

## **COMPARISON OF MARINE PROTECTED AREA POLICIES USING A MULTISPECIES, MULTIGEAR EQUILIBRIUM OPTIMIZATION MODEL (EDOM)**

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## **Abstract**

A multispecies, age-structured spatial model called EDOM is developed and used to evaluate impacts of multiple fishing fleets and marine protected areas on long term (equilibrium) fishery economic performance, catch, and abundance. Populations and fishing are represented on a grid of spatial cells, with linkage among cells due to larval and adult dispersal and inclusion of multiple cells in the home ranges of fish that are resident in or home to each cell for spawning. Recruitment to each cell is assumed to depend on area of suitable juvenile rearing habitat and on compensatory survival responses after larval settlement. Spatial fishing efforts are predicted using either gravity models or an economic optimization that distributes effort so as to maximize total profit for each fleet. The model predicts that imposition of MPA networks designed from habitat criteria will result in improved economic performance only if fishing effort is sub-optimally high outside reserves. Absent such MPAs, it can still be optimum to close some source or nursery areas to fishing, if larval dispersal results in a source-sink metapopulation structure and/or fishing in important nursery areas causes high bycatch mortality of pre-recruit juveniles.

Keywords: population dynamics, marine protected areas, economic optimization, spatial dynamics, EDOM model

## Introduction

Networks of marine protected areas are now widely advocated as a means to deal with overfishing and to protect sensitive habitats and species so as to maintain and restore marine biodiversity. Equilibrium, spatial population dynamics models have been developed to predict the long term efficacy of such networks and to predict impacts on fishery values (Gerber et al. 2003; Gaylord et al. 2005; Botsford et al. 2004; Kaplan and Botsford 2005; Kaplan et al. 2006; Walters et al. 2007; Costello and Polasky 2008; Sanchirico and Wilen 2001). As noted by Kaplan et al. (2006), practical application of such models to compare MPA proposals in stakeholder gaming and optimization settings requires that the models be computationally efficient, i.e. produce predicted population response patterns and fishery performance measures (catch, economic value) in no more than a few seconds for any policy proposal.

Existing models have mainly taken a single-species approach, so as to demonstrate how species with different life-history characteristics (larval dispersal, adult movement, recruitment compensation, age-size dependent fecundity) are likely to benefit or not from different reserve size-spacing patterns. These predictions have been made with either arbitrary fishing mortality patterns outside reserves, or patterns linked to abundance so as to predict effects like concentration of fishing near reserve boundaries. The main findings are: (1) species with high adult dispersal or large home ranges are unlikely to benefit from small reserves, and (2) net benefits of reserves to fishing interests are unlikely to occur unless fishing mortality rates outside reserves are high enough to cause recruitment and/or growth overfishing (i.e. unless fisheries management outside reserves “fails”).

Here we develop a model for guiding MPA design and evaluating MPA performance in settings where multiple fish species are harvested together, by multiple fishing gears or fleets (e.g. recreational, commercial), such that each species suffers fishing mortality rates (or at least bycatch and discard mortality rates) determined by fishing efforts that are distributed in relation to the overall abundance and value of all the species. In order to efficiently compute equilibrium biomasses and egg production of the species over large numbers (hundreds) of spatial grid cells, we use Deriso-Schnute delay-difference models (Deriso, 1980; Schnute, 1987) to predict effects of fishing on size-age structure of the biomass. Larval dispersal and compensatory juvenile survival after larval settlement are modeled with relationships similar to those proposed by Kaplan et al. (2006) and Walters et al. (2007). We think of the spawning biomass on each model spatial cell as the biomass of mature individuals that home to the cell for spawning, and we represent both diffusive (irreversible) movement of fish among such homing cells and also “home range” movements of individuals away from the spawning cell to other cells in conjunction with feeding activities and seasonal migration patterns. We allow model users to set arbitrary fishing effort patterns, to predict effort patterns using gravity (logit choice) models, or to distribute efforts so as to maximize an overall economic profit criterion. The optimized effort distributions provide “least cost” assessments of the impact of arbitrary MPA networks on fishing interests, and we show that these least cost predictions are typically close to the predictions obtained with simple gravity models

where fishing efforts for each cell are predicted to be proportional to landed value of catch (summed over species) in that cell.

We demonstrate application of the model to a region of the north central California coast, where rocky bottom species are harvested by sport and commercial fisheries and where the California Marine Life Protection Act (MLPA) has mandated development of an MPA network aimed primarily at protecting inshore habitats and the rich diversity of species that these habitats support. Planning for MLPA has involved an intensive process of stakeholder involvement to develop multiple MPA network proposals, and screening of these proposals has mainly involved simple static criteria based on size-spacing guidelines intended to protect a high proportion of sedentary species, and on amounts of habitat protected. Population models have been used to develop size-spacing guidelines (particularly variations on the Kaplan et al. 2006 approach), and a key objective in our model development work has been to provide stakeholders and decision makers with the capability to screen policies using models tailored more specifically to the study region than those used to develop overall size-spacing guidelines. For the demonstration we divide the north central planning region into 243 spatial cells each 1km in north-south extent and extending from shore to the limit of California state jurisdiction, model 4 valuable species (lingcod, *Ophiodon elongatus*; cabezon, *Scorpaenichthys marmoratus*; black rockfish, *Sebastes melanops*; and canary rockfish, *Sebastes pinniger*), and 2 fishing fleets (sport, commercial).

## Model assumptions

The model attempts to predict equilibrium spawning biomasses  $B_{is}$  for  $s=1 \dots n_s$  species, over  $i=1 \dots n_c$  grid cells, subject to fishing by  $g=1 \dots n_g$  fishing gears that exert fishing effort  $E_{ig}$  in each grid cell. To make the equations presented below easier to read, we suppress the  $s, g$  subscripts except where necessary, e.g. we refer to  $B_{is}$  simply as  $B_i$  when it is obvious that we are referring to any species  $s$ .

## Representation of habitat spatial structure

We assume that the set of spatial cells, each indexed by  $i$ , are arranged in an arbitrary pattern on an X-Y map coordinate system. The center of each cell is at position  $X_i, Y_i$ , so that the distance between the center of any two cells  $i, j$  is given by  $D_{ij} = ((X_i - X_j)^2 - (Y_i - Y_j)^2)^{1/2}$ . A one-dimensional model (e.g. abundances near a transect running along a coastline) is created just by setting all  $Y_i = 0$ .

Each cell is assumed to have an areal proportion  $H_{is}$  of suitable juvenile habitat;  $H_i$  may differ across the modeled species. For example  $H_{is}$  might be the proportion of shallow hard-bottom habitat for a species whose juvenile nursery distribution is restricted to inshore reef or rocky habitats, and might be the total proportion of hard-bottom habitat for a species whose juveniles rear over a wider depth range.

For case studies with the model on California's north central coast planning region (a 210km stretch of coastline from Point Arena to Pescadero just south of San Francisco),

we have defined the model cells by starting with a GIS raster map of 1x1km rasters, where each raster is assumed to be predominantly one of seven general habitat types (shallow rocky, deep rocky, shallow soft bottom, deep soft bottom, unknown shallow, etc.). Each such raster is assigned a model cell number (i), and habitat areas for i (and geographic mean position  $X_i$ ,  $Y_i$ ) are calculated by adding up the raster areas. This approach makes it easy to assess effects of alternative spatial aggregation choices in defining the model cells; for example the raster data can be accumulated over 1km wide onshore-offshore strips, 2km wide strips, or arbitrarily shaped clusters of rasters. We ended up with 243 model cells after accounting for shoreline curvature and one key offshore feature, the Farallon Islands off the mouth of San Francisco Bay.

