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FISHING THE LINE NEAR MARINE RESERVES IN SINGLE AND MULTISPECIES FISHERIES

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Abstract. Throughout the world “fishing the line” is a frequent harvesting tactic in communities where no-take marine reserves are designated. This practice of concentrating fishing effort at the boundary of a marine reserve is predicated upon the principle of spillover, the net export of stock from the marine reserve to the surrounding unprotected waters. We explore the consequences and optimality of fishing the line using a spatially explicit theoretical model. We show that fishing the line: (1) is part of the optimal effort distribution near no-take marine reserves with mobile species regardless of the cooperation level among harvesters; (2) has a significant impact on the spatial patterns of catch per unit effort (CPUE) and fish density both within and outside of the reserve; and (3) can enhance total population size and catch simultaneously under a limited set of conditions for overexploited populations. Additionally, we explore the consequences of basing the spatial distribution of fishing effort for a multispecies fishery upon the optimality of the most mobile species that exhibits the greatest spillover. Our results show that the intensity of effort allocated to fishing the line should instead be based upon more intermediate rates of mobility within the targeted community. We conclude with a comparison between model predictions and empirical findings from a density gradient study of two important game fish in the vicinity of a no-take marine-life refuge on Santa Catalina Island, California (USA). These results reveal the need for empirical studies to account for harvester behavior and suggest that the implications of spatial discontinuities such as fishing the line should be incorporated into marine-reserve design.

Key words: boundary fishing; California, USA; competitive fishery; cooperative fishing; displacement; effort allocation; fishing impacts; no-take marine protected areas; Paralabrax; Semicossyphus; spatial patterns; spillover.

INTRODUCTION

The function of an MPA [marine protected area] is to change or preempt the distribution and likely the overall level of fishing in space and time ... across a suite of species.

—D. S. Holland (2002:370)

Throughout the world, “fishing the line” is a common harvesting tactic where no-take marine reserves are designated (McClanahan and Kaunda-Arara 1996, Kelly et al. 2000, 2002, Bohnsack and Ault 2002, Goñi et al. 2006). The inherent assumption behind concentrating fishing effort at the boundary of a marine reserve is that the net export of stock from the reserve should enhance catch rates in adjacent unprotected waters (“spillover effect”). Although direct evidence of substantial movement of adults across marine-reserve

boundaries is limited, potential advantages of fishing the line have been documented as increased yield and greater catches of larger individuals near reserve boundaries (Yamasaki and Kuwahara 1989, Shorthouse 1990, Johnson et al. 1999, Murawski et al. 2004).

The disproportionate intensity of fishing effort near a reserve can provide benefits for some harvesters, but the larger scale consequences of boundary fishing for both the fishery and the protected stock are less clear. One common concern is the compression of effort into smaller fishing grounds (Hilborn 2002), especially near the reserve boundary. The unresolved question is whether the intensification of fishing pressure negates the ability of marine reserves to meet their conservation and fisheries management goals (Walters et al. 1999, Roberts et al. 2005) or if reserve benefits (e.g., spillover of adults and export of larvae) are sufficient to compensate for the negative consequences of squeezing fishing into a smaller area (Halpern et al. 2004). Moreover, since fishing the line essentially captures fish that spend part of their life under the protection of the reserve, the spatial distribution of fish inside and outside the reserve should be strongly affected by both the

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spatial distribution of fishing effort and the movement dynamics of fish.

Marine reserves are inherently a multispecies form of management. Since the optimal spatial allocation of fishing effort near marine reserves undoubtedly differs among fished species (e.g., because of differences in their movement, density, and catchability rates), multispecies fisheries will pose unavoidable compromises. Currently, a common method of detecting these cross-species compromises is to compare trends in slope and inflection points of density gradients across marine-reserve boundaries (Kaunda-Arara and Rose 2004). Steeper gradients and inflection points closer to the reserve boundary may imply less spillover than flatter gradients and inflection points further from the reserve boundary. Although the rationale for these predictions seems logical, a number of potential mechanisms could affect fish distribution patterns, including but not limited to fish movement rates, habitat continuity, interspecific interactions, and fishing patterns outside the reserve. In addition, these patterns are likely to change with the spatial and time scale and sample spacing (resolution) of the empirical studies. In the absence of a more comprehensive conceptual framework, it will remain difficult to infer underlying mechanisms and their interactions from simple empirical patterns near reserve boundaries.

Here we focus on understanding the interplay between fish movement dynamics and the spatial allocation of fishing effort near a marine-reserve boundary. We use a theoretical model to project the spatial patterns that are likely to develop for species with different mobility rates. We then apply the model to a multispecies fishery and explore the effects of different rational distributions of fishing effort on the spatial patterns of density and catch per unit effort (CPUE) across the community of species. We conclude by using the model predictions to gain insight into the potential mechanisms driving empirical patterns found in a density gradient study of kelp bass (*Paralabrax clathratus*) and California sheephead (*Semicossyphus pulcher*) populations in the vicinity of a no-take marine-life refuge at Wrigley Marine Science Center on Santa Catalina Island, California, USA.

A SPATIALLY EXPLICIT MODEL OF FISH AND FISHING EFFORT NEAR THE BOUNDARY OF A MARINE RESERVE

We consider a model (Table 1) of a fishery on a finite strip of coastline with a fully protected marine reserve in the center (Fig. 1). The edges of this continuous region are assumed impervious, an appropriate assumption when the surrounding habitat is impenetrable (such as land margins) or when fish can detect a change in habitat (e.g., reef to sandy bottom) and actively choose not to journey beyond that transition. By selecting reflecting edges, we also approximate a small reserve in a large system. This assumption of “reflecting” edges allows us to focus on the spatial patterns of fish density

caused by localized fishing mortality near the reserve boundary.

