

California MLPA Master Plan Science Advisory Team

Methods Used to Evaluate MPA Proposals in the North Coast Study Region (DRAFT) Chapter 8 and Appendix B – Bioeconomic Modeling *Revised February 4, 2010*

8. Bioeconomic Modeling

Status of this chapter: Refinements to the models and this chapter will continue to be made, as needed (revised by modeling work group February 4, 2010); see page 20 and Appendix B3 for changes.

For marine protected areas (MPAs) to function effectively as a network that satisfies various goals of the Marine Life Protection Act (MLPA), they must (1) provide adequate protection from harvest to the portion of a species' (adult) population resident in the MPA, and (2) include a sufficient fraction of the populations' total larval production for populations to persist. The science guidelines for MPA design in the *California Marine Life Protection Act Master Plan for Marine Protected Areas* (Master Plan) support general evaluation of the efficacy of MPAs as refugia and connectivity within alternative MPA proposals, but do not evaluate potential population effects or account for several variables, including conditions outside the MPA proposal (i.e., harvest), spatial structure of the seascape, realistic connectivity across space, and fishing pressure on different species.

Spatially explicit population models account for these factors and facilitate more comprehensive and spatially explicit evaluation of the consequences of MPA design for a proposal's ability to satisfy various goals of the MLPA. Spatially explicit models developed for evaluation of alternative MPA proposals go beyond the current scope of the scientific guidelines in the Master Plan to calculate whether populations will persist and how the proposed MPAs will affect fishery yield and profit. The models include, for example, potential contributions from MPAs that do not satisfy all scientific guidelines, the status of populations outside of MPAs (which depends on fishery management), and the potential costs, in terms of fishery yield, associated with achieving a desired conservation outcome. Further, the models allow us to detect potential situations in which MPAs are sited efficiently, so conservation is gained at minimal cost (or perhaps even a benefit) to consumptive users.

This document briefly describes the key inputs and outputs of two models well-suited for analysis of alternative MPA proposals. Also described are the evaluations that will be performed by these models. Finally, an analysis of genetic connectivity, based on model outputs and designed to complement the MPA spacing evaluation (Chapter 6), is described.

Description of Models

In the MLPA North Central Coast Study Region and MLPA South Coast Study Region planning processes of the MLPA Initiative, two models were developed, vetted, and utilized to evaluate alternative MPA proposals; those models are being extended for use in the MLPA North Coast Study Region. Both models utilize spatial data on habitat, fishery effort, and proposed MPA locations and regulations to simulate the population dynamics of fished species and generate predicted spatial distributions of species abundances, yields, and (in one case) profits for each alternative MPA proposal. The UC Davis "Spatial Sustainability and Yield" model (UCD model) considers each fished species separately, and focuses on sustainability of fished populations under each MPA proposal, using current estimates of fishery stock status to help predict future management success. The UC Santa Barbara "Flow, Fish, and Fishing" model (UCSB model) focuses on the tradeoffs between

fisheries performance (profits) and fish abundance.¹ Importantly, both models incorporate the population dynamic consequences of spatially explicit fishing regulations.

The two models differ in details regarding, for example, how specifically populations' dynamics are modeled, how the steady-state impacts of fisheries outside of protected areas are parameterized, and what units are used to express conservation and economic values. Although they differ in these details, the two models are structurally similar and gave closely agreeing results in the South Coast region. Both models have the ability to be run dynamically or to equilibrium, though running dynamically requires data on the starting stock, across space, of multiple species. In equilibrium mode, they predict the state of the system over the long term rather than its dynamics over time².

Each model includes more or less the same structural elements: (a) larval connectivity across patches driven by ocean currents, pelagic larval duration, and spawning season, (b) larval settlement regulated by species density in available habitat, (c) growth and survival dynamics of the resident (adult) population, (d) reproductive output increasing with adult size, (e) adult movement (e.g., home ranges), and (f) harvest in areas outside of MPAs.

Key Changes to Models

Both models were enhanced during the south coast study region process. Some of these enhancements were driven by differences in biogeography between the two regions (e.g., more heterogeneous flow patterns in southern California), and some were driven by new methods or data (e.g., the desire to integrate data on fisherman behavior into the models). The key changes in the models are:

- Larval dispersal kernel—The models now use output from Regional Ocean Modeling System (ROMS)-based oceanographic models³ to predict connectivity, rather than assuming homogeneous Gaussian kernels along the coastline.
- Spatial dimension—The models represent the coastline as a two-dimensional map (in contrast to the previous one-dimensional representation). This permitted more realistic modeling of complex habitat patterns and offshore islands in the Southern California Bight. A one-kilometer by one-kilometer grid was used for the patches. This grid-scale will be retained for the north coast study region process.
- Fleet dynamics—In the south coast study region process, a version of both models was parameterized with data from Ecotrust's surveys of commercial fisheries in southern California to account for the increased costs of fishing far from shore, rather than assuming the fleet responds

¹ The UCSB model adopts many of the key assumptions of the Equilibrium Delay Difference Optimization Model (EDOM), developed by Walters, Hilborn, and Costello in the MPA North Central Coast Study Region. Both the UCSB and UCD models contain important advances over the versions used in the north central coast to accommodate a more complex biogeography and spatial data on fishing effort in southern California.

² Note that equilibrium models do not account for the costs incurred during the time required to reach steady state.

³ The ROMS model has been developed by oceanographic investigators at UCLA and UCSB who have provided model outputs for use by the spatially explicit population models described in this document. See Chapter 7 – Spacing for additional information on the ROMS model.

only to changes in fish density. The details of the fleet model are given in Appendix B2. The fleet model in the North Coast may also include variable costs of fishing different patches due to distance from port, depending on analysis of Ecotrust data from this new region.

- **Species**—A list of model species has been assembled that covers a wide range of life history and fishery traits of species that occur in northern California (Appendix B3).

Caveats Associated with Model Interpretation

All models necessarily make simplifying assumptions about the nature of real-world processes. Both the UCD and UCSB models rely upon a series of key assumptions about the structural elements (Appendix B1). As such, model results should be interpreted with awareness of the assumptions, although these actually are less restrictive than those required by the verbal and mathematical models that form the basis of the MPA size and spacing guidelines in the Master Plan. For example, the ROMS model used to estimate larval dispersal patterns in the bioeconomic models has limitations in its ability to resolve nearshore circulation, yet is more realistic than the spatially homogenous pattern of connectivity implicitly assumed by the MPA size and spacing guidelines (see “Chapter 7 - Spacing” for more information on the ROMS).

Model outputs also depend on the particular parameter values chosen for each species, so the predictions of the models will be most accurate when appropriate parameter values are known. Both modeling teams are currently searching the biological literature for the best estimates of the necessary life history parameters for each model species, and are preparing an appendix of those parameter values along with the literature source for each estimate. This document will be circulated among SAT members and outside experts to ensure that the best parameter estimates have been used, and that these consensus parameter values will be standardized between the two models.

The spatial distributions of larval settlement and adult biomass predicted by the models are driven by two sets of assumptions: 1) larval dispersal is driven by oceanography as predicted by the ROMS model, and 2) the suitability of a particular location for the settlement and growth of a species is determined by the presence of habitat appropriate for that species. Maps currently under development will represent habitat in a binary fashion; that is, habitat is either hard- or soft-bottom. Using a rasterized version of these maps, the models consider the fraction of the one square kilometer cell which is suitable habitat (either hard or soft substrate of the appropriate depth, depending on species) to be a continuous measure of habitat availability in the cell. The maximum density of individuals in a cell (carrying capacity) is proportional to this measure of habitat availability.

A final caveat is that model results are highly sensitive to the level of fishing outside of MPAs. Because the models are intended to predict a future equilibrium state, it is necessary to predict future fishing levels, an area of high uncertainty. Moreover, the performance of a species under a certain level of fishing also is highly sensitive to the shape of the settler-recruitment relationship (see Table B1 in Appendix B1), which is itself highly uncertain. The precise relationship between fishing effort and the shape of the settler-recruit curve is complex and not perfectly understood, especially in models such as these with considerable spatial complexity. In general, however, it is possible to represent the joint uncertainty in the shape of the settler-recruit curve (biological uncertainty) and in future harvest scenarios (management uncertainty) relative to each other. Specifically, the models describe the shape of the settler-recruit curve in terms of a compensation ratio or critical replacement threshold (CRT), and harvest is described in terms of its effect on the lifetime egg production (LEP) of a species.

For a given value of the CRT, the model results depend roughly on the relative values of CRT and LEP rather than on the particular CRT chosen. In general, the management scenario depends on whether harvest causes lifetime egg production to exceed or fall short of the critical replacement threshold set by the settler-recruit relationship. Expressing the effects of harvest in terms of lifetime egg production also reduces some of the dependence of model results on uncertainty about adult life-history parameters. Therefore, it is possible to represent both biological and management uncertainty by choosing a particular value for the CRT for each species and then simulating population dynamics under several different fishery management regimes relative to that CRT. The models will simulate three fishery management regimes that approximate (1) poor management, (2) MSY-like management, and (3) conservative management, given that CRT. Thus, the model results can illustrate a range of possible performance for each species. For concise interpretation (i.e., coming up with several summary results for each alternative MPA proposal) it may be desirable to weight results across species or possibly weight the probability of different future management outcomes.

