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

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30

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32 protected areas.

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 (>1,000km²) 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.

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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 MPAs (referred to as
64 marine reserves [8]) specifically (mpatlas.org; [9]). Despite the recent establishment of large-
65 scale MPAs (>100,000 km²) [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 km²), 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 ($> 1000 \text{ km}^2$) are
284 isolated ($>42\text{km}$) (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

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350

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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.

Dispersal category	Method	Spatial extent			Temporal resolution	
		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?

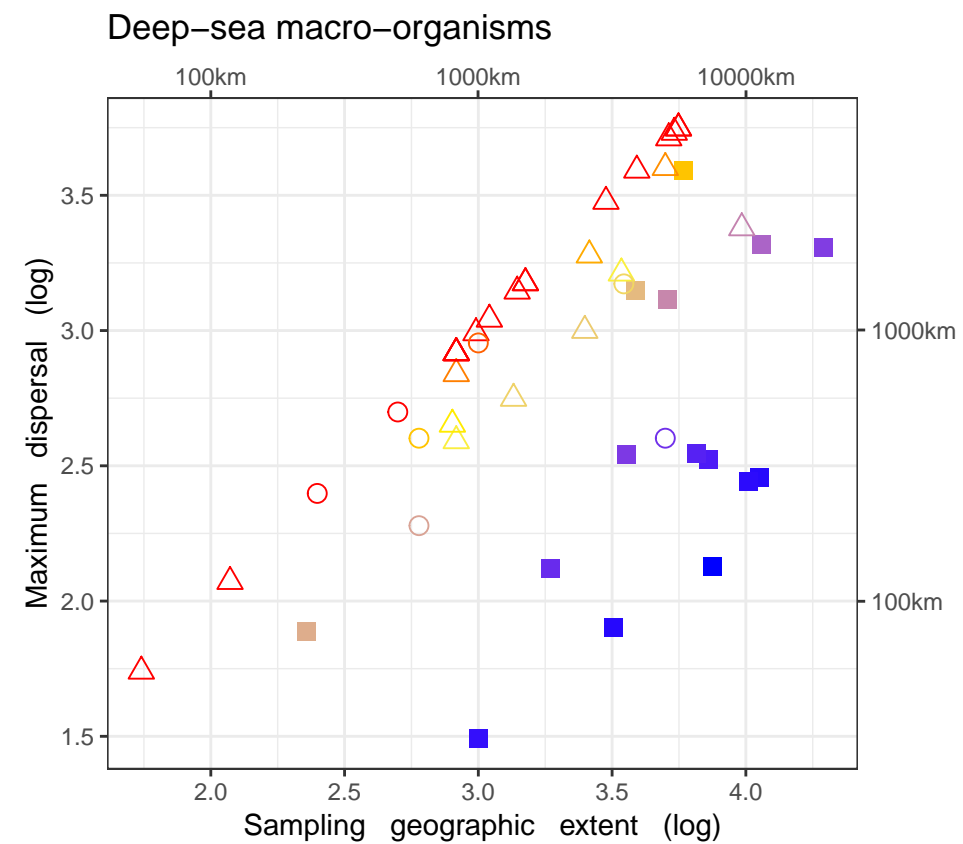
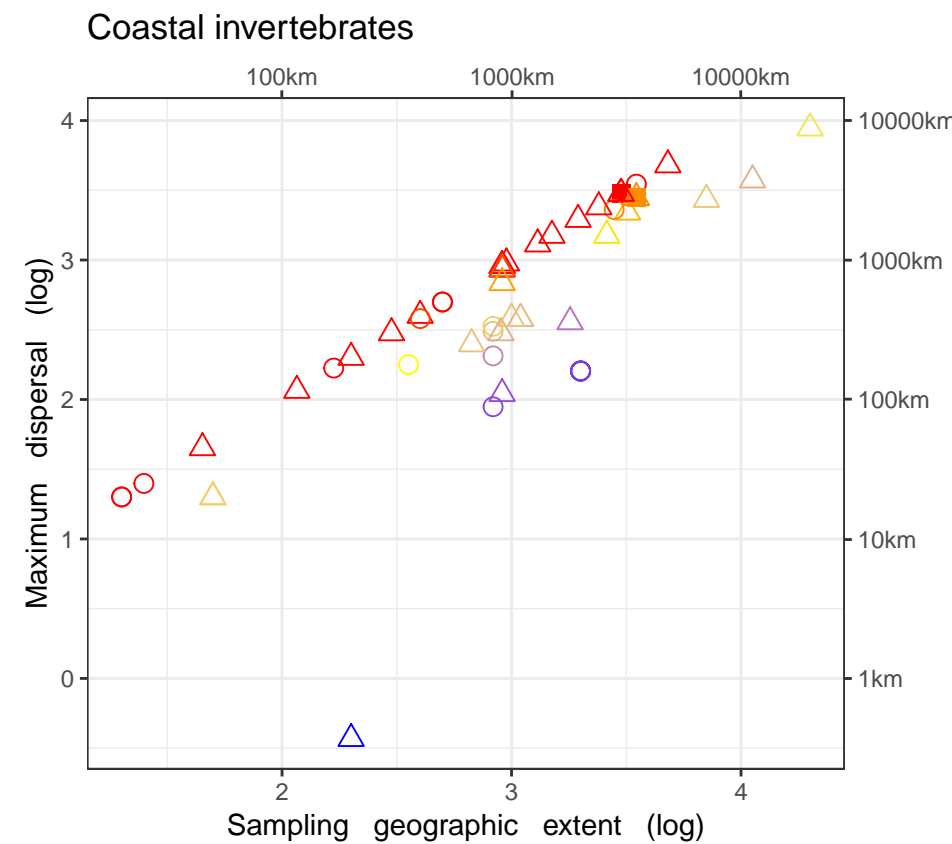
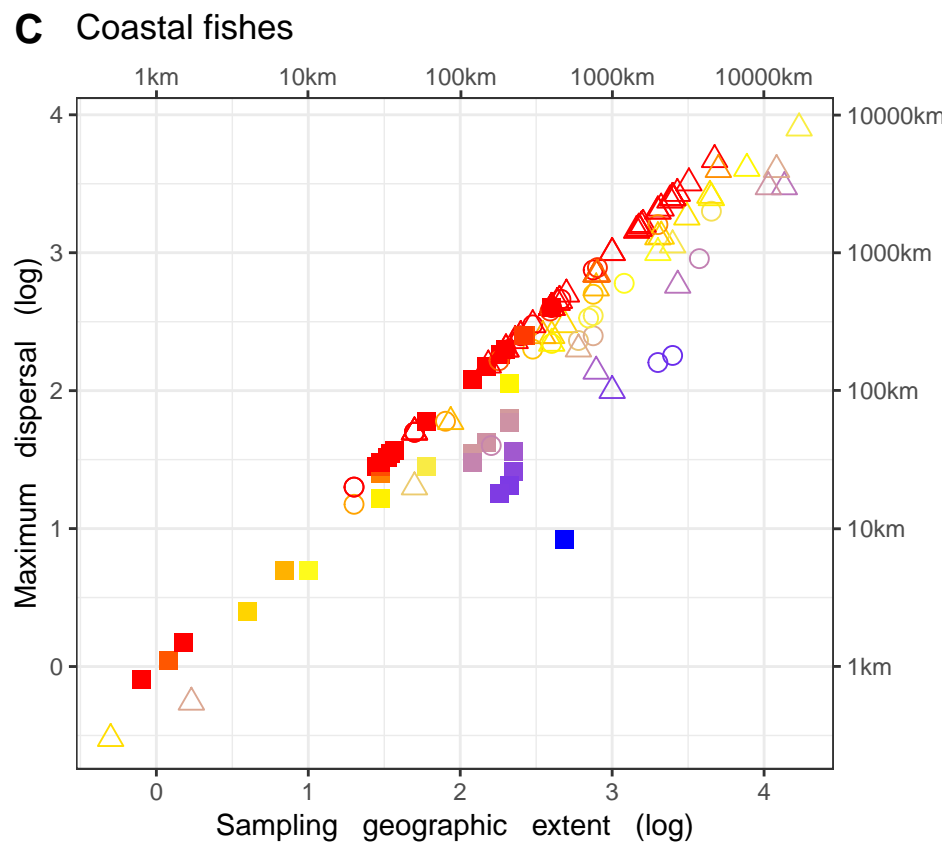
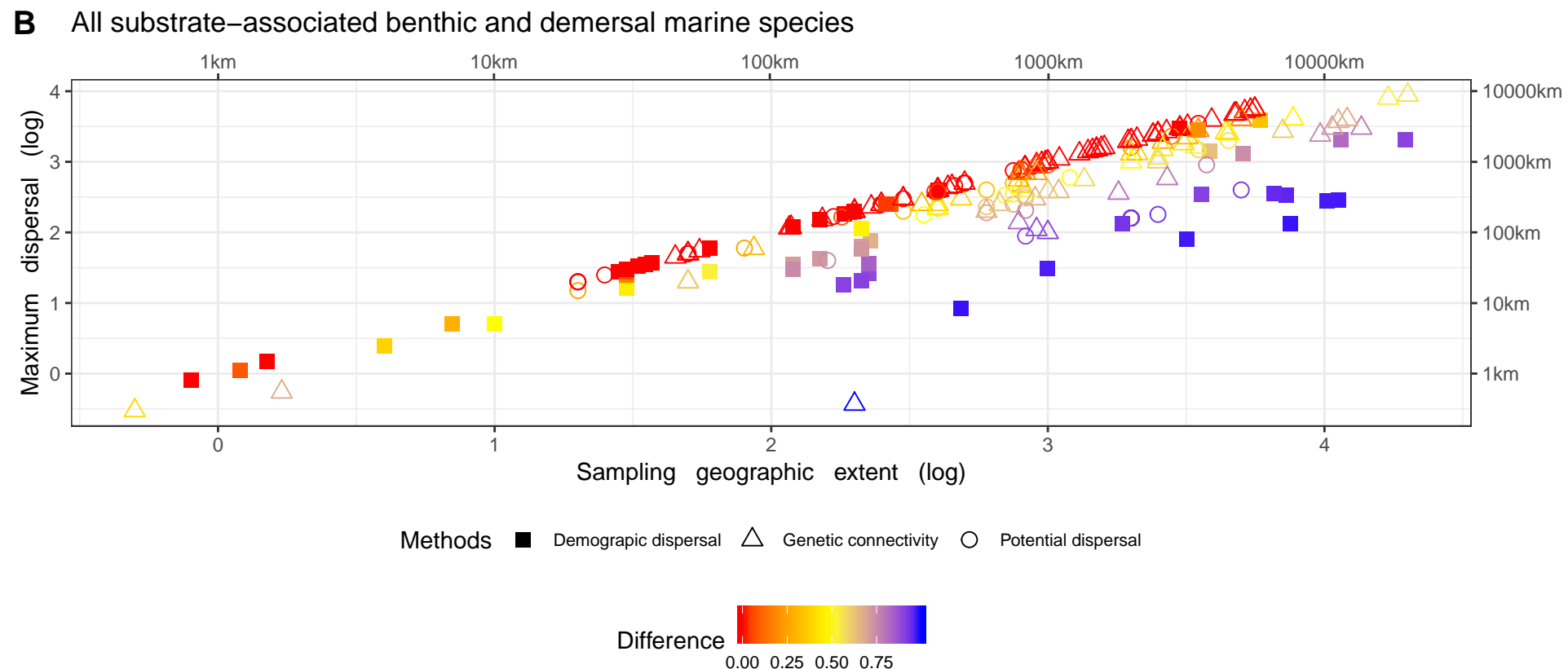
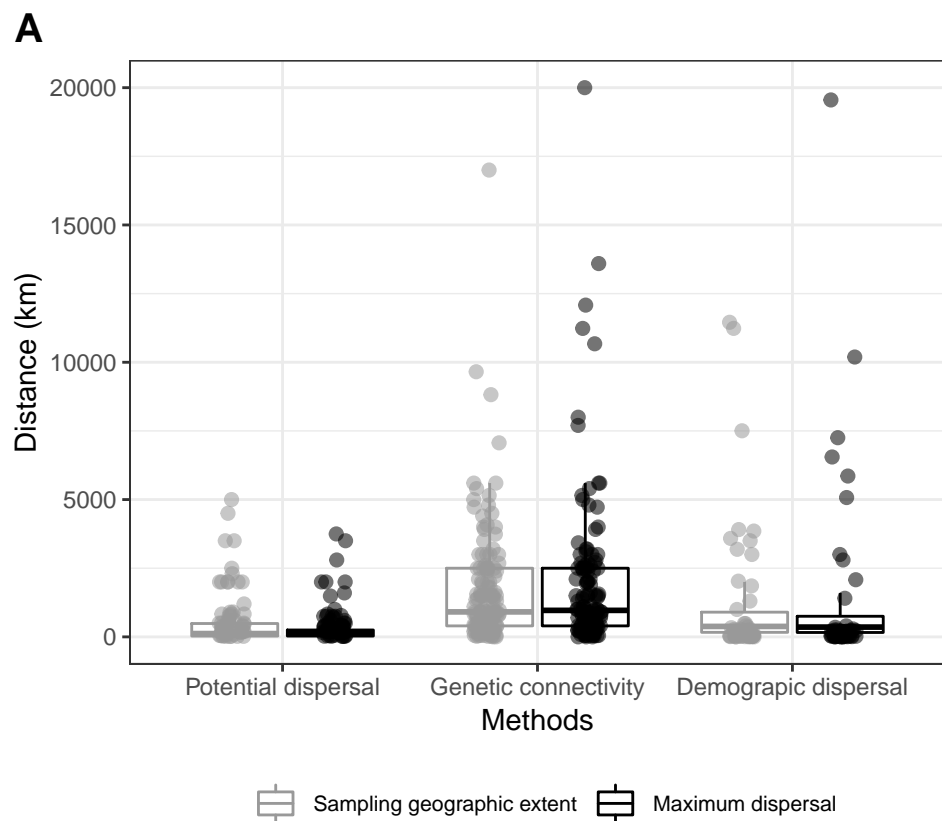
- 786 ▪ Is the restricted spatial scale of sampling designs the only or main
787 cause of the limited geographical dispersal reported in the sea?

- 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



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