In more general GIS terminology, each model cell is defined as a spatial polygon, small enough to represent the smallest MPA size under consideration, and with polygon attributes being the proportions of habitat of different types. The polygons should each have about the same total map area, and when shaped as strips should represent the most likely orientation of MPAs (e.g. as strips running horizontally on the map from shore to the edge of management jurisdiction). This makes it easy to program a model user interface so that users can simply mouse click at any point on the map, and have the corresponding model cell (e.g. strip) be designated as in an MPA or not (closed or open to fishing).

### Delay-difference approximation for exploitable and spawning biomass

To apply eq. (1), we need to predict the average or equilibrium biomasses  $B_i$ . This can be done efficiently, while preserving such key population dynamics relationships as high fecundity of older fish, by using the Deriso-Schnute delay difference model. Suppose in an age-structured population that all fish aged  $k$  and older have equal annual survival rate  $S_t$  (including effects of harvest), and a weight-age relationship that can be approximated by the Ford-Brody growth model  $w_{a+1} = \alpha + \rho w_a$  (this model is typically very good for  $k > 2$ ). Then Deriso and Schnute have shown that total age  $k$  and older biomass  $B_t$  and numbers  $N_t$  are given *exactly* by the difference equations

$$B_t = S_t[\alpha N_{t-1} + \rho B_{t-1}] + w_k R_t \quad (1a)$$

$$N_t = S_t N_{t-1} + R_t \quad (1b).$$

Suppose that  $S_t$  is held constant in cell  $i$  at  $S_t = S_i$ , and that age- $k$  recruitment  $R_t$  in cell  $i$  varies around an average or equilibrium value  $R_i$ . Then (1b) implies equilibrium  $N_i = R_i / (1 - S_i)$ ; substituting this for  $N$  in (1a) and solving for equilibrium  $B_i$  in cell  $i$  results in

$$B_i = [S_i \alpha R_i / (1 - S_i) + w_k R_i] / (1 - \rho S_i) \quad (2).$$

Immigration and emigration can be included in the prediction of  $B_i$  simply by (1) adding predicted biomass immigration rate  $I_i$  into the numerator of (2), (2) including proportional emigration rate  $e_i$  as a loss term in calculation of  $S_i$  ( $S_i = S_{nat}(1 - U_i)(1 - e_i)$ , where  $S_{nat} = e^{-M}$  is natural survival rate and  $U_i$  is annual exploitation rate in cell  $i$  and harvest is assumed to be seasonal so that  $U_i = (1 - e^{-F_i})$ , and (3) adjusting the equilibrium equation for  $N_i$  for immigration using  $N_i = (R_i + NI_i) / (1 - S_i)$  where immigrating numbers  $NI_i$  are approximated as  $I_i / w_I$  using an estimate  $w_I$  of the average body weight of dispersing fish. Total fishing

mortality rate  $F_i$  is calculated as the sum over gears of  $q_g E_{ig}$ , where  $q_g$  is a species-specific catchability. When there is home range movement over multiple spatial cells,  $F_i$  is calculated as a sum over the cells used by  $B_i$  of proportions of time spent in each cell times the  $qE$  sum over gears for that use cell.

$R_i$  is presumably a function of total larval settlement  $L_i$  in cell  $i$ , and there is most likely to be compensatory change in post-settlement juvenile survival rate. We usually expect the net recruitment relationship to be of Beverton-Holt form:

$$R_i = a_i L_i / (1 + b_i L_i) \quad (3).$$

Maximum post-settlement survival rate to age  $k$ ,  $a_i$ , may well be similar among cells, but we expect the carrying capacity parameter  $b_i$  to vary with relative area of suitable juvenile habitat  $H_i$ . To parameterize eq. (5), we specify a base recruitment rate  $R_{oi}$  that is proportional to nursery habitat area  $H_i$  in cell  $i$ , and an initial estimate  $L_o$  of mean (over cells, weighted by unfished biomasses) larval settlement that would be expected when all the  $B_i$  are at unfished equilibrium  $B_{oi}$ . We then assume that recruitment rates per unit nursery habitat area  $R_i/H_i$  vary according to a species (but not cell) dependent relationship with parameters  $a^*$ ,  $b^*$ , and  $c^*$ :

$$R_i/H_i = a^* (L_i H_i^{c^*} / H_i) / [1 + b^* (L_i H_i^{c^*} / H_i)] \quad (4).$$

Here,  $L_i H_i^{c^*} / H_i$  represents effective larval settlement per unit nursery area, where  $c^*=0$  implies that all larvae settling on cell  $i$  are able to find and concentrate on  $H_i$ , while  $c^*=1$  implies that only the proportion  $H_i$  of all larvae settling on  $i$  actually settle successfully on that suitable nursery habitat (note that using a power function  $H^c$  in this setting only makes sense when  $H$  is scaled so as to vary between 0.0 and 1.0, i.e. is scaled as a proportion of total cell area that is usable).. Then  $a^*$  and  $b^*$  are calculated from an assumed Goodyear compensation ratio  $K$  and assumed scaling of  $R$  such that  $R/H=1$  when  $H=1$ , as  $a^*=K/L_o$  and  $b^*=(K-1)/L_o$ . Finally, the cell-specific  $a_i$  and  $b_i$  are calculated from  $a^*$ ,  $b^*$ , and  $c^*$  by scaling back from  $R/H$  to  $R_i$ , as  $a_i=a^* H_i^{c^*}$  and  $b_i=b^* H_i^{c^*} / H_i$ .

Larval settlement  $L_i$  to each cell is found as a sum of proportional contributions from the larval production by every cell, i.e.

$$L_i = \sum_j B_j S_{ij} \quad (5)$$

Here,  $S_{ij}$  is the larval settlement on cell  $i$  per unit spawning biomass in cell  $j$ . In principle  $S_{ij}$  should depend on ocean currents, larval behavior, pelagic larval duration, etc.; lacking some of these data we assume here that the  $S_{ij}$  are calculated with a normal probability kernel with species-specific larval movement distance ( $D_{ij}$ ) standard deviation. Note that we need not specify absolute fecundity or larval survival, since effects of these are represented in the stock-recruit  $a_i$  parameter. Note further that assuming larval production from each cell to be proportional to  $B_j$  implies strong effects of body weight on fecundity. This formulation can be readily extended to cases where larval settlement from each cell  $i$  is displaced from cell  $i$  in some systematic pattern, due for example to advective alongshore transport and differential larval retention patterns, so as to create source-sink patterns. Such extension requires specifying mean locations  $XL_i$  and  $YL_i$  for larval settlement from each  $i$ , then computing settlement on cells  $j$  using distances from these mean settlement positions.

Adult dispersal is modeled as a two-step diffusive process. First, a proportion  $e_i$  of age  $k$  and older fish are assumed to move each year. Of the  $e_j B_j$  dispersing biomass from cell  $j$ , proportions  $SA_{ij}$  (where  $SA_{jj}=0$ ) are assumed to resettle on other cells  $i$  to form the total immigration rate  $I_i$ . The  $SA_{ij}$  values are calculated with a normal probability kernel with species-specific standard deviation, using the distances  $D_{ij}$ .

We also allow the possibility of fish having home ranges larger than one cell, so that movement within home ranges exposes the biomass  $B_i$  of fish whose home range is centered in cell  $i$  to fishing mortality in surrounding cells  $j$ . To do this, we modify the calculation of  $U_i$  as noted above. If  $HE_{ij}$  is an estimate of the proportion of time that fish with home range center in cell  $i$  spend in surrounding cells  $j$ ,  $F_i$  is calculated as  $\sum_j \sum_g q_{sg} E_{ig}$ . We assume that the  $HE_{ij}$  decline in a normally distributed pattern with distances  $D_{ij}$ . This is equivalent to calculating an effective fishable biomass  $B^*_i$  for each cell, where  $B^*$  is a sum over surrounding cells  $j$  of contributions  $HE_{ji} B_j$  of fish with home ranges centered in those surrounding cells.