SAT Recommendations for Using Models to Compare Alternative MPA Proposals

Because the models are built on the best available science, the SAT recommends that these models be among the principal modes of evaluation for each alternative MPA proposal in the MLPA north coast study region. In making this recommendation, the SAT emphasizes that the models' conceptual principles are consistent with those upon which existing MPA size and spacing guidelines are based, and yield similar general conclusions: MPA size relative to adult movement strongly determines MPA effectiveness, and MPA spacing relative to larval dispersal distance strongly determines the ability of MPAs to function as a network. Spatially explicit modeling is more comprehensive because it integrates the effects of MPA size and spacing, habitat distribution, level of fishing, and adult and larval movement to quantify the effectiveness of alternative MPA proposals. Moreover, spatially explicit models are not susceptible to threshold-related sensitivity that can arise from evaluation based on the size and spacing guidelines (i.e., specific sizes and spacing (or ranges of these) are adequate, but others are not). Rather the bioeconomic models estimate the conservation and economic consequences of each proposed spatial configuration of MPAs, so that these can be evaluated directly.

The UCD and UCSB models produce similar outputs that can be used to evaluate these conservation and economic consequences. Both models produce a measure of *conservation value* (e.g. increases in biomass or population sustainability), and a measure of *economic return* (e.g. yield or fishery profitability). Both conservation value and economic return can be described study-region wide (a single number) or can be made spatially explicit (a map or table). The models calculate each output at three spatial scales: Individual one kilometer by one kilometer cells, the entire study region, and at the sub-region scale. Conservation value is essentially a measure of the effectiveness of an alternative MPA proposal at meeting MLPA goals 1, 2, and 6⁴, while economic return reflects the expected changes to fishing yields of implementing MPAs. Specifically, each model will output:

1. Conservation Value

- a. [UCD] Biomass and larval supply (a proxy measure of population sustainability) of representative species, across space, under each alternative MPA proposal (including "No Action")

⁴ Subsections 2853(b)(1), (b)(2), and (b)(6), Fish and Game Code.

- b. [UCSB] Biomass and larval supply of representative species, across space, under each alternative MPA proposal (including “No Action”)
 - c. If A =Conservation Value under Proposal X, and B =Biomass under No Action, then the quotient: $(A-B)/B$ provides a measure of the percentage increase in conservation value compared with No Action.
2. Economic Return
- a. [UCD] Fish yield of representative species, across space, for each alternative MPA proposal
 - b. [UCSB] Fish yield and fisheries profit for the representative species, across space, for each alternative MPA proposal
 - c. Again, by comparing to “No Action”, one can generate a measure of the percentage increase or decrease in economic return from the proposal.

The SAT proposes that each alternative MPA proposal be evaluated by compiling the following outputs:

1. Spatial effects on Conservation Value (as percentage changes versus No Action, presented as a spatial map and averages for each sub-area)
 - a. For each model species
 - b. For an average of all model species
2. Region-wide effects on Conservation Value
 - a. For each model species
 - b. For an average of all model species
3. Spatial effects on Economic Return (presented as a spatial map and averages for each sub-area)
 - a. For each model species
 - b. For an average of all model species
4. Region-wide effects on Economic Return
 - a. For each model species
 - b. For an average of all model species
5. Spatial effects on Recruitment (presented as a spatial map and averages for each bioregion)
 - a. For each model species
 - b. For an average of all model species
6. Spatial fishing intensity.
 - a. For each model species
 - b. For an average of all model species
7. Connectivity diagrams: The larval dispersal kernel shows the intensity of connections from all source to all destination locations.

8. Tradeoff Curves: Plot of Conservation Value against Economic Return for each MPA proposal

All analyses will take place over a range of fishing intensities.

Using Model Outputs to Improve Each MPA Network Proposal

In addition to the outputs being used to compare alternative MPA proposals, both models also produce outputs which can be used to evaluate the strengths and weaknesses of each design. These outputs are intended provide feedback during the iterative design process so that proposals can be adjusted to improve their performance in terms of conservation value and (if desired) economic value.

Three kinds of feedback are provided for each species:

- The models calculate changes in conservation and economic value on sub-area scales. These data can be used to evaluate how the effects of alternative MPA proposals varies over space, and if necessary to revise the proposals to correct spatial imbalances in effects. In each sub-area, conservation value is calculated by comparing biomass in the sub-area with the MPA proposal to biomass in the sub-area without fishing. In each sub-area, economic value is calculated by comparing profit (or yield) in the sub-area with the MPA proposal to profit (or yield) in the sub-area with no new reserves. Examples of these outputs as produced by the UCSB model are given in Figures B4.1 and B4.2 of Appendix B4.
- The models calculate how much biomass is in each MPA, what fraction of the larvae arriving in that MPA were produced within the MPA (self-recruitment), and to what degree the MPA is self-sustaining (self-persistence). The first metric will allow a determination of which MPAs are in locations that support large populations of the target species and which are poorly placed to protect that species. The second metric (self-recruitment) allows a determination of the extent to which each MPA is seeded with larvae originating elsewhere, as opposed to being replenished primarily by larvae spawned within that MPA. The third metric (self-persistence) is related and determines whether the MPA would persist in isolation; this is subtly different from self-recruitment, in that an MPA may receive a huge influx of larvae from other sources (low fraction of self-recruitment) but might nonetheless persist on its own. Conversely, an MPA may be highly self-recruiting, but if the total number of self-produced larvae is very low, the population in the MPA may not be persistent. Examples of these outputs as produced by the UCSB model are given in Figures B4.3 and B4.4 of Appendix B4.
- The models calculate how conservation value and economic value would vary for an alternative MPA proposal if one of the proposed MPAs was not implemented. That is, the model is run for a particular alternative MPA proposal, which contains m individual MPAs. Then m additional model runs are made. In each run, one of the MPAs is 'deleted' from the proposal. The outcome of these deletion runs is then compared to the run with the full proposal. By comparing the performance of the proposal with and without each individual MPA, the relative importance of each MPA can be determined. If the proposal with a particular MPA removed performs similarly to the whole, intact proposal, then the given MPA is not contributing greatly to various MLPA goals, and could be altered to improve its effectiveness at meeting those goals. Alternatively, if removing an MPA causes a decrease in overall performance, then that MPA is performing well at meeting those goals and should probably not be reduced in size or repositioned. Examples of these outputs as produced by the UCSB model are given in Figures B4.5 and B4.6 of Appendix B4.

- The models calculate the change in larval supply to each spatial cell under each alternative MPA proposal. This value is calculated as the percentage change in larvae settling in a cell in a given proposal, relative to the number of larvae settling in that cell under the “No-Action” Alternative, or Proposal 0. This statistic reveals which portions of the study region are expected to experience an increase (or decrease) in larval replenishment as a result of MPA implementation. Additionally, the model results also display the locations where those additional larval settlers were spawned; i.e., the locations where MPAs increase the production of successful larvae (“successful” larvae are those that actually disperse to another cell within the study region). This statistic quantifies the degree to which a given MPA actually increases the replenishment of itself, other MPAs, and the fished areas outside of MPA boundaries. This statistic can be compared across MPA proposals to determine which MPA configurations lead to the greatest increase in successful larval production. Examples of these outputs as produced by the UCD model are given in Figure B4.7 of Appendix B4.

In interpreting these outputs, it is important to recognize that the performance of an alternative MPA proposal or a particular MPA within that proposal is determined by the interplay of multiple factors, often in nonlinear ways. Therefore “improving” the performance of a particular MPA could be accomplished by varying any one of a number of factors (including size, shape, coverage of habitat in the vicinity, distance to neighboring MPAs, position relative to oceanographic retention zones, etc.). However, lessons drawn from simpler models of population dynamics within MPAs (e.g., Crowder et al. 2000, Botsford et al. 2001, 2009, Gaines et al. 2003, Kaplan and Botsford 2005, Kaplan 2006, Moffitt et al. 2009) do suggest the consequences of adjusting different MPA features. In general, MPAs will afford better protection to a species if it is made larger relative to the home range radius of that species. An MPA is more likely to be self-sustaining and independently persistent if it is larger (so that a greater fraction of larvae produced within that MPA return to replenish the population within the MPA) and if it is positioned in a location with higher oceanographic retention (larger values on the diagonal of the larval connectivity matrix). MPAs also may support large populations if they are situated such that they receive large inputs of larvae from ‘upstream’ locations, although then the performance of the ‘downstream’ MPA is tied to the persistence of the population in the ‘upstream’ location. Similarly, it may be advantageous to locate MPAs such that they export many larvae to ‘downstream’ locations (determined by looking at the off-diagonal elements of the connectivity matrix in the horizontal rows corresponding to that MPA as a larval origin). However, the successful export of larvae still will depend on whether the ‘source’ MPA maintains a large, persistent population.

