

An equilibrium model for predicting the efficacy of marine protected areas in coastal environments

Carl J. Walters, Ray Hilborn, and Richard Parrish

Abstract: Quantitative models of marine protected area (MPA) proposals can be used to compare outcomes given current biological knowledge. We used a model of a linear coastline, with 200 discrete cells each spanning 1.6 km of coast. This model is used to evaluate alternative proposals for marine protected area networks, predicting equilibrium changes in abundances and harvests while accounting for dispersal of larvae and older fish, changes in fecundity with reduced mortality in reserves, impacts of displaced fishing effort on abundances outside reserves, and compensatory (stock–recruitment) changes in postsettlement juvenile survival. The model demonstrates that modest dispersal rates of older fish can substantially reduce abundance within protected areas compared with predictions from models that ignore such dispersal. The strength of compensatory improvements in postsettlement juvenile survival is the most critical factor in determining whether a reserve network can rescue populations from the impacts of severe overharvesting. We use the model to compare specific alternative proposals for protected area networks along the California coast, as mandated through California’s Marine Life Protection Act, and show that achieving the goals of the Act depends primarily on the fisheries management regulations outside of protected areas and that the size and configuration of MPAs has little impact.

Résumé : Des modèles quantitatifs des propositions de zones de protection marines (MPA) peuvent servir à comparer les résultats escomptés, compte tenu des connaissances biologiques actuelles. Nous utilisons un modèle comprenant une côte linéaire avec 200 cellules distinctes couvrant chacune 1,6 km de côte. Le modèle sert à évaluer des propositions de rechange pour un réseau de zones de protection marines en prédisant les changements des abondances et des récoltes à l’équilibre, tout en tenant compte de la dispersion des larves et des poissons plus âgés, du changement de fécondité relié à la diminution de la mortalité dans les réserves, des impacts sur l’abondance des efforts de pêche relocalisés hors des réserves et les changements compensatoires (stock–recrutement) de la survie des jeunes après leur établissement dans le milieu. Le modèle démontre que les taux de déplacement modestes des poissons plus âgés peuvent réduire considérablement les abondances dans les zones protégées, en contraste des prédictions des modèles qui ignorent ces déplacements. L’importance de l’amélioration compensatoire de la survie des jeunes après leur établissement est le facteur le plus critique pour déterminer si un réseau de réserves peut sauver une population des effets d’une récolte excessive. Nous utilisons le modèle pour comparer des propositions spécifiques de rechange de réseaux de zones de protection le long de la côte de la Californie, tel que requis par la loi californienne de protection de la vie marine (California Marine Life Protection Act), et nous démontrons que l’atteinte des objectifs de la loi dépend principalement des règlements de gestion des pêches à l’extérieur des zones de protection et que la taille et la configuration des MPA ont peu d’effet.

[Traduit par la Rédaction]

Introduction

A number of relatively simple, one-dimensional models have been proposed for evaluating population impacts of networks of marine protected areas (MPAs) distributed along coastal shorelines and extending offshore far enough to protect animals that undergo ontogenetic offshore movements (e.g., Botsford et al. 2004; Gaylord et al. 2005; Kaplan and Botsford 2005). The basic idea in these models has been to divide the shoreline into a large number of small (e.g., 1 km or 1 nautical mile (= 1.852 km)) spatial slices or cells, then

predict changes in abundance within each of the cells. Typically, these models have accounted for linkage among cells through larval dispersal and for compensatory changes in juvenile survival rates after larval settlement. However, they have not accounted for dispersal of older animals or changes in fishing impacts in remaining open areas because of displacement of fishing effort out of reserve areas and (or) fisheries regulations aimed at reducing overall fishing mortality rates whether or not reserves are present. Models that do account for movement of older animals and spatial redistribution of fishing effort (Walters et al. 1999; Walters

Received 6 June 2006. Accepted 5 March 2007. Published on the NRC Research Press Web site at cjfas.nrc.ca on 27 July 2007. J19349

C.J. Walters. Fisheries Centre, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

R. Hilborn. School of Aquatic and Fisheries Science, Box 355020, University of Washington, Seattle, WA 98195-5020, USA.

R. Parrish.¹ P.O. Box 1125, Pebble Beach, CA 93953, USA.

¹Corresponding author (e-mail: clupeid@sbcglobal.net).

and Martell 2004; Hilborn et al. 2006) have led to much less optimistic predictions about the yield benefits of protected areas.

There is a need for relatively simple models that can be used to compare and screen alternative MPA proposals (differing in spacing and sizes of reserves) to give some idea of how different proposals will impact a range of species with widely different life histories, without resorting to very complex (and expensive to develop) models like Ecospace. The model of Hilborn et al. (2006) did not consider age structure or differential larval dispersal. Absent, simple, but realistic models, quantitative design guidelines, and proposals for MPA networks are liable to be based on intuitive guesses or simplistic percent target rules, and networks implemented on the basis of such guesses can have severe impact on fishing interests without achieving the intended conservation goals.

Here we propose a simple model that can be easily implemented using a spreadsheet, which accounts for dispersal of both larval and older fish, compensatory juvenile mortality, redistribution of fishing effort, and changes in mean fecundity of fish in protected areas due to accumulation of older, highly fecund individuals. We use the model to demonstrate for a range of indicator species that proposals for an MPA network along the California coast would very likely not meet intended conservation objectives unless accompanied by fisheries harvest management in remaining open areas that maintains biomass outside of reserves.

A key factor that has motivated our model development is that computer simulation studies (e.g., fig. 11.10 in Walters and Martell 2004; see also Meester et al. 2001) warn that impacts of heavy fishing pressure near MPA boundaries can have impacts on abundance that extend well into the MPA, beyond typical dispersal distances for the impacted species. Two mechanisms cause this effect: (i) individuals with home ranges near the boundaries are still subject to risk of harvest, and more importantly, (ii) dispersal imbalance effects, which have not been widely recognized by proponents of MPAs. Dispersal imbalance effects occur when there is movement out of sites near the boundary, which is not balanced by movements into the site because of lack of source animals from outside the MPA boundary. Models with density-dependent movement (more movement of individuals from high-density sites near the core of the MPA; see e.g., Abesamis and Russ 2005) predict even larger imbalance effects on overall MPA abundance. Such effects are difficult to measure in patchy environments and may take years to develop after a MPA is created, but can considerably reduce the long-term abundance benefits of localized protection from fishing.

