

## Habitat-specific larval dispersal and marine connectivity: implications for spatial conservation planning

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**Abstract.** Connectivity via larval dispersal is an important ingredient in setting effective marine reserve networks. Simple guidance for establishing spacing between individual protected sites can provide reliable rules of thumb to help ensure connectivity. Spacing rules for protected network design are relatively new to marine spatial planning, though so far they have been generically and indiscriminately applied to all types of habitats based on a single range of distance values. Here we address the extent to which such rules capture subtleties associated with dispersal distances varying among species in different regions and habitats. We applied a 50–100 km global spacing rule ( $SR_{glob}$ ), also recently applied in the California Marine Life Protection Act (MLPA) process and based on available global larval dispersal data, to a previously assessed network in the Gulf of California. Using larval dispersal data for species within this region ( $SR_{reg}$ ), we associated each species with eight unique habitats ( $SR_{hab^*}$ ) and we evaluated connectivity by means of different spacing rules ( $SR_{glob}$ ,  $SR_{reg}$  and  $SR_{hab^*}$ ) using graph-theory. The existing spacing rule employed by the MLPA process ( $SR_{glob}$ ) was found to be robust and conservative when applied to the Gulf of California or to its different habitats (i.e., the lower limit for dispersal distance includes the distance for all species in the Gulf). We found that species in different habitats exhibit statistically distinct dispersal profiles. Therefore, some habitats could be evaluated with more relaxed spacing rules (i.e., larger distances), than those proposed by the rules of thumb. Our work identifies a conservation planning trade-off when implementing spacing rules: already proposed rules are robust but at the cost of efficiency. Habitat-specific spacing rules should be considered for more efficient marine conservation planning solutions.

**Key words:** graph theory; Gulf of California; larval dispersal; marine connectivity; Marine Life Protection Act; marine protected areas networks; rules of thumb; spacing rules.

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### INTRODUCTION

Marine Protected Areas (MPAs) are known to enhance the abundance, size and diversity of species (Halpern 2003, Lester et al. 2009, Claudet

et al. 2010). To meet the large-scale conservation challenges facing ocean ecosystems, several nations are building networks of MPAs (Mora et al. 2006, Planes et al. 2009, Gaines et al. 2010). Doing so successfully requires a detailed under-

standing of the ecological and physical characteristics of ocean ecosystems. Ideally, for MPA networks to be successful in protecting marine populations, individual MPAs must be adequately connected to other MPAs via larval dispersal or adult movement to promote recovery from eventual local extinctions (Sala et al. 2002, Shanks et al. 2003, Planes et al. 2009, Gaines et al. 2010). To ensure such connectivity, maximum spacing between MPAs can be set as a rule of thumb to allow some larval exchange between them (Shanks et al. 2003, Palumbi 2004, Halpern et al. 2006). In this paper, we examine the reliability of general rules of thumb to alternative assumptions about larval dispersal patterns. As an applied example, we consider the relevance of the simple rules of thumb recently employed by the Californian Marine Life Protection Act (hereinafter MLPA) process to the Gulf of California, Mexico. The Gulf of California is considered a conservation priority area both in Mexico as well as internationally due to its high productivity and diversity values (Carvajal et al. 2004).

The development of general guidelines for the design of MPA networks represents an urgent need for policy makers and managers (Foley et al. 2010). While complex simulation modeling tools may be informative about the effects of any conservation action, these models are highly time-consuming and expensive. These spatially-explicit larval dispersal models are mainly based on coupling the biological parameters of larval dispersal with dynamic physical oceanographic data (Tremblay et al. 2008). There is an acute need for simple and robust rules of thumb to design MPA networks in a cost-affordable and timely manner (Moffitt et al. 2011). At the same time, the design of MPA networks should be a bottom-up process (Agardy 2005), with proposals originally made by stakeholders (as in the MLPA process) and evaluated by a technical-scientific-management panel. This is an iterative process where stakeholders improve their protection proposals using 'evaluation tools' that they both understand and believe. Modeling tools are often not understood or trusted by stakeholders, and in such cases rules of thumb may be particularly useful (Airmé et al. 2003). Thus, general rules of thumb not only play an important role in the scientific evaluation of MPA networks, but they also allow

bottom-up decision processes (involvement of stakeholders), which are basic in the design of conservation actions (Klein et al. 2008).

Spacing guidelines have been proven as a simple and useful way for MPA network design, although their efficacy varies with the spatial ecology of the species (Moffitt et al. 2011). These guidelines have been used in the MPA network design process recently completed along the coast of California, USA (CDFG 2013). Implementation of the California MLPA has been one of the most sophisticated marine reserve design processes carried out to date. Among the employed criteria, a spacing rule checks for connectivity of the protected habitat in a simple way since it requires protected patches of the same habitat to be less than 50–100 km apart (CDFG 2013). This guideline was based on available knowledge of the distribution of larval dispersal distances of fish species (CDFG 2013).

Spacing rules have so far been generic distance values that are applied indiscriminately to all habitats and species (Moffitt et al. 2011). In the MLPA process, for example, the connectivity of each habitat type is evaluated separately but the threshold value (50–100 km) is the same for all types of habitats. However, under the assumption of a close relationship between habitats and differential fish assemblages (Ward et al. 1999, Mumby et al. 2008, Dalleau et al. 2010), dispersal distances might be different among species inhabiting different habitats. Species inhabiting a given habitat may present average dispersal distances below the generic spacing value and thus this habitat would be under-connected. In contrast, habitats harboring species with dispersal distances above the spacing rule would be connected beyond sufficiency. In this latter case, the MPA network would include some habitat patches that are not strictly needed (from a connectivity perspective). Identifying such situations could yield a more efficient design of MPA networks.

The Gulf of California offers a prime study area for evaluating these alternative spacing rules, given its diversity of habitats, proximity to California MLPA target region, and history of marine spatial planning, yet continued need for reserve design implementation. In 2006, a marine ecoregional assessment for the Gulf of California and the near-shore Pacific coast of southern Baja



Fig. 1. MPA network proposal for the Gulf of California. Colored polygons represent different priority areas ( $n = 54$ ). This proposal is derived from the EcoRegional Assessment for Marine Conservation: Gulf of California and west coast Southern Baja California Peninsula (Ulloa et al. 2006).