Using Models to Evaluate Genetic Connectivity

The science guidelines for MPA spacing are to place MPAs no more than 50-100 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 the Master Plan). This 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. For example, 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 threshold guidelines can be misconstrued by non-experts to suggest that connectivity is maximized below that range and negligible at greater distances. In reality, some locations may be more connected based on geographic, physical and oceanographic characteristics, while other may be less connected than the threshold guidelines suggest. 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.

The SAT has noted that bioeconomic models can directly calculate the levels of demographic connectivity. That is, the bioeconomic models provide additional information about connectivity between MPAs that is complementary to the MPA spacing evaluation. Moreover, the bioeconomic models provide continuous measures of the ecological 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 large distances. 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. However, in a fragmented MPA array, genetic information would not be able to pass from one sub-population in an MPA to another protected sub-population, making the overall population less able to respond to and adapt to changing conditions (e.g., climate change). To operate as an ecological network, MPAs should be connected by the exchange of alleles. For this reason, the existing bioeconomic modeling framework has been adapted to explicitly calculate patterns of genetic connectivity.

The genetic connectivity extension of the existing bioeconomic models represents dynamics in patches which have a maximum carrying capacity of 100 individuals in N patches (the same number of patches used in the standard bioeconomic model). The results are sensitive to the value used for carrying capacity, but consistent results are obtained across model runs as long as the carrying capacity is held constant. 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 a measure of the genetic connectivity between i and all other patches. This metric is calculated for each of the N patches in turn. That is, each patch is considered to be the initial origin of allele B and transmission times are calculated to each of the other patches, which are assumed to start out as homozygous A . This iterative procedure provides a pairwise estimate of connectivity among all the 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.

The model operates at the steady-state equilibrium obtained from the original demographic model. That is, all life-history parameters, habitat, fishing rates, etc., are assumed to be constant at their equilibrium levels for the duration of the genetic connectivity simulations. The genetic connectivity between each pair of patches is calculated for each of the fishery management scenarios (unsuccessful management, MSY-type management, and/or conservative management) and for the unfished scenario. Connectivity is reported as the difference in connectivity afforded by a proposed network of MPAs (or MPA array), relative to the unfished state. If $C_{ij}(F)$ is the connectivity (average number of generations) between patches i and j under fishing conditions F , then the percent change in connectivity for an MPA array is:

$$Z_{ij} = [1 - C_{ij}(\text{fished})/C_{ij}(\text{unfished})] \times 100$$

Values of Z near zero indicate that the proposed network of MPAs (or MPA array) maintains the same level of connectivity found in an unfished population. More negative values indicate that gaps in MPA

spacing may be causing a loss in connectivity in the network. Note that Z_{ij} is undefined because $C_{ij} = 0$, and that $Z_{ij} = 0$ if there is no connectivity between i and j in the unfished state (i.e., a natural connectivity barrier). Visual inspection of a plot of Z values typically reveals where genetic breaks have arisen and can be used to gauge where MPA spacing may be adjusted to prevent this break in the network of MPAs.

Figure 8-1. Example of Spatial Map of Conservation Value Generated by UCD Model

The map from the MLPA South Coast Study Region shows the equilibrium biomass for one species (kelp bass) in each model cell.

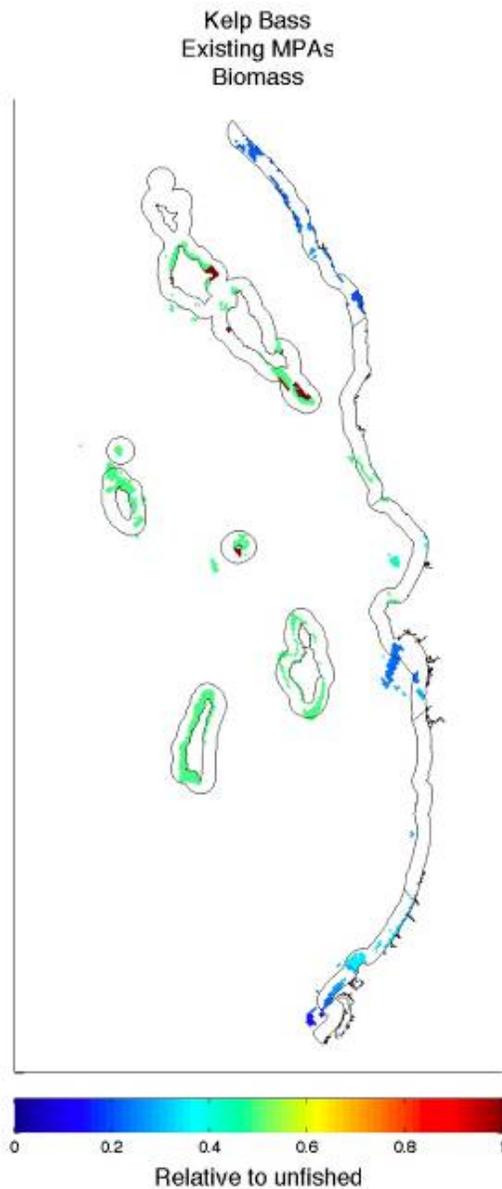


Figure 8-2. Example of Spatial Map of Economic Return Generated by UCD Model

The map shows the equilibrium yield for one species (kelp bass) in each model cell in the MLPA South Coast Study Region.

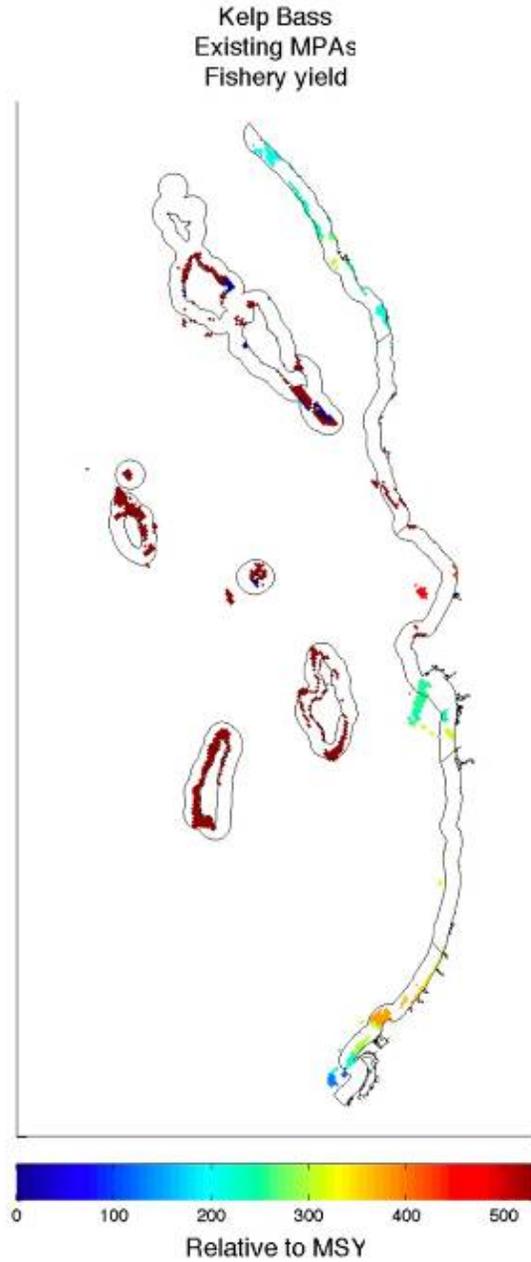


Figure 8-3. Example of Spatial Map of Recruitment Generated by UCD Model

The map from the MLPA South Coast Study Region shows the equilibrium larval recruitment for one species (kelp bass) in each model cell.