In our model, fish population dynamics are governed by density-dependent logistic growth and diffusive movement at species-specific rates that are constant in space and time. A compensatory (negative) relationship between population growth and density has been observed in a number of marine populations including fish, lobster, and abalone (Shepherd 1990, Pollock 1993, Koslow et al. 1995, Hixon and Carr 1997, Anderson 2001). Density-dependent demographic rates such as survival and fecundity arise from (1) resource limitation (food, settlement sites, refuge sites, etc.), (2) direct interference among conspecifics, and/or (3) increases in the per capita predation rate in response to prey aggregation (Sánchez Lizaso et al. 2000, Rose et al. 2001, Holbrook and Schmitt 2002). Turchin (1991, 1998), Holmes et al. (1994), and many other authors suggest that diffusion is an appropriate approximate description of movement for a variety of populations. Numerous empirical and theoretical studies support this: examples include turbot (Sparrevoorn et al. 2002), chinook salmon (Zabel 2002), green crab (Grosholz 1996), and marine microorganisms (Okubo 1980). Further explanation of the characteristics, assumptions, and appropriateness of diffusion to describe population movement can be found in Holmes et al. (1994), Lima and Zollner (1996), Turchin (1998), and Okubo and Levin (2001).

Outside the reserve, local fish density is also regulated by fishing. Fishing has two components: total fishing effort, E , which causes mortality in proportion to the local fishing intensity applied at each location, and the catchability, q (Schaefer 1954). In nonspatial models, these terms are often subsumed as the fishing mortality rate, $F = qE$. After reserve establishment the total fishing effort must be reallocated to areas outside the reserve. Total E may change for the region if fishery managers alter regulations or if vessels voluntarily leave the fleet. Although the establishment of new reserves can influence these decisions (Halpern et al. 2004), we focus here on the optimal spatial reallocation of fishing effort under the assumption that total fishing effort remains fixed. Catchability, q , defined as the fishing mortality per unit of fishing effort, is a complex parameter that can vary with species, stock availability, environmental conditions, gear attributes, vessel characteristics, and a crew's skill (reviewed in Arreguin-Sanchez 1996). Improvements in catchability are often attributable to technological advances in gear efficiency, selectivity, and vessel power.

To simulate systems that are fished at and above maximum sustainable yield, we consider catchability coefficients, q , that range from the value that would generate peak catch in the absence of a reserve to levels of intense overexploitation (see *Benchmarks*). We focus on variation in q to compare how the fixed total fishing effort, E , should be redistributed in systems with marine reserves.

TABLE 1. A spatially explicit model of fish and harvesters near a marine-reserve boundary.

Independent and State Variables:	
x	Spatial coordinate, one dimensional
t	Time
$n(x, t)$	Density of fish at location x at time t (no. fish/length)
Parameters:	
<i>Environment</i>	
L	Length of coastline occupied by the fishery
L_R	Reserve length, where $L_R < L$
<i>Movement</i>	
D	Diffusion constant, independent of space and time [(length) ² /time]
<i>Growth</i>	
r	Intrinsic rate of increase, constant in space and time (1/time)
K	Local carrying capacity (no. fish/length)
<i>Fishing</i>	
q	Catchability coefficient defined as the fishing mortality per unit of fishing effort [length/(time × harvester)]
$qn(x)$	Catch per unit effort (CPUE) at location x , assumed to be a linear functional response of stock availability [no. fish/(time × harvester)]
$e_U(x)$	Fishing intensity in unprotected waters outside the reserve boundary, where $e_U(x) = 0$ if $ x \leq \frac{L_R}{2}$ (no. harvesters/length)
E_B	Fishing effort at the reserve boundary $x = \pm \frac{L_R}{2}$ (no. harvesters)
$e(x)$	Fishing intensity at location x , constant in time such that $e(x) = e_U(x) + \left(\frac{E_B}{2}\right) \left\{ \delta\left(x - \frac{L_R}{2}\right) + \delta\left(x + \frac{L_R}{2}\right) \right\}$ (no. harvesters/length)†
Population Dynamics at Steady State:	
For $x = \pm \frac{L}{2}$, $\frac{\partial n}{\partial x} = 0$	Reflecting region edges
For $ x < \frac{L}{2}$, $\frac{\partial n}{\partial t} = 0 = rn\left(1 - \frac{n}{K}\right) + D\frac{\partial^2 n}{\partial x^2} - qe(x)n$	Reaction-diffusion equation inside the region edges
For $x = \frac{L_R}{2}$, $-D\frac{\partial n}{\partial x}\Big _- = -D\frac{\partial n}{\partial x}\Big _+ + q\frac{E_B}{2}n$	Spillover at the (right hand) reserve boundary line; a similar expression holds for the left hand boundary at $x = -\frac{L_R}{2}$
where the subscripts + and - represent derivatives evaluated to right and left of the line.	
Composite Metrics:	
$N = \int_{-L/2}^{L/2} n(x)dx$	Total population size (no. fish)
$C = q \int_{-L/2}^{L/2} n(x)e(x)dx$	Total catch (no. fish)
$E_U = q \int_{-L/2}^{L/2} e_U(x)dx$	Total fishing effort in unprotected waters outside the reserve (no. harvesters)
$E = \int_{-L/2}^{L/2} e(x)dx = E_U + E_B$	Total fishing effort, constant in time (no. harvesters)
Fishery Objectives:	
<i>Coordinated Fleet</i>	
Find $e_U(x)$ and E_B that maximize C .	
<i>Competitive Fishery</i>	
Find $e_U(x)$ and E_B such that $n(x)$ is constant for $\frac{L_R}{2} < x < \frac{L}{2}$ (details in Appendix A).	

† The local fishing intensity function $e(x)$ incorporates a Dirac delta function, a limiting form of other functions whose unit is (length)⁻¹ and total integral $\int_{-\infty}^{\infty} \delta(x)dx$ is equal to 1 (Nisbet and Gurney 2003; see Appendix D). As applied here, it denotes a function that is zero almost everywhere, except at the reserve boundary line where it represents a very narrow and tall spike.

Since $F = qE$, derived optimal patterns for q can be readily translated into spatial patterns of fishing mortality, F .

Given these constraints on harvesting, we seek the optimal spatial allocation of fishing effort near a no-take marine reserve for two fishing strategies: one that mimics a coordinated fleet controlled either by a sole owner or cooperative and another that simulates the behavior of a purely competitive industry with many autonomous

participants. The objective in the first scenario (coordinated fleet) is to find the spatial arrangement of fishing effort that maximizes collective catch. By contrast, in the second scenario (competitive fishing industry) individual benefits are maximized by equalizing catch per unit effort among participants. This latter objective is analogous to an ideal free distribution (Fretwell and Lucas 1970, Gillis 2003).