California was conducted in order to identify geographic priorities based on the status of biodiversity, habitat condition, threats and socio-political conditions in the ecoregion (Ulloa et al. 2006; Fig. 1). This analysis identified 54 priority areas for conservation covering 26% of the ecoregion. In this paper, we address the extent to which simple rules of thumb capture subtleties associated with regional and habitat-specific dispersal. Our general approach was to compare the MLPA spacing rule ( $SR_{glob}$ ), which was derived from species dispersal distances around the globe, with new spacing rules specific for the Gulf of California but providing the same

level of connectivity as the MLPA process (CDFG 2013). Specifically, we calculated a spacing rule based on a subset of species found in the Gulf of California region ( $SR_{reg}$ ) and another set of rules further differentiating species found in specific habitats in the region ( $SR_{hab*}$ ). We then applied the three different spacing rules ( $SR_{glob}$ ,  $SR_{reg}$ ,  $SR_{hab*}$ ) to the proposed network of 54 priority areas for conservation. The differences in network connectivity resulting from different spacing rules were assessed by means of graph-theory metrics. Our work provides insight on understanding connectivity in the Gulf of California as well as understanding the efficacy of

the proposed MPA network in conserving habitats.

## METHODS

### *Regional and habitat specific spacing rules*

The MLPA Science Advisory Team assumed that patches of the same habitat within a range of 50–100 km were connected (CDFG 2013). Under this spacing rule (50–100 km), all protected patches would be connected for species with dispersal distances larger than 100 km, but isolated for species with dispersal distances smaller than 50 km. For those species with dispersal distances between 50 and 100 km, the network of protected habitat patches would be composed of a number of isolated sub-networks. This represents a tradeoff to protect the intended majority of species with greater dispersal distances so as to not require the entire coastline to be a reserve in order to fully conserve the short distance dispersers. The value of 50–100 km employed in the MLPA process is based on available knowledge of the frequency distribution of larval dispersal distances of fish species worldwide (CDFG 2013), and thus it can be considered a global spacing rule ( $SR_{glob}$ ) for all fish species (i.e., not specific to any particular area). It should be noted that other taxonomic groups, such as invertebrates and algae, presumably would require much shorter inter-patch distances to ensure connectivity among MPAs (Kinlan and Gaines 2003), and were not considered here. Spacing rules have been proposed for ranges from 10–20 km (Shanks et al. 2003) to 100 km (Sala et al. 2002). In this sense, the 50–100 km interval evaluated in this work represents the upper half of the values proposed for MPA spacing in the scientific literature. Our goal is assessing to what extent applying this generic spacing rule for different marine systems (i.e., regions or habitats) might produce conservation inequalities, with some systems showing higher connectivity levels than others. In other words, are regional or habitat specific spacing rules more appropriate as compared to a global rule?

We first calculated the percentage of fish species whose populations are connected under  $SR_{glob}$ , i.e., percentages of species at dispersal distances larger than 50 and 100 km separately to identify the range. Since 50–100 km is a generic

value not specific to any particular area, we built a frequency distribution of global dispersal distances based on data from Lester et al. (2007). This dataset is comprised of pelagic larval duration data for 499 demersal fish species of many different taxonomic groups, regions and ecosystems worldwide, and constitute the most comprehensive worldwide database of pelagic larval duration on fishes to date. Pelagic larval duration values were transformed to dispersal distance values based on the relationship  $DD = 1.33 \times PLD^{1.30}$ , where PLD is pelagic larval duration and DD is dispersal distance (Siegel et al. 2003). Although the use of pelagic larval duration may introduce some bias in the estimation of dispersal distance (e.g., Shanks 2009, but see Faurby and Barber 2012), this method allow us to evaluate the connectivity for a large number of species worldwide. Use of more refined estimators (e.g., Thorrold et al. 2006, Bradbury and Bentzen 2007) is only possible for a tiny subset of these species, which would render comparison among habitats in the Gulf of California impossible.

A regional spacing rule for the Gulf of California ( $SR_{reg}$ ) was also obtained by calculating for the subset of species present in the Gulf the same connection level as the  $SR_{glob}$ , i.e., the distance range that protected the same percentage of species as the  $SR_{glob}$ . For this purpose, we first constructed a frequency distribution of dispersal distances by selecting from the global dataset (Lester et al. 2007) those species that are listed in different regional species lists (Appendix A) as being present in the Gulf of California. The  $SR_{reg}$  was then defined as the distance range that protected the same percentage (i.e., quantile) of species as the  $SR_{glob}$ . In the same way, we also estimated habitat-specific spacing rules in the Gulf ( $SR_{hab*}$ ). We obtained habitat-specific frequency distributions of dispersal distances by assigning each of the species present in the Gulf to a given habitat based on a literature review (Thomson et al. 1979, Allen and Ross 1994, Froese and Pauly 2011; Appendix B). The main marine habitats present in the Gulf were obtained from Ulloa et al. (2006), resulting in the mapping of eight habitats (Table 1). We then defined the  $SR_{hab*}$  by calculating for the subset of species present in each habitat the distance range that provided the same connection level as the



Table 1. Spacing rules determined by inclusion of all species globally (per MLPA process), or limited to those species found regionally in the Gulf of California and various habitats within the Gulf. Spacing rules, including lower, middle and upper limits values, are determined by the distance (in km) needed to connect the same proportion (55–94%) of fish species as the MLPA spacing rule (50–100 km) between reserve patches.

Species constraint	Species	Patches	Spacing rule		
			Lower (km at 94%)	Middle (km at 76%)	Upper (km at 55%)
Global (MLPA)			50		100
Regional (Gulf)	64		64.8	84.8	118.3
Habitat-specific					
Sandy beach	11	86	79.0	95.4	119.1
Rocky shores	48	80	63.6	81.2	105.5
Estuary	9	55	74.0	78.2	105.2
Rocky reefs	49	127	63.7	81.6	106.7
Hard 0–30 m	52	39	63.9	82.3	109.8
Hard 30–100 m	30	38	74.0	108.5	156.5
Soft 0–30 m	20	98	84.7	107.0	129.4
Soft 30–100 m	15	131	90.5	117.7	156.1

$SR_{glob}$ .

