## Persistence and Yield in MPA Networks: Results from Spatially Explicit Population Models

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Models of species persistence and fishery yield in marine protected area (MPA) networks are an important tool to help understand how MPAs affect fish and fisheries. The purpose of our research is to use models to identify changes in fishery yield and fish population distribution and persistence in nearshore California. Because the Oregon MPAs will not be specifically designed as fishery management tools, some aspects of these models may not be relevant to evaluation of reserve size and spacing here in Oregon. Nevertheless, the removal of fishing pressure is a primary effect of any MPA, our models can provide insight into how populations of fished species will respond to MPAs and how multiple MPAs can interact as a network connected by larval dispersal.

In California, most goals of the Marine Life Protection Act (MLPA) implicitly require that MPAs support persistent populations (Figure 1).


Figure 1. Diagram of population persistence in a network of MPAs, with larvae retained within natal MPAs and also settling in neighboring MPAs

The criterion for population persistence is replacement. Just as in a human population, persistence requires that each fish replace itself with at least one offspring (a 'recruit') over its entire lifetime. In most fish populations it is difficult to keep track of offspring during the larval phase (when mortality and dispersal are both quite high), so the replacement concept is described in terms of the number of eggs that each fish much produce in its lifetime in order to ensure that at least one survives to recruit.

In a natural fish population, the expected lifetime egg production (LEP) for a new recruit is calculated by summing the expected egg production at each age (which increases with age) times the probability of surviving to that age (which decreases with age). In a fished population, individuals are less likely to reach older ages (the age distribution of the population is truncated), so LEP decreases. We can thus describe the intensity of fishing effort in terms of the fraction of natural egg production (FLEP) that results. If FLEP is low enough, fish are no longer producing enough eggs to replace themselves, so the population is no longer persistent. The value of FLEP at which this occurs is termed the critical replacement threshold (CRT). For many fish populations, the CRT is found at $F L E P=0.35$ ( $35 \%$ of natural lifetime egg production), and we use that value in our
models. Using FLEP as a "common currency" for evaluation of population persistence obviates the need to use many (difficult to estimate) parameters and allows us to identify the best configurations of reserve size and spacing for a wide range of taxa given a particular level of fishing.

The general relationship between FLEP and recruitment is shown by the yellow curve in Figure 2. For high values of FLEP, recruitment stays at the unfished maximum of 1 (individuals are replacing themselves); as FLEP decreases below 0.35 , recruitment decreases to zero (replacement is insufficient). The long-term, steady state levels of recruitment for several levels of fishing are shown by the colored dots. The location of the dot is found by plotting a line with slope 1/FLEP and finding the intersection of that line with the yellow curve. Notice that if FLEP $<0.35$, the dot is at zero and the population goes extinct. In this figure we have used an angular "hockey stick" curve to illustrate the FLEP-recruit relationship; this is just an approximation of the real curve, which would be smoother and less angular.


Figure 2. Diagram of the "hockey stick" relationship between FLEP and recruitment. FLEP can be used as a common currency to characterize the relationship between fishing pressure and population replenishment.

In a coastal population, neighboring subpopulations may exchange larvae with each other. In this case, any given subpopulation may not retain enough larvae for each fish to replace itself directly, but may be replenished by larvae arriving from neighboring subpopulations (Fig. 1). Thus larval exchange can allow a network of subpopulations to persist, even if any one subpopulation would not persist in isolation. We term this a network effect.

Network effects may be especially important in the presence of MPAs, because egg production in unfished areas (where FLEP is high) can replenish fished areas (where FLEP is low). Likewise, MPAs that are too small to persist in isolation may be replenished by larvae dispersing from neighboring MPAs or fished areas (Figure 3).


Figure 3. Diagram showing the model structure of dispersal, FLEP and recruit effects in fished and MPA areas

For populations along the California coastline, a reasonable first approximation is to model a one-dimensional linear coastline. In an initial modeling effort, we evaluated the effectiveness of the California size and spacing guidelines for networks of MPAs along an infinite coastline with uniformly distributed, homogenous habitat. In general, MPAs that conformed to the guidelines supported persistent populations of species with moderate to low larval dispersal distances and home range widths (Figure 4). Home range width often had a stronger effect on persistence than larval dispersal distance, so it may be desirable to create wider reserves to accommodate species with large home ranges.

## First approach:

Infinite coastine, uniformly distributed habitat
MPAs placed according to size \& spacing guidelines
(50-100 km spacing, 5-20 km size)


Figure 4. Modeling results for an infinite coastline with uniformly distributed habitat with and MPA network that met the recommended CA size and spacing guidelines. The response surface indicates the fraction of the coastline supporting a persistent population for different combinations of larval dispersal distance and adult home range width. Results indicate that species with shorter larval dispersal and smaller home ranges are more likely to have persistent populations within this type of MPA network.

To evaluate MPAs for the North Central Coast Study Region (between Pigeon Pt and Pt Arena), we developed models that incorporated the spatial distribution of habitat in the study region and simulated population dynamics for 8 commercially important species. The goals of this effort were to:

- Evaluate proposed MPAs for persistence and yield
- Compare each proposal to the "no action" scenario (current regulations only)

The model results for several representative MPA proposals reveal the essential lessons from this effort (Figure 5). Proposals in which most MPAs fell short of the size and spacing guidelines still performed better than the No Action scenario. However, proposals that more closely matched the preferred size and spacing guidelines supported persistent populations for a wider range of larval dispersal distances and adult home range widths. Once again, species with wider home ranges were the least likely to sustain persistent populations.


Figure 5. Results for several representative MPA proposals from the North Central Coast. The axes of each figure are the same as in Fig. 4.

Another factor determining MPA performance is the management of fisheries outside of the MPAs (Figure 6). If fisheries are managed poorly ("overfishing"), MPAs may be necessary to sustain persistent populations, and increasing the area dedicated to MPAs may actually increase fishery yield. However, if fisheries are managed sustainably, MPAs are less important to persistence, there are fewer benefits to increasing MPA area, and MPAs may impose economic costs by reducing fishery harvests. Consequently, a reliable assessment of the performance of a particular MPA proposal requires decision makers to specify what sort of management will occur outside MPA boundaries.

Result \#2:
MPA performance depends on management outside MPAs


Figure 6. The effect of fishery management on MPA performance. Each panel shows the performance of 4 MPA proposals (symbols) under 3 different management scenarios (sustainable, unsustainable, or highly unsustainable fishing). MPAs are evaluated based on the ability to support persistent populations (upper left), fishery yield (bottom right), and the trade-off between those two factors (bottom left).

The general conclusions of our modeling efforts are:

1. Species that move in large home ranges as adults are not protected well by MPAs
2. Increasing MPA size is more useful than reducing spacing in terms of improving persistence and fishery yield (especially for species with high adult movement)
3. Spatially explicit models can be valuable tools to determine if conservation and economic targets are being met
4. MPA success depends on current and future fishery management outside MPAs
5. Decision makers must specify their beliefs about future and/or commitment to managing fisheries

In general, we recommend using size and spacing guidelines as a starting point for designing MPAs, but emphasize that models such as these should be used to compare different MPA proposals in order to quantify their ability to support populations and fisheries.