The simplifying assumptions made here are conservative and potentially underestimate the ability of the reserve to simultaneously enhance standing stock and catch, because all fisheries' benefits must arise solely through the spillover of adults. The model: (1) ignores other ways that reserves can export production to fished areas outside, e.g., through larval export or movement of non-fished juvenile stages across the reserve boundary; (2) does not incorporate the potential for the reserve stock to include larger, more fecund individuals (Halpern 2003, Halpern et al. 2004) that possibly produce higher quality young (Berkeley et al. 2004); and (3) does not consider situations in which the cessation of fishing improves habitat quality inside reserves (Rodwell et al. 2003). Each of these factors could allow reserves to sustain a higher total fishing effort (e.g., Gaylord et al. 2005). Thus, to counter losses of catch due to the displacement of fishing effort, the spillover of adult fish across the reserve boundary to surrounding unprotected waters must exceed the prior potential harvest inside the reserve.

Our aims are threefold: First we compare the optimal spatial distribution of fishing effort near the marine reserve for the two fishing strategies and assess how this allocation may vary for fish species with different rates of mobility. Second, we explore the spatial patterns of fish density and CPUE that can arise from spatially heterogeneous fishing intensity in the vicinity of a marine reserve. Third, we evaluate the region-wide consequences of spatially variable fishing effort using two metrics: total population size and catch.

Our interest is in steady-state solutions of the model equations that characterize the long-term (asymptotic) dynamics of the system. The model is too complex to calculate explicit analytic expressions for these steady states, except in relatively uninteresting simple situations. For example, in the absence of fishing (i.e., $e(x) = 0$ everywhere), the steady-state population density is everywhere equal to the carrying capacity, K . Conditions for population persistence and the optimal allocation of fishing effort are more complex when fishing can vary over space. For a specified fishing effort, however, numerical solutions of the model equations can be computed by standard methods; we used FEMLAB version 2.3 (Comsol, Burlington, Massachusetts, USA), a MATLAB (MathWorks, Natick, Massachusetts, USA) toolbox for solving partial differential equations using the finite element method. All simulations reported here used a fine-scale mesh (5000+ points) relative to the parameter scale in order to minimize computational artifacts, especially near the reserve boundaries.

BENCHMARKS

We use an unrestricted access scheme ($L_R = 0$; L_R represents the reserve length), in which the fishery is open to exploitation at all locales across the coastline, as a baseline for choosing parameter values and assessing the effectiveness of heterogeneously allocated

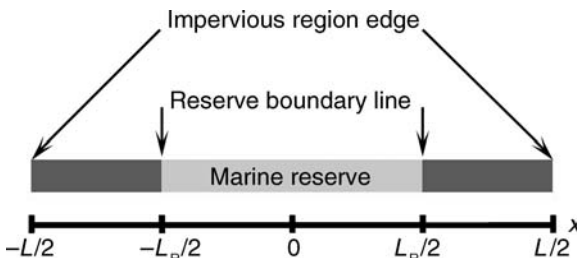


FIG. 1. Schematic of a fishery, where x is a one-dimensional spatial coordinate; L is the length of coastline occupied by the fishery; and L_R is reserve length. The system depicted in the model is symmetrical about the reserve mid-point, represented here as 0. The boundary line of the marine reserve is indiscernible to fish.

fishing effort. When spatial access to the entire fishery is unlimited, the most productive tactic for both a coordinated fleet and a competitive industry is to homogeneously allocate fishing effort across the entire region (i.e., $e(x) = E/L$ for $-L/2 < x < L/2$; L represents length of coastline occupied by the fishery) (Neubert 2003). Because the region edges are impervious and all biological and fishing parameters are constant across the region, species movement rates are arbitrary for the unrestricted access scheme. Population persistence in the absence of a reserve requires the intrinsic growth rate to be greater than the mean fishing intensity (i.e., $r > qE/L$ or $r > F/L$). When these conditions are met, the lack of spatially heterogeneous parameters generates a homogeneous pattern of fish density and CPUE across all spatial locales. Maximum sustainable yield occurs when $q = rL/2E$ or $F = rL/2$, corresponding to a total population size of $N = (K/2)L$ and catch of $C = (rK/4)L$ (Case 1999:235). Hereafter, these values are referred to as q_{MSY} , N_{MSY} , and C_{MSY} , respectively. When catchability exceeds q_{MSY} under the unrestricted access scheme, both the total population and catch are reduced below N_{MSY} and C_{MSY} (i.e., the population is overfished). Furthermore, the fish population cannot persist if the catchability equals or exceeds $2q_{MSY}$.

The interpretation of most empirical studies relating spillover with density gradients explicitly or implicitly assumes a uniform distribution of effort outside the reserve. Most existing theoretical models in the marine-reserve literature make a similar assumption. Thus, we also contrast our results to a restricted access scheme in which fishing effort is uniformly distributed in the unprotected area outside of a marine reserve (i.e., $e(x) = E/(L - L_R)$ for $-L/2 < x < -L_R/2$ and $L_R/2 < x < L/2$). In this case, inclusion of a no-take marine reserve squeezes the fishing effort into a smaller area, such that self-replenishment in the unprotected area requires $r > qE/(L - L_R)$ and $q < 2q_{MSY}(1 - L_R/L)$. Because fishing pressure on the unprotected stock accelerates as the fraction inside the reserve increases (Halpern et al. 2004), the compression of fishing effort may reduce the

stock to zero in the unprotected area unless this region is augmented by spillover from the reserve. In this model we assume that fishing-induced depletion of unprotected stocks may be renewed only by spillover of adults, not by the export of young. However, when fishing mortality exceeds population growth in the non-reserve area, region-wide population persistence of this source-sink system is dependent upon the species-specific movement and intrinsic growth rates, as well as the size of the reserve and unprotected areas. When the unprotected stock is not self-replenishing, regional population persistence requires

$$L_R > 2\sqrt{\frac{D}{r}} \times \arctan\left(\sqrt{\frac{qE}{r(L-L_R)} - 1}\right) \times \tanh\left\{\frac{1}{2}\sqrt{\frac{L-L_R}{D}[qE - r(L-L_R)]}\right\}$$

(equation adapted from Shigesada et al. [1986]; see Table 1 for an explanation of variable abbreviations). The parameter values used in the present study satisfy this inequality.

