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

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Abstract :

Long-distance (>40-km) dispersal from marine reserves is poorly documented; yet, it can provide essential benefits such as seeding fished areas or connecting marine reserves into networks. From a meta-analysis, we suggest that the spatial scale of marine connectivity is underestimated due to the limited geographic extent of sampling designs. We also found that the largest marine reserves (>1000 km(2)) are the most isolated. These findings have important implications for the assessment of evolutionary, ecological, and socio-economic long-distance benefits of marine reserves. We conclude that existing methods to infer dispersal should consider the up-to-date genomic advances and also expand the spatial scale of sampling designs. Incorporating long-distance connectivity in conservation planning will contribute to increase the benefits of marine reserve networks.

Highlights

► Marine dispersal distance estimates are limited by the spatial scale of sampling design and therefore biased downwards. ► Active larval behavior, oceanographic eddies and fronts, tsunamis, marine debris, and translocations are potentially important, but overlooked, dispersal vectors over long distances. ► The largest marine reserves have the highest potential for massive and long-distance benefits but are the most isolated reserves. ► Long-distance dispersal has important consequences for the design of marine reserve networks.

Keywords : connectivity ; global network ; long-distance dispersal ; marine reserves ; marine protected areas

Benefits from marine reserves: where are we?

Marine resources are declining at an alarming rate [1, 2], with more than half of the oceanic area exploited by industrial fishing [3]. In response, marine protected areas (MPAs) have been established in an effort to conserve biodiversity and sustain fisheries [4-7]. Yet, only 3.7 % of the ocean is presently covered by MPAs and less than 2% by no-take MPA**s** (referred to as marine reserves [8]) specifically (mpatlas.org; [9]). Despite the recent establishment of large-scale MPAs (>100,000 km^2) [10], the current trend of protection is not keeping pace with the increasing human footprint on marine resources [11, 12]. In particular, the Aichi Biodiversity Target 11 established by the Convention of Biological Diversity to protect at least 10% of the ocean by 2020 is unlikely to be achieved [9, 13, 14]. In consideration of the ever-growing human population, fishing technological developments and per capita consumption rates, a new target of 30% protected area by 2030 was proposed at the 2016 International Union for Conservation Nature (IUCN) World Conservation Congress in line with scientific advice [6, 15]. There is thus an urgent need to better understand the full range of benefits provided by marine reserves to optimize future conservation efforts.

Theoretical and empirical studies support the positive effects of marine reserves within their boundaries and in their vicinity [16-19]. Indeed, marine reserves unambiguously host more and larger - and thus more fertile - individuals than fished areas (e.g. [5, 20, 21]). They also contribute to preserve genetic diversity [22], increase human wellbeing [23], alleviate poverty [24] and facilitate adaptation to climate change [25]. In addition, when properly designed and enforced, they have the potential to increase catches of commercial species in surrounding fishing grounds [26, 27] due to juvenile or adult **spillover** (see glossary) [28, 29]. However, such direct benefits have been typically documented at short distances from reserve boundaries, i.e. from a few hundred meters to less than 40 km [16, 30 , 31]. In contrast, little is known about the benefits of marine reserves in areas that are 40 to hundreds of kilometers away from their boundaries [32].

The concept of long-distance (>40 km) **dispersal** is not new in marine ecology and the oceans have been assumed to function as mostly open, well-connected systems until the last two decades [33, 34], when evidence of local recruitment started to accumulate [35, 36]. However, the large-scale impacts of marine reserves resulting from long-distance dispersal of larvae [37], juveniles and adults [38] are still poorly documented. The potential for long-distance dispersal is highest for **pelagic species**, which is consistent with their widespread geographic distributions [39]. Yet, recent findings based on telemetry and genetic tools indicate that **benthic** and **demersal species** (hereafter called benthos), including those in the deep sea, can also disperse up to hundreds of kilometers [32, 40-42]. This recognition of high dispersal capabilities calls for more studies on the effect of dispersal far from reserves and for a better integration of long-distance dispersal in the design of reserve networks.

Here we review the potential long-distance benefits of marine reserves, including those provided by relatively rare long-distance dispersal events. We focus on the benthos since their adult stages can be more easily assigned to protected versus non-protected areas compared to pelagic species which have large home ranges, often larger than most MPAs [43]. First, through an extensive literature screening, we characterize the spatial scale of dispersal for the benthos. We then discuss how existing methods can be enhanced to expand the scale of connectivity analyses. Finally, we discuss the potential long-distance benefits of marine reserves for both conservation and fisheries and how a well-connected network can enhance those benefits.

Spatial scale of dispersal and connectivity in the marine realm: do we capture the full picture?

We define marine connectivity as the exchange of individuals among marine populations [44]. This exchange can take place through dispersal of individuals as larvae, juveniles, or adults. When individuals reproduce successfully thereafter, **demographic connectivity** translates into **genetic connectivity**. Determining the spatial scale of marine connectivity is crucial for our understanding of the population dynamics, genetic structure and biogeography of marine organisms, and accordingly for the design of marine reserves.