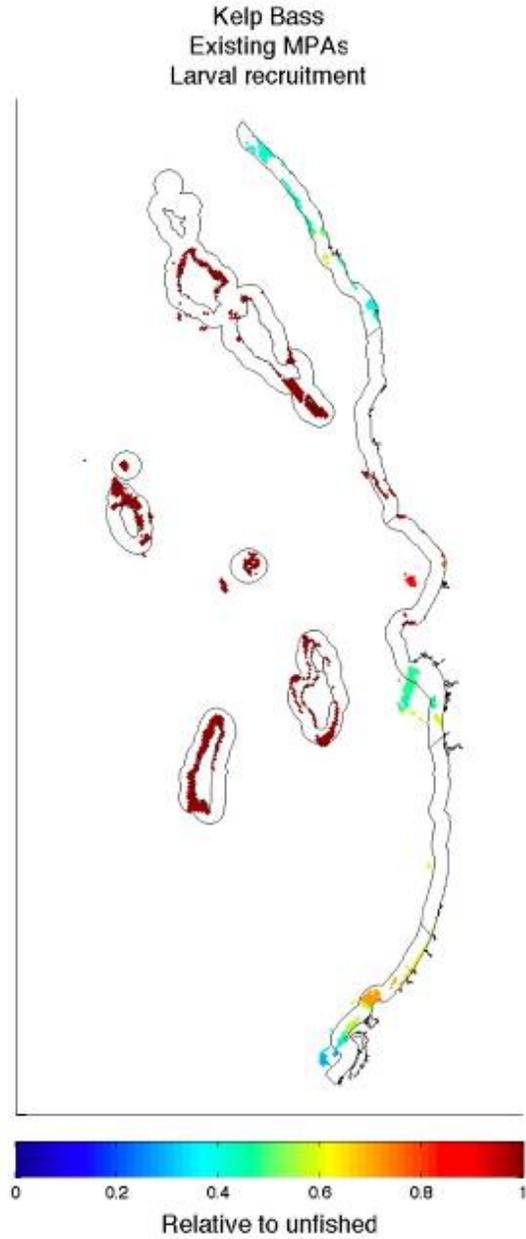


Figure 8-4. Example of Spatial Map of Fishing Generated by UCD Model

The map from the MLPA South Coast Study Region shows the equilibrium fishing rate for one species (kelp bass) in each model cell.

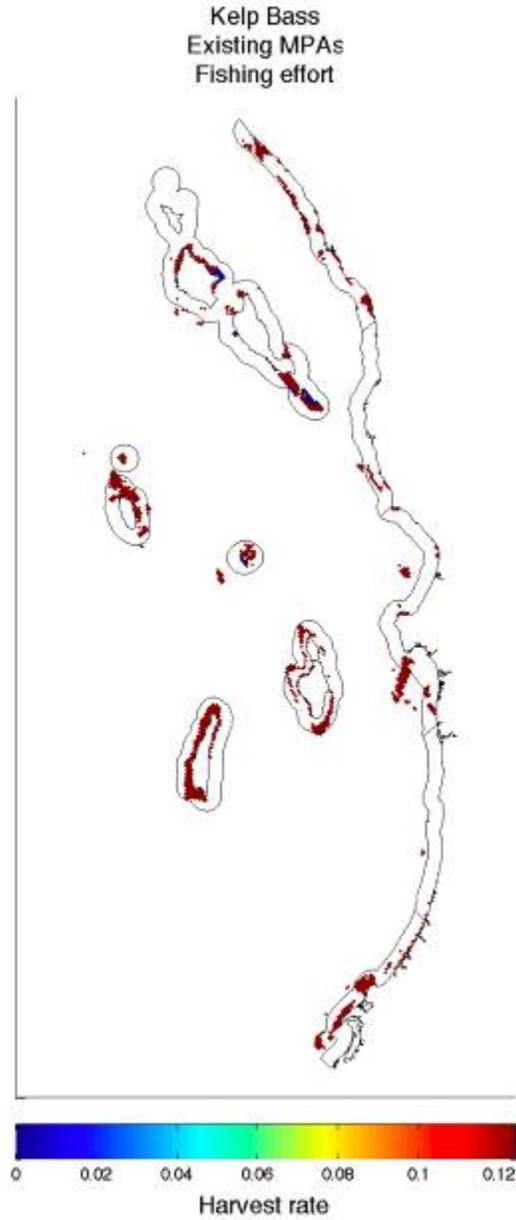


Figure 8-5. Example of Connectivity Matrix Used by Models

Color intensity at each point shows the probability of dispersal of kelp bass larvae from an origin patch (along vertical axis) to a destination patch (along horizontal axis). Points are grouped geographically for the MLPA South Coast Study Region.

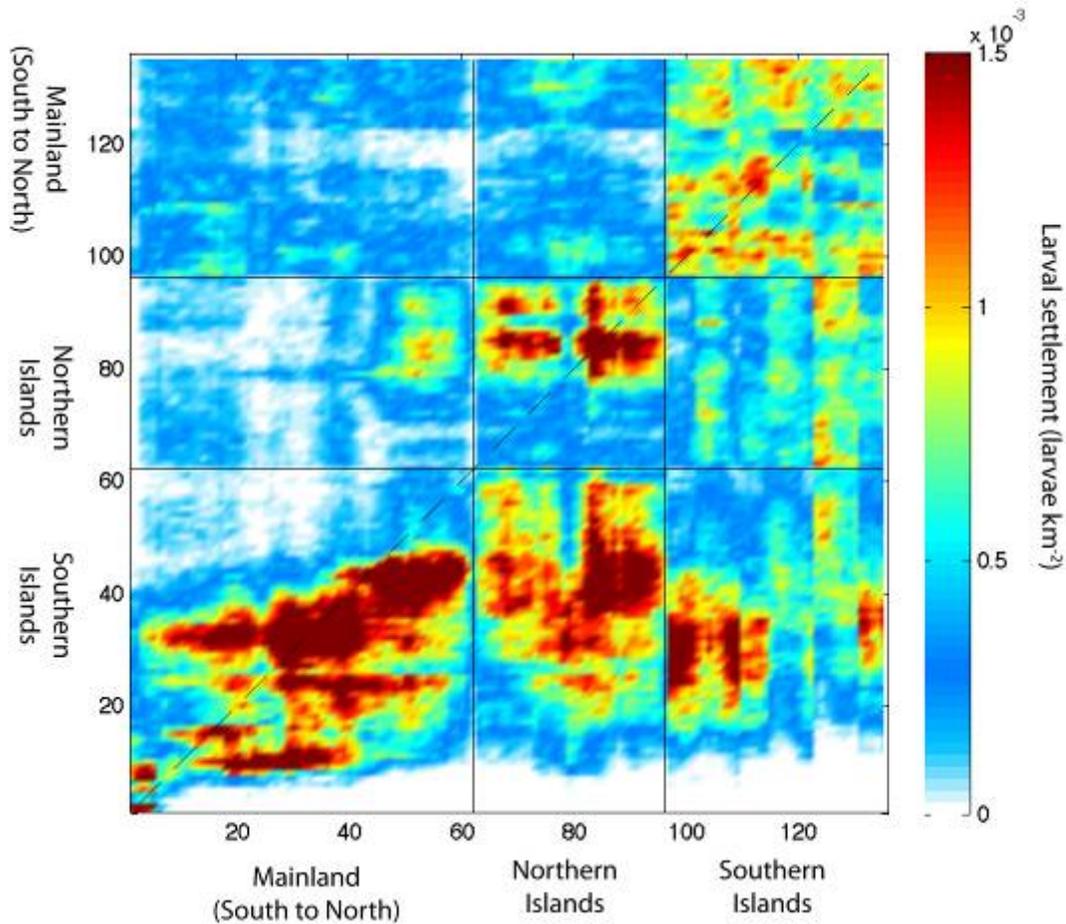
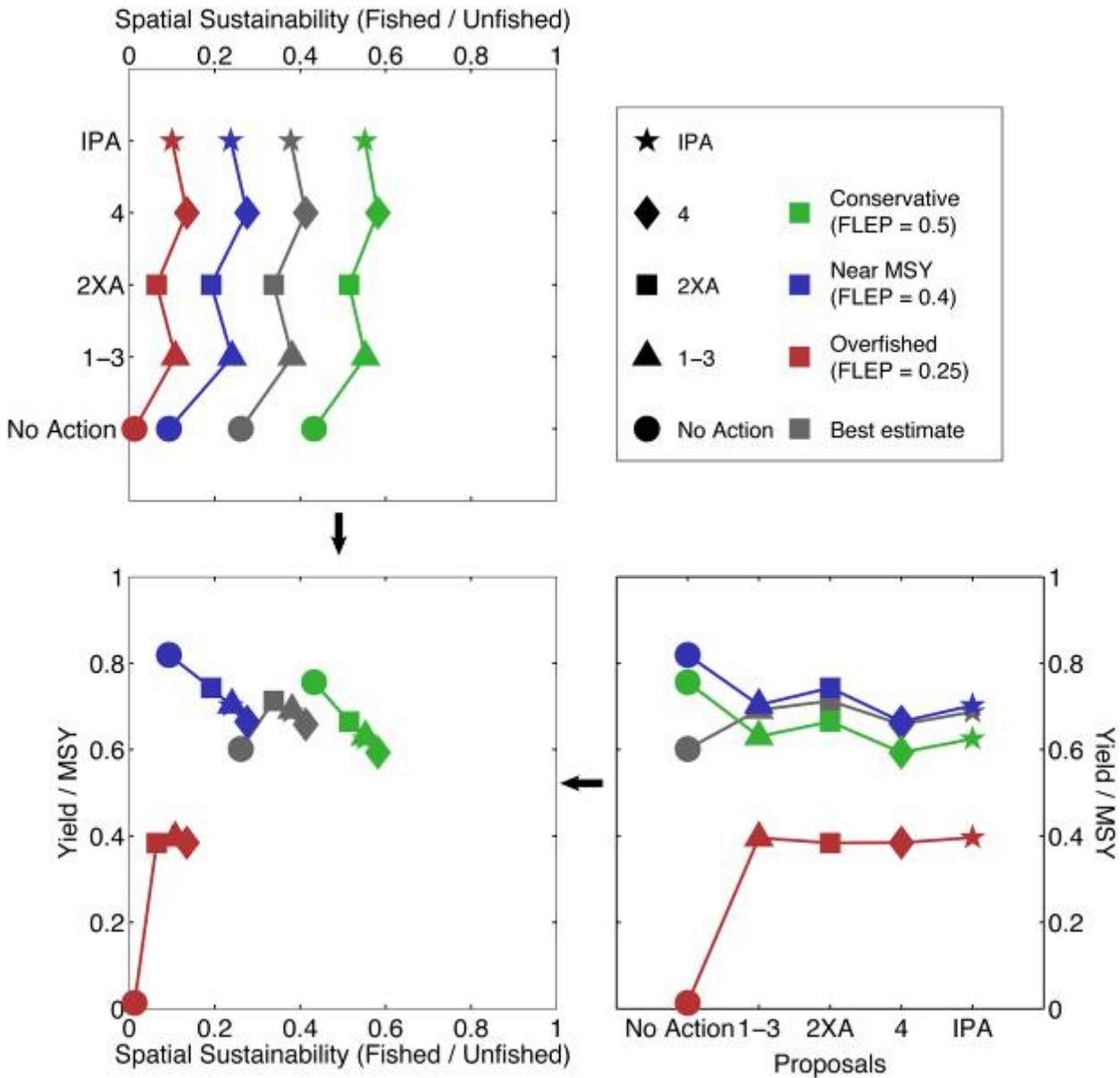