Irrespective of the spatial allocation of fishing effort in the unprotected area and catchability, the stock will be self-sustainable within the marine reserve if the reserve is large enough so that on average an individual resides in the reserve long enough to reproduce before emigrating. The condition for self-replenishment of a diffusively moving, non-fished population is well known as the KISS model and its analytical expression can be written as $L_R > \pi\sqrt{D/r}$ (Kierstead and Slobodkin 1953, Kot 2001:293).

Using these benchmarks, we categorize species by their relative movement rates into three groups based upon the size of reserve necessary to guarantee population persistence: (1) limited, in which the population is self-sustainable in a reserve that is at least 10% of the total region; (2) moderate, in which the population is self-sustainable in a reserve that is at least 25% of the total region; and (3) high, in which the population is self-sustainable in a reserve that is at least 50% of the total region.

In subsequent calculations, we set the reserve size to one-third of the nominal length of coastline. Emerging global networks have reserve fractions in this neighborhood (e.g., Great Barrier Reef Marine Park, Queensland, Australia; Channel Islands National Marine Sanctuary, California, USA). Alternatively, our length choice can be used to represent a single small reserve in a large system, in which we restrict our investigation to spatial scales that can be influenced by adult movement out of the reserve. With a reserve spanning one-third of the coastline length, species exhibiting limited to moderate mobility rates would have self-sustainable

reserve stocks regardless of how the stock is exploited beyond the reserve boundaries. Highly mobile species could require a viable exploited stock, because the reserve is only two-thirds as large as needed to guarantee persistence on its own.

In the next sections, we explore the spatial patterns of fish density and CPUE that can arise from homogeneously and heterogeneously distributed fishing effort near a marine-reserve boundary for species in these three mobility categories.

Uniform distribution of fishing effort

Catch and CPUE for fisheries with unrestricted spatial access are maximized by a homogeneous distribution of both fishing effort and fish when biological parameters are constant across space and the surrounding habitat is impenetrable. When fishing effort is distributed uniformly outside of a marine reserve, fish density becomes heterogeneous (Fig. 2A) with highest densities inside and near the reserve boundary. The gradient in density across the region is greatest for species with limited mobility whose stock inside the reserve grows close to carrying capacity, while the unprotected stock can become severely depleted. Fish density becomes more uniform with greater mobility because fish in the reserve cross the reserve boundary more frequently, which (1) reduces stock size inside the reserve and (2) increases stock size outside the reserve via replenishment. Further numerical solutions show that fish density in both the reserve and unprotected area decreases with increasing catchability. Sharper density gradients result from increases in catchability (e.g., with improving gear efficiency). This leads to a higher outward flux of biomass across the reserve boundary and a greater loss of stock inside the reserve.

Spillover to surrounding unprotected waters also has important repercussions for densities within the reserve: high movement rates reduce densities far below the carrying capacity, especially at locations near the boundary (“edge effect”). The zone of depressed fish density within the reserve widens as fish mobility increases. Therefore, spatially restricting fishing effort still has a strong influence on protected stocks. Overall, total population size is as large (highly mobile species) or larger with a reserve than without, especially for overexploited populations (Fig. 3A, B).

Fish density declines across the reserve boundary. Consequently, when fishing effort is uniformly distributed in the unprotected area, highest CPUE is attained at the reserve boundary. Catch per unit effort declines with distance from the reserve boundary to an asymptotic value. The rate of decline in CPUE increases as fish mobility is reduced (Fig. 2D). A uniform distribution of fishing effort outside of a marine reserve does not capitalize on spillover. As a result, there is a discrepancy between fish availability and local fishing intensity. Under this scheme, an excess proportion of fishing effort