To obtain a global estimate of the spatial scale of marine connectivity for the benthos, we conducted an extensive – but non-exhaustive – literature review over the last decade in the ISI Web of Science (supplementary text S1, supplementary file S1). Of the 460 papers identified, 130 were included in our meta-analysis as they contain information about maximum sampling geographic range and maximum inferred demographic or genetic connectivity for a total of 243 species.

The different methods used to estimate dispersal distance apply to different spatial and temporal scales (Table I of Box 1). The median potential dispersal distance averaged across all studies based on biophysical models (226 km, interquartile range = 160 - 415 km, number of species = 56) was at least four times higher than the demographic (realized and effective) median dispersal distance (42 km, interquartile range = 27 – 250 km, number of species = 55;

Figure 1A; Box 1). These results indicate that studies are either overestimating potential dispersal or underestimating demographic dispersal, with some exceptions where both estimates are congruent (e.g. [45]). However, assessing the full spatial extent of dispersal is challenging due to the inherent difficulty of tracking or recapturing organisms over long distances. With a few exceptions (e.g. [32, 41, 46]), most empirical studies of demographic connectivity were conducted at scales smaller than 40 km [47]. Estimating demographic connectivity at larger spatial scales and over multiple generations would require sampling significantly more individuals and in more distant populations, which would entail high, possibly prohibitive, costs. Genetic assignment approaches at the population level might be scaled-up more easily than mark-recapture or parentage analysis methods and constitute a promising approach when populations are genetically differentiated [48, 49]. For example, putative first-generation migrants between two populations separated by 400 km were detected in the Omani Clownfish (*Amphiprion omanensis*) using assignment tests [40]. If populations are locally adapted, the use of genetic markers that are under divergent selection can contribute to increase the power of such approaches, and can even be used in the absence of neutral genetic structure [50]. Genetic **isolation by distance** at the population or individual level [51] provides dispersal estimates that are consistent with demographic dispersal estimates obtained from parentage analysis (Box 1) [52]. When a reference genome and **haplotype** data are available, the consideration of **admixture tracts** [53] and **blocks of identity by descent** [54] constitutes another promising avenue to detect recent dispersal events, that can also apply in isolation by distance contexts [55].

Our literature review also reveals that genetic connectivity, based on Wright's Fixation Index (F_{ST}), tends to provide higher estimates than any other method (Figure 1A: median = 910 km, interquartile range = 315 - 2346 km, number of species = 126). Yet, genetic connectivity differs from demographic connectivity as it integrates the effects, not just off migration, but also genetic drift, mutation and selection. Translating genetic connectivity into demographic estimates of dispersal is not straightforward [56]. This notably implies estimating effective population sizes [57] or assuming specific population genetic models that are often unrealistic in real-world situations [58]. Furthermore, **gene flow** over large geographic distances might result from **stepping-stone dispersal** over multiple generations without necessarily implying direct long-distance dispersal events [59].

Globally, the data show a universal positive correlation between the geographic sampling scale of the study and the maximum dispersal or connectivity averaged across all studies and organisms ($R = 0.7$, $p < 0.001$; Figure 1B). The relation holds true when analyzing the data per type of dispersal estimate (potential vs. demographic vs. genetic). In 45 % of the studies, the dispersal distance was equal to the maximum geographic extent of the sampling. This reached 48 % when data were restricted to coastal fishes, 41 % for invertebrates and 41 % for deep sea organisms (Figure 1C). These results suggest that estimates are limited by the spatial scale of the sampling, resulting in a global underestimation of the extent of demographic and genetic connectivity.

For genetic connectivity, an absence of population structure can also result from a lack of statistical power to detect subtle population genetic structure when a small number of genetic markers are used. With the advent of **next-generation sequencing** technologies, this limitation can now be overcome by typing hundreds to millions of **single nucleotide polymorphism markers** [60, 61].

A variety of mechanisms can contribute to long-distance dispersal in marine ecosystems (Figure 2). Foremost, the hydrodynamic forces at play in the marine environment are expected to have a strong influence on the dispersal of **pelagic larvae** [62]. In addition, the conditions encountered in the pelagic environment might influence growth, survival and pelagic larval duration, all of which can in turn induce extreme values in spatial and temporal connectivity patterns. Active larval behavior can also play an important role for the benthos [63, 64]. Extreme events, such as tsunamis [65], and oceanographic eddies and fronts [66] are also important, but overlooked potential dispersal vectors over long distances. They can favor the survival and establishment of individuals beyond their usual dispersal range. Furthermore, marine debris of natural or anthropogenic origin can constitute effective oceanic rafts for dispersal [67, 68]. These debris provide refuges for larvae and adults of **sessile species**, allowing the movement and potential establishment of a variety of species over large distances. For instance, mussels from Japan arrived on the west coast of the US after nearly six years at sea on debris produced by the 2011 East Japan earthquake [65]. Ice blocks also allow invertebrates to disperse across distances of about 20 km per day [69]. Anthropogenic vectors such as international vessel traffic, restocking from aquaculture [70], and species translocation (Box 2) also have the potential to modify the natural spatial and temporal patterns of marine connectivity [71]. Overall, the occurrence of long-distance dispersal events, even if rare, suggest that marine reserves can have an effect far beyond their boundaries, which calls for a re-evaluation of the spatial extent of their potential benefits.