Figure 8-6. Example of Tradeoff Curve Produced by Models

This example shows a comparison of four MPA proposals and the no action alternative (Proposal 0) from the MLPA South Coast Study Region. The top left panel shows the Conservation Value metric (total biomass as a proportion of biomass in a scenario without fishing for each proposal) and the bottom left panel shows the tradeoff curve for both metrics for each proposal. Model results were generated using three different assumptions about the future success of fishery management outside of MPAs: conservative management, MSY-type management, and unsuccessful management. These different fishery management scenarios are indicated by different colors in the figure.



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- Botsford LW, Hastings A, Gaines SD (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol Lett* 4:144-150.
- Botsford LW, White JW, Coffroth MA, Paris C, Planes S, Shearer TL, Thorrold SR, and Jones GP (2009) Connectivity and resilience of coral reef metapopulations in MPAs: matching empirical efforts to predictive needs. *Coral Reefs* 28: 327-337
- Crowder LB, Lyman SJ, Figueira WF, Priddy J (2000) Source-sink population dynamics and the problem of siting marine reserves. *Bull Mar Sci* 66:799-820
- Gaines SD, Gaylord B, Largier JL (2003) Avoiding current oversights in marine reserve design. *Ecol Appl* 13:S32-S46
- Kaplan DM (2006) Alongshore advection and marine reserves: consequences for modeling and management. *Mar Ecol Prog Ser* 309:11-24
- Kaplan DM, Botsford LW (2005) Effects of variability in spacing of coastal marine reserves on fisheries yield and sustainability. *Can J Fish Aquat Sci* 62: 905-912.
- Moffitt EA, Botsford LW, Kaplan DM, O'Farrell MR (2009) Marine reserve networks for species that move within a home range. *Ecol Appl*: in press.

Appendix B. Bioeconomic Modeling

B1. Model Assumptions for Key Structural Elements in Spatially Explicit Bioeconomic Models

Table B1-1. Assumptions of the University of California, Davis (UCD) and University of California, Santa Barbara (UCSB) Bioeconomic Models

UCD Model Assumptions	UCSB Model Assumptions
<p>Larval Dispersal: Adults of representative species in each 1 km x 1 km habitat cell throughout the study region spawn larvae that are randomly distributed within that cell. The probability of larvae moving from that cell to any other in the study region is calculated using output from the ROMS, for which larvae are assumed to behave as passive, neutrally buoyant particles. Dispersal pathways are calculated by averaging across several years of ROMS circulation output. For each species, dispersal pathways are calculated using known spawning seasons and pelagic larval durations for the species. ROMS dispersal probabilities are calculated for five km radius circles distributed along the coastline of the study region; these data are mapped onto the 1 km x 1 km habitat grid used in the population models. Successful settlement for larvae ‘arriving’ at each model cell is contingent on the presence of suitable habitat in that cell.</p>	<p>Larval Dispersal: Same as UCD model.</p>
<p>Larval Settlement: Settling larvae experience intra-cohort density-dependent mortality. That is, the mortality rate of settlers depends on the density (fish per square meter) of other settlers arriving at that location, reflecting competition for habitat and predator refuges that is typical of the species being modeled.</p>	<p>Larval Settlement: Settling larvae experience intra-cohort density-dependent mortality as in the UCD model. Because this density-dependence represents competition for habitat and refuges, its strength depends on the proportion of the cell that is suitable habitat. For a given number of settling larvae, more will survive to adulthood in a cell with abundant suitable habitat than in a cell with mostly poor habitat.</p>
<p>Adult Growth and Reproduction: Growth, survival, and egg production are based on published data. In general, individuals grow to a maximum length, their weight is proportional to length cubed, and egg production is proportional to weight. Thus old, large individuals produce more eggs than young small individuals. Survival</p>	<p>Adult Growth and Reproduction: Growth for each species is based on previously published growth curves. Survival is independent of fish age and is based on published estimates of mortality in the absence of fishing. Egg production is assumed to be proportional to the total weight of adult fish.</p>

UCD Model Assumptions	UCSB Model Assumptions
is constant with age except for species for which more precise data are available.	
Adult Movement: Adults move within home ranges. Individuals with home ranges spanning MPA boundaries experience fishing pressure in proportion to the amount of their home range that is outside the MPA. This creates a spillover effect for adults with home ranges centered just inside MPAs.	Adult Movement: Each year a fraction of the fish of each age class in each cell leave the cell and are distributed evenly among all neighboring habitable cells (any cell adjacent at the sides or corners which contains appropriate habitat). We assume, for each species, that this fraction is proportional to the typical diameter of a home range. The model is reasonably insensitive to the scaling of this diffusive movement rate.
Fishing Pressure: Fishing regulations follow those set forth in each draft proposal, and both recreational and commercial fishing are considered. Initially, in the absence of better information, fishing effort will be modeled assuming that effort is equal across space but total effort is redistributed and increases outside of MPAs after MPA implementation. Pending collaboration with UCSB and Ecotrust, fishing effort will vary over space depending on fish abundance and travel costs (distance from port) using a fleet model that is parameterized based on data from the northern California commercial fishing fleet.	Fishing Pressure: We assume that fishers are acting to maximize their own profits. Assuming a large number of fishers acting independently, this means that fishing effort will be distributed such that at the end of each season marginal profits are the same in all patches. The current calculation of profits accounts for the “stock effect” in which fish are cheaper to extract from large than from small populations. We also have developed a version of the model that accounts for the costs of traveling to isolated patches. The model used in the north coast may account for these travel costs depending on analysis of Ecotrust data on the spatial pattern of commercial and recreational fishing.

B2. Summary of Methods for Parameterizing Fishing Fleet Component of Spatially Explicit Bioeconomic Models

Note: These methods are currently under development.

Both the economic and conservation outcomes of implementing an MPA network will depend on how areas outside of the MPAs are fished. The UCSB and UCD models therefore predict not only how MPAs will change fish populations but also how fishing effort will be distributed throughout the region. Because of the broad spatial scale and the large number of fishers involved, the models do not seek to predict decisions made by individual fishers but instead to predict the aggregate distribution of fishing effort for each species.

The description of the spatial distribution of fishing effort in the bioeconomic models can take on several forms, of increasing complexity. The simplest description is a uniform distribution of fishing effort (except in MPAs, where effort is restricted or prohibited). A somewhat more realistic description is to allow fishing effort to be redistributed across space as a function of profit. This approach is based on the expectation that effort on each species will be distributed

across patches so that marginal profits from fishing the species are the same in all fished patches. If this was not the case, and one patch had higher marginal profits than another, fishers would be expected to reduce effort in the less profitable patch and allocate more effort to the more profitable patch. To calculate the level of fishing effort that equalizes marginal profits in each patch, the models need to know how profit in each patch varies as a function of fishing effort.

Profit in each patch is calculated as revenue minus costs, where revenue is a function of fishing effort and fish biomass in the patch, and costs are a function of fishing effort in the patch, distance of the patch from the nearest port and typical weather conditions in the patch. A simple form is assumed for this relationship:

$$\text{Profit in patch } i = \alpha_1 f(E_i, B_{i0}) - [\alpha_2 D_i + \alpha_3 W_i + \alpha_4] E_i$$

Where $f(E_i, B_{i0})$ gives yield as a function of effort and biomass in patch i , D_i is the distance of the patch from port, W_i reflects typical weather conditions in the patch, and the α terms are unknown parameters giving the relative importance of the different factors.