California is the first state to plan an extensive series of marine protected areas under the legislation Marine Life Protection Act (MLPA). The MLPA mandates development of a network of marine reserves along the California coast, with basic goals of protecting marine communities and unique habitats. Planning for implementation of the Act's requirements has focused on the central coast area from Point Conception near Santa Barbara to Pigeon Point near Santa Cruz. A science advisory team has developed recommendations for MPA size and spacing based on review of movement and larval dispersal characteristics of a wide range of species, and these recommendations have been used to guide

development of three alternative network proposals or plans (details and maps available at www.dfg.ca.gov/mrd/mlpa/centralcoast.html). Each of these proposals would protect 15%–20% of coastal areas from the impacts of at least demersal fishing.

A serious complicating factor in evaluation and comparison of these proposals is that the California Department of Fish and Game (with management responsibility for fisheries inside the state 3 mile limit (1 mile = 1.609 km)) and National Marine Fisheries Service (NMFS) (offshore species) have initiated extensive trawl and gill net fishing bans, species closures, large offshore closures for rockfish conservation, and protection of essential fish habitat, all aimed at rebuilding and sustainably managing a collection of species that have been classified as overfished. These species already being afforded management protection include red abalone (*Haliotis rufescens*), widow rockfish (*Sebastes entomelas*), bocaccio (*Sebastes paucispinis*), lingcod (*Ophiodon elongatus*), and inshore species like cabezon (*Scorpaenichthys marmoratus*). One of these, lingcod, has recently been declared by NMFS to be recovered.

Consequently the development of MPA proposal alternatives has taken place in an environment of extreme uncertainty. There is a need to account for high ecological complexity (species with a wide variety of life histories and dispersal characteristics); there is gross uncertainty about population parameters related to spatial processes (adult mortality and larval dispersal); and there is considerable uncertainty about the efficacy of other fisheries management measures. In such environments, and especially when a wide range of expertise and stakeholder interests are involved, even quite simple models can go a long way toward clarifying likely differences in outcomes among policy alternatives and in obtaining consensus about needs for adaptive management in implementation of the program (Walters 1997). Indeed, development of the model described below was motivated mainly by the possibility of using it in future adaptive management planning processes for the California coast.

In this paper, we construct a general model of a linear coastline broken into many small areas, as in Botsford et al. (2004), and use this model to evaluate specific proposals for the central coast of California proposed under the MLPA.

Materials and methods

When MPAs are to be placed along a coastline like California's, where each MPA is intended to protect an inshore–offshore band that includes both juvenile nursery and older fish residence areas, the most important population impacts of protection can be quantified by using a simple, one-dimensional spatial model with a large number of spatial cells or local sites that are linked through dispersal of both larvae and older animals. We develop the model by first providing an overall dynamic accounting and solution structure, then examine each element of that structure in more detail.

General dynamic structure and numerical solution method

We divide a coastline into $i = 1 \dots n$ spatial cells, each extending a longshore distance of 1 mile and extending off-

shore for an unspecified distance large enough to protect all life stages of a species. We assume initially that all of these cells are equally suitable for the species in terms of habitat conditions. If N_i is the number of older individuals in the cell (summed over all ages from an arbitrary age of recruitment or maturity), the dynamics of N_i can be approximated by the continuous recruitment–movement–mortality rate relationship:

$$(1) \quad dN_i/dt = r(L_i) - MN_i - F_iN_i - 2mN_i + m(N_{i-1} + N_{i+1})$$

where $r(L_i)$ is local recruitment rate as a function of local larval settlement rate L_i , M is natural mortality rate, F_i is fishing and (or) bycatch mortality rate specific to cell i , m is movement rate of older animals out of cell i to the adjacent cells, and mN_{i-1} and mN_{i+1} are movement rates of animals into cell i from surrounding cells.

For evaluation of the long-term impacts of protection, we need not solve eq. 1 over time, and can instead try to find the long-term mean or equilibrium N_i implied by $dN/dt = 0$. This equilibrium abundance field must satisfy the relationship:

$$(2) \quad N_i = [r(L_i) + m(N_{i-1} + N_{i+1})]/(M + F + 2m)$$

This is obtained just by setting dN/dt to zero and solving eq. 1 for N_i . Owing to the nonlinear dependence of L_i and $r(L_i)$ on larval transport and survival patterns and on mean fecundity of the N_i in each cell, eq. 2 cannot be solved analytically for the long-term N_i ; however, it can be easily solved by numerical relaxation methods. The simplest such method involves substituting successive estimates of L_i , N_{i-1} , and N_{i+1} into the right-hand side of eq. 2 and using the resulting estimates of N_i as the inputs for the next iterative substitution. However, that method converges very slowly.

The following procedure converges very rapidly (within 10–20 iterations) for most parameter combinations: (1) set N_i to the initial, trial values $N_i^{(1)}$ (e.g., $N_i^{(1)} = R_0/(M + F_0 + 2m)$, where R_0 is initial recruitment, and F_0 is initial fishing mortality rate); (2) use these estimates to solve eqs. 3–6 below for larval production, recruitment rates, and spatial F_i (setting F_i for closed areas to zero); (3) treating the resulting recruitment and F_i estimates as fixed constants, solve a tridiagonal equation system for equilibrium N_i , where each equation in the system is given by $r(L_i) = MN_i + F_iN_i + 2mN_i - m(N_{i-1} + N_{i+1})$. This results in a vector $N_i^{(eq)}$ of new N estimates; and (4) combine these with the previous estimates using a relaxation weight W of around 0.9 to give a next iterative estimate $N_i^{(2)} = WN_i^{(eq)} + (1 - W)N_i^{(1)}$. Then use these estimates in step 2 to begin another iteration, repeating steps 2–4 until the N_i estimates stop changing. Note that for each iteration, we calculate updated estimates of F_i under various hypotheses about redistribution of fishing effort and update the $r(L_i)$ function to represent changes in larval source abundances and mean fecundities.