## Finding Maximum Equilibrium Economic Value

Total equilibrium profit  $V_g$  for gear  $g$  over the mosaic of areas  $i=1 \dots n_c$  is assumed to vary as

$$V_g = \sum_i \left[ \sum_s P_s U_s(E_{ig}) B^*_{is} - c_{ig} E_{ig} \right] \quad (6)$$

where  $E_{ig}$  is fishing effort on area  $i$ ,  $U_s(E)$  is exploitation rate by gear  $g$  on species  $s$  as a function of effort,  $B^*_{is}$  is equilibrium biomass exposed to fishing on area  $i$  (a function of  $U_{is}$  and of dispersal from other sites),  $P_s$  is the landed price per biomass of species  $s$  (assumed independent of gear type, and scaled up from model biomass per habitat area to total biomass estimated from stock assessment models) and  $c_{ig}$  is cost per  $E$  of fishing. To represent competing effects of multiple gears fishing in the same cell,  $U_s(E_{ig})$  is calculated as

$$U_s(E_{ig}) = q_{sg} E_{ig} / F_{is} (1 - e^{-F_{is}}) \quad (7)$$

where  $F_{is}$  is the total fishing rate on species  $s$  in cell  $i$ :  $F_{is} = \sum_g q_{sg} E_{ig}$ .

It is instructive to examine how  $V_g$  varies with  $E_{ig}$  in the case where the optimum  $E$ 's are all expected to be low enough so that  $U_{sg}$  for every  $s$  and  $g$  is approximately equal to just  $q_{sg} E_{ig}$ . In that case,  $V_g$  can be approximated as just  $V_g = \sum_i E_{ig} B^*_{ig} - \sum_i c_{ig} E_{ig}$ , where  $B^*_{ig}$  is the weighted sum over species of prices times biomasses times catchabilities:

$B^*_{ig} = \sum_s P_s B^*_{is} q_{sg}$ . Differentiating this approximation for  $V_g$  with respect to  $E_{ig}$  and setting the resulting derivative to zero implies that the  $E_{ig}$  that maximize  $V_g$  will satisfy (up to zero constraints on  $E_i$ )

$$E_{ig} = - \frac{B^*_{ig} - c_{ig} + \sum_{j \neq i} E_{jg} \partial B^*_{jg} / \partial E_{ig}}{\partial B^*_{ig} / \partial E_{ig}} \quad (8)$$

The denominator of this expression represents the effect of fishing in area  $i$  on abundances in area  $i$ , and the sum in the numerator represents effect of fishing in area  $i$  on abundances and catches in other areas  $j$  (not including  $i$ ). Note that terms of the form  $\partial B^*_{jg} / \partial E_{ig}$  generally have negative sign.

Eq. (8) implies a very interesting pattern of optimum  $E_{ig}$  when there is a subset of areas that act as “sources” of recruitment and dispersal to other “sink” areas (that do not send recruits and dispersers to the source areas), i.e. the source areas are  $i$ 's for which the terms  $\partial B^{**}_{jg}/\partial E_{ig}$  in the denominator of (8) are large negative for sink areas  $j$  (fishing in  $i$  causes loss of recruits to those sink areas). In this case the optimum fishing pattern will involve  $E_{ig}=0$  for the source areas, i.e. the source areas should be closed to fishing so as to act as “seed sources” for the other areas. We have been seeing this seed-source closure pattern in mosaic closure optimizations for tuna (R. Ahrens, University of B.C. Fisheries Centre, pers. comm.): the optimization wants to close areas like the western Pacific and western Indian, where there are high recruitment rates and from which tuna grow and disperse. A worrisome point is that absent spatial regulation, the high-abundance source areas tend to attract the most fishing, i.e. site choice by fishermen tends to produce exactly the opposite spatial pattern of fishing from that which would maximize overall profit  $V$ .

Another useful result from examining eq. (8) is that it predicts optimal efforts to be approximately proportional to fish availability as represented by  $B^{**}_{ig}$ , provided differences among cells in the denominator sum of sensitivities to fishing in cell  $i$  are ignored. This means that a simple gravity model, where  $E_{ig}$  is predicted as  $E_{ig}=ET_g B^{**}_{ig}/\sum_j B^{**}_{jg}$  and  $ET_g$  is total effort summed over all cells, can be used as both a predictor of how fishing effort will be distributed given myopic choices by fishers to concentrate where fish are most abundant, and also as a starting point in numerical searches for optimal effort distributions. In the California case example, we have found the gravity model effort predictions to be quite close to the efforts found by numerical optimization of  $V_g$ , except in cases where source-sink or sensitive species concentrations imply a need to prevent fishing in some cells.

There are two approaches to finding the  $E_i$  that maximize  $V$ . One is simply brute force, using some general constrained nonlinear search procedure such as the GRG2 algorithm of Solver in Excel. The second is to apply a fixed-point method to the approximation eq. (8): starting with initial equilibrium  $B^{**}_{ig}$  for  $E_{ig}=E_{oig}$ , compute the partial derivatives  $\partial B^{**}/\partial E$ , then compute  $E_{1ig}$  from eq. (3) and set all the  $E_{ig}$  to  $\max\{0, WE_{1ig} + (1-W)E_{oig}\}$  for some suitable relaxation weight  $W$  (we obtained stable results with  $W=0.1$  to  $0.2$ ). Repeat this iteration until the  $E_{ig}$  stop changing.

An alternative reference fishing pattern for MPA planning is to compute the  $E_i$  at bionomic equilibrium, by allocating total effort using a gravity model then increasing that total until  $V_g=0$  (i.e., until profits are dissipated). This equilibrium effort distribution presumably represents the worst case overfishing that could be economically sustained, possibly involving substantial loss of spatial stock structure so that the remaining  $E_i$  are concentrated in relatively few spatial cells.

The gravity and optimization models have an important implication for management planning that involves limitation of total fishing effort  $ET_g$ , namely that the  $ET$  needed to generate a given total fishing mortality rate  $F$  can be much lower when fish are patchily



distributed than would be predicted by assuming even distribution of fishing over patches or spatial cells. The models predict effort on cell  $i$  to be approximately

$E_{ig} = ET_g B^{**}_{ig} / \sum B^{**}_{ig}$ ; assuming catch on each cell is approximately proportional to  $E_{ig}$ ,  $F$  for each cell varies as  $qE_{ig}$  and total  $F$  over all cells varies as  $F = qE_{ig} B^{**}_{ig} / \sum B^{**}_{ig} = qET_g B^{**}_{ig} / (\sum B^{**}_{ig})^2$ . This relationship can be expressed in terms of the variance in  $B^{**}$  among cells,  $\sigma^2_{B^{**}}$ , as

$$F = q(ET_g/n_c)[1 + CV^2_{B^{**}}] \quad (9)$$

Here,  $ET_g/n_c$  is the mean effort per cell, and  $CV_{B^{**}}$  is the coefficient of variation of  $B^{**}$  among cells, i.e.  $\sigma^2_{B^{**}}$  divided by the mean  $B^{**}$  per cell. This equation predicts that overall  $F$  felt by the biomass complex  $B^{**}$  will be inflated by the factor  $1 + CV^2$  from the  $F$  predicted by assuming even distribution of effort over cells, or equivalently that  $ET_g$  needs to be reduced by the factor  $1/(1 + CV^2)$  in order to meet a given  $F$  target that would be predicted to occur at  $ET_g = Fn_c/q$  if effort were evenly distributed.