We tested for differences in the original frequency distributions of dispersal distances to compare different spacing rules ( $SR_{glob}$ ,  $SR_{reg}$ ,  $SR_{hab^*}$ ). The strongly imbalanced sample size of the different groups prevented use of classic parametric tests (Zar 1996), thus we used randomization tests (Manly 2007). For testing differences in the mean values of the dispersal distances in the simplest comparison of two groups, such as  $SR_{glob}$  vs  $SR_{reg}$  with sample size  $n_{glob}$  and  $n_{reg}$ , we first pooled the dispersal data of the two groups, randomly split the dataset into two groups of size  $n_{glob}$  and  $n_{reg}$  and calculated the difference between their means. We repeated this process 10000 times to obtain the distribution of our statistic (differences in the means) under the null hypothesis that there were no differences between the groups. The null hypothesis is rejected if the observed difference in the mean for the two groups falls below the 2.5th or beyond the 97.5th percentile of the distribution (two-tailed test). When testing for differences between more than two groups, the statistic employed was the sum of the absolute values of all pair-wise differences in the means. Also worthy of note: when performing multiple pair-wise comparisons for a randomization test, the Bonferroni correction doesn't apply as in classical parametric tests (Churchil and Doerge 1994, Cheverud 2001).

### Conservation planning in the Gulf of California

To examine the policy and spatial planning implications of using global ( $SR_{glob}$ ), regional ( $SR_{reg}$ ) or habitat-specific ( $SR_{hab^*}$ ) spacing rules, we considered the three scenarios for the network of 54 priority areas in the Gulf of California proposed by Ulloa (2006; Fig. 1). This ecoregional plan has been subsequently complemented with a national prioritization effort (CONABIO-CONANP-TNC-PRONATURA 2007). This more recent analysis mainly expands some conservation sites; in particular the 14 sites located in the northern Gulf are merged into two large conservation areas. For our analyses we rely on the original network of 54 priority sites, which allows us to consider a spatial scale of conservation sites that is relevant to connectivity. However because these two proposals largely match, our connectivity analysis is relevant to both planning efforts.

Connectivity under the three spacing rules was measured by means of two basic metrics from graph theory: the edge/node ratio and the number of components. The former indicates the ratio between the number of connections and the number of patches being positively related to network connectivity, whereas the latter reflects the number of isolated or non-connected sub-networks present in the whole network and is negatively related to connectivity. Graph analysis was performed using the *igraph* package in R (R Development Core Team 2010). Inter-patch distances were assessed using the *raster* library in R

(R Development Core Team 2010). To do this, the habitat maps were transformed to a raster map of  $1 \times 1$  km cell size and we calculated the shortest path between groups of cells (i.e., patches), taking into account cells that cannot be traversed (i.e., with land in between).

## RESULTS

### *Regional- and habitat-specific spacing rules*

Our dispersal distance data for 64 fish species in the Gulf of California comprised 22 different families (Appendix A). The number of species in each habitat ranged from 52 (for hard substrate from 0 to 30 m deep) to 9 (for estuaries) (Table 1 and Appendix B). Probability density functions for estimates of larval dispersal distances from the region of the Gulf and the habitat-specific groups are shown in Fig. 2.

Considering fish species globally ( $n = 499$ ; Lester et al. 2007), 94% of all the species have dispersal distances of more than 50 km and 55% have dispersal distances of more than 100 km (Fig. 2). Therefore the  $SR_{glob}$  (50–100 km) provides connectivity for 55–94% of the species worldwide. Strong variations exist when considering habitat-specific groups of species in the Gulf (Table 1). In particular, when applying the  $SR_{glob}$  the largest variability and lower degree of protection was detected for estuarine species (100% of all the species have dispersal distances of more than 50 km but only 44% have distances of more than 100 km), whereas for species associated to hard and soft bottoms at 30–100 m depth, protection was the largest (100% for 50 km and 80% for 100 km dispersal distances).

If the goal in the Gulf of California is to provide connectivity levels similar to those provided by the  $SR_{glob}$ , the spacing rule in the Gulf ( $SR_{reg}$ ) should be slightly larger (65–120 km) (Table 2). Habitat-specific spacing rules in the Gulf could also be less restrictive, particularly for hard and soft bottoms at 30–100 m depth (habitats 6 and 8:  $SR_{hab6} = 74$ –157 km;  $SR_{hab8} = 90$ –156 km) (Table 2).

Regarding the comparison of the different spacing rules ( $SR_{glob}$ ,  $SR_{reg}$ ,  $SR_{hab*}$ ), randomization tests revealed significant differences among the mean dispersal distances of the eight habitats ( $p = 0.0101$ ). Pair-wise comparisons showed that differences were statistically significant ( $p <$

0.025), particularly between soft bottom habitats at depth 30–100m (marginally at depth 0–100 m) and the remaining habitats (Appendix C). In contrast, pair-wise differences were smaller than expected by chance ( $p > 0.975$ ) between mean values of rocky shores and rocky reef habitats and marginally between sandy beach, rocky shores, and rocky reef habitats. This indicated that for dispersal purposes, these habitats are probably better represented as a combined habitat. Dispersal distances of fish globally were not statistically different from those for the Gulf of California ( $p = 0.8954$ ).

### *Evaluation of the network for different spacing rules*

The number of patches included in the network proposal for the Gulf of California varied among habitats, ranging from 38 to 131 (shallow hard and soft bottom habitats, respectively). Overall, results indicated a stronger connectivity for all habitats and for the connectivity metrics employed when considering a regional ( $SR_{reg}$ ) spacing rule rather than the global ( $SR_{glob}$ ) spacing rule (Table 3). In turn, there was stronger connectivity when considering habitat-specific ( $SR_{hab*}$ ) spacing rules rather than the regional ( $SR_{reg}$ ) spacing rule.

The least interconnected network of protected patches, as measured by the edge/node ratio, corresponded to estuaries. On average, each patch of protected estuarine habitat is connected to 1–2 other patches, however the edge/node ratio varies depending on the specific spacing rule applied. The habitats with the largest edge/node ratio are soft bottoms at 30–100 m depth followed by rocky reefs. In soft bottoms at 30–100 depth, each protected patch is on average connected to 3–10 patches, although the exact mean number varies depending on the spacing rule used for the evaluation (3–6 according to  $SR_{glob}$ ; 5–10 according to  $SR_{hab*}$ ).