Local recruitment dynamics

The really critical term in eqs. 1–2 is the recruitment function $r(L_i)$, which involves issues of both how far larvae are dispersed (how L_i is formed as a sum of larval contributions from other cells) and whether there is strong density dependence in postsettlement survival rates (whether or not

juvenile nursery habitats are fully seeded so that recruitment is independent of larval settlement). In the absence of strong longshore advection of larvae in particular direction(s), we would expect dispersive mixing processes to result in a normally distributed pattern of larval settlement from spawning in each cell, with a spread or standard deviation parameter proportional to larval duration and mixing velocities per unit time. The normal distribution assumption for larval settlement implies that if there are no larval sources outside the study region, average L_i on each cell i should consist of a sum of larval contributions from potentially all other cells, with the functional form:

$$(3) \quad L_i = k \sum_{j=1}^n \bar{f}_j N_j e^{-0.5(j-i)^2/S^2}$$

Here, k is a scaling constant for total larval settlement from each source cell, S is the standard deviation of the spatial distribution of larval settlement (e.g., $S = 10$ implies that settlement of larvae produced in a cell drops off rapidly beyond 10 miles from that cell), and \bar{f}_j is mean relative fecundity of animals in cell j (see below; for simple simulations that ignore impact of harvesting on mean fecundity, set $\bar{f}_j = 1.0$). Note that summing over all cells j implies that larval settlement on cell i may include contributions from any or all of the other cells j . The exponential term in eq. 3 results in a normally distributed pattern of larval settlement from each source cell, as would be expected if larval dispersal is essentially a random walk process without directional advection along the coast.

Using eq. 3 to predict average larval settlement to each cell i , the key issue then becomes prediction of how $r(L_i)$ varies with L_i . In the absence of evidence of recruitment suppression at high N_i due to cannibalism or spacing behaviors by the animals already present in cell i , we would expect the recruitment function to be of a saturating or Beverton–Holt form, i.e.,

$$(4) \quad r(L_i) = \alpha L_i / (1 + \beta L_i)$$

where α is the maximum survival rate of larvae from settlement to recruitment, and α/β is the maximum recruitment rate (carrying capacity of the cell to produce recruits). We hypothesize a base or reference natural settlement rate L_0 for each cell, calculated by setting $k = 1$, $i = n/2$, and all N_j in eq. 3 to a base unfished abundance $N_j = R_0/M$, where R_0 is an average natural recruitment rate per cell. Then we can parameterize the recruitment relationship in terms of R_0 , L_0 , and the Goodyear compensation ratio (K , ratio of maximum larval survival at low densities to survival at unfished natural abundance) by setting

$$(5) \quad \alpha = KR_0/L_0 \\ \beta = (K - 1)/L_0$$

Note that in this parameterization of the Beverton–Holt function, absolute larval production per spawner (k) does not matter, since only the product $k\alpha$ actually appears in the recruitment prediction. Meta-analyses of stock–recruitment data indicate that we should expect K to be in the range 5–100 (see e.g., Goodwin et al. 2006), with most likely values for long-lived benthic species in the range $K = 10$ –50. The

critical parameter in this representation is K , which determines how much larval settlement can be reduced before net recruitment $r(L_i)$ is impaired; R_0 is simply a scaling parameter that is determined by (or implies or represents) the units of measurement of N_i .

In assuming that local recruitment depends only on local larval settlement (eq. 4), we join other modelers (e.g., Botsford et al. 2004; Gaylord et al. 2005; Kaplan and Botsford 2005) in ignoring postsettlement, longshore movement by juveniles prior to recruitment to the older population N . This is not a serious issue for species where juvenile nursery habitat is widely distributed along the coast, since for such species, juvenile movement just acts like wider spreading of larvae in the first place (we could account for it by increasing S in eq. 3). But for species that depend on very restrictive nursery habitats (e.g., estuaries) from which juveniles fan out to occupy other habitats as part of their ontogeny, we really should include calculations of prerecruit juvenile movement using the same approach as eq. 3 but applied to the survivors from density-dependent mortality effects in the restricted nursery areas.

The above formulation allows for variation among species in the following basic life history parameters: M , natural longevity (annual natural mortality rate); m , adult diffusive movement rate between cells (per year); F , base (and policy) fishing mortality rate (per year); S , larval dispersal distance (standard deviation of normal settlement curve, miles); K , compensatory improvement in juvenile survival at low stock sizes. The only major population dynamics factors that are not represented in the above equation system are (i) changes in mean larval production per adult with changes in age-size composition (i.e., increases in mean fecundity \bar{f}_j per N_j in spatial cells that have lower total mortality rates $M + F_i$ and (ii) spatial variations in juvenile and adult habitat capacity, as might be reflected in spatial variation in the juvenile carrying capacity parameter β and in adult dispersal rate m (i.e., higher dispersal rates out of areas with relatively poor habitat). It is not difficult to model spatial variation in mean fecundity with variation in $M + F_i$ for species that are not highly dispersive (low movement rates m). Omitting this variation results in somewhat conservative predictions about the benefits to larval production of reducing local mortality rates (when dispersal rates are high, mean fecundity cannot increase in protected areas, since loss of older animals into fished areas prevents the development of a natural age structure; only relatively small (e.g., 5%), annual emigration rates are enough to substantially lower mean fecundity for long-lived species). We have tested a simple method for representing variable fecundity, assuming \bar{f}_j is proportional to a power of the ratio of numbers per recruit to unfished numbers per recruit (see below), and found no substantial change in the basic predictions. It is likewise simple to model variation in nursery capacities (β) among cells and m .

For simple policy-screening exercises involving general comparisons of how well alternative MPA proposals are likely to perform at enhancing abundances of animals with a range of different life histories (M , m , S , F , K values), it is probably best not to complicate the comparisons by including variations in spatial habitat and effects of increased longevity-fecundity. In simple game-playing exercises where we have varied the life history parameters widely, we

have found that predictions are typically not particularly sensitive to the M and S parameters. The parameter m determines the extent to which there will be substantial increases in biomass inside reserves. For longer-lived species ($M < 0.2$), the reserve must be greater than 5–10 times the mean dispersal distance to lead to major increases inside reserves. The most critical parameters for predicting the overall outcome are the parameters F and K . These are exactly the same parameters that are most critical in comparisons of fisheries harvesting policies in general, using standard stock assessment models.

Spatial variation in fishing effort

When using the model to evaluate MPA proposals that involve closing a large proportion of the cells to fishing (by setting F_i for those cells to zero or to some lower predicted poaching rate), a key consideration is what to assume about fishing effort displaced from the cells after closure. One simple option is to assume historical F_i , which amounts to assuming that total fishing effort will be reduced so that the F_i in each remaining cell does not increase. A more realistic option is to assume that displaced effort is spread across the remaining open cells, so that F_i for each cell changes from a base value F_0 to a higher value $F_i = F_0/(1 - c)$, where c is the proportion of the cells closed to fishing under the proposal. A still more realistic option is to use a gravity or multinomial logit model to predict spatial redistribution of fishing effort, so as to recognize likely concentration of fishing effort near MPA boundaries where abundances are enhanced by spillover effects of m .