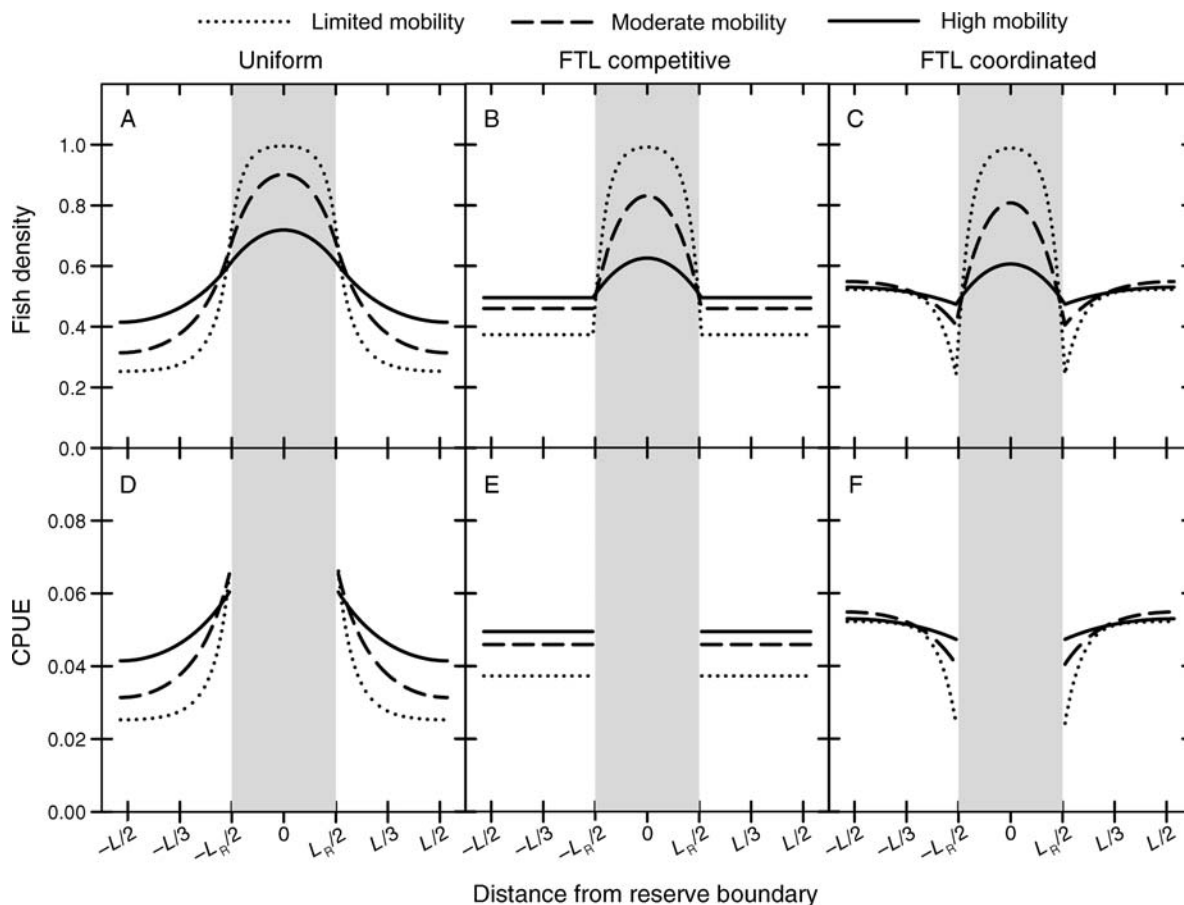


FIG. 2. Steady-state spatial patterns of fish density and catch per unit effort (CPUE) in the vicinity of a marine reserve (shaded area) with respect to three distributions of fishing effort. (A, D) Fishing effort is uniformly distributed. A harvesting strategy with a fishing-the-line (FTL) component is implemented for (B, E) a competitive fishing industry and (C, F) a coordinated fleet, respectively. Spatial patterns are similar for various gear efficiencies explored in this model; here we show results for $q = q_{MSY} = 0.1$, $r = 1$, $K = 1$, $L = 4\pi$, $L_R = L/3$, and $E = 5L$, where MSY relates to maximum sustainable yield in the absence of a reserve. In each panel, spatial patterns of fish density and CPUE are shown for three fish movement rates, $D = 0.16$ (limited), 1 (moderate), and 4 (high). See Table 1 for explanations of variables.

is invested at more distant locales where little or no catch is acquired. When spillover from the reserve is not targeted, catch is often well below C_{MSY} (Fig. 3C), except when $q > q_{MSY}$ for a limited species mobility range (Fig. 3D).

Optimal spatial allocation of fishing effort of a competitive fishing industry

In a competitive fishery, individual harvesters adjust their position to maximize CPUE. As a result, the steady-state outcome is a distribution of harvesters that equalizes CPUE (see Appendix A). For convenience we refer to this as the “optimal” distribution of fishing effort. The optimal arrangement of fishing effort near a marine-reserve boundary for a competitive industry has two components; some harvesters should concentrate their fishing effort at the reserve boundary (i.e., fish the line), while the remainder should distribute homogeneously across the remaining unprotected area (i.e., E_B

$\neq 0$ and $e_u = \text{constant}$). Those fishing the line harvest the spillover from the marine reserve, while the remaining effort exploits the production of fish in the adjacent unprotected waters.

The proportion of effort that should be allocated to fishing at the reserve boundary is dependent upon the movement dynamics of the target species. When $q = q_{MSY}$, the proportion of fishing effort for a competitive industry that should fish the line (E_B/E , herein called the optimal fish-the-line [FTL] ratio) increases with fish mobility (Fig. 4A). The proportion of effort that should be allocated to fishing at the boundary is small for less mobile species and approaches the proportion of coastline inside the reserve (i.e., $E_B/E \cong L_R/L$) as the spillover rate increases. Increasing the catchability coefficient causes a rise in the optimal FTL ratio for both limited and moderately mobile species (Fig. 4B) but does not alter the asymptotic FTL ratio seen for highly mobile species.

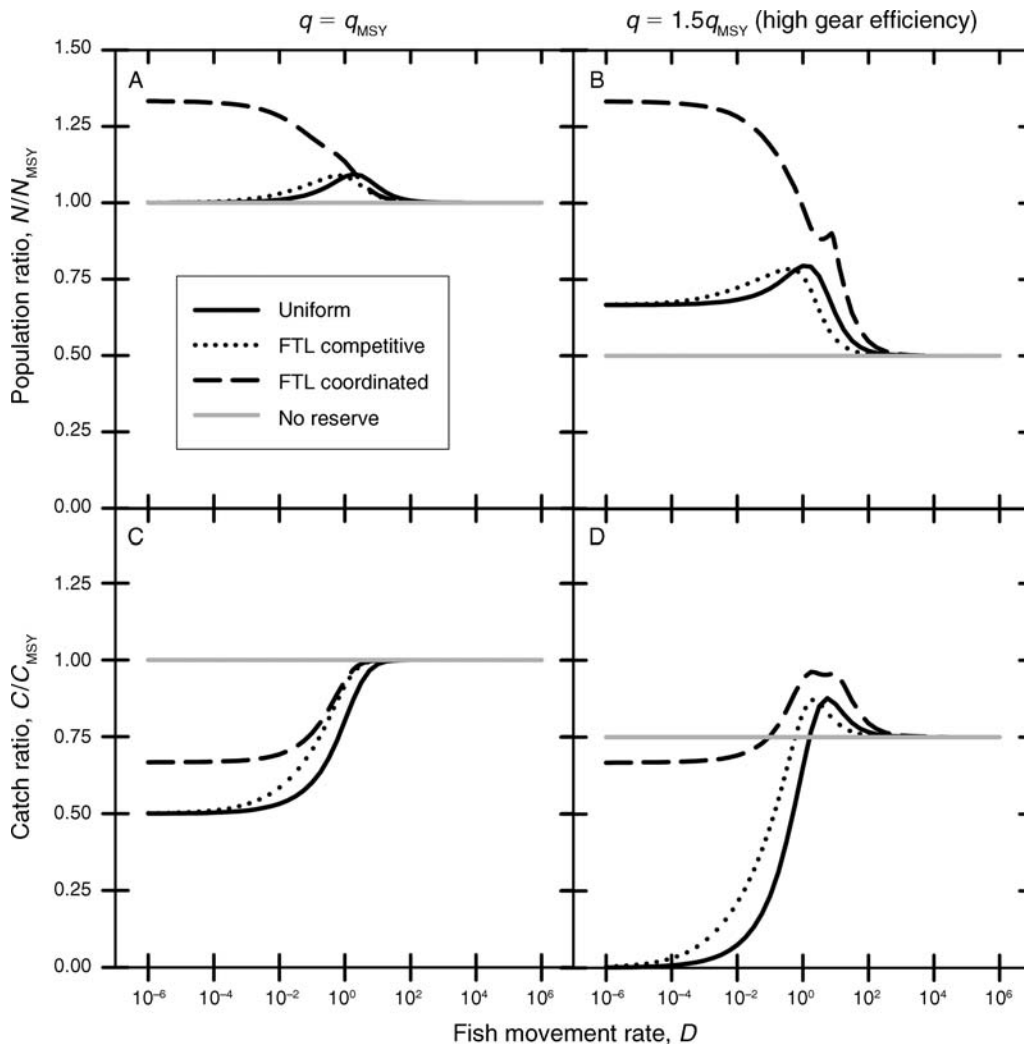


FIG. 3. The ratio of steady-state population size (N) and catch (C) to the quantities N_{MSY} and C_{MSY} (as defined in *Benchmarks* and related to maximum sustainable yield in the absence of a reserve) as a function of fishing effort, fish movement rate (D), and gear efficiency (q). FTL is fishing the line. Values of parameters r , K , L , L_R , and E are equal to those used in Fig. 2. See Table 1 for explanations of variables.

