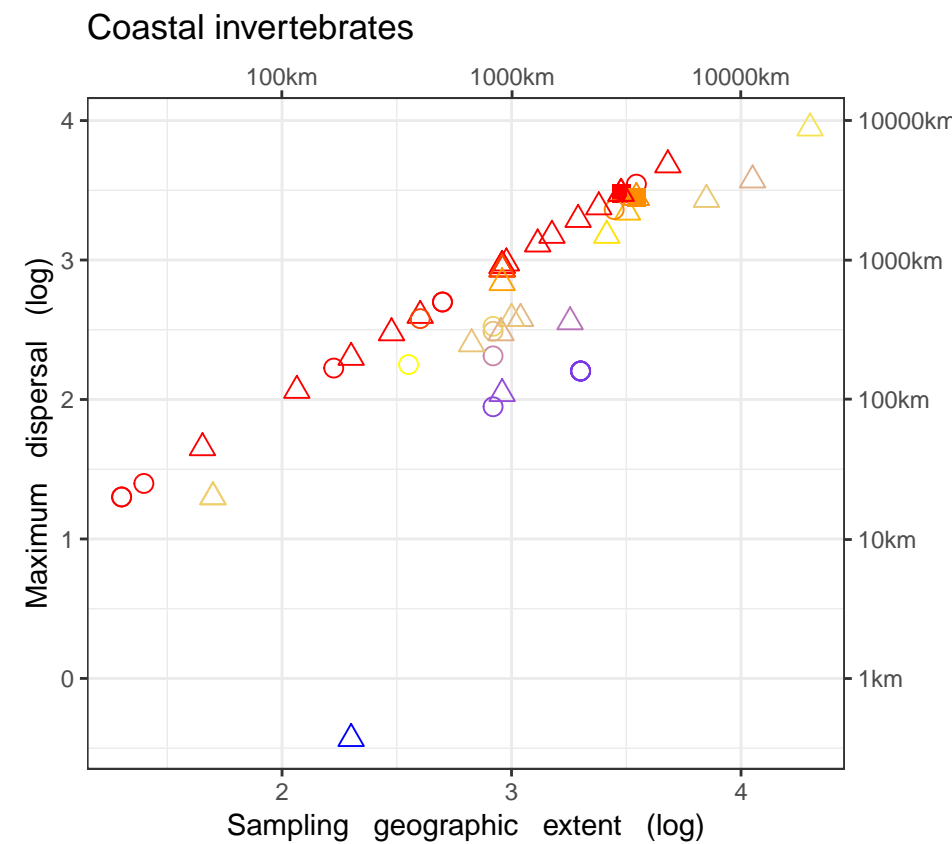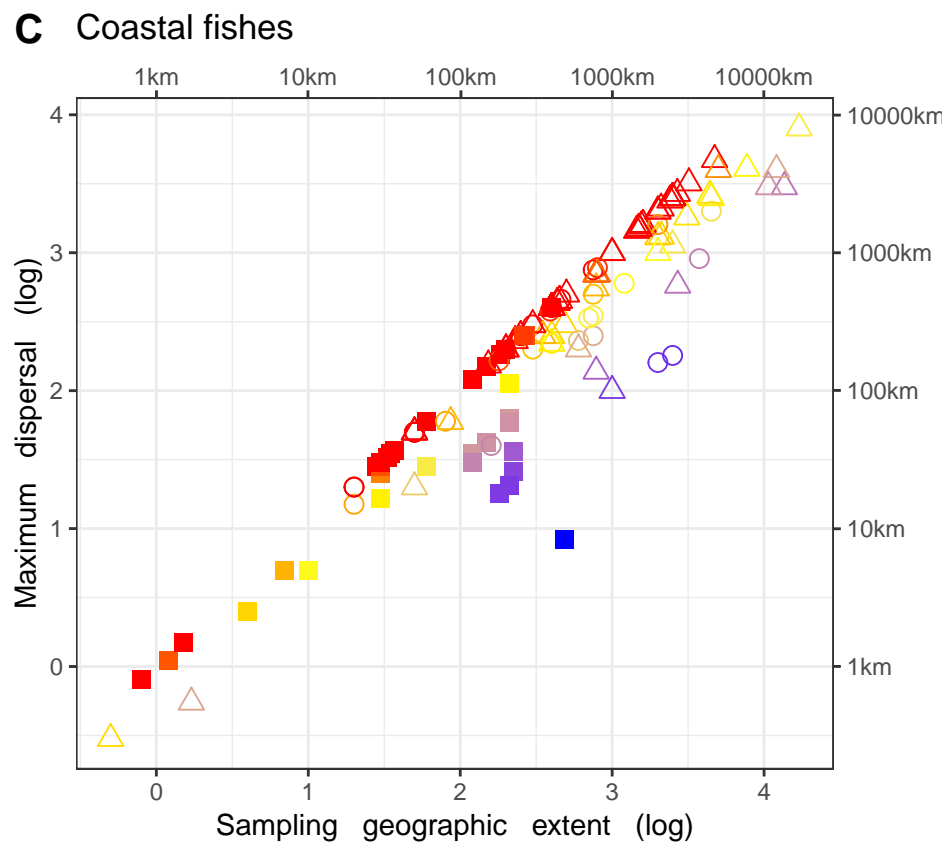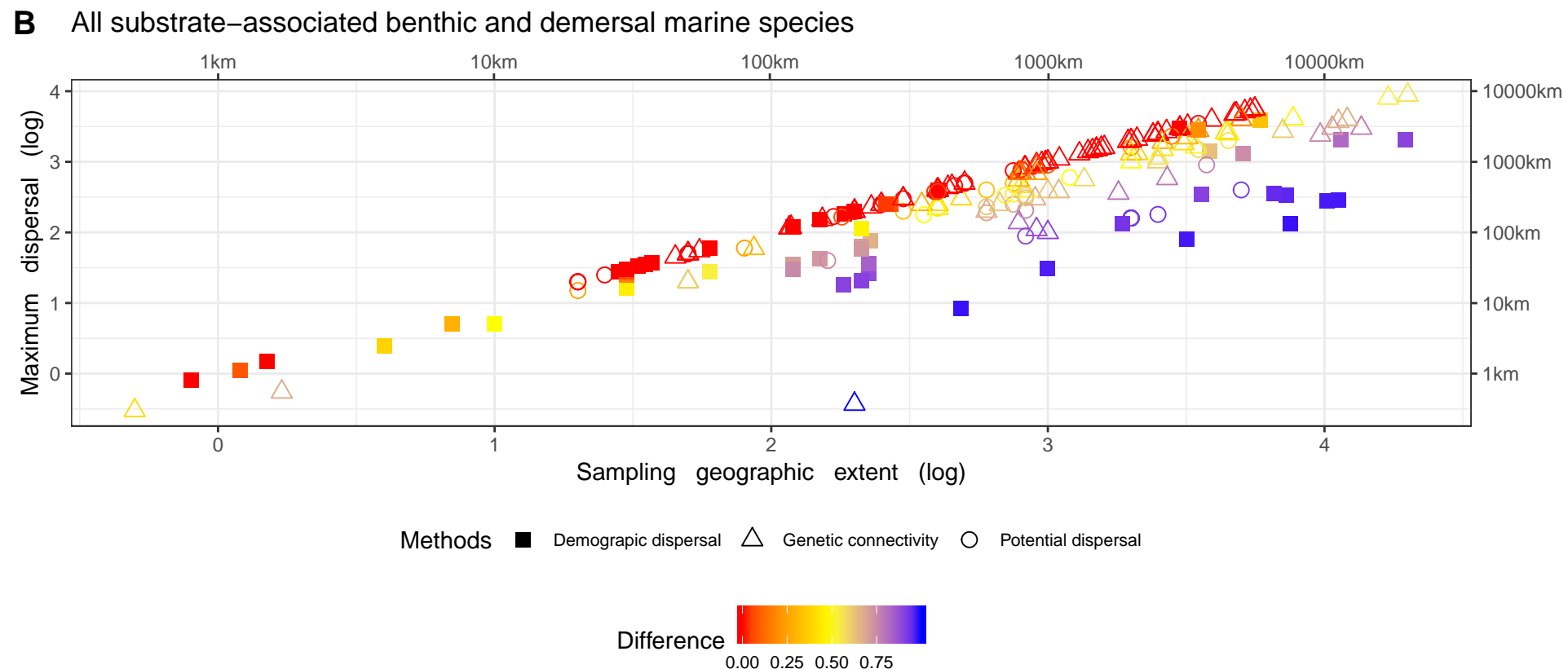785   missing when we do not consider the long-distance (>40 km) dispersal?
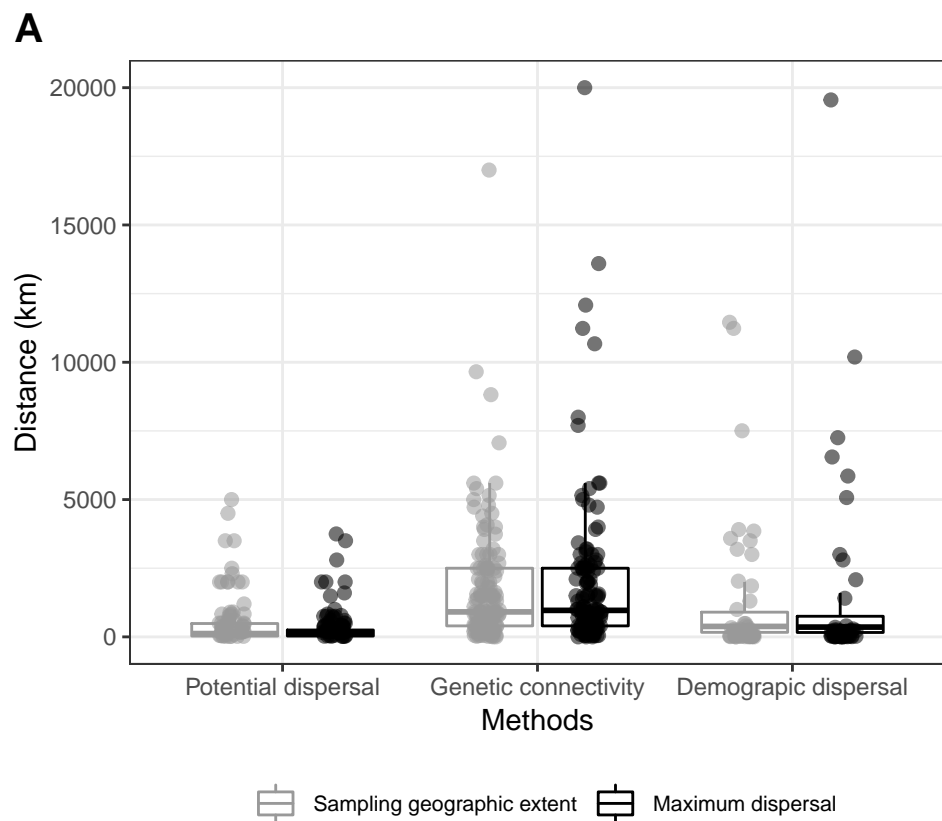
786   • Is the restricted spatial scale of sampling designs the only or main
787   cause of the limited geographical dispersal reported in the sea?

788   • What are the quantitative effects of marine reserves at long distances
789   (>40 km)?

790   • Is the unknown long-distance dispersal sufficient to connect large
791   isolated marine reserves?

792   • To which extent future marine reserve networks should be composed of
793   few but large reserves instead of many small when we consider species
794   long-distance dispersal?

795

A

B All substrate−associated benthic and demersal marine species

Methods: ■ Demograpic dispersal △ Genetic connectivity ○ Potential dispersal

Difference 0.00 0.25 0.50 0.75

C Coastal fishes

Coastal invertebrates

Deep−sea macro−organisms

PROCESSES
1. Active dispersal
2. Passive dispersal by current
3. Drifting or floating debris
4. Translocation

BENEFITS
A. Increase of biomass (Fisheries)
B. Maintenance of biodiversity
C. Maintenance of cultural species

Marine Reserve