# California MLPA Master Plan Science Advisory Team
# MPA Spacing Work Group Progress Report:
# Spacing Guidelines and Other Metrics for Connectivity among MPAs

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***October 29, 2009 Draft***

## Goal

The task of the MLPA Marine Life Protection Act (MLPA) Master Plan Science Advisory Team (SAT) Marine Protected Area (MPA) Spacing Work Group was to examine supplements and/or alternatives for the spacing guidelines currently used to advise and evaluate MPA arrays. The need for a metric of connectivity emerged from the observation that the MPA size and spacing guidelines originally were intended as proxies for direct evaluation of adult movement (MPA size) and larval movement (MPA spacing) among MPAs in the context of MLPA goal 6, that MPAs should, to the extent possible, be designed and managed as a network.

## Limitations of Current MPA Spacing Guidelines

The current MPA guidelines are to place MPAs no more than 50-100 kilometers (km) apart for an objective of facilitating dispersal of important bottom-dwelling fish and invertebrate groups among MPAs, based on currently known scales of larval dispersal (from *California Marine Life Protection Act Master Plan for Marine Protected Areas*). The threshold guideline is easy to use for design of MPAs, but it has two substantial limitations. First, the threshold-based guideline is discrete and does not provide information about contributions of MPAs that are close to the maximum spacing, such that MPAs that are 99 km apart fall within the range of the guideline, while MPAs 101 km apart do not. The 50-100 km value was chosen based on examination of empirically-determined larval dispersal distances, with the understanding that connectivity decreases monotonically with increasing distance. However, the use of those single values can be misconstrued by non-experts to suggest that connectivity is maximized below that range and negligible at greater distances. In reality, biological connectivity is not likely to follow such discrete thresholds. Additionally, the MPA spacing guideline is a proxy measure that does not account for spatial variability in dispersal (such as the existence of breaks or discontinuities in larval dispersal) or better sources of information on dispersal, such as numerical ocean circulation models.

As the spatially explicit bio-economic models have come into use as an additional SAT evaluation tool, it has been noted that the models can directly calculate the levels of demographic connectivity that the size and spacing guidelines are intended to capture. That is, the bioeconomic models provide additional information about connectivity between MPAs that is complementary to the spacing evaluations. Moreover, the bioeconomic models provide continuous measures of the conservation effects of MPA proposals (i.e., they are not threshold-based) and they can explicitly account for spatial heterogeneities in dispersal. However, although the bioeconomic models in their current form take dispersal and connectivity into account, they do not directly evaluate whether MPAs are functioning as a network. As an extreme example of this distinction, consider an MPA array made of up several large MPAs separated by a large distance. If those MPAs are self-persistent, the bioeconomic models would reveal that the MPA array is demographically sustainable and would persist

through time, despite low or no connectivity between MPAs. In a fragmented MPA array like this genetic information would not be able to pass from one sub-population to another, making the population less able to respond to changing conditions (e.g., climate change). The requirement that MPAs operate as a 'network' implies that MPAs should be connected by the exchange of alleles among MPAs. For this reason, the MPA spacing workgroup sought to explore more direct measures of genetic connectivity based on the existing bioeconomic modeling framework.

## Potential Metrics of Connectivity: A Progress Report

The work group agreed that any additional measure of genetic connectivity would need to possess four key features in order to be useful: It should 1) build upon the existing bio-economic models, since they have been thoroughly vetted by the SAT; 2) estimate the rate of genetic transmission across the network at equilibrium, using a metric such as the rate of movement of a neutral allele between MPAs; 3) reveal 'gaps' in connectivity between proposed MPAs; and 4) provide actionable recommendations for revising MPA proposals to improve connectivity.

At present, the work group has considered three potential approaches to estimating connectivity. These are all rather similar but vary in computational complexity and the type of biological information they provide. None is fully developed at this point, so the following discussion is a progress report.

### *Approach 1*

The first approach would involve an extension of the existing bioeconomic models that would explicitly represent genetic connectivity. A preliminary version of this type of model has been developed. This model extension simulates genetic connectivity among patches which have a maximum carrying capacity of $X$ individuals in $N$ patches. The model tracks the allele frequency of a single haploid locus in each patch. Genetic connectivity between patches is assessed by assuming that all patches are homozygous for a single allele $A$, except for patch $i$, which is homozygous for an alternative allele, $B$. The time it takes (in generations) for one copy of allele $B$ to arrive in every other patch is then a possible measure of the genetic connectivity between $i$ and all other patches. This metric then could be assessed for every patch, providing a pairwise estimate of connectivity among patches. This model maintains a finite, integer number of individuals in the population (rather than operating in units of population density), so in each timestep, some number of individuals (and the alleles they carry) are randomly lost from the population due to mortality. This introduces stochastic genetic drift into the model, so multiple model runs are used to approximate the long-term probability of genetic connectivity.