Long-distance benefits of marine reserves

We consider a long-distance benefit of marine reserve any change in biomass, biological processes (e.g. recruitment) or biodiversity (including genetic diversity as raw material for adaptation) at distance greater than 40 km from reserve boundaries that contributes to improve ecosystem function or human livelihoods (e.g. fisheries, tourism, culture) (Figure 2). Long-distance benefits from reserves can occur at different spatial and temporal scales depending on the vector of dispersal (Box 1, Figure 2), and this includes both direct and stepping-stone dispersal processes.

Parentage analyses have demonstrated dispersal from marine reserves at more than 40 km [32, 46]. For example, Almany *et al.* [46] revealed connectivity patterns with direct exchanges of larvae over up to 150 km among reefs with varying levels of protection. **Larval dispersal** from reserves towards exploited areas located at more than 100 km has also been suggested by biophysical models [37, 72]. Yet, empirical studies showing an effect of marine reserves on fished areas are largely restricted to spatial scales smaller than 40 km (e.g. [26, 73, 74]). Scaling-up these studies is challenging for a variety of logistic reasons, including the difficulty to sample and monitor individuals over large spatial scales.

Even if long-distance dispersal events from marine reserves are rare, a few successful migrants can be sufficient to re-colonize areas where local populations have been extirpated or to expand species distributions in response to global change [75]. Long-distance dispersal between populations that are genetically differentiated or locally adapted can moreover contribute to limit inbreeding, increase genetic diversity and facilitate adaptation to a changing environment [25, 76]. However, in case of local adaptation, long-distance dispersal can also reduce fitness of recipient populations through immigration of locally maladapted alleles [77].

Active translocations from marine reserves can also contribute to restore locally depleted or extinct populations [78]. For example, the Bumphead Parrotfish (*Bolbometopon muricatum*) is highly targeted by spear fishers due to its large size and therefore population densities tend to be low in areas close to human populations [79]. This species is only abundant in reserves and on the most protected reefs such as in Palau where it aggregates to spawn. These populations have been used as a source of eggs and larvae for active translocations (Box 2). Nearly 500 translocation projects of 242 marine species have been recorded [78]. However, still few projects take advantage of large stocks in marine reserves. It should also be emphasized that translocations entail a number of risks (e.g. disease, invasion, gene pool mixing). Overall, marine reserves could support a wide variety of long-distance benefits that are potentially underestimated and that should be considered for the design of reserve networks.

Implications of long-distance dispersal for marine reserve design

An underestimate of dispersal ability can profoundly influence the design of marine reserve networks. Long-distance dispersal can potentially connect distant and isolated reserves, and sustain biodiversity and biomass in exploited areas located at more than 40 km from their boundaries. In this respect, long-distance dispersal provides a fresh perspective on two long-lasting and active debates in the marine reserve literature.

First, long-distance dispersal has implications for the unresolved single-large-or-several-small (SLOSS) marine reserve debate. Simulations suggest that a network of well-connected reserves on a scale of 10-100 km can meet both conservation and fisheries goals [7, 80]. However, the idea that a network constituted of many small reserves spaced within species maximum dispersal distance [4] maximizes reserve benefits to fisheries has been recently revisited and challenged. Based on a spatially explicit model of population dynamics, De Leo & Micheli [81] show that for larval dispersal >10 km, one or two large reserves are more efficient in terms of fisheries gains than 10 or 20 small reserves covering the same area. This is notably due to the fact that large (>100 km^2), old (>10 years, [5]) and well-managed reserves tend to increase fish density and biomass [5, 82], and that large females over-contribute to reproduction since the relation between female body mass and reproductive output is hyperallometric for the vast majority of fishes (i.e. a 2-kg female has a higher reproductive output in terms of egg number, volume and energy, than two 1-kg females [83]). We can therefore expect large, old and well-managed reserves to disproportionately contribute to larval seedling within a network when dispersal distances are greater than ten kilometers. Using a rigorously calibrated metapopulation model with empirical data from the Great Barrier Reef, Hopf et al. [84] also show that reserves are unable to compensate for the increased mortality outside reserve boundaries when they are small or at the periphery of the metapopulation [84]. In contrast, the establishment of a single large reserve, that is able to seed overexploited areas through dispersal, is expected to result in higher population growth within reserve boundaries and shorter recovery times after overexploitation outside the reserve. Finally, a global analysis indicates that when larval dispersal distances are long (>40 km), the magnitude of biomass increase within large reserves is expected to be sufficient to compensate for the redistributed fishing pressure associated with reserve establishment [85].