Modification of the biological parameters, reserve size, or region length does not alter these qualitative findings. The optimal arrangement of fishing effort always includes a fishing-the-line component in addition to some effort homogeneously distributed outside the reserve. Only the optimal FTL ratio changes. For example, if the cessation of fishing improves habitat quality, thereby increasing the intrinsic growth rate or carrying capacity within the protected area, more effort should be allocated to fishing at the boundary as reserve productivity rises. However, the benefit of increased productivity due to improvements in habitat quality could be counteracted by decreases in mobility. If enhanced habitat quality led to a decrease in movement of individuals inside the reserve, because food or shelter are more readily available, then the optimal FTL ratio would likely decline as the spillover rate is reduced.

The spatial pattern of fish density resulting from the two-component distribution that maximizes CPUE in a competitive fishery (Fig. 2B) is in marked contrast to the sloping pattern of density resulting from a uniform distribution of fishing effort (Fig. 2A). Predictably, fish density outside the reserve and CPUE are constant across space for a competitive industry (Fig. 2B, E).

Enhancements to total population size and catch due to reserve establishment are similar to those predicted by spatially implicit models of marine protected areas (reviewed in Gerber et al. 2003). Total population size increases for limited and moderately mobile species with smaller gains for more mobile species (Fig. 3A, B). As with spatially implicit models, reserve establishment can boost catch under a limited set of conditions for moderately mobile species (Fig. 3C, D). When fishing effort is distributed optimally, implementation of a

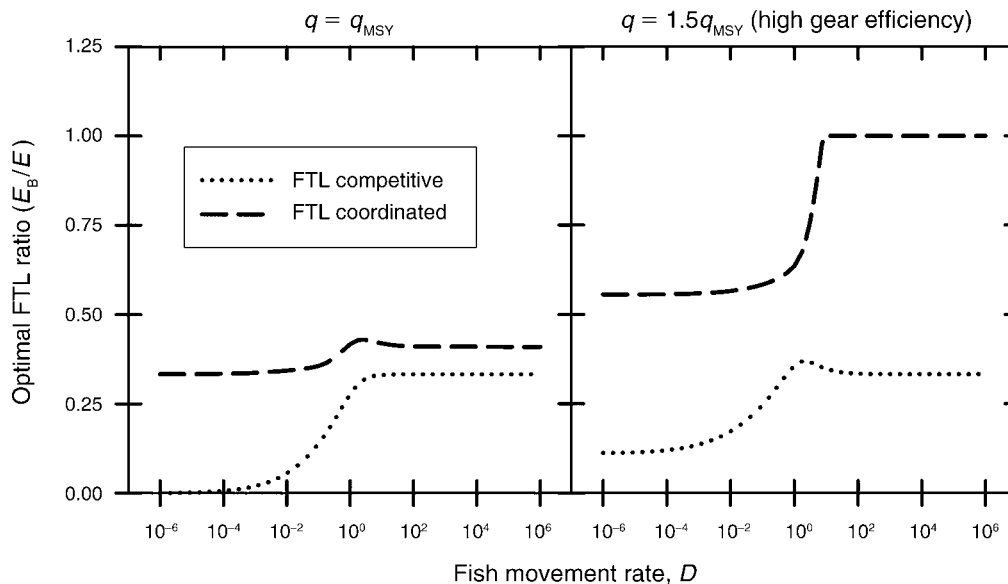


FIG. 4. Optimal fishing-the-line (FTL) ratio at steady state for a competitive fishing industry and a coordinated fleet as a function of fish movement rate (D) and gear efficiency (q). Values of parameters r , K , L , L_R , and E are equal to those used in Fig. 2. See Table 1 for explanations of variables.

reserve can result in a double payoff, simultaneously increasing total population size and catch only for a moderately mobile population that is overexploited (i.e., $q > q_{MSY}$). When part of the region is protected from fishing, catch is reduced for more static populations, whereas total population size and catch of highly transient species are less affected by reserve designation.

These model predictions are particularly important for the interpretation of empirical data in which it is common that density gradients vary continuously at and near a boundary. For example, it has been assumed that the steeper the curve and the closer to the boundary the inflection point, the slower the dispersal rate (for example see Kaunda-Arara and Rose 2004: Fig. 3). Such interpretation is challenged by distributions such as in Fig. 2B.

Optimal spatial allocation of fishing effort of a coordinated fleet

The optimal allocation of fishing effort near a marine-reserve boundary is more complex for a coordinated fleet. We have been unable to develop a general mathematical argument analogous to that in Appendix A for a competitive fishery, but intuition, supported by extensive numerical analyses, establish that there will be a fishing-the-line component. Work by Neubert (2003) suggests that when one marine reserve is established as a management tool in our model, the optimal harvesting strategy of a coordinated fleet may also include the creation of additional voluntary non-fished areas. Here, catch would be maximized by fishing the lines of multiple marine reserves (e.g., Neubert 2003: Fig. 1c–f). Because optimization of spatial fishing effort for a coordinated fleet is highly dependent upon parameter

values and the region length, we focus on presenting trends comparable to the results of the competitive industry. As such, we restrict the following analysis to a fishery containing a single marine reserve. Under this limitation, numerical investigations suggest that a binary distribution consisting of a fishing-the-line component and a uniform distribution outside the reserve may maximize collective catch for a coordinated fleet. This is not a rigorous result, and it is possible that the distribution outside the reserve may take a more complex form. However we feel confident in asserting that the optimal distribution of effort will, in general, include a fishing-the-line component. Results based on our assumed binary distribution provide conservative estimates of catch and may thus overestimate predictions of total population size, but the assumed scenario is appropriate for examining localized patterns and is a probable case as few fisheries are likely to self-impose sizeable non-fished areas in the vicinity of a management-designated marine reserve.