Spatial variation in fishing effort can be predicted with a multinomial logit (gravity model) based on the assumption that the average utility of each area to fishers is proportional to the logarithm of abundance in that area. This leads to the spatial effort or fishing mortality allocation model:

$$(6) \quad F_i = F_{\text{total}} N_i^{1/\nu} C_i / \sum_j N_j^{1/\nu} C_j$$

Here ν is a standard deviation among fishers in perception of the utility of fishing in cell i compared with other areas (higher ν spreads effort more evenly along the coast), F_{total} is the total number of spatial cells times the base assumed fishing rate F_0 per cell, and C_i is set to 1.0 for cells that are open to fishing and to 0 for closed cells.

Spatial variation in habitat quality

Habitat quality for both juveniles and older fish of any species is likely to vary considerably along any large coastline. Spatial variations in habitat quality or carrying capacity among cells can be represented by variation in dispersal rates and recruitment carrying capacities. For each cell, assume that relative habitat quality can be represented by a 0–1 index value h_i , where $h_i = 1$ represents the best quality habitat and $h_i = 0$ represents completely unsuitable habitat. A simple way to estimate h_i is to examine distributions of fishing effort prior to establishment of reserves, since effort is likely to be concentrated in cells with higher habitat quality and fish abundance. Then we simply multiply the recruitment α for each cell by h_i in predicting recruitment and further assume that emigration rates (m out of the cell) in-

crease to m/h_i for cells with low h_i , while immigration rates (m into the cell) decrease to h_i/m for cells with low h_i .

Changes in mean fecundity

Spatial variation in \bar{f}_i can be represented by estimating the equilibrium size–age structure of each cell and adjusting that cell’s contribution to total larval production accordingly. It has been pointed out (e.g., Gaylord et al. 2005) that protected areas will allow buildup of older, more fecund animals, and these animals will make disproportionate contributions to total larval production. Fish typically mature at about 8%–10% of their maximum body weight, and fecundity is typically proportional to body weight above the weight at maturity. For slow-growing species like widow rockfish, such growth–fecundity patterns result in age–fecundity patterns like that shown in Fig. 1.

When a long-lived stock is heavily exploited, such an age–fecundity pattern can obviously lead to large decreases in mean fecundity when mean age is severely reduced by fishing. For example, if widow rockfish were exploited at an annual exploitation rate of 25% at ages 4 and older for long enough so that the population age structure could stabilize, the annual egg production per recruit in the exploited (age 4+) population would drop from around 6.6 eggs per recruit (relative scale) for an unfished population to only 0.5 eggs per recruit under harvesting. This implies a drop in relative mean fecundity per age 4 and older animal from 0.05 to only 0.01 (in this calculation, eggs per recruit is calculated as survivorship to age times fecundity at age, and eggs per fish is eggs per recruit divided by numbers of fish present per recruit).

Based on calculations like these, we might expect a gain of as much as fivefold in mean egg production by fish resident in MPAs. Unfortunately, such gains can only be expected for completely sedentary species. It is not difficult to calculate the equilibrium age structure for each spatial cell along a coast by numerically integrating the die-off rate equation for a typical cohort in each cell i :

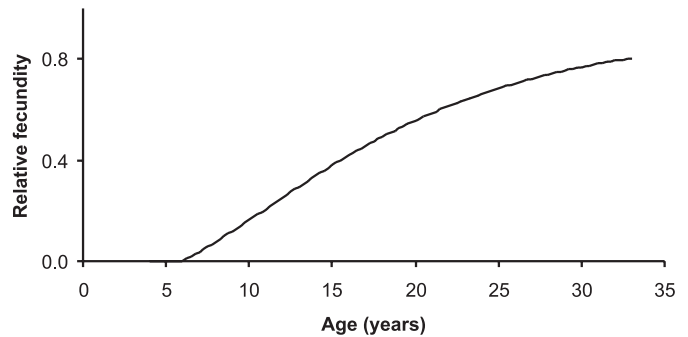
$$(7) \quad dN_i/dt = -(M + F_i + 2m)N_i + m(N_{i+1} + N_{i-1})$$

Note that this equation includes a dispersal loss term, $2mN_i$, representing dispersal to other cells, and a gain term, $m(N_{i+1} + N_{i-1})$, for immigration of animals (of the same age) from surrounding cells. Because of the cross-cell linkage and possibility of highly variable F_i among cells i , eq. 7 has to be integrated using very short time steps (0.25 years or less), along with some iterative method for estimating the mean of the gain term $m(N_{i+1} + N_{i-1})$ over each integration time step. But an important point about eq. 7 is that each cohort within cell i suffers a loss rate of $2mN_i$ to adjacent cells, which may or may not be balanced by immigration from those cells, even when $F_i = 0$. Thus, it can be seriously incorrect, especially for small MPAs and animals with high m values, to assume that unfished cells will reach the unfished equilibrium age structure predicted by the natural stock decay equation $dN_i/dt = -MN_i$ for a typical cohort in the absence of fishing and movement.

Assessment of m of older fish

The instantaneous movement rate m of older fish in eq. 1

Fig. 1. Age–fecundity relationship for widow rockfish (*Sebastes entomelas*), assuming von Bertalanffy $K = 0.1$ and maturity at 9% of maximum body weight.



can obviously have a large impact on predictions of N_i . Note that if the spatial cells are of unit long-shore width, the sum of terms $-2mN_i + m(N_{i+1} + N_{i-1})$ in eq. 1 is a discrete approximation of the diffusion term $D\partial^2 N/\partial x^2$ that appears in continuous one-dimensional (x) spatial models for movement treated as a random walk process (Okubo 1980). That is, m is the same as the diffusion coefficient usually called D in such models.

A useful mathematical result about such random diffusion processes is that if a set of animals are tagged at some point in space and then allowed to move for some time t (e.g., 1 year), their distribution is expected to be normal with position mean 0 (no net advection along shore) and variance $2Dt = 2mt$ (Goel and Richter-Dyn 1974). So if there are tagging data that provide a distribution of annual ($t = 1$) movement distances, the standard deviation S of this distribution (a measure of average movement distance) is an estimate of $(2m)^{1/2}$ (i.e., $m \approx S^2/2$).

The m parameter is not a discrete-time movement proportion and hence can have very large values. The total dispersal loss across any cell boundary from cell i is predicted to be mN_i , and for highly mobile animals this flux can obviously be many times the number of animals N_i present in the cell at any moment.