When using the number of clusters as a measure of connectivity, sandy beach and rocky reefs were the least connected habitats. In both cases, the network of protected patches contained up to 18 isolated sub-networks. However, the number depends on the spacing rule applied for the evaluation and there was large variation along the lower and upper limit of the spacing rules. Differences in the evaluation among

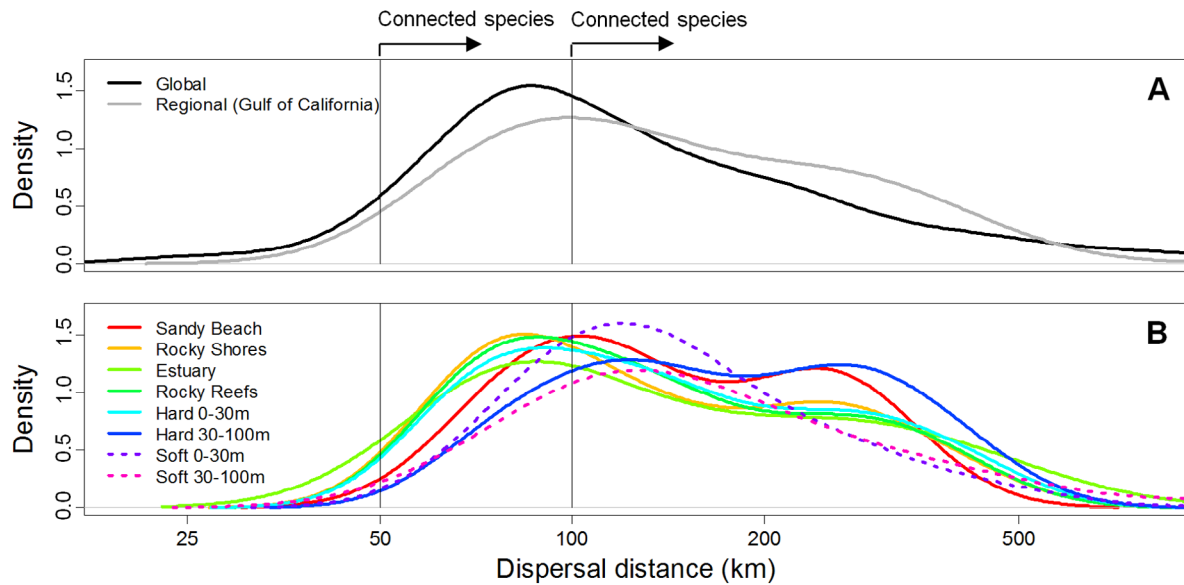


Fig. 2. Probability density functions of larval dispersal distances for species globally and those specific to the Gulf of California (A), and limited to habitats within the Gulf (B). Dashed lines represent the two soft-bottom habitats showing statistical differences in their dispersal distances from the other habitats. In both cases the vertical lines indicate the limits of the spacing rule used in the MLPA ( $SR_{glob}$ ) (50–100 km). The proportion of species protected under a given spacing rule, are those having dispersal distance greater than the spacing rule value (i.e., to the right of the vertical line).

Table 2. Dispersal distances (mean  $\pm$  SD) and proportion of species connected by inter-patch distances of 50 or 100 km (per MLPA process) applying only species constrained to the given spacing rule. Mean and standard deviation in kilometers are given for dispersal distance. For instance, limiting species to those found within the Gulf of California region yields a mean dispersal distance of 272 km. Patches within 50 km of each other allow for larval connectedness for 100% of the species, but only 66% of these species have dispersal distances exceeding 100 km.

Species constraint	Dispersal distance (km)	50 km (%)	100 km (%)
Global (MLPA)	201 $\pm$ 322	94	55
Regional (Gulf)	272 $\pm$ 496	100	66
Habitat-specific			
Sandy beach	163 $\pm$ 83	100	73
Rocky shores	161 $\pm$ 103	100	58
Estuary	175 $\pm$ 129	100	56
Rocky reefs	160 $\pm$ 103	100	61
Hard 0–30 m	168 $\pm$ 109	100	65
Hard 30–100 m	198 $\pm$ 108	100	83
Soft 0–30 m	385 $\pm$ 709	100	80
Soft 30–100 m	623 $\pm$ 948	100	87

Table 3. Evaluation of the connectivity of the MPA network proposal for eight habitats in the Gulf of California using two metrics: edges/node ratio (top) and the number of clusters (bottom). See *Methods* for a description of these metrics. In each case, for each habitat the MPA network proposal in the Gulf is evaluated by means of the three spacing rules  $SR_{glob}$ ,  $SR_{reg}$ ,  $SR_{hab}^*$  (see Table 1 for the values). For each spacing rule the metrics for the upper and lower limits are given.

Species constraint	Patches	$SR_{glob}$	$SR_{reg}$	$SR_{hab}^*$
Edges/nodes ratio				
Sandy beach	84	1.35–2.40	1.61–3.02	1.84–3.11
Rocky shores	75	1.72–3.27	2.07–3.92	2.04–3.45
Estuary	52	1.11–1.71	1.27–1.90	1.37–1.73
Rocky reefs	123	2.25–5.36	3.08–6.62	3.02–5.88
Hard 0–30 m	39	1.44–2.90	1.74–3.51	1.72–3.26
Hard 30–100 m	38	1.37–2.66	1.71–3.18	1.95–4.05
Soft 0–30 m	97	2.15–4.18	2.74–4.92	3.62–5.57
Soft 30–100 m	131	2.68–5.68	3.57–6.82	5.07–9.76
Number of clusters				
Sandy beach	84	18–5	15–4	9–4
Rocky shores	75	15–8	15–6	15–6
Estuary	52	14–7	12–7	11–7
Rocky reefs	123	20–6	16–4	17–4
Hard 0–30 m	39	11–5	9–5	9–5
Hard 30–100 m	38	9–6	7–6	7–4
Soft 0–30 m	97	10–3	7–2	3–2
Soft 30–100 m	131	9–2	5–2	2–2

spacing rules were evident when considering the number of resulting clusters (Table 3). In the case of soft bottoms at 30–100 m depth (and considering the lower limit of the SR), the application of the  $SR_{glob}$  (50 km) yields the existence of 9 clusters, the  $SR_{reg}$  (65 km) yields 5 clusters, and the  $SR_{habSD}$  (90 km) yields only two clusters (Fig. 3). This habitat, evaluated with the habitat-specific spacing rule, is the most connected among the eight habitats in this study. Large differences in the connectivity levels also arise in more weakly connected habitats, such as sandy beaches. Considering the lower limit of the SR, the application of the  $SR_{glob}$  (50 km) yields the existence of 18 clusters, the  $SR_{reg}$  (65 km) yields 15 clusters, and the  $SR_{habSB}$  (79 km) yields 9 clusters (Fig. 4).