Numerical simulations indicate that a coordinated fleet should allocate a greater proportion of effort at the reserve boundary compared to a competitive industry (Fig. 4). The FTL ratio should increase as both the species-specific movement rate and catchability rise. With the parameters used here, the proportion of effort that should be allocated to fishing at the reserve boundary ranges from 33% to 100%. Because the minimum optimal FTL ratio (when movement rates are low) is proportional to the fraction of coastline set aside as a marine reserve ($\min E_B/E \cong L_R/L$), an effective tactic for a coordinated fleet is for all displaced effort to reallocate to the line and to move additional

effort to the boundary when targeting moderately to highly mobile species.

Applying very intense fishing effort at the reserve boundary has two benefits for a coordinated fleet, despite generating considerable variability of CPUE among individuals and across space (Fig. 2F). First, heavily fishing the line effectively exploits spillover from the marine reserve by ensuring that few fish are able to return to the reserve once they have spilled over. This high fishing mortality creates a dip in fish density at the reserve boundary (Fig. 2C). Second, the sharp density gradient at the reserve boundary amplifies the transfer rate of fish from the marine reserve to the surrounding unprotected waters. Consequently, both density and CPUE increase with distance from the protected area for fisheries exploited by a coordinated fleet.

Contrary to concerns that fishing the line could offset potential reserve benefits, heavy fishing at a reserve boundary in order to maximize collective catch often results in a larger total population size compared to effort distributions that are uniform or equalize CPUE (Fig. 3). While intensively fishing the line can cause local depletions close to the protected area, the increase of fish density, both inside the reserve and at locales less intensively exploited further away from the reserve boundary, contributes significantly to the overall standing stock (Figs. 2C and 3A, B). The contribution of stock in the fished area to the overall population increase can be considerable as fishing-the-line effort intensifies, because the “edge effect” inside the reserve becomes more pronounced (leptokurtic), while the mean density outside the reserve becomes larger (Fig. 2A–C).

As is the case when optimizing CPUE for a competitive industry, enhancements to total population size deriving from reserve establishment are greatest for species with limited and moderate mobility (Fig. 3A, B). Not surprisingly, catch is higher for a coordinated fleet compared to the other distributions of fishing effort considered here (Fig. 3C, D). Nevertheless, conditions in which catch can be increased in the presence of a marine reserve are limited to heavily exploited, moderately mobile species; otherwise catch is equivalent to maximum sustainable yield for highly mobile species and below maximum sustainable yield for less mobile species.

APPLICATION TO MULTISPECIES FISHERIES

The above analyses focus on optimizing the distribution of fishing effort for a single-species fishery. However, a marine reserve protects an ensemble of species from local fishing pressure and will simultaneously influence multiple species through direct and indirect effects (Micheli et al. 2004). Using nonspatial models, others have explored the impacts of joint harvesting of two or more species that have either noninteracting or interacting populations (e.g., through competitive or predator–prey interactions; Clark 1976, Mesterton-Gibbons 1996, Supriatna and Possingham

1998, Micheli et al. 2004). Here we explore an indirect linkage between two exploited species that are connected by the effort distribution of a common competitive industry.

Multispecies model predictions

As indicated in the previous sections, the optimal spatial allocation of fishing effort depends strongly on the movement dynamics of an individual species (e.g., Fig. 4). Therefore, fishing effort cannot simultaneously be distributed optimally for species with different mobility rates. As such, fishing-the-line behavior is likely to have different impacts on coexisting species in the fishery. We now explore the consequences of basing the spatial distribution of fishing effort for a multispecies fishery upon the optimality of one species.

Obviously in mixed-species fisheries, abundance, biomass, and value are important considerations for determining catch patterns, but often fish movements alone can drive the fishery effort distribution (fisher behavior) near marine-reserve boundaries. Because the spillover rate is the flux across the reserve boundary, it should depend on both the abundance of a species and the mobility of individuals. As a result, if the abundances of two species are roughly equivalent, the most mobile species in a mixed-species fishery should differentially affect the spatial allocation of fishing effort in the vicinity of a marine reserve barring significant differences in the value of the fish species. Given this logical argument, we examine the effects on a less mobile species when the fishing effort distribution is predicated on a more mobile species. When competitive multispecies fisheries prioritize catch of a highly mobile species, the distribution of fishing effort will be suboptimal for a less mobile species. Although the density and CPUE of the more mobile species is homogenized outside the reserve, species with more limited mobility exhibit dips in their density and CPUE close to the reserve boundary. This localized depletion of slower species is sustained by excess fishing effort attracted to exploit the higher spillover of the more mobile species from the reserve (Fig. 5A, B). While CPUE of the most mobile species is equalized among independent participants, combined (multispecies) CPUE is spatially and individually variable, with harvesters located further from the boundary gaining higher returns (Fig. 6). As such, harvester distributions directed towards equalizing combined CPUE should be based upon the mobility rates of all targeted species. For example, combined CPUE variability across space (and therefore across individuals) is much lower when the fishing effort distribution is an average of the optimal FTL ratio for the slower and faster species ($CPUE\ SD = 0.749 \times 10^{-3}$) as opposed to distributions that are maximized for just one of these species ($CPUE\ SD = 3.54 \times 10^{-3}$ and $SD = 4.13 \times 10^{-3}$ for fishing effort distributions based on the less and more mobile species, respectively). In view of this, the optimal FTL ratio for a multispecies fishery will