For relatively sedentary species with distinct home ranges, distributions of movement distances are likely to show two distinct patterns, with many animals showing apparently zero movement and others showing relatively large movements. In such cases, it is tempting but incorrect to think of m as consisting of the product of two factors: a probability of moving at all multiplied by half the square of the mean distance moved for those individuals that do disperse. Suppose instead that N_i is viewed as divided at any moment into two behavioral types of animals: S_i sedentary individuals and D_i actively dispersing individuals ($N_i = S_i + D_i$). The rate dynamics of these components can be represented by the pair of equations (where $Z = F + M$)

$$(8) \quad \begin{aligned} dS_i/dt &= r(L_i) - Z_i S_i - eS_i + sD_i \\ dD_i/dt &= eS_i - Z_i D_i - sD_i - 2mD_i + m(D_{i+1} + D_{i-1}) \end{aligned}$$

Here, e represents the (relatively low) movement rate of animals from sedentary to dispersive state, and s represents the

Table 1. Simple model parameters for five test species found along the California coast.

Simple model parameters	Red abalone	Widow rockfish	Lingcod	Bocaccio	Cabezon
Base recruitment (R_0)	1	1	1	1	1
Annual adult mortality (M)	0.1	0.125	0.25	0.15	0.3
Fishing mortality rate (F)	0.08	0.06	0.25	0.056	0.2
Adult emigration rate (\sim miles \cdot year $^{-1}$)*	0.01	0.5	6	6	1.5
Larvae per adult (k)	100	100	100	100	100
Goodyear compensation ratio (K)	3	20	10	4	10
Larval transport distance parameter (S)	0.3	40	15	45	1.5

Note: Red abalone (*Haliotis rufescens*), widow rockfish (*Sebastes entomelas*), lingcod (*Ophiodon elongatus*), bocaccio (*Sebastes paucispinis*), cabezon (*Scorpaenichthys marmoratus*).

*1 mile = 1.609 km.

(likely very high) movement rate of dispersing animals back into the sedentary state. The equilibria of these equations ($S_i = [r(L_i) + sD_i]/(Z_i + e)$ and $D_i = [eS_i + m(D_{i+1} + D_{i-1})]/(Z_i + s + 2m)$, respectively) can be found by the same iterative procedures as described above for N_i . We have found that these solutions are very close to those of the simpler diffusive model with $m = e$, that is the slow rate of movement into the dispersive state dominates the effective value of m for the population as a whole.

For animals that have relatively large home ranges but rarely disperse (very low e in eq. 8), another alternative to treating movement as dispersive is to assume no dispersive movement at all, but to account instead for partial exposure of N_i to fishing mortality rates in other spatial cells. In this formulation, it is necessary to calculate F_i , which now needs to be defined as the effective fishing mortality rate suffered by animals whose home ranges are centered in cell i , as a sum of proportions of time that cell i animals spend in surrounding cells multiplied by effort-based fishing mortality risks for each of those cells. This results in the same qualitative effect as dispersal imbalance near the border of protected areas, namely depression in abundance for spatial cells near such borders. However, just how far that depressing effect extends into a multicell MPA depends on the details of how much time animals are assumed to spend in cells surrounding the center of their home ranges.

Results

We used the model to examine how the five historically overfished indicator species mentioned above might respond under the three alternative proposals for the central coast study area. To do this, we first obtained rough estimates of the model parameters for each species (Table 1) from information in stock assessment documents and from syntheses of information by the California science advisory team. Then we divided the central coast study region into 200 spatial cells, each roughly 1 mile wide. Using maps of the proposed closures, we designated each cell as closed ($F_i = 0$) or open ($F_i > 0$) to fishing for each of the proposals; all of the test species are benthic, so we made no distinction between types of protected area (e.g., we ignored the fact that some MPAs would be open to fishing for pelagic species). Only a few of the proposed MPAs extend offshore far enough to fully protect the rockfishes, but we assumed for those proposed MPAs that coordination of state and federal protective measures will eventually lead to permanent offshore, as well

as inshore, protection; at present, federal regulations have nearly shut down demersal fishing offshore of all the proposed MPAs as rockfish conservation areas and (or) essential fish habitat closures.

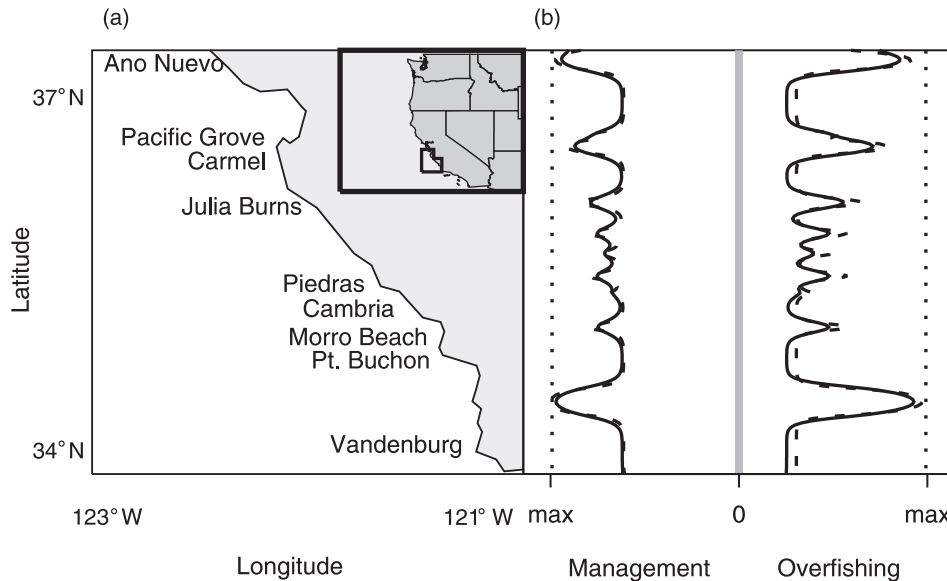
In relation to uncertainty about future fisheries management, we examined two alternative scenarios for future fishing mortality rates in areas remaining open to fishing: one where management target F s are met through the current conservative regulations and one where regulation fails and much higher F s (e.g., 0.2 for rockfish) prevail in open areas. We did not model possible enforcement failures within MPAs, a particular concern for red abalone, where very high prices and easy access to shallow waters have likely created severe poaching problems.