The fishing effort pattern that maximizes eq. (6) may well involve overfishing one or more of the species. If such solutions are considered unacceptable, and a maximum tolerable fishing mortality rate  $FM_s$  is specified for each species  $s$ , the maximization can be “constrained” to prevent  $F_s$  for each species ( $F_s = \text{total catch}/\text{total biomass}$  for species  $s$ ) by subtracting a penalty term  $FP$  from  $V_g$  where

$$FP = p_1 \sum_s (F_s/FM_s)^{p_2} \quad (10).$$

Here, the penalty weight  $p_1$  is set to a small enough value (e.g. 0.00001) to avoid instability in the numerical optimization search, and the penalty power parameter  $p_2$  is set to a large value (e.g. 10.0). Including such terms in the spatial effort optimization typically results in a “mosaic closure” pattern where spatial cells having high abundance of species  $s$  that have low  $FM_s$  are closed to fishing (Walters and Martell 2004).

## Software implementation

We developed a Visual Basic application called EDOM (Equilibrium Delay-difference Optimization Model) to implement the calculations described above. The EDOM user interface makes it easy for model users (scientists, stakeholders) to check sensitivity of the model predictions to parameter changes, quickly enter new MPA options by clicking on map displays of the study region, and compare MPA options in terms of economic performance and expected equilibrium abundance patterns.

EDOM can compute and display equilibrium biomasses over  $n_c = 243$  cells for  $n_s = 4$  species and  $n_g = 2$  gears in about 0.5 sec on fast notebook computers available as of 2007, so model users see apparently instantaneous answers to simpler “what if” questions about parameter sensitivity and impact of altering MPA boundaries and locations. Effort optimizations for 11 MPA policy alternatives, to generate maximized economic performance and biomass-catch indicator comparisons among the options, with a few minutes of computer time.

The EDOM application, with sample data files for the California MLPA case study, is freely available by email from the senior author. System requirements are Win XP, 1mb RAM, and 2mb disc space. EDOM runs on some computers with Win Vista.

## Case study: California Marine Life Protection Act

We evaluated 10 MPA network proposals that have developed to date for the north central coast planning region of California (Fig. 1). These proposals were developed by stakeholders and California Department of Fish and Game staff. They differ widely in MPA sizes and locations, and in total area of hard bottom habitats protected. The most extreme proposals (C, Jade A) would close over half the hard bottom area to all (recreational and commercial) bottom fishing.

Using population dynamics parameter estimates (Table 1) from Pacific Fisheries Management Council stock assessment reports and expert judgment of scientists involved in MLPA planning, EDOM predicts equilibrium spawning abundance patterns along the central California coast (Fig. 2) that are very similar to predictions from previous modeling exercises (Kaplan et al. 2006, Walters et al. 2007). Spawning biomasses ( $B_{is}$ ) are predicted to be highest in spatial cells having higher proportions of suitable juvenile nursery area (hard bottom), and harvestable biomasses ( $B^*_{ig}$ ) are predicted to be more widespread for species like lingcod that are assumed to have larger home ranges.

Predicted biomass distribution patterns ( $B_i$ ) like Fig. 2 are obviously very sensitive to estimates of the distribution of nursery habitat and to assumed recruitment compensation ratios  $K$ , particularly since such ratios determine whether areas of low natural larval settlement (and/or high fishery impact on larval production) are still likely to achieve normal recruitments per habitat area. Predicted distributions are also very sensitive to assumptions about  $c^*$ , the parameter controlling whether settling larvae are able to successfully concentrate on areas of suitable habitat. But they are quite insensitive to the body growth parameters and related fishery impacts on mean body size and fecundity, except when recruitment compensation ratios are assumed to be very low (e.g.  $K < 5.0$ ). And surprisingly, they are relatively insensitive to assumptions about larval transport distances except in scenarios where very high fishing mortality rates are assumed for cells not closed to fishing (when there is almost no spawning biomass outside reserves, larval connectivity among reserves along with recruitment compensation determines whether recruitment and spawning biomass accumulation can occur successfully within reserves). For high fishing effort scenarios when MPAs are present, predicted biomass patterns are also sensitive to assumed home range sizes and adult dispersal rates (spawning biomasses cannot build up inside small reserves for species with large home ranges and/or high dispersal rates).

If fishing effort outside MPAs is assumed to be high (no effective regulation of total fishing effort, a “management fails” scenario), predicted biomass response to imposition of MPAs is greatest for species with weak recruitment compensation (small Goodyear compensation ration  $K$ ), small home ranges, and wide larval dispersal. Progressively more restrictive MPA policies (Fig. 1) can lead in this fishing scenario to increases in catch and overall net economic value for all fisheries (Fig. 3a), i.e. a win-win option for biodiversity conservation and fishing interests.

However, the current situation in California is that fishing efforts for bottom fish have been radically reduced through commercial license retirements and sport fishing regulations including closed seasons. If this low effort scenario persists for the long term, predicted responses to more restrictive MPA proposals (Fig. 3b) involve a pure tradeoff relationship between abundance (biomass) versus catch and net economic value. This tradeoff relationship is predicted to be much less severe if efforts outside MPAs are regulated so as to be near those predicted by maximizing net economic value (Fig. 3c), i.e. effective management of fishing effort could considerably reduce the negative effect of MPAs on fishery performance. With suboptimally low fishing efforts in the future, fishing interests would lose up to 50% of net economic value under the most restrictive MPA policies, but it should be possible to reduce this loss to 20% or less through optimal effort management.

When larval dispersal is assumed to follow a random walk pattern (normal distribution of larval settlement along the coast both north and south from each larval source cell), Fishing effort distributions predicted using both gravity models and optimization are very similar (Fig. 4). Fishing is predicted to be concentrated in areas of high  $B^*$  and along the boundaries of MPAs. However, the optimization tends to reduce fishing in important nursery or larval source areas for less mobile stocks that are sensitive to overfishing (e.g. canary rockfish), when more productive and mobile species (e.g. lingcod) can still be taken outside such areas, i.e. the optimization “anticipates” some economic benefit for local protection of sensitive species that would be invisible to myopic fishers selecting fishing areas based solely on local abundance. This tendency for the optimization to protect some areas becomes much stronger when larval production rates are arbitrarily reduced from most cells (the cells are set to be “sinks”), but are left high in some “source” cells; in this case the optimization calls for complete closure of the source cells to fishing even when no cells are pre-designated to be in MPAs. We have no idea whether such a source-sink structure does occur along the California coast, but sensitivity of the optimization results to assuming such structure indicates that examination of larval drift and settlement patterns using more detailed hydrodynamic transport and larval behavior models should be a high priority for future model development in the case region.

We calculated total profits from commercial fishing ( $V_g$  of eq. 6) for various MPA options and assumptions about whether optimum fishing patterns are followed in the future (Fig. 5), using reference fish prices of \$1.00/kg for all species and a location independent fishing cost  $c_g$  scaled so as to give cost per effort equal to 50% of income per effort at abundances calculated from recent stock assessments (Scholz et al. 2006; Wilen and Abbott, 2006). If fishing efforts remain low into the future, we predict that equilibrium total profits will drop still further under all MPA plans if effort now occurring in MPAs is simply lost when MPAs are imposed (Fig. 5a). If total effort now occurring is redistributed to remaining open areas (gravity model or by optimization) following imposition of MPAs, loss in economic value will still be reduced somewhat (Fig. 5b). If future efforts are allowed to rebuild to levels predicted to be optimum by maximizing eq. 6, losses associated with the more restrictive MPA options could be

further reduced (Fig. 5c). For the more restrictive MPA options, loss of 50% of the productive hard bottom fishing area results in corresponding 50% loss in economic value under the Fig. 5a effort scenario, but as little as 20% of economic value if efforts are allowed to rebuild to optimum levels.