## DISCUSSION

Addressing connectivity of MPA networks has been identified as a key frontier in marine conservation research (Gaines et al. 2010). In order to maximize the efficiency of size and spacing rules, we need first to assess their general reliability (e.g., Moffit et al. 2011). Here, we examine the extent to which such existing rules of thumb perform in the context of dispersal distances varying among species in different regions and habitats. The results from this study may be used to evaluate connectivity of different habitats and how this inter-habitat variability may affect the efficiency of marine conservation planning actions.

Our results show that the existing spacing rule employed in the MLPA process ( $SR_{glob}$ ), which requires MPA to be within 50 and 100 km, is very robust when applied to the Gulf of California. The robustness of the  $SR_{glob}$  relies in that fact that it is strongly conservative. The lower limit (50 km) includes the dispersal distance of 94% of the species globally (according to the database in Lester et al. 2007) and all the species (100%) in the Gulf for which their dispersal distance is available. The higher limit of the  $SR_{glob}$  (100 km) includes 55% of all species at a global scale and 66% in the Gulf.

While much work has been conducted on taxon-specific dispersal distances (e.g., Shanks et al. 2003), there has been little research on habitat-specific dispersal. Our work reveals remarkable

differences in the dispersal distances of species across different habitats. In particular, we found that: (1) deep water species generally possess larger dispersal rates than the species inhabiting most of the remaining habitats, and (2) species inhabiting rocky shores, sandy beaches and rocky reefs have shorter dispersal distances and are strongly similar.

These results indicate that some habitats may be included in marine reserve designs with more relaxed rules (larger distances) than those proposed by the  $SR_{glob}$  or by the  $SR_{reg}$ . This is particularly true for deeper habitats that present  $SR_{hab*}$  values that do not largely overlap with the  $SR_{glob}$  or the  $SR_{reg}$  (Table 1). Such is the case for rocky shores and deep soft bottom habitats, whose spacing rules have to be 64–105 km and 90–156 km respectively, to ensure conservation levels similar to that provided by the MLPA. As a consequence of this variability in habitat-dependent spacing rules and dispersal distances, the evaluation of protected habitat networks strongly differs in some habitats depending on the employed spacing rule. For example, the evaluation of soft bottom habitat at 30–100m depth with  $SR_{glob}$  or  $SR_{reg}$  would conclude that further conservation planning efforts are needed to ensure connectivity of this habitat, whereas the evaluation of this habitat by means of a habitat-specific spacing rule reveals that all the conservation sites inside the Gulf of California are adequately connected (Fig. 3). As a consequence, the use of habitat-specific spacing rules promotes more efficient marine conservation planning. These results highlight a conservation planning trade-off when implementing spacing rules: the generic spacing rule  $SR_{glob}$  is robust (since it is highly conservative) but at the cost of efficiency, since its application may yield redundant sites for connectivity purposes. This situation will be exacerbated when more restrictive spacing rules (i.e., <50 km) are used.

A further implication of the existing differences in the dispersal distances among different habitats is that for a given target study area, its overall dispersal profile will depend on the representation of the different habitats in the area. In our case, results show that the connectivity of all the species of the Gulf of California as a whole were adequately addressed by the generic  $SR_{glob}$ . However, it is clear that this will