We evaluated three specific proposals considered in the MLPA process, known as package 1, package 2, and package 3R. Package 3R formed the basis of the final recommendation, and there was considerable disagreement among stakeholders as to the costs and benefits of these three packages.

Sample results are shown from integrating eq. 7 (Fig. 2a), then calculating average fecundity per animal from the age-fecundity relationship in Fig. 1 for a species with growth and mortality characteristics similar to widow rockfish and a relatively low annual movement rate of $m = 0.5$ (roughly, 0.5 miles per year) under package 3R. Peaks in mean fecundity occur where there are protected areas (using California coast proposals as example; see below). But we see from this example that predicted mean fecundity per age 4 and older fish only approaches the unfished fecundity mean near the center of the largest MPA (off Vandenberg Air Base, California). When we repeat the calculations assuming a lower fishing mortality rate, $F = 0.07$, near the current Pacific Fisheries Management Council target for long-term management, we obtain the pattern shown in the portion of the panel labeled management. Even in this far more sustainable scenario, mean fecundity is reduced considerably in most areas from the natural baseline and again only approaches it in the largest MPA. Peaks in mean fecundity are predicted to occur in proposed protected areas, but mean fecundity only reaches the expected value for an unfished stock near the center of the largest proposed MPA (off Vandenberg Air Base, approximately 16 km wide MPA).

The approximate mean fecundity lines in Fig. 2 (dashed) are those obtained by predicting mean fecundity as $(N_i/N_0)^p$, where N_i/N_0 is the ratio of equilibrium numbers per recruit to numbers per recruit in an unfished population, with the

Fig. 2. Predicted spatial variation in mean fecundity for a species like widow rockfish (*Sebastes entomelas*) (mean adult dispersal distance $0.8 \text{ km}\cdot\text{year}^{-1}$, $M = 0.1$, vulnerable to fishing at age 4), measured along the California coast southward from San Francisco Bay to Cape Conception. (a) The coastline with some locations labeled (inset shows location on US west coast). (b) Mean fecundity over space for two scenarios: one with high fishing mortality rate ($F = 0.25$) outside marine protected areas (MPAs) and one with much lower rate ($F = 0.07$) proposed for long-term management by Pacific Fisheries Management Council. Dotted lines indicate mean fecundity in the absence of any fishing, solid lines are predicted mean fecundity, and dashed lines are the approximate mean fecundity.



empirical power parameter $p = 1.3$. As noted above, this approximation was used to model spatially variable fecundity in some runs of the simple model and made essentially no difference to the overall patterns predicted by the model.

The result of the mean fecundity analysis is that gains in population viability due to survival of animals to older, more fecund ages can be expected only for species that are highly sedentary and subject to high, uncontrolled exploitation rates outside MPAs. Planners should not expect such gains from most fish species in coastal ecosystems.

Basic results of the simplest analysis (with no spatial variation in habitat quality, fishing effort concentrated near MPA boundaries) show that except for completely sedentary species like red abalone, widespread restoration to productive stock sizes is unlikely to be achieved through any of the MPA proposals unless accompanied by successful fisheries management (achievement of relatively low F s) in open areas (Fig. 3). The model predicts that a fundamental weakness in all of the proposals is that the MPAs are too small (most are 5–10 km longshore) to protect species with even relatively low ($m = 1$) movement rates of older animals. For these species, dispersal imbalance effects lead to reduced abundances (and mean fecundities) all the way to the centers of all but the largest (off Vandenberg Air Base, for package 1) MPAs that were proposed. The dispersal imbalance effects lead in turn to much lower predictions of total larval production than would be expected if $m = 0$, and that lower larval production leads in turn to persistence of recruitment overfishing effects if stocks outside MPAs remain depleted. We found that there were reasonably small differences in yield or total abundance among the three packages, that yield was generally higher without any MPAs in place, and that the abundance and yield depended primarily on the fisheries regulations outside of MPAs.

We ran a wide variety of sensitivity tests on the predictions, varying particularly the adult movement parameter m and including spatial variation in habitat quality with the h_i estimated by examining areas of concentration of fishing effort (assuming effort tends to concentrate in areas where good habitat has led to fish concentrations). The tests on m show that basically the same results as shown in Fig. 3 can be expected for fish species with $m > 0.5$ (i.e., for fish species that move on average more than about 0.5 mile per year). The different life histories and different MPA packages examined serve as large-scale sensitivity tests for the basic biological and regulatory parameters.

Adding complex longshore habitat structure to the analysis (Fig. 3f) leads to a much more complex spatial pattern, but still about the same differences among policies as for the flat world scenarios (other panels of Fig. 3). However, because of the heavy bias towards hard-bottom habitat in each of the MPA proposals, it does result in larger increases in total abundance with all of the MPA proposals. The percentage of hard-bottom habitat inside MPAs with the variable habitat model (36.8%–47.8%) is more than twice the nominal percentage (14.9%–19.3%) in the constant habitat model.

It appears that there will be negative consequences for fishery yields under all the MPA packages if other fisheries management measures are successful (Table 2). We calculated equilibrium total catch for each proposal simply by summing $F_i N_i$ over all spatial cells for the model case where there is spatial variation in habitat quality (as in Fig. 3) and where fishery management is successful at achieving the target fishing rates in Table 1. In that case, MPAs simply concentrate fishing so as to reduce N_i and catch per effort in open areas relative to what it would be if all cells were well managed, and this reduction in CPUE leads to considerable loss in total yield and in lower overall F s than intended.

Fig. 3. Predicted equilibrium patterns of relative abundance for a selection of indicator species, calculated using the spatial model with constant habitat quality. The y axis of the each graph is geographic position, from just below San Francisco Bay at the top to Point Conception at the bottom. Each panel has the abundance in a management scenario and an overfished scenario; higher values of the management scenario are to the left, higher values of the overfished scenario are to the right. The dashed lines represent abundance in the absence of fishing, solid lines represent abundance with marine protected areas (MPAs), and dotted lines represent abundance with fishing but no MPA. Abundance is measured in relative (per recruit) units. Note that predicted abundances drop off near the range limits because of not accounting for dispersal of larvae and older animals into the modeled area from outside regions, while accounting for dispersal losses to those regions. Parameter values for simulations are as shown in Table 1 (except that fishing rates for red abalone (*Haliotis rufescens*) and widow rockfish (*Sebastes entomelas*) are set to 0.3 to simulate high historical fishing impact). Panel *f* represents predicted spatial distributions for bocaccio (*Sebastes paucispinis*); model including spatial habitat variation is assumed to be correlated with spatial distribution of fishing effort. Lingcod (*Ophiodon elongatus*), cabezon (*Scorpaenichthys marmoratus*).