The median nearest-neighbor distance between marine reserves is estimated at 12 km globally (interquartile distance: 4 to 40 km) (Supplementary text S2). This geographical pattern is highly variable, with some reserves being very isolated (e.g. the Parque Natural Obô do Príncipe in São Tomé and Príncipe at 4130 km from the nearest reserve, the Monumento Natural do Arquipelago de Sao Pedro e Sao Paulo at 940 km off the coast of Brazil) (Figure 3A, supplementary text S2). Fortunately, 76 % of reserves are found closer to the nearest reserve than the median demographic dispersal distance estimated in our literature review (42 km) (Figure 3B). It implies that three-quarters of marine reserves are potentially demographically embedded in a connected network providing spatial insurance. The median nearest-neighbor distance in the 24 % remaining reserves is estimated to be 129 km, with a very skewed distribution (Figure 3B). Notably, 83% of large reserves (> 1000 km^2) are isolated (>42km) (Figure 3C). The mean nearest neighbor of this subset of large marine reserves is 359 km away, decreasing their potential contribution to the global network. Therefore, the largest marine reserves, allowing large spillover of individuals and providing benefits for both biodiversity and human population, are the least connected. However, we did not consider how sea surface currents could modify our assessment of connectivity among isolated reserves.

Second, long-distance dispersal has also implications for prioritizing the conservation of human-impacted versus non-impacted areas. Intuitively, one can see little benefit in placing reserves in isolated areas which are difficult to access and therefore *de facto* protected [86]. On the other hand, reserves close to dense human populations can mitigate but not eliminate the high anthropogenic pressure outside but also inside their boundaries [87]. It has therefore been suggested that reserves located at an intermediate level of human pressure might offer the maximum benefits in terms of fish biomass within their boundaries [87]. For top predators like sharks, only isolated marine reserves with low human pressure can be effective [87]. The realization of long-distance dispersal would also make a case for the protection of such areas isolated from human pressure. More generally, it would suggest to reconsider the design of marine reserve networks with fewer but larger reserves, including isolated ones, to sustain large populations of large individuals, even of top predators, that can massively seed larvae towards fishing grounds. Tools that integrate species dispersal in conservation planning are now available to reach both conservation and fisheries management objectives in a multispecies framework [88]. The consideration of long-distance dispersal would certainly modify the outputs of conservation plans.

Concluding remarks

Marine dispersal has been extensively documented at short distance (mostly <40 km). We suggest that this has been due, at least in part, to logistic constraints and a restricted geographic extend of the sampling design (e.g. the median sampling distance in parentage analyses is only 33 km, interquartile range = 29 – 60 km, number of species = 22). While a significant fraction of dispersal indeed occurs at small spatial scales, the fraction of the **dispersal kernel** that we are missing is largely unknown (see Outstanding Questions). A few recent empirical studies have demonstrated dispersal of fish at larger spatial scales (up to 400 km), but even these estimates were limited by the maximum sampling distance [40]. Dispersal estimates from biophysical modelling studies at larger spatial scales suggest even longer dispersal distances (median sampling distances = 600 km, interquartile range: 237-1400, Figure 1A). Such long-distance connectivity patterns remain challenging to validate empirically, but have potentially important consequences in terms of reserve design and benefits. The more isolated reserves are, the more critical long-distance dispersal becomes to maintain source-sink dynamics between protected and exploited populations. Thus, long-distance benefits imply a more regional and network-based perspective, which entails specific challenges. Long-distance dispersal will often cross countries as well in-shore-offshore boundaries. The designation of marines reserves is largely carried out by individual countries and they rarely able coordinate efforts with other countries and high-seas authorities [89]. Furthermore, the focus on marine reserves is strongly constrained by the perspective of local stakeholders [15], which is perfectly justified but should nonetheless not obliterate a broader perspective.

We suggest scaling-up dispersal studies at regional instead of local scale. We can now genotype a large number of genetic markers, which provides the opportunity to apply population-level assignment tests at large spatial scales and in a context of low spatial structure [90]. Such studies can be guided by high-resolution biophysical models to target the specific populations among which long-distance distance dispersal occurs. A large number of single nucleotide polymorphism markers will also provide the statistical power to detect very subtle population structure, which will allow refining genetic connectivity estimates [90, 91]. Finally, approaches based on admixture tracts [53] and blocks of identity by descent [54] are largely untapped. The combination of genetic, chemical and biophysical approaches within an integrative statistical framework also appears to be a promising approach to estimate long-distance dispersal [92] and guide the design of new reserve networks to keep pace with ever increasing threats on marine ecosystems.

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Figure Legends

Figure 1: The spatial scale of sampling constraints dispersal estimates

(A) Boxplot representing the maximum dispersal distance and the sampling geographic extent across all studies. Central lines represent median values and whiskers first and third quartiles. (B) Mean maximum dispersal distance increases with the maximal sampling geographic extent and (C) the pattern remains consistent among groups: fish, invertebrates and deep-sea organisms (>200 m). In (B) and (C), the color gradient displays the difference between maximal dispersal estimate and sampling geographic extent, with warmer colors (red) indicating that the maximum dispersal distance is closer to the maximal sampling geographic extent. The methods used to estimate connectivity include tracking, parentage analysis, assignment tests and isolation by distance (= demographic dispersal) described in Box 1 (see

B and C), biophysical models (potential dispersal), and genetic connectivity estimated from Fixation Index (F_{ST}). See supplementary method S1 and supplementary file S1 for details on the data used to generate the figure.