The modelers are collaborating with Ecotrust to determine the values of these α parameters. For each species, the α parameters are refined to obtain the best match between the spatial distribution of fishing effort predicted by the model (assuming the current set of existing MPAs) and the actual current distribution of fishing, documented by Ecotrust. Then, these best parameter values will be used in evaluating alternative MPA proposals, and will allow the models to predict how fishing effort will be distributed under that proposal, and thus how fishing outside of MPAs will effect conservation and economic outcomes of the proposal.

Note that while “profit” implies the sale of harvested resources, it is possible to calculate the relative benefit of recreational fishing in each location in an analogous manner because recreational fishermen place a value, though not necessarily monetary, on the fish they catch.

B3. Summary of Life History Parameters Used in Models

Life-history parameters for each modeled species are obtained by searching the published scientific literature, stock assessments, and the 2000 Pacific States Marine Fisheries Commission report prepared by G. Cailliet et al. These parameters will be vetted by the SAT modeling work group and a panel of experts on northern California fish and kelp forest ecosystems, including other SAT members

Parameters Used

Movement: Because management with MPAs involves creating differences in conditions (i.e., fishing mortality rate) over space, the effects of individual movement have a critical effect on sustainability and yield. Two kinds of biological movement are important, dispersal during the larval stage and swimming movement during juvenile and adult stages.

Juvenile/Adult Swimming: Most of the species that will be protected and sustained by MPAs either have limited adult movement or move within a specified home range. For some of these species, the sizes of the home ranges have been estimated using acoustic tags. This type of movement can be considered well known for species that have been studied in this way. In general, home range size is reported in terms of diameter, which facilitates implementation in a one-dimensional model. There is greater confidence in estimates derived from acoustic tagging studies than from simple tag-recapture studies.

Larval Dispersal: The models use estimates of larval dispersal derived from the ROMS-based Lagrangian particle-tracking model developed by UCLA and UCSB. In this approach, each species is characterized by pelagic larval duration (PLD) and spawning season.

Life History: Both reproduction and yield depend on the sizes of individuals, which depends on how fast they grow through life. Here, the relationship of body size versus age is presented in terms of the dependence of length on age in the most commonly used form, a von Bertalanffy growth function. The parameter L_{∞} represents the mean length for very old individuals, the parameter k represents the growth rate at young ages, and the parameter t_0 essentially describes the length of an individual at age 0. The relationship of body size versus age also is presented in terms of weight, which is calculated from size via an allometric relationship, $W = aL^b$. The values of a and b are given for each species.

Reproduction depends on the age of maturity and fecundity. Fecundity, f , the number of eggs produced by a female of a certain age or size in a year, is commonly assumed to be proportional to weight, but is sometimes also calculated from an allometric (or other) relationship with length.

Mortality consists of two components, fishing mortality and natural mortality. Here we present instantaneous natural mortality rates.

The size ranges that are available to be caught by the fishery are either specified by regulation or estimated from fishery or other data.

Compensation Ratio / Critical Replacement Threshold: Species persistence, and thus all model results, depends heavily on the shape of the settler-recruit relationship. This relationship describes the per-capita mortality of settlers as a function of settler density; settlers surviving this initial bout of post-settlement mortality are considered 'recruits' into the benthic population. This curve is generally described in terms of the slope at the origin; it is assumed that the curve has a Beverton-Holt functional form and that the asymptotic maximum density can be made non-dimensional by scaling all model results to the baseline un-fished case.

The settler-recruit curve is analogous to the stock-recruit curves utilized in non-spatial fishery models. The slope at the origin of the stock-recruit curve can be described as a non-dimensional compensation ratio, which is the ratio of per-capita settler survival at very low densities (settlers = 0) to per-capita survival of settlers at the highest possible density in the un-fished state. The inverse of this number ($1/CR$) also is referred to as the critical replacement threshold (CRT) because it is the fraction of lifetime egg production (FLEP) below which the population is not persistent. That is, if $CR = 5$, $CRT = 1/5 = 0.2$, and if fishing reduces lifetime

egg production below 20% of its unfished maximum, the population will collapse. Estimates of the CR generally are difficult to obtain except for species that have been fished below the CRT and therefore collapsed. As a consequence the CR is known for only a few fished species. Dorn (2002) estimated a CR of approximately 3 for several collapsed species of north Pacific rockfishes. This CR is likely to be a conservative estimate, especially since some species are likely to be somewhat more resilient than those rockfish species. Therefore, both models use a reasonable but nonetheless conservative estimate of $CR = 4$ ($CRT = 0.25$) for the settler-recruit curves for each species.

Although the choice of CR will affect the model results, by far the largest effect will be on the sensitivity of the population to fishing. This effect on sensitivity to fishing largely should be accounted for by the methods used to choose fishing effort outside of reserves. Because fishing effort in each of the future fishing scenarios is chosen as some constant fraction of CRT (or MSY, in the case of the UCSB model), the potential for the choice of CR to affect model outcomes should be much reduced.

Species Notes

The effects of alternative MPA proposals will be evaluated for a suite of seven species: black rockfish, brown rockfish, cabezon, redbtail surfperch, red abalone, red sea urchin, and Dungeness crab. The text and tables that follow provide the life history parameters used for each model species and the literature source for that parameter. Unless otherwise noted, all distances are in kilometers, all organism body lengths are in centimeters, and all masses are in kilograms. A literature search for parameter estimates is currently underway for brown rockfish (*Sebastes auriculatus*) and redbtail surfperch (*Amphistichus rhodoterus*).

Table B3-1. Black rockfish (*Sebastes melanops*)

Parameter	Value	Source
Pelagic larval duration	4-6 mo	Love et al. 2002, Laroche and Richardson 1980
Spawning season	Jan-May	Leet et al. 2001
Home range diameter	9-16 km	Mathews and Barker 1984, Culver et al. 1987, Starr and Green 2007
Length-at-age (cm TL)		
von Bertalanffy equation:		
$L(t) = L_{\infty} (1 - \exp(-k(t - t_0)))$		
L_{∞}	44.2	Bobko and Berkeley 2004
k	0.33	
t_0	0.075	
Weight-at-length (cm, kg)		
$W = aL^{\hat{a}}$		
\hat{a}	1.68×10^{-5}	Ralston and Dick 2003
a	3	
Maximum age	50 yr	Love et al. 2002
Age at maturity	7 yr	Bobko and Berkeley 2004
Natural mortality rate	0.14	Ralston and Dick 2003, Sampson 2007
Available to fishery	4 yr	CDFG Regulations

Table B3-2. Brown rockfish (*Sebastes auriculatus*)

Parameter	Value	Source
Pelagic larval duration	1-2 months	
Spawning season	Dec-Jun in NCSR	
Home range diameter	< 2 km	Lea et al 1999
Length-at-age (cm TL)		
von Bertalanffy equation:		
$L(t) = L_{\infty} (1 - \exp(-k(t - t_0)))$		
L_{∞}	51.4	Love and Johnson 1998
k	0.16	
t_0	-0.55	
Weight-at-length (cm, kg)		
$W = \hat{a}L^{\hat{a}}$		
\hat{a}	4.4×10^{-5}	Love and Johnson 1998
\hat{a}	2.74	
Maximum age	20	Stein and Hassler 1989
Age at maturity	4	Love and Johnson 1998
Natural mortality rate	0.112	Gowan 1983
Available to fishery	?	

Table B3-3. Cabezon (*Scorpaenichthys marmoratus*)

Parameter	Value	Source
Pelagic larval duration	3-4 mo	Cope and Punt 2005
Spawning season	Nov-Mar	Leet et al. 2001
Home range diameter	60 m	C. Merelis et al., unpublished data
Length-at-age (cm TL)		
von Bertalanffy equation:		
$L(t) = L_{\infty} (1 - \exp(-k(t - t_0)))$		
L_{∞}	62.12	Cope and Punt 2005
k	0.18	
t_0	-1.06	
Weight-at-length (cm, kg)		
$W = aL^{\hat{a}}$		
\hat{a}	9.2×10^{-6}	Cope and Punt 2005
\hat{a}	3.187	
Maximum age	13 yr	Cope and Punt 2005, Love 1996
Age at maturity	3 yr	Cope and Punt 2005
Natural mortality rate	0.25	Cope and Punt 2005
Available to fishery	4 yr	CDFG Regulations

Table B3-4. Red abalone (*Haliotis rufescens*)

Parameter	Value	Source
Pelagic larval duration	4-7 d	Prince et al. 1987
Spawning season	Apr-July	Leet et al. 2001
Home range diameter	100 m	Ault and Demartinit 1987
Length-at-age (cm TL)		
von Bertalanffy equation:		
$L(t) = L_{\infty} (1 - \exp(-k(t - t_0)))$		
L_{∞}	19.24	Tegner et al. 1992
k	0.217	
t_0	0	
Weight-at-length (cm, kg)		
$W = aL^{\hat{a}}$		
\hat{a}	1.69×10^{-4}	Ault 1982
\hat{a}	3.02	
Maximum age	30 yr	Leaf 2005
Age at maturity	3 yr	Rogers-Bennett et al. 2004
Natural mortality rate	0.15	Tegner et al. 1989
Available to fishery	8 yr	CDFG Regulations