A very interesting result is obtained when efforts are first optimized for commercial fishing as in Fig. 5c, but then net values are calculated for recreational fishing under the various MPA options. In this case, higher optimized “economic” net values for recreational fishing are obtained when moderate area is protected in MPAs (Fig. 6). That is, recreational fishing interests actually stand to benefit from MPAs if it is known that commercial fishing efforts outside MPAs will be relatively high but not responsive to increases in abundance and spillover caused by the MPAs.

We ran a few optimization trials where allowable fishing mortality rates  $FM_s$  were arbitrarily set to very low values (e.g. 0.02) for one or another species  $s$ . The results from those trials were very similar to the mosaic closure patterns reported by Walters and Martell (2004). When  $FM_s$  is set low for a sedentary species (e.g. cabezon), the optimum effort pattern involves closing all spatial cells where that species is concentrated. When  $FM_s$  is set low for a species with large home range (e.g. lingcod), the optimum pattern is reversed, and involves closing many cells to which the species moves while concentrating fishing effort in the remaining cells where sedentary species are most abundant.

The California MLPA calls for an adaptive management process to evaluate performance and possibly adjust MPAs over the long term. Monitoring for adaptive management will presumably include monitoring of abundances inside MPAs with outside reference areas, hopefully in a before-after (BACI) “experimental” design. Most of the MPA proposals involve a strong “selection bias” toward protecting areas with relatively more hard-bottom habitat. Comparisons of predicted equilibrium biomasses averaged over cells inside and outside MPAs “before” (at equilibrium with respect to current fishing effort) and after MPA implementation (Fig. 5) indicate that a monitoring program would immediately (before time for recovery) see almost double (1.7 times) the mean total spawning biomass from density sampling inside MPAs than outside, i.e. simple inside-outside comparisons would indicate that MPAs had been successful at increasing abundance, even before such increase could have occurred. At long term equilibrium, total spawning densities inside MPAs are predicted for most policy options to be 3-5 times the mean densities outside MPAs, a difference that should be easily detectable with monitoring methods such as visual diver and ROV counts and test fishing catch rates. Predicted biomass ratios both before time for recovery to have occurred and after are well within the range of inside-outside and before-after biomass ratios reported by Halpern (2003), warning that many of the MPA “effects” that he reported could also be due to selection bias rather than before-after changes.

## Discussion

The case study results presented above are similar to those obtained with single-species models that make the same general assumptions about dependence of recruitment on

spatial patterns of larval dispersal and nursery habitat area, e.g. Kaplan et al. (2005, 2006) and Walters et al. (2007). They are also qualitatively similar to predictions that we have obtained with a much more complex Ecospace model (Walters et al. 1999, 2008) that includes both age-structured population dynamics and trophic interaction effects, constructed from an Ecopath model of the California current ecosystem developed by Field et al. (2005). When habitats and dispersal are roughly homogeneous, all of these models agree that MPA networks are unlikely to generate net increase in fisheries. However, our model reveals that if appropriately designed, MPA networks may be capable of enhancing fisheries when: (1) fishing effort cannot be controlled such that there is a high risk of overfishing in unprotected areas, (2) there is some source-sink structure in larval dispersal such that protection of key source areas would increase recruitment to substantial sink areas of nursery habitat, or (3) relatively immobile and unproductive species are concentrated in areas that would attract unacceptably high fishing efforts for various reasons (e.g. low fishing costs, high abundances of more productive and mobile species). In such cases, spatial dynamic models such as EDOM are critical for efficient reserve siting.

There has been much discussion among scientists involved in the California MLPA case about the importance of spacing reserves so as to provide for maintenance of metapopulation structure through “connectivity” among reserves by larval dispersal, and larval dispersal distances have been treated as a critical uncertainty for model predictions. In fact, such larval connectivity is much less important (for predictions about maintenance of metapopulation structure) when severe overfishing is expected outside reserves than is compensatory survival response after larval settlement (recruitment  $K$  and  $c^*$  parameters). Absent strong compensatory responses, the models predict that large overall decreases in larval production (loss of larval production from spawning outside reserves) will result in inadequate recruitment within reserves to maintain natural abundance levels in those reserves, even if fish within the reserves exhibit natural age-size structure in terms of proportions of older, more fecund fish. Because of this compensation issue, the models also warn against using simplistic guidelines based on single species assessments about total area that should be protected, e.g. “if assessment models say that spawning biomass should be maintained at 20% or more of unfished levels, at least 20% of the total area should be protected so as to have natural spawning biomass”.

Comparison of optimized to myopic (gravity model) effort distributions when no MPAs are present (Fig. 4 a) suggests that seasonal time-area closures should be considered as an alternative to no-take reserves, in cases where such closures can effectively reduce annual fishing mortality in areas where sensitive (to overfishing) species are concentrated and where one or more such sensitive species have relatively small home ranges. This finding depends on there being at least some negative correlation between productivity and mobility, i.e. on there being opportunity to harvest more productive species at higher rates in parts of their home ranges where it is not beneficial to have seasonal closures; such negative correlations are probably common, due to obvious major distinctions like sedentary rockfishes being caught in fisheries that also take more productive and mobile species like cods and lingcod. The economic gains from spatial effort reduction measures

are predicted to be relatively minor for the species mix included in the California MLPA case study (on order 5-10% increase in net economic value by moving from gravity model to optimized efforts), but could be considerably larger in other regions.

It is not clear that equilibrium models like EDOM should be the only type of model used to compare MPA network options in terms of population dynamics performance. Such models can certainly provide more realistic predictions about long term performance than simplistic calculations based on habitat areas protected or guidelines about overall percentage of area that ought to be protected, by avoiding pitfalls of reasoning like those mentioned in the previous paragraph and by forcing explicit consideration of some parameters that determine population responses. But equilibrium analysis ignores at least two really important dynamic issues: (1) the possibility of multiple equilibria in population size, such that depressed populations might be “trapped” at low equilibria by mechanisms such as depensatory predation and fishing mortality that are ignored in simple compensatory recruitment models; and (2) time transients in benefits and costs to economic stakeholders, which would be represented in dynamic models by calculating “net present value” as a discounted sum over time of net benefits. Point (2) is particularly worrisome for cases like California rockfish, where current populations of some species are very low and where recovery may take several decades and involve sporadic recruitment variation related to oceanographic factors. Why for example should a California sportfisher support some MPA or effort reduction plan that will take away his fishing opportunities, when the only comfort we can offer is that his/her grandchildren will see improved fishing? If we present only the equilibrium analysis, we may mislead that sportfisher by not warning him/her to think about how long it will take for benefits to accrue, and to whom those benefits will go. It is easy for scientists and conservationists to advocate use of evaluation models that take only a long view, both for computational convenience and because we are not the people who will suffer the short term losses.

We have resorted to equilibrium calculations for computational convenience (which is particularly critical when optimizing). But once an MPA network is defined, a fully functional age structured dynamic model could easily coupled to EDOM to facilitate dynamic predictions. In addition to illuminating dynamic tradeoffs, this would assist in experimental design for monitoring and evaluation.