Figure 2: **Potential long-distance dispersal processes and marine reserve benefits from** The main processes that contribute to long-dispersal distance are indicated with numbers and the main benefits due to long-dispersal distance are indicated with letters. The marine reserve is represented by a circle. (1) Active dispersal can drive larvae or adults far from the reserve boundaries, independently of the sea currents. (2) Larvae are pelagic and disperse passively due to currents. (3) They can associate with floating and drifting debris. (4) Translocation involves deliberately moving organisms from one site (“productive” reserves) to another (e.g. overexploited population). Thus, long distance dispersal can (A) increase biomass in fished areas far from the reserve, (B) potentially maintain species and genetic diversity across reserves, (C) maintain commercially and culturally important species that were the target of protection in the reserve.

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

(A) Map showing the neighbor distance for each marine reserve, i.e. the distance to the nearest marine reserves. To improve the visibility of the figure, we used both size and color of the circles to indicate the nearest-neighbor distance of each marine reserve. Small yellow circles indicate the most connected marine reserves (e.g. Scandinavian region or Australia) while large blue circles indicate the most isolated reserves (e.g. Western African coast). (B) Distribution of nearest-neighbor distances between marine reserves. The median and mean nearest-neighbor distances are 12 km and 65 km, respectively. The dashed red line indicates the demographic median dispersal distance estimated for all organisms from the meta-analysis (42 km). (C) The nearest-neighbor distance increases with the no-take surface area of marine reserves (from 752 no-take marine reserves).

Box

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

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

A. Potential dispersal (inferred from biophysical models)

Biophysical models can be used to simulate larval dispersal trajectories over large spatial and temporal scales (Table I) [96]. These models usually incorporate three elements: a physical model that simulates the ocean hydrodynamics, a particle tracking model that simulates the passive movement of virtual larvae, and optionally a coupled model that simulates the activity of the larvae when information on their ecology, behavior and physiology is available [97]. This third element is often lacking and it is therefore important to better understand the biology of marine larvae. Biophysical models are becoming increasingly complex and realistic, yet they always need to be validated with empirical data [98].

B. Realized dispersal (dispersal took place, but dispersers can or cannot successfully reproduce)

Specific dispersal events can be inferred using genetics. Parentage analyses identify dispersal events by using individual genotypes to assign juveniles to their parents [99]. This approach provides a snapshot of dispersal events over one generation. It requires considerable effort to sample and genotype a large number of juveniles and potential parents. Similarly, population genetic assignment tests use individual genotypes to assign individuals to their population of origin [48]. This approach relies on the occurrence of genetic structure among populations [100], but can also be applied in the absence of population genetic structure if populations are locally adapted [50]. Various tracking methods can also identify dispersal events. Acoustic telemetry can be used to observe the movement of individuals, often adults, providing the opportunity to directly observe dispersal [101]. Electronic and physical tags can provide information on the movement of individuals. Some, however, have the drawback that individuals need to be recaptured to retrieve the data. Otolith analyses can also provide evidence of dispersal when the microchemistry or stable isotope composition of populations differ [102, 103]. When these approaches are applied to many individuals, it is possible to derive empirical distributions of dispersal kernel [104]. Yet the fact that individuals disperse does not necessary imply that they will successfully reproduce.

C. **Effective dispersal** (dispersal took place and dispersers successfully reproduced)

In the presence of **genetic isolation by distance** [105], it is possible to estimate dispersal at ecological timescales (tens of generations, [106]). This approach can be applied at the individual or population level. Another interesting avenue to infer dispersal is **cline analysis** [50]. Additional approaches based on **coalescent theory** [57] or the **site frequency spectrum** [107] go deeper back in time (tens to thousands of generations) and are therefore less relevant at ecological timescales.

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

Box 2

Translocation is the process by which living organisms are deliberately removed from one site for release in another. This definition excludes captive or cultivated organisms, sometimes genetically modified, that are massively released into the wild to support agriculture, fisheries, aquarium trade or pest control. The translocation process begins with the capture of wild organisms in a donor site and ends with post-release monitoring in the receiving site. Translocation has only recently become prominent in the oceans, particularly in coastal environments, where human impacts are the highest [67]. Translocations are equivalent to long-dispersal events.

Translocation in terrestrial environments is historically more common from non-protected to protected areas in order to prevent vulnerable organisms from being killed (e.g. African megafauna). In this scenario, protected areas are considered a sink, so the benefit is limited to individuals that are more likely to survive under protection. However, following the IUCN recommendations, conservation translocation must yield a measurable conservation benefit at the level of the population, species or ecosystem. Protected areas thus need to shift their role to become a source of translocated organisms and to provide long-distance benefits through human assistance. Marine reserves host more abundant and larger individuals, thus producing more larvae and juveniles than exploited areas [6, 19]. The challenge is now to capture these small larvae and juveniles, which are under high predation risk, to seed locally depleted or extinct populations elsewhere. This recently burgeoning strategy seems extremely promising. For instance, Palau, a small island nation created one of the largest marine reserves on the planet in 2015. Palau is now a sanctuary for marine animals that are globally endangered or under severe threats like the Bumphead Parrotfish (*Bolbometopon muricatum*) which has critical and unique ecological functions in coral reef ecosystems [68]. The extremely high density of Bumphead Parrotfish in Palau induces massive spawning aggregations from which eggs can be collected and juveniles can be grown in tanks and then released at other sites where this species has been depleted (Figure I). Humans protect individuals through the period of high mortality and then release sub-adults in other reserves where populations have been exploited or are still being exploited to restore a certain density. This example highlights how marine reserves can play a pivotal role in long-distance translocations and broaden the geographic extent of their benefits in the near future.