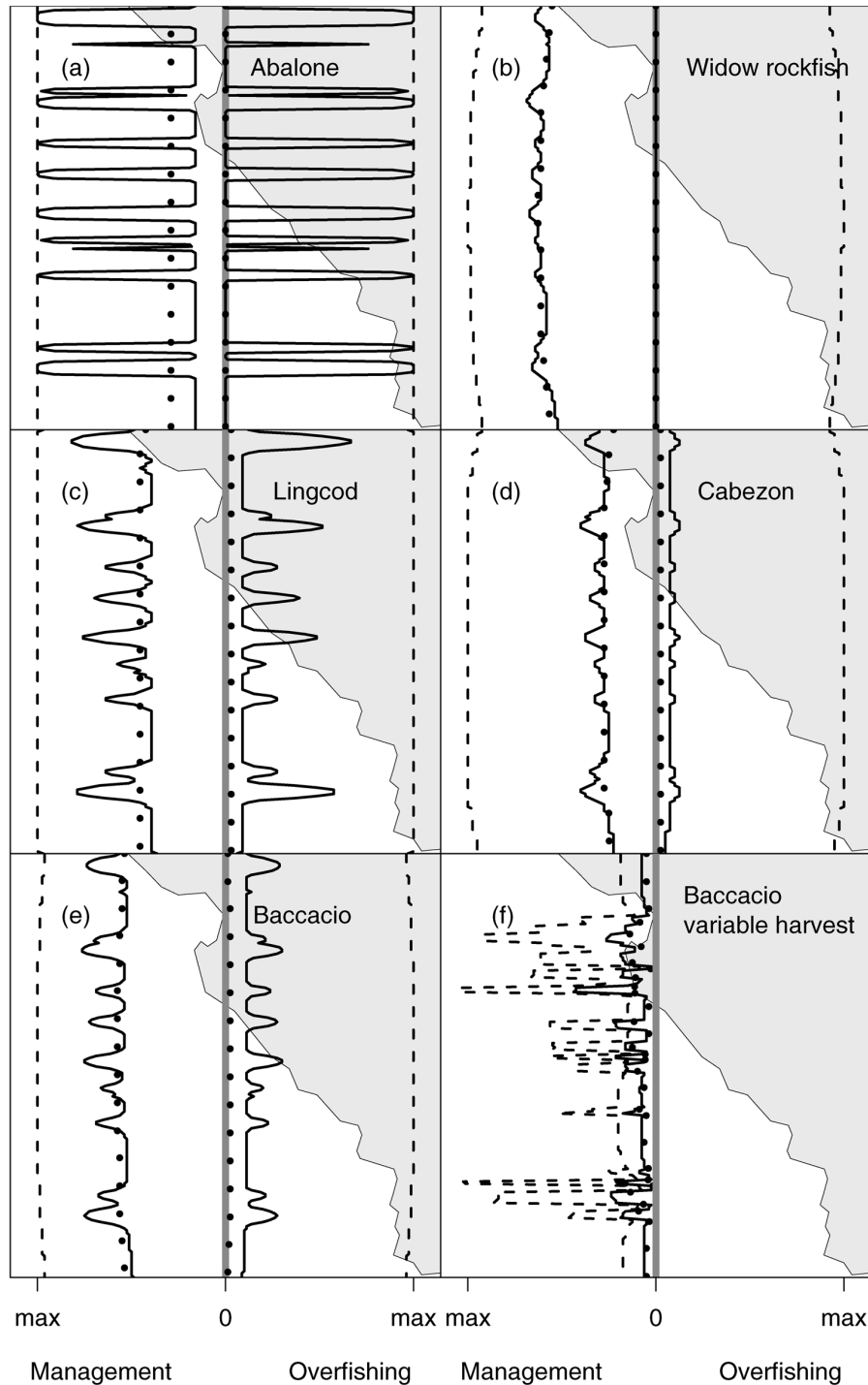


Table 2. Equilibrium relative abundances and yields predicted by the simple spatial model, with variable habitat quality (correlated with historical fishing effort concentrations) and fishing effort responses to spatial variation in abundances.

	Red abalone	Widow rockfish	Lingcod	Bocaccio	Cabazon
Abundance					
Without fishing	683.8	637.8	296.8	474.1	249.2
Without MPAs	205.0	293.1	72.2	232.2	100.2
Package 1	293.4	323.2	99.4	253.0	119.7
Package 3R	317.2	322.6	95.0	258.1	122.5
Package 2	329.6	319.9	92.9	256.3	122.8
Catch					
Without fishing	0.0	0.0	0.0	0.0	0.0
Without MPAs	21.1	32.2	25.1	20.8	27.4
Package 1	13.1	30.0	25.2	19.5	23.1
Package 3R	11.2	30.2	26.3	19.5	23.7
Package 2	10.3	30.4	26.2	19.6	23.5
Fishing mortality (<i>F</i>)					
Without fishing	0.00	0.00	0.00	0.00	0.00
Without MPAs	0.10	0.11	0.35	0.09	0.27
Package 1	0.04	0.09	0.25	0.08	0.19
Package 3R	0.04	0.09	0.28	0.08	0.19
Package 2	0.03	0.10	0.28	0.08	0.19

Note: Note that values for “Without MPAs” (marine protected areas) option are predicted using current fisheries management policy (i.e., assuming that current fishing mortality rate goals are met by other means than protected areas). Red abalone (*Haliotis rufescens*), widow rockfish (*Sebastes entomelas*), lingcod (*Ophiodon elongatus*), bocaccio (*Sebastes paucispinis*), cabazon (*Scorpaenichthys marmoratus*).

A matter of considerable concern in scientific discussions of the California proposals has apparently been larval dispersal distances, with planning documents mentioning the need for MPA spacing that will allow for connectivity in larval settlement among reserves. The model indicates that if overfishing does persist outside reserves, roughly 40%–50% of larval settlement will eventually be from fish resident in reserves because of even modest buildup in abundances and mean fecundities. Further, this prediction is largely insensitive to assumed average larval transport distances (*S* parameter), except for species like red abalone or cabazon that have extremely short larval dispersal distances.