Another potentially serious weakness in the EDOM assumptions is that we ignore the possibility of species-selective fishing practices aimed at meeting different fishing mortality rate goals. When effort is assumed to take all species with equal (or at least constant) species-specific catchabilities, it is typical for the effort pattern that maximizes net total value to cause overfishing on at least one stock that has lower  $F_{msy}$  than the others, unless that “weak” stock is a very large proportion of total harvestable biomass. Likewise, the best overall effort pattern forgoes some yield from more productive species ( $F < F_{msy}$ , e.g. for lingcod in the California case). Further, we know that at least some species like cabezon, can be taken quite selectively through targeted fishing. One option for dealing with such possibilities (need to protect less productive stocks, opportunity to selectively harvest others) is simply to create more gear types representing the selective fisheries, and to optimize those independently from the less selective gear types. At the

extreme, we could use the common fisheries assessment practice of simply optimizing effort for each species separately, without pretending to know how such effort patterns might be achieved by management regulations. Compared to these alternatives, EDOM provides a most conservative (lowest) assessment of potential net economic value, since any of the alternatives would reduce or entirely avoid overfishing of any species.

While we can easily identify various ways to make the model more realistic and credible from an ecological and economic perspective, it is not clear that much will be gained by doing so. The main value of the model is for making broad comparisons across alternative protected area network proposals, and those comparisons are apparently quite insensitive to details of model formulation and parameter values. Simply by exposing future fisheries management regimes under which win-win versus abundance-catch tradeoff would occur, the model emphasizes that responsible MPA planning cannot be done with simplistic assumptions about future fisheries management. By providing a timely way to assess how both ecological and economic performance indicators are likely to change when MPAs are added or modified, the software should provide stakeholders charged with designing and recommending network proposals an open, objective way to move toward proposals that are acceptable to all interest groups.

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## Tables

Table 1. Population dynamics parameter estimates used in case study demonstration of the EDOM model for a region of the California coast. Estimates compiled from stock assessment reports of the Pacific Fisheries Management Council (<http://www.pcouncil.org/groundfish/gfsafe0406/gfsafe0406.html>), expert judgments by scientists, and stock reduction analyses conducted by the senior author using PFMC catch and trend data and the SRA modeling approach recommended by Walters et al. (2006).

	Lingcod	Cabezon	Black Rockfish	Canary Rockfish
<b>Annual survival rate (e-M, yr-1)</b>	0.84	0.78	0.79	0.94
<b>Body growth intercept (a, kg)</b>	1.17	0.42	0.19	0.25
<b>Body growth slope ®</b>	0.95	0.93	0.90	0.96
<b>Weight at maturity (wk, kg)</b>	2.23	0.57	0.74	0.28
<b>Recruitment compensation ratio (K)</b>	10.00	5.00	2.00	20.00
<b>Mean larval dispersal distance (km)</b>	10.00	45.00	45.00	45.00
<b>Adult emigration rate (e, yr-1)</b>	0.01	0.01	0.01	0.02
<b>Mean adult dispersal distance (km)</b>	5.00	5.00	5.00	10.00
<b>Adult home range radius (km)</b>	10.00	0.50	7.00	3.00
<b>Unfished spawning biomass (tmt)</b>	30.00	3.50	24.00	80.00
<b>Ratio of current to unfished biomass</b>	0.20	0.30	0.30	0.10

## Figure captions

- Figure 1. Spatial locations and sizes of MPAs (white) for 10 network proposals developed for the north central coast of California.. Map rasters extend from shore to the offshore limit of California state jurisdiction. Number next to each proposal name (A, B, etc.) is rough percentage of hard bottom area included in MPAs. Reference locations are: PA-Point Arena, SP-Salt Point, BB-Bodega Bay, PR-Point Reyes, SF-mouth of San Francisco Bay, HM-Halfmoon Bay, FA-Farallon islands. Larger areas of hard bottom shown as dots.
- Figure 2. Spatial distributions of spawning biomass, harvestable biomass, and larval settlement predicted by EDOM for four bottomfish species that are important in the central California nearshore fisheries. X axis of the graphs is spatial position along the coast from Pt. Arena in the north to Pescadero in the south, with cells representing the offshore Farallon islands shown as the last 20 X positions (see locations in Fig. 1, e.g. PA, SF). (a)-(c) show spawning biomass (B), vulnerable biomass (B\*), and larval settlement (L) for no MPA option; (d)-(f) show these variables for MPA proposal C; panel (d) shows closed cells (black dots) for this proposal.
- Figure 3. Predicted relationships for the north central California coast area between equilibrium biomasses of four indicator fish species and catches of those species, for three alternative assumptions about fishing outside MPAs. a—low fishing efforts outside MPAs, so that more restrictive MPA proposals like C, Jade A cause little gain in biomass but large loss in catch; b—high (overfishing) efforts outside MPAs, so more restrictive proposals result in both higher biomass and higher catches (net benefit to fisheries of “spillover” from MPAs); c—efforts optimized outside of MPAs, for which MPAs cause a severe tradeoff between abundance and catch.
- Figure 4. Differences between spatial effort patterns predicted with simple gravity models versus with optimization for overall net economic value. (a) no MPAs, (b) MPA proposal C. Note that both models predict effort concentration in areas of high abundance, and along MPA boundaries; note also much higher efforts for cells open to fishing in the MPA proposal C case, and reduced efforts in the no MPA case in areas where less productive, less mobile species are concentrated.
- Figure 5. Ratios of predicted mean biomass density per spatial cell, inside and outside of MPAs before and after enough time for biomass to reach equilibrium. Long term ratios evaluated at optimum fishing effort pattern. (a) ratios before enough time to reach equilibrium; high values indicate “selection bias” toward MPA placement in areas of higher abundance; (b) ratios after enough time to reach equilibrium.

Figure 1.

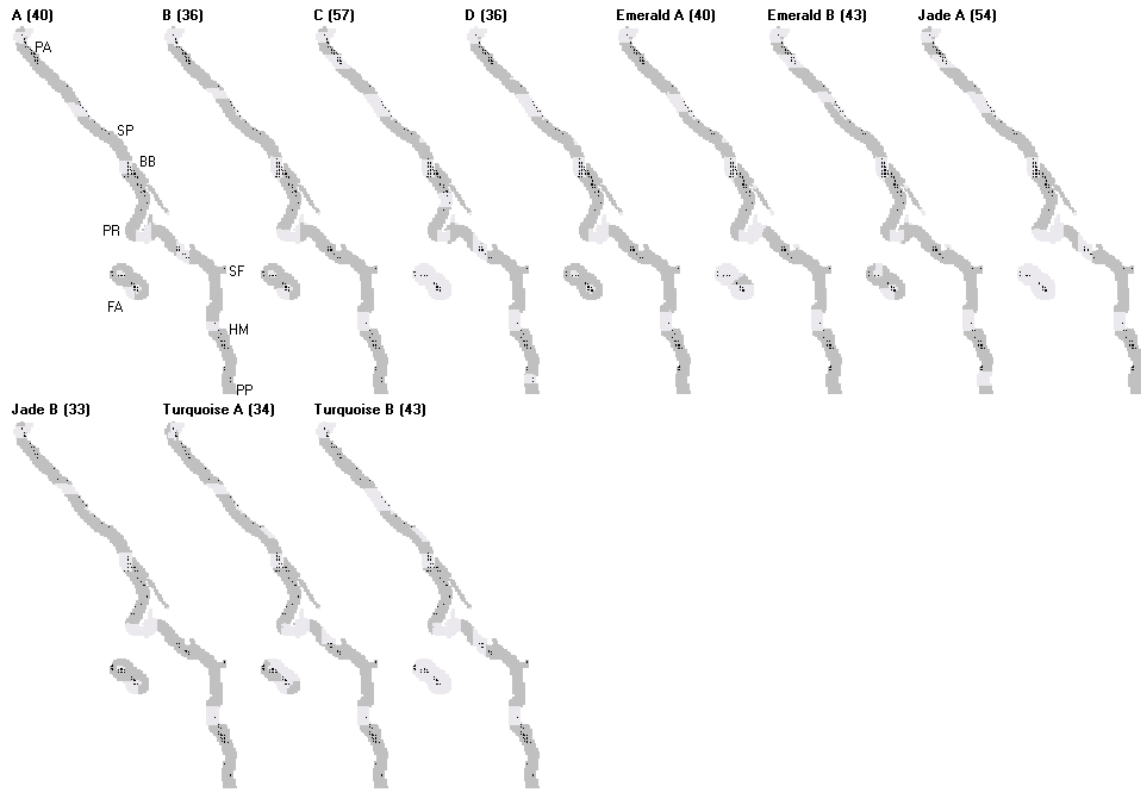


Figure 2.