Figure I. The translocation process for the threatened Bumphead Parrotfish (*Bolbometopon muricatum*) species from Palau. This island nation hosts the highest density of Bumphead Parrotfish worldwide (A) due to severe fishing restrictions. Massive spawning aggregations produce eggs (B) that can be caught without damage using nets (C). Larvae are then grown in optimal conditions to avoid mortality and juveniles (D) can be released to restore depleted or extinct local populations on overexploited reefs (E) but also revitalize a key functional role on coral reefs by bio-eroding dead corals (F). Photos from Tom Bowling (Biota Palau).

Glossary

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

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

Blocks of identity by descent: Continuous blocks of the genome that share the same alleles inherited from a common ancestor**.**

Cline analysis: A framework that uses the relation between the genetic variation and the geography or environment to estimate dispersal and selection.

Coalescent theory: A model that traces back gene variants from populations to their common ancestor.

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

Dispersal: In this context, any movement of individuals or propagules from a source location followed by successful immigration into a novel location with potential for gene flow.

Demographic connectivity: The process by which the dispersal of propagules, juveniles or adults affects population growth and vital rates.

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

Genetic connectivity: A measure of gene flow and other evolutionary processes among populations.

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

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

Isolation by distance: A pattern whereby genetic distance increases with geographic distance. It can be used to estimate dispersal distance from population or individual genotype data and regression analysis.

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

Next-generation sequencing: Sequencing technologies that allows millions of DNA-fragments to be sequenced in a single run.

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

Pelagic species: Species living mainly in the water column.

Sessile species: Species that are fixed to a substratum for most of their life. Many sessile species, however, have other stages in their life cycle, usually as eggs or larvae, that allow for active or passive dispersal.

Spillover: The net movement of (adult and juvenile) organisms across the boundary of a reserve into a fished area.

Stepping-stone dispersal: A dispersal process involving intermediate steps across several generations.

Single nucleotide polymorphism markers: Molecular markers used to detect genetic variation among individuals that correspond to a difference in a single DNA building block, called a nucleotide.