Discussion

The results shown here are very discouraging from the perspective of using MPAs as a tool for fish stock and ecosystem restoration and are very similar to the relatively pessimistic results obtained with much more complex models like Ecospace. MPAs of the size and spacing proposed for the hallmark California case will only offer substantial protection to a very small proportion of marine fish and invertebrate species, making up only a small percentage of the biomass and production of that coastal ecosystem (see Field et al. 2006 for a review of biomass distributions across the California Current ecosystem).

The scenarios in Fig. 3 indicate that monitoring programs could expect to see substantial increases in abundance within MPAs relative to surrounding fished areas, as has now been widely observed in studies of MPA performance (Halpern and Warner 2002). The basic problem is that inside–outside abundance comparisons do not involve a sound baseline (i.e.,

do not reveal how much more abundant some species could or should be if widely protected). In short, it is meaningless to show that some species is twice as abundant within an MPA than outside, if even the inside abundance is only a tiny percentage of the unharvested population size. For most species in most places, there is little recourse but to use population dynamics models, with attendant uncertainty about parameter values, to establish such baselines or performance reference points.

Equilibrium spatial models can be solved quickly for policy screening and tests of sensitivity to parameters, but they do not give any indication of how long MPA effects might take to develop (a key issue in adaptive management planning). They can serve the same role in protected area planning as do equilibrium yield-per-recruit models in fisheries harvest policy analysis: to give a sense of the best long-term settings for policy variables (like age at first capture) without specifying how such settings might be implemented. But after first screening for policies that make long-term sense, it is usually relatively easy to develop more detailed models to examine time patterns and other possible pitfalls in the equilibrium calculations.

It would be foolish to claim that such equilibrium models can be precisely parameterized by fitting to field data, as we would do with ordinary stock assessment models. While such exercises might reveal some basic patterns such as variation in habitat quality h_i , they do not represent a wide variety of fine-scale processes that shape fish distributions in time and space. To capture all of these processes via some model-fitting procedure would require a much more complex parameterization with all sorts of nuisance parameters (for factors like historical recruitment variability) that are

not likely in fact to be critical for average, long-term policy performance. While we will doubtless move in the direction of such realistic models to understand some fine-scale processes, it is important to develop simpler models as policy-screening tools.

It would seem that for species that have been severely reduced by historical fishing, particularly those that have life history ontogeny involving inshore nursery areas and later movement into deeper waters, there is the possibility that nursery areas are now widely underseeded with larvae (i.e., are not producing nearly as many offshore recruits as they could). If this is the case, then even onshore-offshore protection (MPAs that extend well offshore) will not insure rapid population recovery, since abundance even in the MPAs may be limited by inadequate recruitment rather than depressed survival. For such species, the main connectivity among MPAs will be due mainly to relatively large-scale larval dispersal rather than to along-shore movement of older fishes. But if even larval settlement into MPAs is depressed because of large-scale historical overfishing, then recovery in MPAs will be slow enough that (unless a very high proportion of the offshore population is protected) most larval settlement will have to come from spawning outside the MPAs. That is, it may be wrong to suppose that MPA spawning abundances will recover rapidly so as to provide widespread larval seeding including connection through larval transport with other MPAs.

Our results are consistent with Allison et al. (1998), who found that protected areas are not sufficient to assure conservation of marine species. However, our results show that protected areas are also not necessary, stocks can be rebuilt and maintained by reducing fishing mortality rates alone, and none of the biology in the model we used suggests protected areas provide additional benefits to abundance and yield.

The model we present, or similar models that include spatial structure of populations, adult and larval dispersal, and the spatial allocation of fishing effort in response to changes in abundance, are straightforward to implement and can be used to quantitatively evaluate alternative MPA proposals. While such models are dependent upon specific assumptions, particularly dispersal assumptions, such models should be used when alternative MPA designs are being evaluated.

Acknowledgements

This work resulted from a peer review of the MPA proposals for the central coast of California funded by the Cali-

fornia Fisheries Coalition. RH was additionally supported in this work by a grant from the National Science Foundation (Award No. 0308440).

References

- Abesamis, R.A., and Russ, G.R. 2005. Density-dependent spillover from a marine reserve: long-term evidence. *Ecol. Appl.* **15**: 1798–1812.
- Allison, G.W., Lubchenco, J., and Carr, M.H. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecol. Appl.* **8**(Suppl.): S79–S92.
- Botsford, L.W., Kaplan, D.M., and Hastings, A. 2004. Sustainability and yield in marine reserve policy. *Am. Fish. Soc. Symp.* **42**: 75–86.
- Field, J.C., Francis, R.C., and Aydin, K. 2006. Top-down modeling and bottom-up dynamics: linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. *Progr. Oceanogr.* **68**: 238–270.
- Gaylord, B., Gaines, S.D., Siegel, D.A., and Carr, M.H. 2005. Marine reserves exploit population structure and life history in potentially improving fisheries. *Ecol. Appl.* **15**: 2180–2191.
- Goel, N.S., and Richter-Dyn, N. 1974. *Stochastic models in biology*. Academic Press, New York.
- Goodwin, N.B., Grant, A., Perry, A.L., Dulvy, N.K., and Reynolds, J.D. 2006. Life history correlates of density-dependent recruitment in marine fishes. *Can. J. Fish. Aquat. Sci.* **63**: 494–509.
- Halpern, B.S., and Warner, R.R. 2002. Marine reserves have rapid and lasting effects. *Ecol. Lett.* **5**: 361–366.
- Hilborn, R., Micheli, F., and DeLeo, G. 2006. Integrating marine protected areas with catch regulation. *Can. J. Fish. Aquat. Sci.* **63**: 642–649.
- Kaplan, D.M., and Botsford, L.W. 2005. Effects of variability in spacing of coastal marine reserves on fisheries yield and sustainability. *Can. J. Fish. Aquat. Sci.* **62**: 905–912.
- Meester, G.A., Ault, J.S., Smith, S.G., and Mehrotra, A. 2001. An integrated simulation modeling and operations research approach to spatial management decision making. *Sarsia*, **86**: 543–558.
- Okubo, A. 1980. *Diffusion and ecological problems: mathematical models*. Springer-Verlag, New York.
- Walters, C. 1997. Challenges in adaptive management of riparian and coastal ecosystems. *Conserv. Ecol.* **1**(2): 1. [online]. Available from www.consecol.org/vol1/iss2/art1/.
- Walters, C.J., and Martell, S.R. 2004. *Fisheries ecology and management*. Princeton University Press, Princeton, N.J.
- Walters, C.J., Christensen, V., and Pauly, D. 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems*, **2**: 539–544.