
Long-Distance Marine Connectivity: Poorly Understood but Potentially Important

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20 **Most Marine Protected Areas are not islands**

21 We agree with Costello & Connor [1] that most marine reserves should not be considered as
22 totally isolated islands. On the other hand, the marine environment is not a homogeneous
23 habitat either. Landscape connectivity quantifies the extent to which the movements of genes,
24 propagules and individuals between populations (i.e. dispersal) are facilitated or hindered by
25 the structure and composition of the landscape [2]. Landscape [3] and seascape [4,5] genetics
26 in particular provide a framework (concepts, tools, community) that considers explicitly the
27 suitability of habitats outside marine reserves for the estimation of genetic connectivity [6].
28 Yet, although tools are available (Box 1), the vast majority of studies that estimate
29 connectivity in the context of marine conservation and strategic management planning still
30 ignore seascape resistance models (Box 1). In this respect, it is true that marine reserves in
31 particular, and marine populations more generally are often envisioned as islands. We
32 advocate for sampling designs that are more continuous across the landscape, including areas
33 and populations inside and outside marines reserves but also in between (e.g. [7]).

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35 **Long-distance connectivity is poorly understood**

36 Since the contribution of long distances (i.e. >40km) to marine dispersal kernels is currently
37 unknown [8], we cannot yet provide strong recommendations for the spacing among marine
38 reserves on the basis of long-distance connectivity. We suggest that long-distance dispersal is
39 likely to have been underestimated [8]. However, this does not necessarily imply that it is
40 important from a demographic perspective, nor that the role of local retention and local
41 dispersal, for which evidence has accumulated over the last two decades, is not. Furthermore,
42 long-distance dispersal events are expected to be rare, which has implications at different
43 spatial and temporal scales than local dispersal events. On the other hand, long-distance

44 connectivity could also result from more frequent stepping-stone dispersal events over several
45 generations. By no means, does our review suggests that dispersal, because it is spatially
46 extensive, is not important for conservation and management planning. We believe, on the
47 contrary, that seascape connectivity studies are needed to advise on the minimal distance
48 among marine reserves. In this respect, we concur with Costello & Connor [1] that future
49 connectivity studies should account for the seabed and water column habitat, as well as
50 fishing pressure within these habitats. Seascape genetics opens promising perspectives to do
51 so. It will also open perspectives to forecast the effect of climate change on species range
52 shifts accounting for connectivity [9].

53

54 **Long-distance connectivity is potentially important for threatened marine biodiversity**

55 Many marine species are overexploited and threatened [10]. Long-distance dispersal can
56 potentially connect distant and isolated populations within marine reserves and sustain
57 biodiversity and biomass in exploited areas located more than 40 km from marine reserve
58 boundaries. Rare long-distance dispersal from marine reserves due to a few successful
59 migrants can also be sufficient to re-colonize areas where local populations have been
60 extirpated, or expand species distributions in response to global change. Long-distance
61 dispersal between populations that are genetically differentiated or locally adapted can
62 moreover contribute to limiting inbreeding, increasing genetic diversity, and facilitating
63 adaptation to a changing environment. One open question here is to what extent long-distance
64 dispersal contributes to connect the largest marine reserves (>1000 km²) in the global
65 network, which can provide the greatest benefits but are also the most isolated ones (closest
66 reserves >359 km) [8].

67 **Spatial planning should be multi-specific and multi-objectives**

68 We agree with Costello & Connor [1] that planning should focus on area and creation of
69 reserve networks that contain representative range of habitat. However, without consideration
70 for connectivity, efficiency of marine protected networks will be lower. A recent conservation
71 planning study showed that combining representation and connectivity objectives provides the
72 best strategy for enhanced biodiversity persistence in network of marine reserves [11].
73 Therefore, we do not recommend disregarding connectivity in conservation and management
74 planning, but instead to develop multi-species and multi-objective strategies. Such
75 applications are still scarce not only in marine but also terrestrial systems, but again the tools
76 are available [11]. We agree with Costello & Connor [1] that such multi-objective strategies
77 should also account for a representative range of benthic and pelagic habitats within
78 biogeographic realms [12].

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81 **Box 1: Connectivity between marine ecosystems – Seascape genetics**

82 Seascape genetics integrates the concepts and tools used to describe the patterns and
83 understand the processes of marine connectivity in a spatially explicitly context that considers
84 habitat characteristics.

85

86 (i) The first step to estimate marine connectivity in a seascape genetics context is the
87 assessment of resistance surfaces from seascape variables. Resistance surfaces are spatial
88 layers that represent the extent to which the conditions in each grid cell covering the study
89 area constrain movement or gene flow ([6], chap 8, p129-144). Seascape variables include
90 current flow, habitat, climatic variables, bathymetry, chlorophyll etc, as well as fishing data
91 that are increasingly publicly available¹. Seascape variables are then converted to resistance
92 cost surfaces and costs are assigned ranging from 1 (no resistance to movement) to 100
93 (strong barriers to movement). Cost can be determined by expert opinion or estimated from
94 genetic data.

95 (ii) A second step is the conversion of the resistance surface into a seascape connectivity
96 measure (i.e. a matrix of connectivity distances). Such conversion is typically based on least-
97 cost paths or circuit theory ([6], chap 8, p129-144). Least-cost analysis identifies the least
98 costly route that an organism can take from one area to another, while the circuit theory
99 approach ([6], chap 8, p129-144) calculates resistance matrices between populations or
100 individuals and estimates all potential movement pathways across the landscape based on the
101 cumulative cost of movement due to landscape resistance.

102

103 (iii) Finally, the connectivity measure resulting from resistance surface is correlated to genetic
104 distances to detect statistically significant seascape drivers of genetic differentiation and to
105 select the most important drivers to be used for estimating resistance surfaces. Various

106 approaches can be used to assess the correlation between genetic distance and multiple
107 seascape distances: multiple regression on distance matrices or mixed linear model
108 accounting for non-independence of pair-wise matrix data ([6], chap 5, p77-96).

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111 1- see [4] for an exhaustive list. Additional links are:

112 www.gebco.net ; <http://gmed.auckland.ac.nz> ; www.oracle.ugent.be

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