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

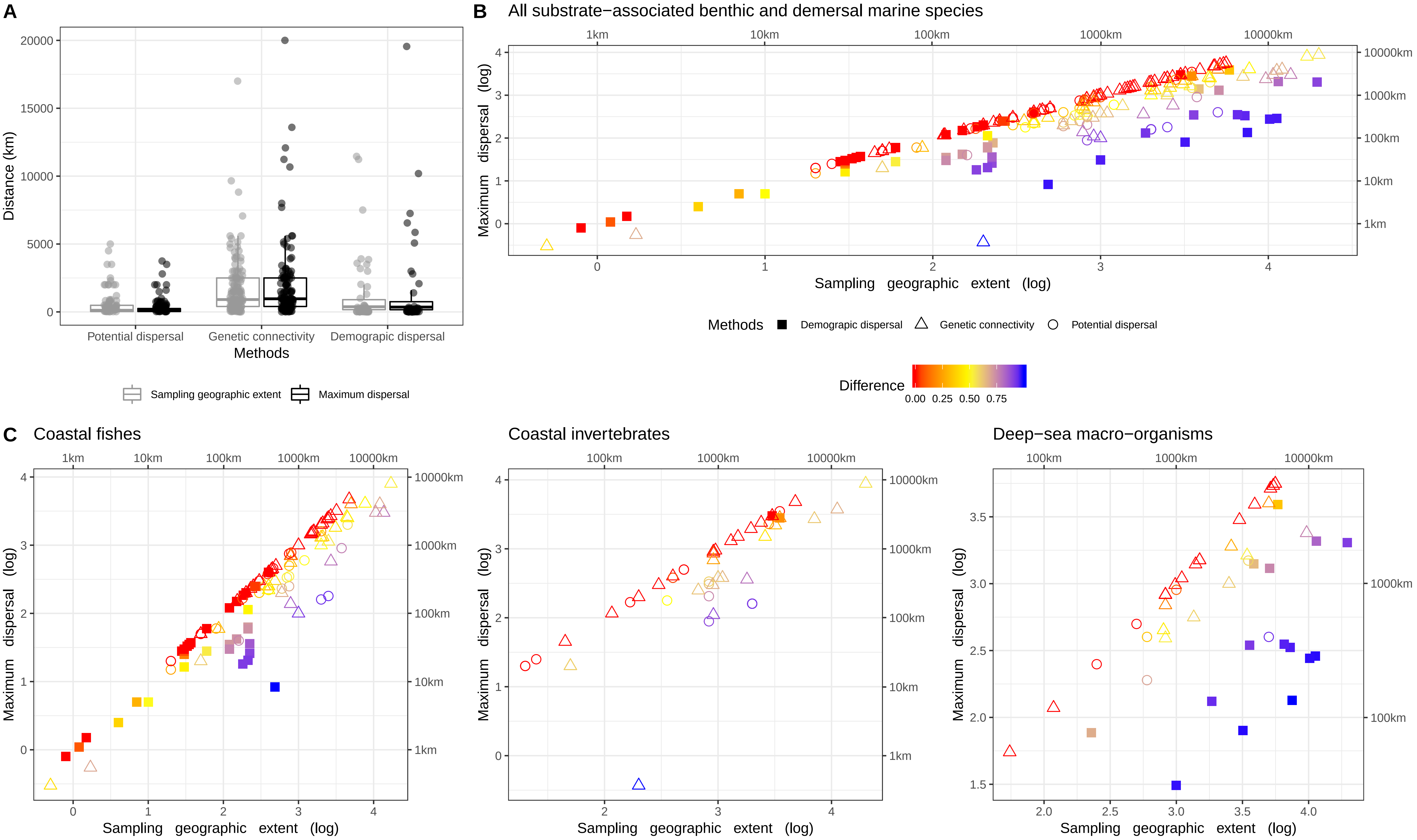
Highlights

- Marine dispersal estimates are limited by the spatial scale of sampling design and therefore biased downwards;
- Active larval behavior, oceanographic eddies and fronts, tsunamis, marine debris and translocations are potentially important, but overlooked, dispersal vectors over long distances;
- The largest marine reserves have the highest potential for massive and long-distance benefits, but are the most isolated ones;

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

Box 3: Outstanding questions Box

- What proportion of the dispersal kernel of marine species are we missing when we do not consider the long-distance (>40 km) dispersal?
- Is the restricted spatial scale of sampling designs the only or main cause of the limited geographical dispersal reported in the sea?
- What are the quantitative effects of marine reserves at long distances (>40 km)?
- Is the unknown long-distance dispersal sufficient to connect large isolated marine reserves?
- To which extent future marine reserve networks should be composed of few but large reserves instead of many small when we consider species long-distance dispersal?