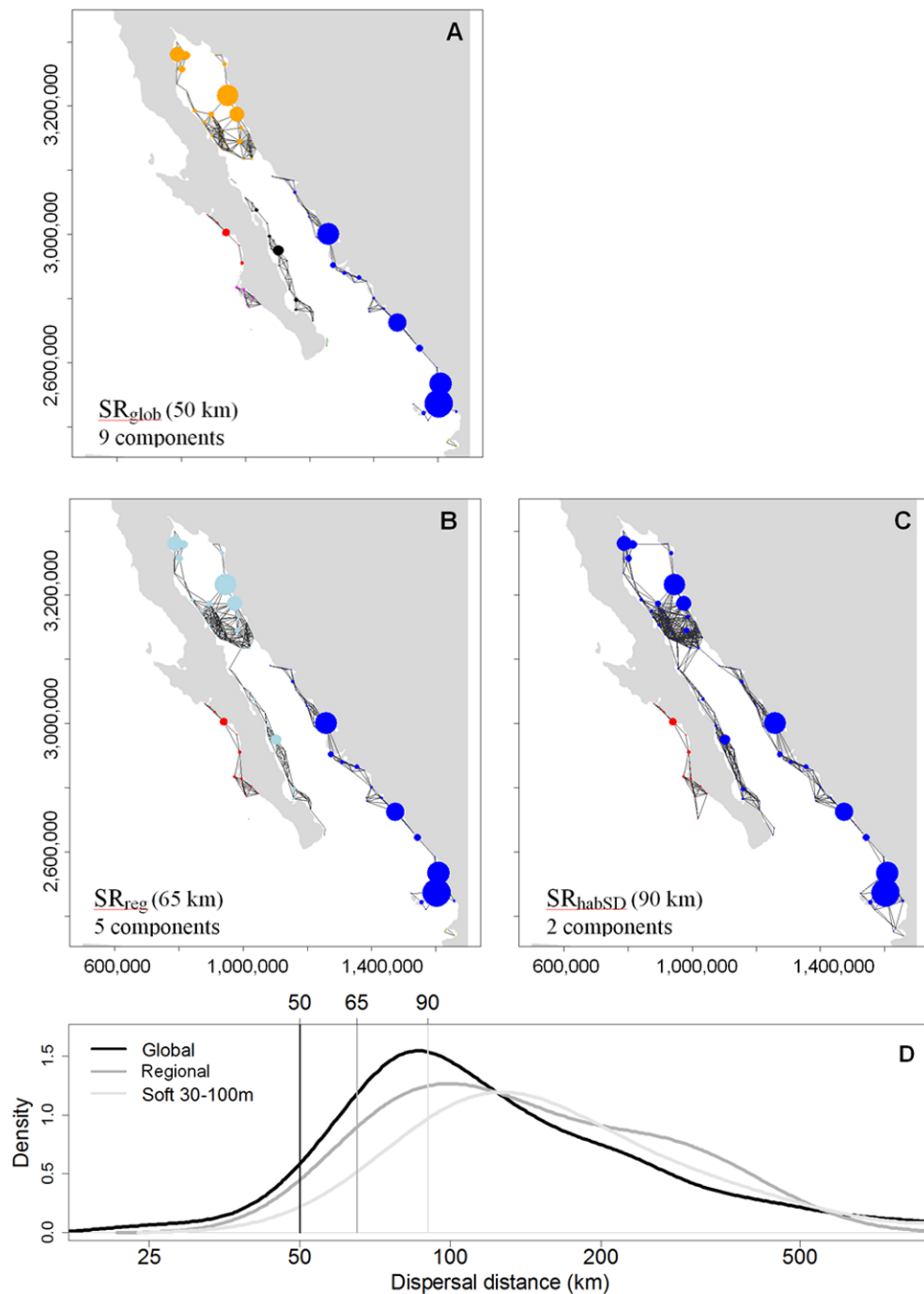


Fig. 3. Connectivity networks for the soft bottom habitat at 30–100 m depth (habSD) in the Gulf of California under the ERA. Node (patches) and edges (connections) are shown. The diameter of the circle is proportional to the area of the patch, which are uniquely colored by connected component. Three connectivity evaluation thresholds are considered: the lower limit of the  $SR_{glob}$  (A),  $SR_{reg}$  (B) and  $SR_{habSD}$  (C); these values are 50, 65 and 90 km, respectively. The plot below (D) is of the probability density functions of larval dispersal distances and spacing rules for global, regional and habitat-specific species. The number of components represents the number of isolated subnetworks.

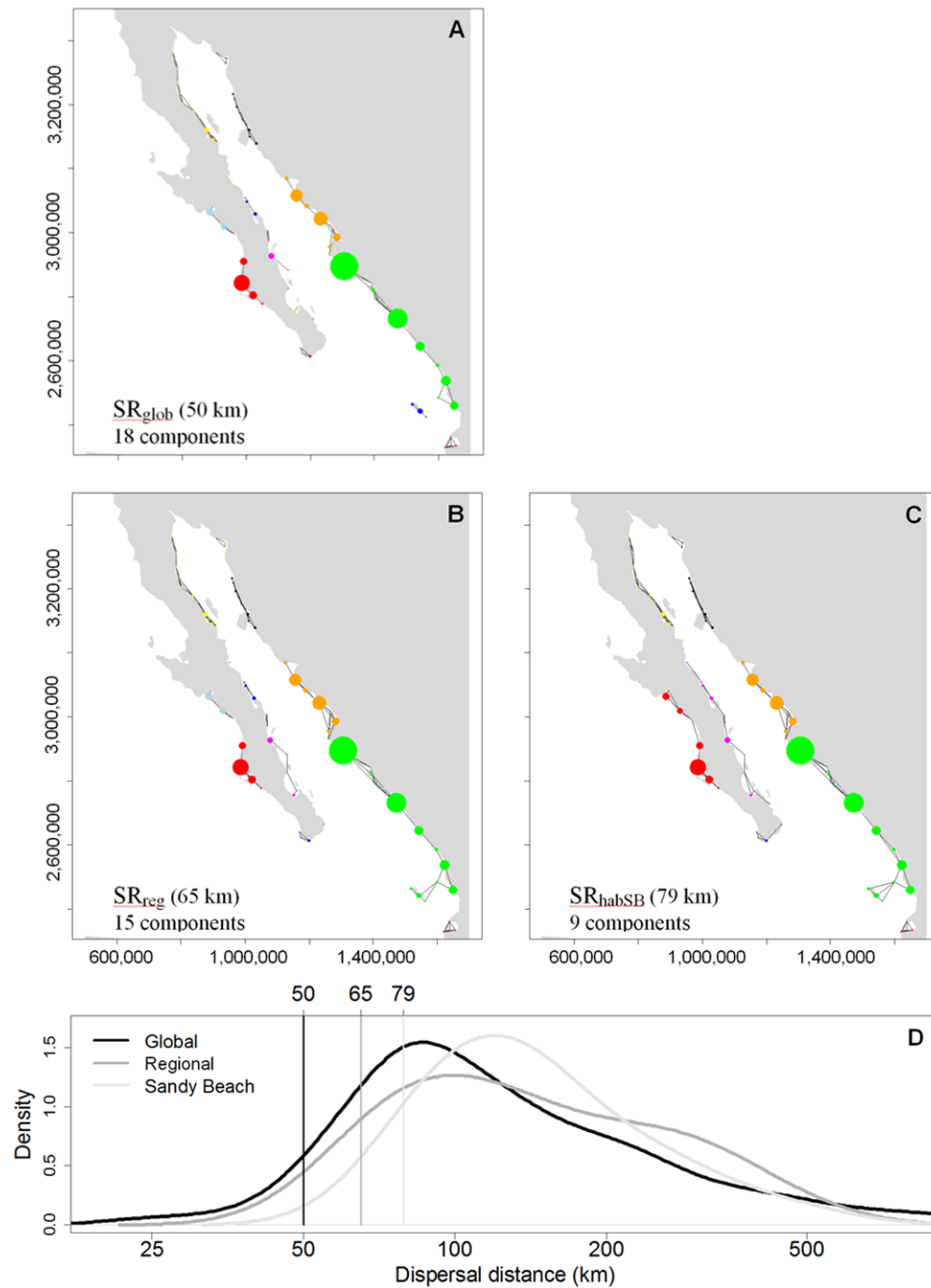


Fig. 4. Connectivity networks of the sandy beach habitat in the Gulf of California (HabSB) under the EcoRegional Assessment (Fig. 1). Node (patches) and edges (connections) are shown. The diameter of the circle is proportional to the area of the patch, which are uniquely colored by connected component. Three connectivity evaluation thresholds are considered: the lower limit of the  $SR_{glob}$  (A),  $SR_{reg}$  (B) and  $SR_{habSB}$  (C); these values are 50, 65 and 79 km, respectively. The plot below (D) is of the probability density functions of larval dispersal distances and spacing rules for global, regional and habitat-specific species. The number of components represents the number of isolated subnetworks.

not be the case in other study areas where the proportion of habitat may change, for example in areas mainly composed by deep habitats, where  $SR_{glob}$  can be needlessly conservative and thus inefficient.