Table B3-5. Red sea urchin (*Strongylocentrotus franciscanus*)

Parameter	Value	Source
Pelagic larval duration	7-19 wk	Leet et al. 2001
Spawning season	Dec-Mar	Rogers-Bennett et al. 1995
Home range diameter	10 m	Rogers-Bennett et al. 1995
Length-at-age (cm TL)		
von Bertalanffy equation:		
$L(t) = L_{\infty} (1 - \exp(-k(t - t_0)))$		
L_{∞}	11.8	Morgan 1997, Morgan et al. 2000
k	0.22	
t_0	0	
Weight-at-length (cm, kg)		
$W = aL^{\hat{a}}$		
\hat{a}	1	
\hat{a}	3	
Maximum age	30 yr	Morgan 1997, Morgan et al. 2000
Age at maturity	3 yr	Morgan 1997, Morgan et al. 2000
Natural mortality rate	0.08	Morgan 1997, Morgan et al. 2000
Available to fishery	5 yr	CDFG Regulations

Table B3-6. Dungeness crab (*Cancer magister*)

Parameter	Value	Source
Pelagic larval duration	3-4 mo	Leet et al. 2001
Spawning season	Nov-Feb	Leet et al. 2001
Home range diameter	5-10 km	
Length-at-age (cm TL)		
von Bertalanffy equation:		
$L(t) = L_{\infty} (1 - \exp(-k(t - t_0)))$		
L_{∞}	24	L. Botsford, unpublished data
k	0.345	
t_0	0.068	
Weight-at-length (cm, kg)		
$W = aL^{\hat{a}}$		
\hat{a}	3.165×10^{-4}	
\hat{a}	2.76	
Maximum age	7 yr	
Age at maturity	4 yr	
Natural mortality rate	0.2	
Available to fishery	4 yr (males only)	CDFG Regulations

B4. Examples of Bioeconomic Model Output to Be Used as Feedback on Individual MPA Performance (examples taken from the MLPA South Coast Study Region)

The following figures are examples of model outputs that will be provided as part of the evaluation of alternative MPA proposals. These example results were produced by the UCSB model based on a proposal of three MPAs: MPA A - near San Diego, MPA B - near Santa Barbara and MPA C – at San Nicolas Island.

Figure B4-1. Conservation Value (Biomass as a Fraction of Unfished Biomass) for All Regions and for Each Subregion Separately

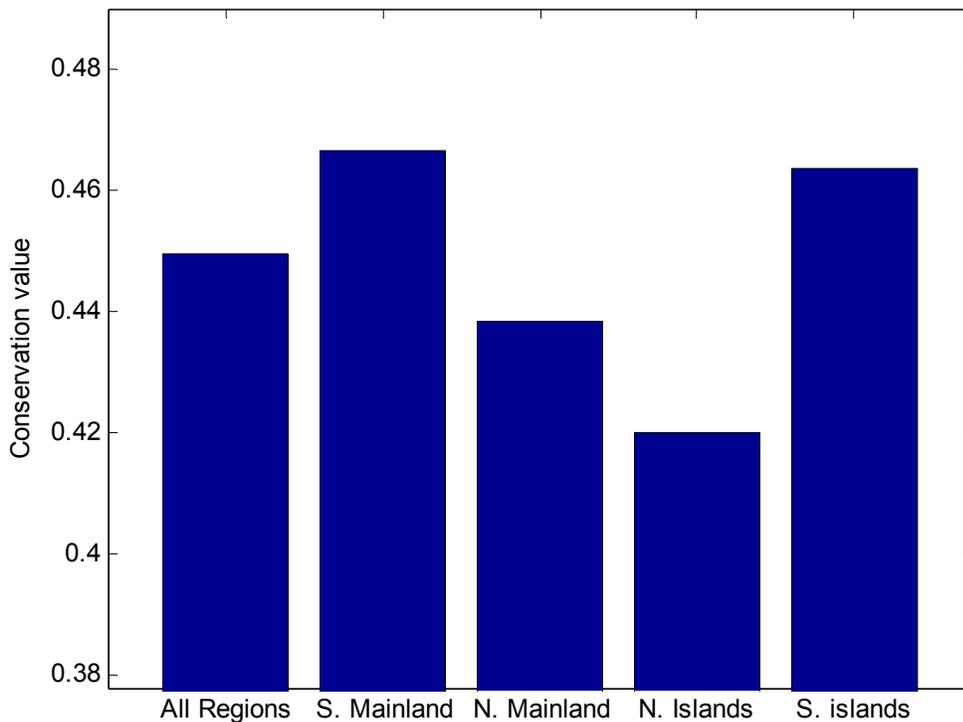


Figure B4-2. Economic Value (Profit with Reserves as a Fraction of Maximum Sustainable Profit without Reserves) for All Regions and for Each Subregion Separately.

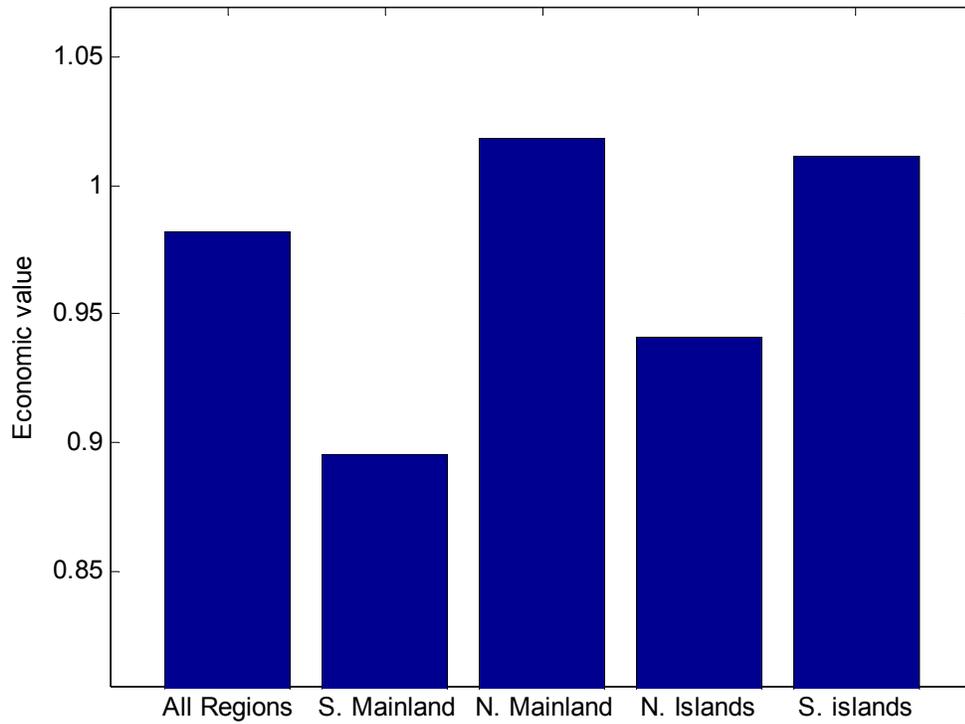


Figure B4-3. The Mass of Fish in Each Reserve, as a Fraction of the Total Mass of Fish in the Entire MPA Network.

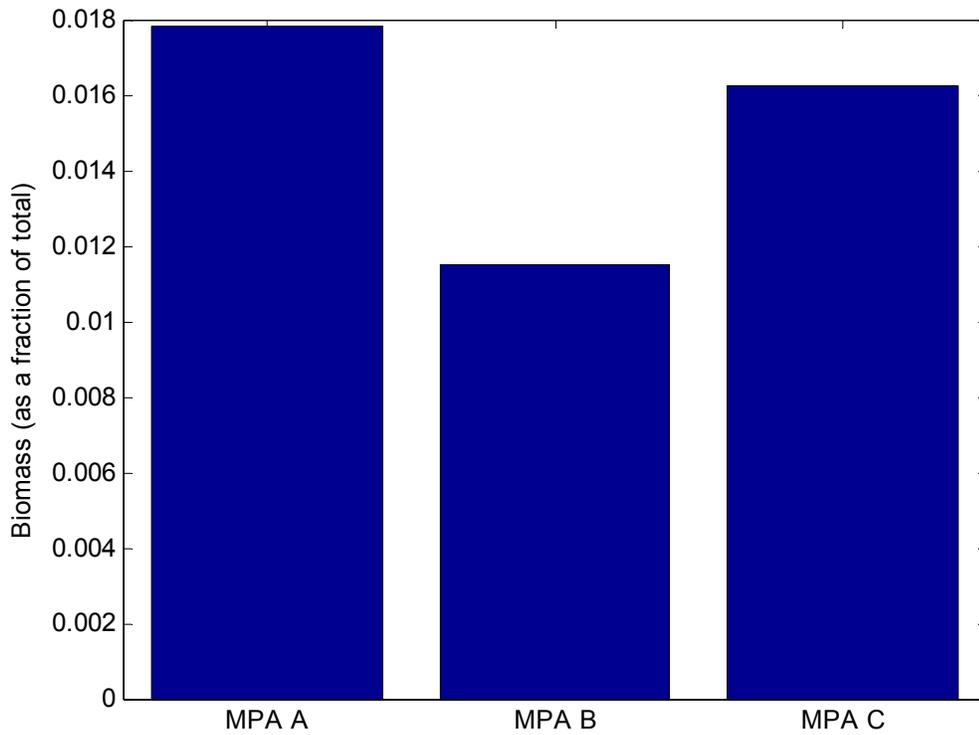


Figure B4-4. The Fraction of Larvae Settling in Each Reserve and Produced within the Reserve.