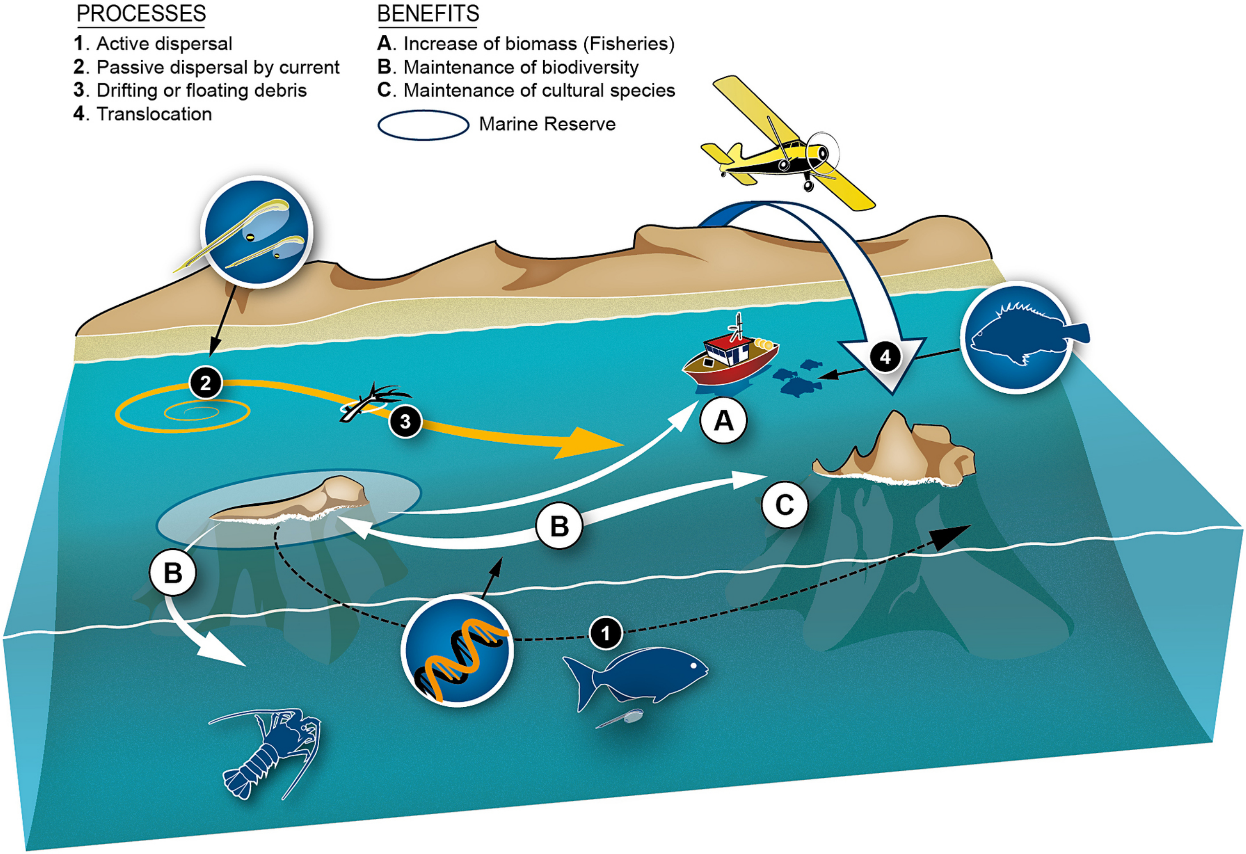


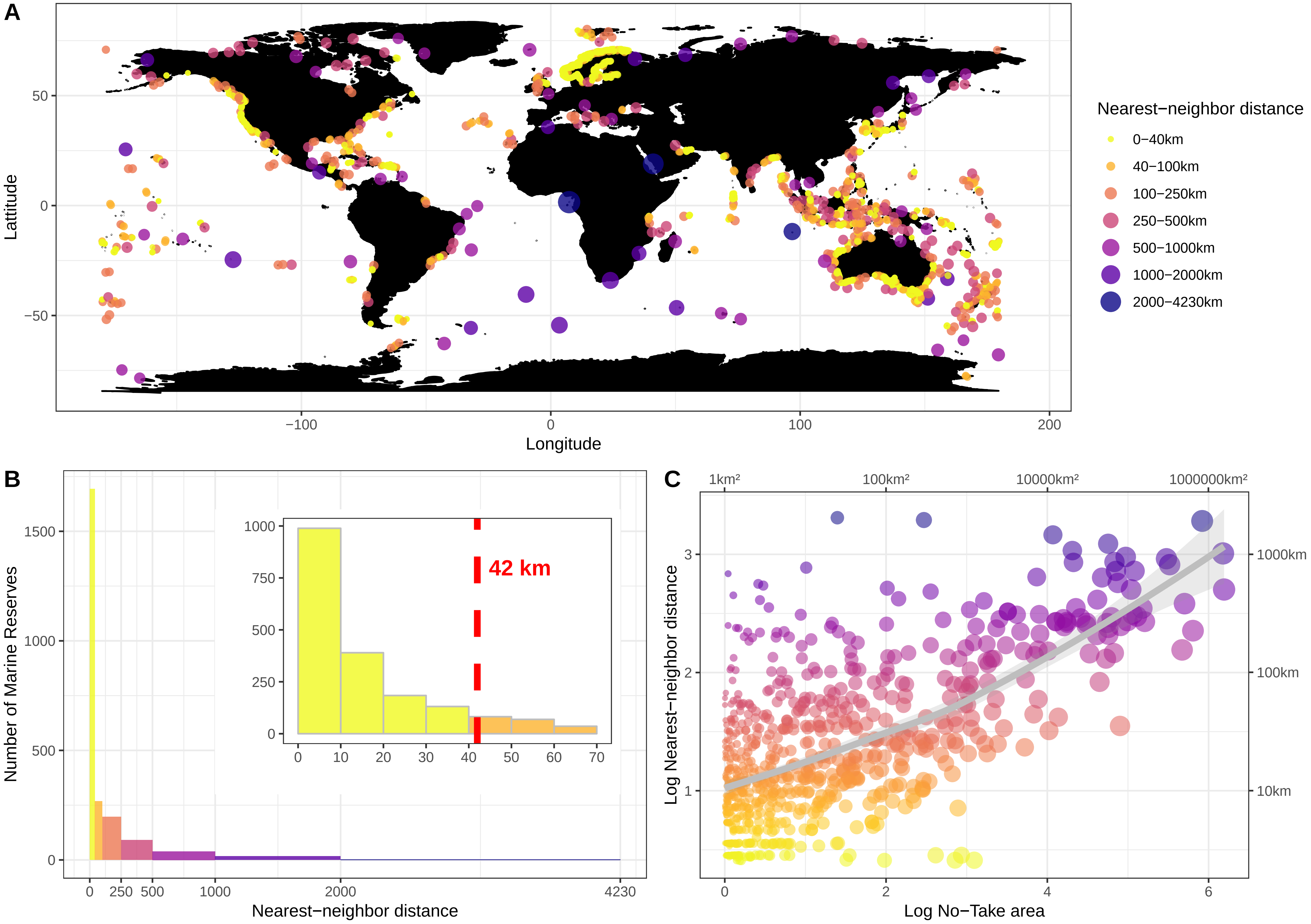
All substrate−associated benthic and demersal marine species

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
4
2
3
A
C
B
B
1


A
Latitude
50
0
−50
Longitude
−100
0
100
200
Nearest−neighbor distance
0−40km
40−100km
100−250km
250−500km
500−1000km
1000−2000km
2000−4230km
B
Number of Marine Reserves
0
500
1000
1500
Nearest−neighbor distance
0
250
500
1000
2000
4230
1000
750
500
250
0
0
10
20
30
40
50
60
70
42 km
C
1km²
100km²
10000km²
1000000km²
Log Nearest−neighbor distance
1
2
3
10km
100km
1000km
Log No−Take area
0
2
4
6