Our results should be treated with caution and with the underlying assumptions in mind, which raises three relevant issues. Firstly, this study does not evaluate the spacing rules by means of evaluating their outcome with more complex and realistic spatially-explicit population dynamic models such as Moffit et al. (2011). In this sense, the present study explores the robustness or consistency among different spacing rules of thumb. Secondly, we have used a relatively simple estimate of dispersal distance, starting from pelagic larval duration data and using a general relationship between this metric and dispersal (Siegel et al. 2003). This method has allowed us to evaluate the connectivity for eight habitats and a large number of the species but at the cost of possible bias in the assessment of dispersal distance (e.g., Shanks 2009, but see Faurby and Barber 2012). Finally, given the variability of larval life histories and dispersal distances among major taxonomic groups, with dispersal peaks at different orders of magnitude (Kinlan and Gaines 2003), it is not feasible to develop a single spacing rule to address connectivity for all taxonomic groups. Our study has only included fish species and not other taxonomic groups such as invertebrates and algae, which presumably would require much more smaller inter-patch distance to ensure connectivity among MPAs (Kinlan and Gaines 2003).

Our results highlight the importance of developing habitat-specific spacing rules in efficient marine conservation planning. These results complement those of Moffit et al. (2011), who assessed the reliability of the rules of based on life traits of the target species. Despite these efforts, much work remains to understand rules of thumb before they are widely applied. For example, current spacing rules have been evaluated in temperate marine systems but not in arctic or tropical marine ecosystems where dispersal profiles could shift. The development of reliable rules of thumb for evaluating connectivity represents a promising tool that could be implemented in a variety of scenarios and study areas around the world.

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## SUPPLEMENTAL MATERIAL

## APPENDIX A

Table A1. Species considered in the Gulf of California. Data bases employed to identify species in the GOC: Ulloa06 = Ulloa et al. 2006, GBIF = Global Biodiversity Information Facility (<http://www.gbif.org/>), CONNABIO = Connabio-remib, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Red mundial de información sobre biodiversidad ([http://www.conabio.gob.mx/remib/doctos/remib\\_esp.html](http://www.conabio.gob.mx/remib/doctos/remib_esp.html)); PLD = pelagic larval duration estimations from Lester et al. (2007); DD = Dispersal distances (in km) estimation obtained from PLD values (in days; see *Methods* for further details).

Family	Species	Ulloa06	GBIF	CONNABIO	PLD	DD	
Acanthuridae	<i>Acanthurus nigricans</i>		x	x	59.7	271	
	<i>Acanthurus triostegus</i>		x	x	65	302	
Achiridae	<i>Achirus lineatus</i>		x		23	78	
Atherinopsidae	<i>Leuresthes tenuis</i>		x	x	40	161	
Batrachoididae	<i>Porichthys notatus</i>		x		31.5	118	
Blenniidae	<i>Ophioblennius atlanticus</i>		x		28.5	104	
	<i>Ophioblennius steindachneri</i>		x		50	215	
Chaetodontidae	<i>Forcipiger flavissimus</i>		x	x	50.7	219	
Cirrhitidae	<i>Cirrhitichthys oxycephalus</i>		x	x	51	221	
	<i>Oxycirrhites typus</i>		x	x	69	327	
Clinidae	<i>Heterostichus rostratus</i>		x		35	135	
Cottidae	<i>Leptocottus armatus</i>			x	60	273	
Gobiidae	<i>Lythrypnus dalli</i>		x	x	75	364	
	<i>Lythrypnus zebra</i>		x		82.5	412	
Labridae	<i>Bodianus diplotaenia</i>		x	x	39.7	159	
	<i>Halichoeres chierchiae</i>		x	x	29.5	108	
	<i>Halichoeres dispilus</i>		x	x	39.3	157	
	<i>Halichoeres melanotis</i>		x	x	35.7	139	
	<i>Halichoeres nicholsi</i>		x	x	31.4	117	
	<i>Halichoeres notospilus</i>		x	x	37.9	150	
	<i>Halichoeres semicinctus</i>		x	x	29.9	110	
	<i>Iniistius pavo</i>		x	x	59	267	
	<i>Novaculichthys taeniourus</i>			x	54.2	239	
	<i>Oxyjulis californica</i>		x		39.4	158	
	<i>Semicossyphus pulcher</i>		x	x	46.1	193	
	<i>Thalassoma duperrey</i>		x		89.2	456	
	<i>Thalassoma grammaticum</i>		x		61.8	283	
	<i>Thalassoma lucasanum</i>		x	x	72.2	347	
	<i>Xyrichtys mundiceps</i>			x	59.2	268	
	Labrisomidae	<i>Malacoctenus hubbsi</i>		x		24	83
	Lutjanidae	<i>Hoplopagrus guentherii</i>		x	x	21.5	72
<i>Lutjanus argentiventris</i>			x	x	22	74	
<i>Lutjanus guttatus</i>			x	x	24.4	85	
<i>Lutjanus novemfasciatus</i>			x	x	22	74	
<i>Lutjanus viridis</i>			x	x	37.9	150	
Merlucciidae	<i>Merluccius productus</i>		x		88	448	
Ostraciidae	<i>Ostracion meleagris</i>		x	x	69	327	
Paralichthyidae	<i>Citharichthys sordidus</i>		x	x	272	1944	
	<i>Citharichthys stigmaeus</i>		x	x	325	2451	
	<i>Paralichthys californicus</i>		x		32	120	
Pleuronectidae	<i>Hypsopsetta guttulata</i>		x	x	39	156	
	<i>Microstomus pacificus</i>		x		365	2850	
Pomacentridae	<i>Abudefduf concolor</i>		x	x	19.7	64	
	<i>Abudefduf declivifrons</i>		x	x	21.9	74	
	<i>Abudefduf saxatilis</i>		x	x	18.8	60	
	<i>Abudefduf taurus</i>		x		21.2	70	
	<i>Abudefduf troschelii</i>		x	x	19.4	63	
	<i>Chromis atrilobata</i>		x	x	28.9	105	
	<i>Chromis limbaughi</i>		x	x	23.5	81	
	<i>Chromis punctipinnis</i>		x		35.2	136	
	<i>Hypsypops rubicundus</i>		x	x	20	65	
	<i>Microspathodon bairdii</i>		x	x	28.9	105	
	<i>Microspathodon dorsalis</i>		x	x	25.9	91	
	<i>Stegastes acapulcoensis</i>			x	23.8	82	
	<i>Stegastes flavilatus</i>		x	x	27	97	

Table A1. Continued.