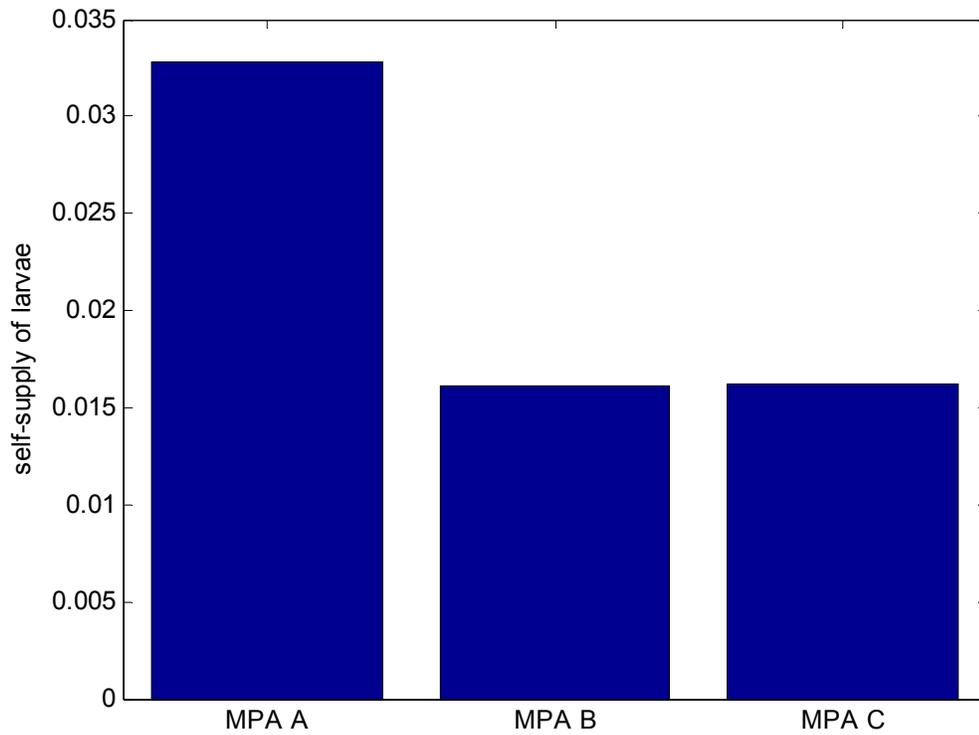


Figure B4-5. Conservation Value for the Entire MPA Network, Subsets of the MPA Network, and No MPAs

Conservation Value (Biomass as a Fraction of Unfished Biomass) for the entire MPA network with all reserves as well as with all reserves except Reserve A, all except Reserve B, all except Reserve C and no new MPAs

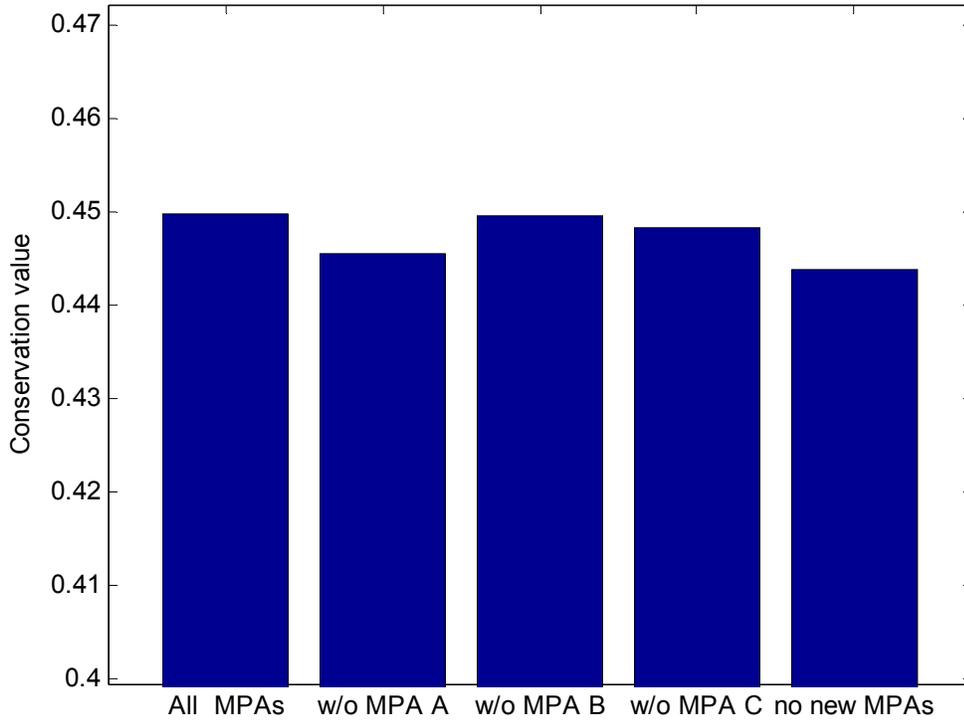


Figure B4-6. Economic Value for the Entire MPA Network, Subsets of the MPA Network, and No MPAs

Economic Value (profit with reserves as a fraction maximum sustainable profit without reserves) for the entire MPA network with all reserves as well as with all reserves except Reserve A, all except Reserve B, all except Reserve C and without new MPAs.

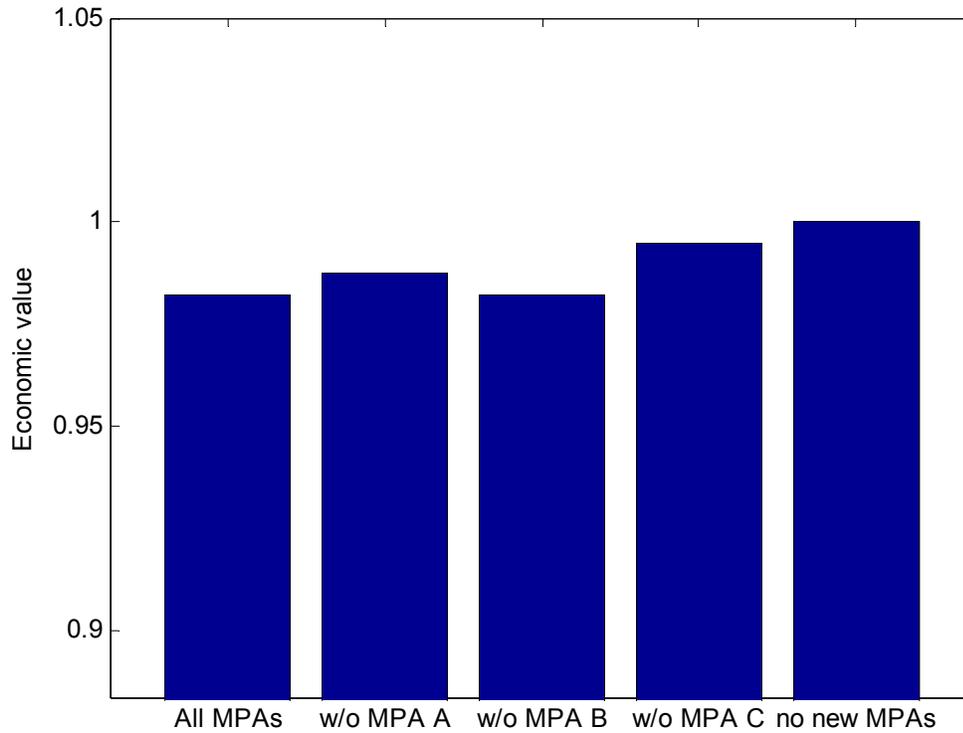


Figure B4-7. Change in Larval Production and Larval Supply for a Hypothetical MPA Proposal

Left panel: Percent change in the production of successfully dispersing larvae, relative to Proposal 0 (both under unsuccessful fishery management scenario). Right panel: Percent change in larval settlement, relative to Proposal 0. The successful larval settlers depicted in the right panel were produced at the locations depicted in the left panel.