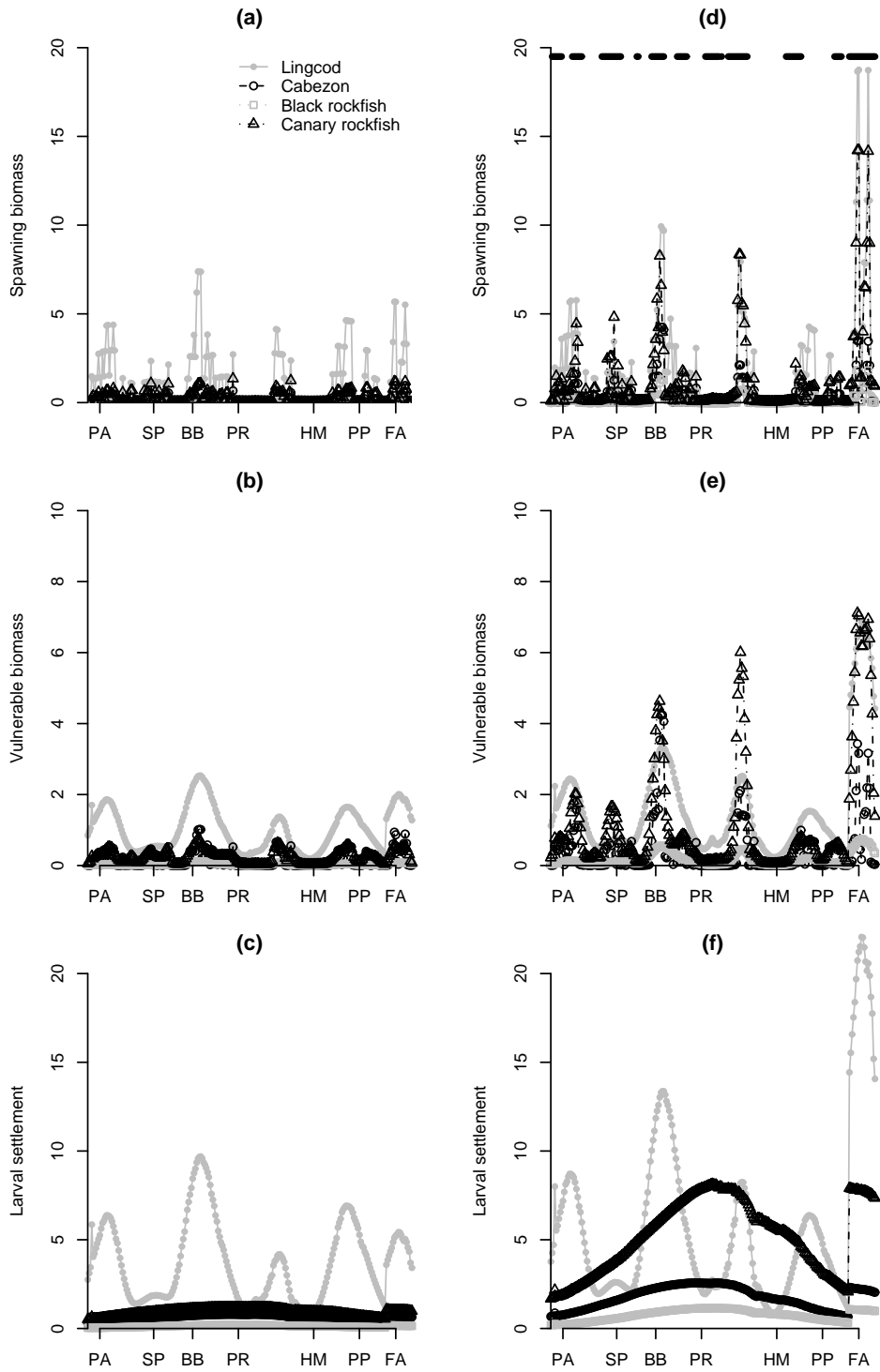


Figure 3.