### *Approach 2*

The second approach is similar to the first, in that it builds upon the existing bio-economic models and tracks the frequency of a neutral allele in the population. In this approach, population abundance is tracked as density, rather than numbers of individuals, so there is no longer stochastic genetic drift. This precludes measuring genetic connectivity in terms of the

time required for a single allele copy to migrate among patches. Instead, this approach would measure connectivity in terms of the time required for new allele *B*, introduced in patch *i*, to reach equilibrium in the population, or to reach some threshold frequency in another patch.

### *Approach 3*

The third approach is a Markov chain approximation to population dynamics. This approach requires constructing a connectivity matrix, **M**, in which each entry $m_{ij}$ describes the number of individuals per generation spawned in patch *i* that successfully disperse and enter the adult population in patch *j* (accounting for density-dependent settler mortality at equilibrium and other details). This value reflects both the lifetime reproduction of individuals in *i* (which varies depending on whether *i* is in an MPA or not) and the probability of dispersal from *i* to *j*. Raising **M** to the power *n* produces a second matrix, $\mathbf{M}^n$, for which each entry indicates the total number of descendents in patch *j* after *n* generations that would originate from a single individual in patch *i* at the starting time. This value could then be used as a proxy for the genetic connectivity between *i* and *j*. The advantage of this method is its extreme ease of computation. In theory, this simplification could be applied to either of the first two approaches to obtain a rapid solution, although the mechanics of this have not yet been fully worked out.

Regardless of the exact calculations developed, the general concept is to estimate a connectivity metric for the “no fishing” scenario and for an MPA proposal with fishing, then to estimate the difference between the two. This difference (in units such as the number of generations for allele transmission between patches) then could provide an overall measure of the level of connectivity afforded by the MPA array (the mean difference in connectivity from the no fishing case) and could indicate which specific regions of the coast would have decreased genetic connectivity in that MPA array (which regions have less connectivity than they would in the no fishing case; i.e., where there are gaps in connectivity). The latter results could presumably be used to revise the MPA array to improve connectivity, although at present it is unclear exactly how to link the evaluation (e.g., two MPAs have reduced connectivity) to a precise recommendation for change (e.g., Should the 'source' MPA be increased in size, or moved closer, or is a third MPA needed between those two?); establishing that linkage would be a priority if one of these connectivity metrics were developed further.

Preliminary results from the genetic model lead to two initial conclusions. First, on a simple linear coastline with diffusive larval dispersal, genetic distance as measured by the genetic connectivity model is directly related to the linear distance between patches. (This is consistent with the concept of isolation-by-distance in population genetic theory.) However, when a more complicated dispersal matrix is used, such as those derived from the Regional Ocean Model System (ROMS) numerical circulation model used in the MLPA South Coast Study Region, there is no longer a simple relationship between geographic distance and genetic connectivity. Second, a genetic connectivity model of this type is computationally intensive, somewhat difficult to interpret by laypeople, subject to key assumptions (such as population size, whether dispersal matrices represent generation-scale processes, and more technical genetic assumptions), and would require further technical development and vetting before implementation.

## Preliminary Recommendations

Spacing guidelines provide a proxy of coast-wide genetic connectivity, whereas a population model that explicitly represents genetic connectivity could provide a more direct measure of connectivity between MPAs in a network. If the coastline in question has relatively simple circulation that is well approximated by a spatially homogenous advection-diffusion circulation model (e.g., a Gaussian dispersal kernel), then the current distance-based evaluations provide a reasonable approximation to genetic connectivity with the benefit of simple computation and interpretation.

If, however, dispersal matrices derived from numerical circulation models are available for the north coast, *and* those matrices reveal considerable heterogeneity and complexity in dispersal that deviates substantially from advection-diffusion approximations (as in the south coast study region), then it may be worthwhile for the MPA spacing workgroup to devote more effort to developing and vetting an explicit genetic component for the bioeconomic models that could augment the existing spacing evaluations.