Family	Species	Ulloa06	GBIF	CONNABIO	PLD	DD
	<i>Stegastes leucorus leucorus</i>			x	33.5	128
	<i>Stegastes rectifraenum</i>		x	x	21.5	72
	<i>Stegastes redemptus</i>			x	27.7	100
Sciaenidae	<i>Atractoscion nobilis</i>		x	x	53.5	235
Serranidae	<i>Paralabrax clathratus</i>		x		28	101
	<i>Paralabrax maculatofasciatus</i>		x		24.5	85
	<i>Paralabrax nebulifer</i>		x		26	92
Tripterygiidae	<i>Axoclinus nigricaudus</i>		x		18	57
Zanclidae	<i>Zanclus cornutus</i>		x	x	57	255

## APPENDIX B

Table B1. Assignment of species to the eight habitats mapped for the Gulf of California. SB = Sand Beach; RS = Rocky shores; ES = Estuary; RR = Rocky reefs; HS = Hard bottom, 0–30 m; HD = Hard bottom 30–100 m; SS = Soft bottom 0–30 m; SD = Soft bottom 30–100 m.

Family	Scientific Name	SB	RS	ES	RR	HS	HD	SS	SD
Acanthuridae	<i>Acanthurus nigricans</i>		x		x			x	x
	<i>Acanthurus triostegus</i>	x	x		x			x	x
Achiridae	<i>Achirus lineatus</i>			x		x			
Atherinopsidae	<i>Leuresthes tenuis</i>	x				x		x	
Batrachoididae	<i>Porichthys notatus</i>	x	x			x	x		
Blenniidae	<i>Ophioblennius atlanticus</i>		x		x			x	
	<i>Ophioblennius steindachneri</i>		x		x			x	
Chaetodontidae	<i>Forcipiger flavissimus</i>		x		x			x	x
Cirrhitidae	<i>Oxycirrhites typus</i>				x			x	x
	<i>Cirrhitichthys oxycephalus</i>		x		x			x	x
Clinidae	<i>Heterostichus rostratus</i>				x			x	x
Cottidae	<i>Leptocottus armatus</i>			x			x		
Gobiidae	<i>Lythrypnus dalli</i>		x		x			x	x
	<i>Lythrypnus zebra</i>		x		x			x	x
Labridae	<i>Halichoeres melanotis</i>		x		x	x		x	x
	<i>Iniistius pavo</i>		x	x		x	x	x	x
	<i>Semicossyphus pulcher</i>		x		x			x	x
	<i>Halichoeres chierchiae</i>	x	x		x			x	x
	<i>Halichoeres notospilus</i>		x		x			x	
	<i>Halichoeres semicinctus</i>		x		x	x		x	x
	<i>Halichoeres nicholsi</i>				x	x		x	x
	<i>Halichoeres dispilus</i>		x		x	x	x	x	x
	<i>Bodianus diplotaenia</i>		x		x	x	x	x	x
	<i>Thalassoma lucasanum</i>		x		x			x	x
	<i>Novaculichthys taeniourus</i>	x	x		x	x			
	<i>Xyrichtys mundiceps</i>	x				x			
	<i>Thalassoma duperrey</i>		x		x			x	
	<i>Thalassoma grammaticum</i>		x		x			x	x
	<i>Oxyjulis californica</i>				x			x	x
Labrisomidae	<i>Malacoctenus hubbsi</i>		x					x	
Lutjanidae	<i>Hoplopagrus guentherii</i>	x	x		x			x	x
	<i>Lutjanus viridis</i>		x		x			x	
	<i>Lutjanus guttatus</i>	x	x	x	x	x		x	
	<i>Lutjanus novemfasciatus</i>		x	x	x			x	x
	<i>Lutjanus argentiventris</i>		x	x	x			x	x
Merlucciidae	<i>Merluccius productus</i>			x		x	x	x	x
Ostraciidae	<i>Ostracion meleagris</i>		x		x			x	
Paralichthyidae	<i>Citharichthys sordidus</i>					x	x		
	<i>Citharichthys stigmaeus</i>						x		
	<i>Paralichthys californicus</i>	x		x		x	x		
Pleuronectidae	<i>Hypopsetta guttulata</i>			x		x	x		
	<i>Microstomus pacificus</i>					x	x		
Pomacentridae	<i>Chromis limbaughi</i>		x		x			x	x
	<i>Abudefduf concolor</i>		x		x			x	

Table B1. Continued.

Family	Scientific Name	SB	RS	ES	RR	HS	HD	SS	SD
	<i>Microspathodon bairdii</i>		x		x			x	
	<i>Hypsypops rubicundus</i>		x		x			x	
	<i>Stegastes flavilatus</i>		x		x			x	x
	<i>Abudefduf declivifrons</i>		x		x			x	
	<i>Chromis atrilobata</i>				x			x	x
	<i>Abudefduf saxatilis</i>		x		x			x	
	<i>Microspathodon dorsalis</i>		x		x			x	
	<i>Stegastes rectifraenum</i>		x		x			x	
	<i>Abudefduf troschelii</i>		x		x			x	
	<i>Stegastes acapulcoensis</i>		x		x			x	
	<i>Stegastes leucorus leucorus</i>		x		x			x	
	<i>Stegastes redemptus</i>		x		x			x	
	<i>Chromis punctipinnis</i>		x		x			x	x
	<i>Abudefduf taurus</i>		x		x			x	
Sciaenidae	<i>Atractoscion nobilis</i>	x	x					x	x
Serranidae	<i>Paralabrax clathratus</i>					x	x	x	x
	<i>Paralabrax nebulifer</i>		x		x	x	x		
	<i>Paralabrax maculatofasciatus</i>	x	x		x	x	x		
Tripterygiidae	<i>Axoclinus nigricaudus</i>		x		x			x	
Zanclidae	<i>Zanclus cornutus</i>		x		x			x	x
Total		11	48	9	49	20	15	52	30

## APPENDIX C

Table C1. Results of the pair-wise comparisons among dispersal distance of habitat-specific species. P-values of randomization tests are given. SB = Sand Beach; RS = Rocky shores; ES = Estuary; RR = Rocky reefs; HS = Hard bottom, 0–30 m; HD = Hard bottom 30–100 m; SS = Soft bottom 0–30 m; SD = Soft bottom 30–100 m. Significant values (two tailed-test:  $p < 0.025$  and  $p > 0.975$ ) are italicized.

Species constraint	SB	RS	ES	RR	HS	HD	SS	SD
SB		0.059	0.205	0.068	0.117	0.680	0.683	0.857
RS			0.289	<i>0.014</i>	0.237	0.883	0.959	<i>0.996</i>
ES				0.281	0.130	0.399	0.498	0.817
RR					0.284	0.907	0.963	<i>0.997</i>
HS						0.788	0.953	<i>0.993</i>
HD							0.826	<i>0.968</i>
SS								0.565