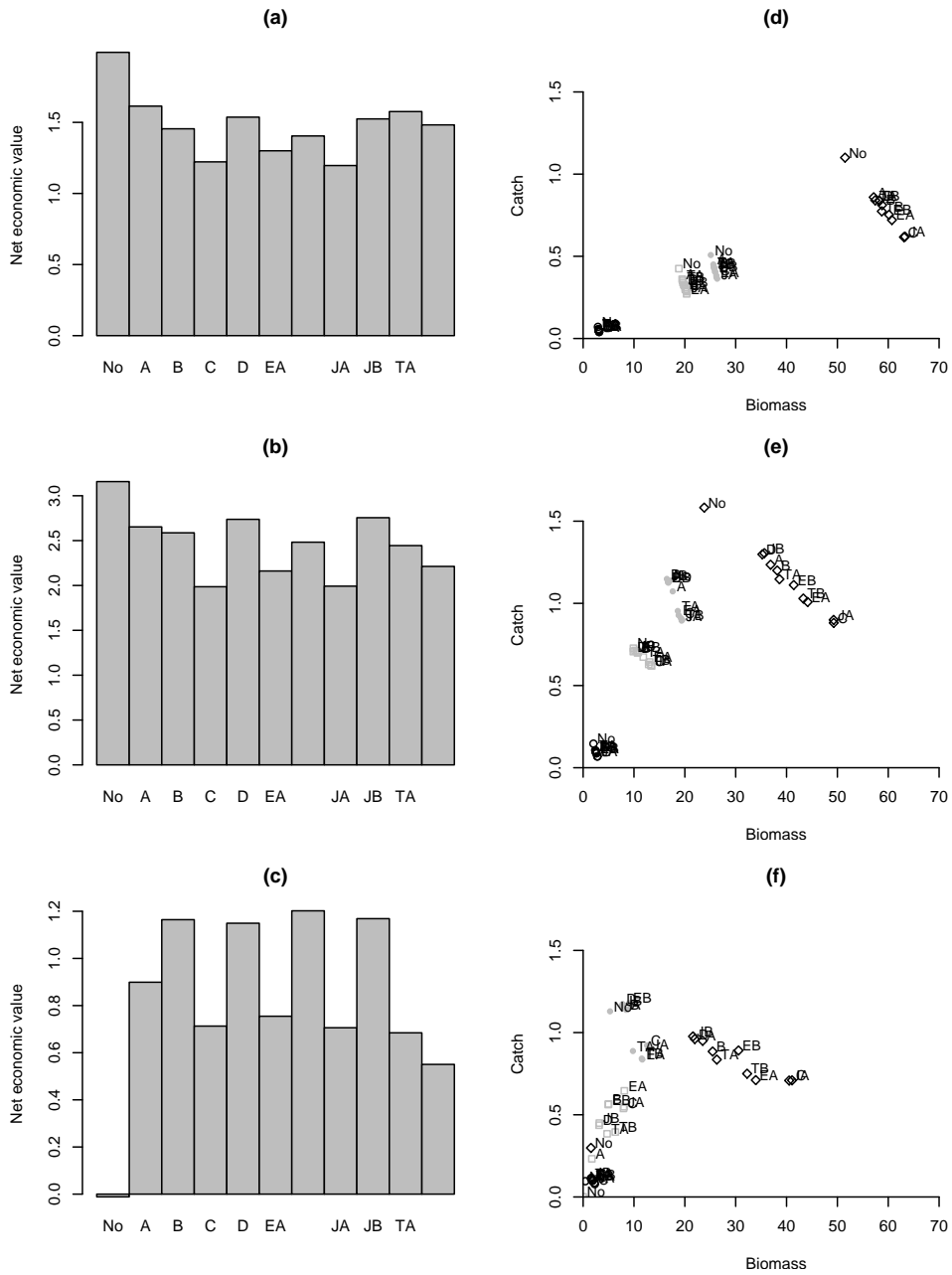
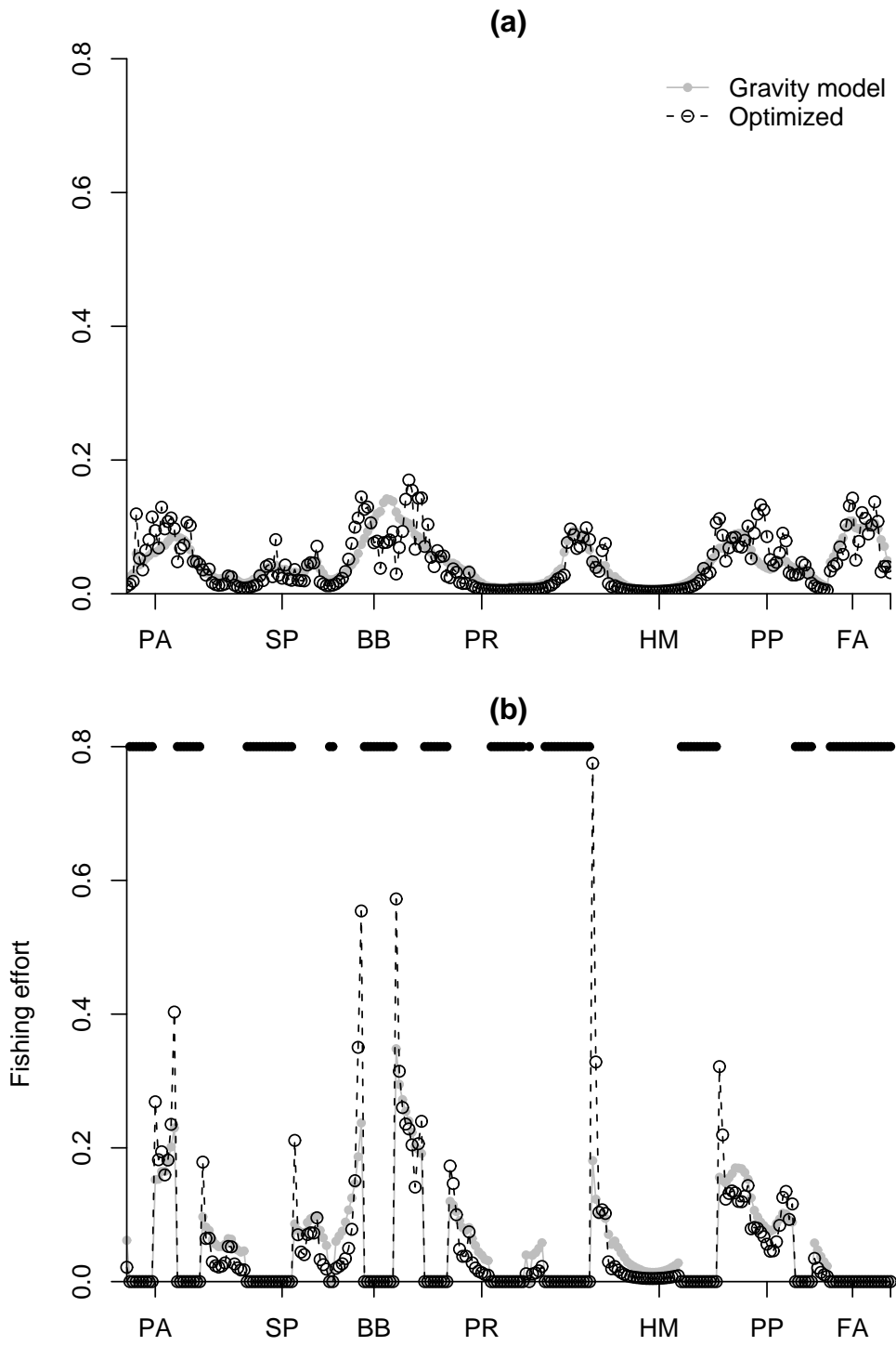


Figure 4



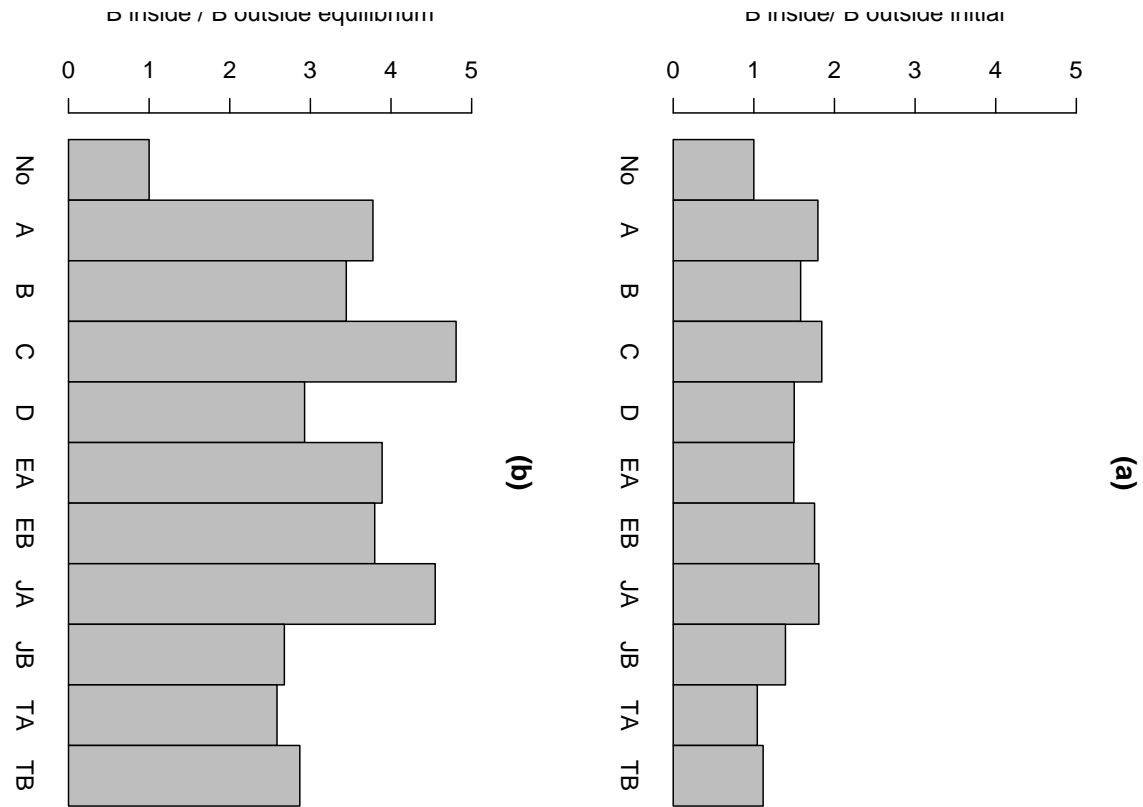


Figure 5.