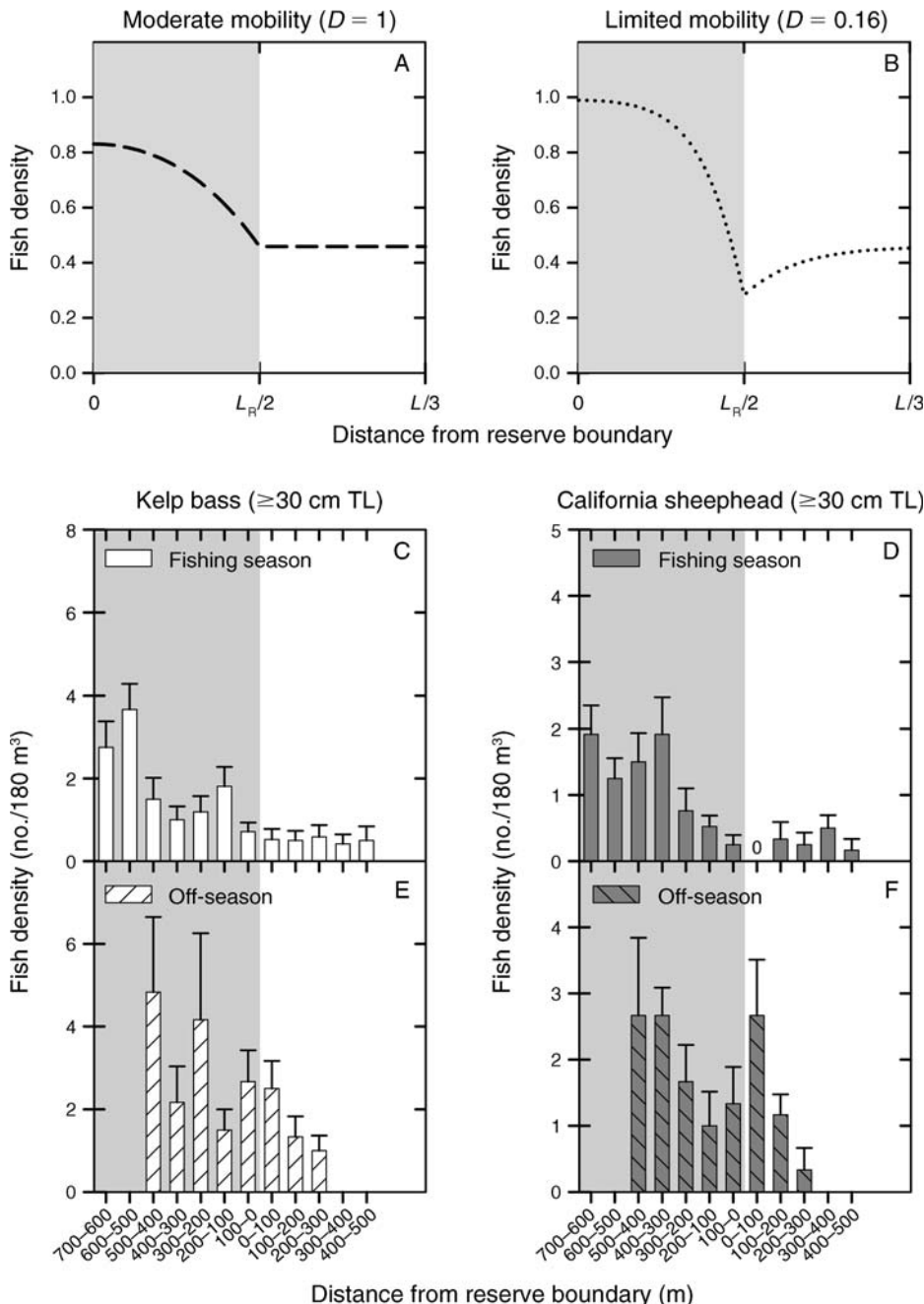


FIG. 5. (A, B) Model predictions of multispecies fish distributions at steady state based upon the optimal fishing-the-line (FTL) ratio of the moderately mobile species for a competitive fishing industry. The system depicted in the model is symmetrical about the reserve midpoint; therefore we show spatial patterns for one-half of the region where the shaded area represents density predictions inside the reserve. Values of parameters are equal to those used in Fig. 2. (C–F) Densities (mean + SE) of harvestable kelp bass (*Paralabrax clathratus*) and California sheephead (*Semicossyphus pulcher*) (TL, total length) from replicate transects with respect to distance from the reserve boundary of the Catalina Marine Science Center Marine Life Refuge in southern California, surveyed during fall 2001 (fishing season) and winter 2002 (off-season). Mean fish densities are shown for 12 100-m sections during the fishing season (seven within [shaded] and five outside the reserve boundary) and eight 100-m sections during the off-season (five within and three outside the reserve). See Appendix B for methodology.

lie between the FTL ratio of the slowest species and the most mobile species. As a result, the greater the disparity in movement rates between species caught in a multispecies fishery, the more likely that the less mobile

species will show dips in density at the reserve boundary. Although these analyses have held K constant across species and explored the isolated consequences of differences in movement rates, large differences among

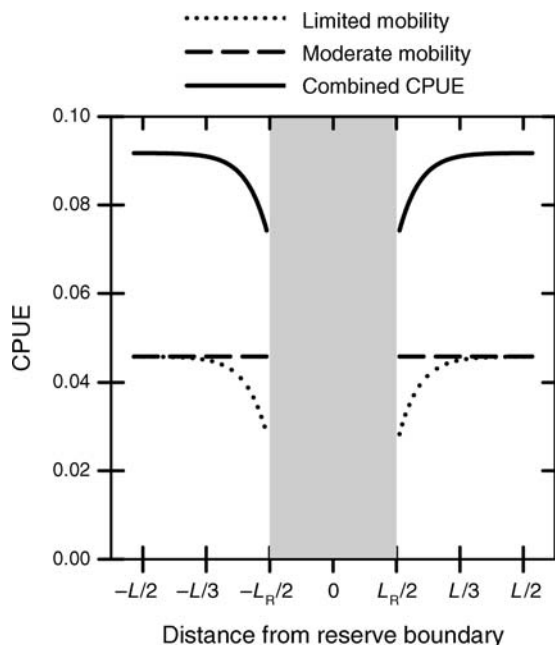


FIG. 6. Spatial patterns of multispecies catch per unit effort (CPUE) at steady state in the vicinity of a marine reserve (shaded area) based upon the optimal fishing-the-line (FTL) ratio of the moderately mobile species for a competitive fishery. This figure is a counterpart to Fig. 5A and B with parameter values $q = q_{MSY}$, $E_B/E = 0.279$, $D = 0.16$ (limited mobility), and $D = 1$ (moderate mobility). The solid line represents the sum of the dotted and dashed lines, such that $CPUE(\text{combined}) = CPUE(D = 0.16) + CPUE(D = 1)$. See Table 1 for explanations of variables.

species in their density inside the reserve (i.e., as a result of higher K) should generate similar disparities in rates of spillover. Therefore, multispecies fisheries may generate predictable spatial patterns with less mobile, less abundant species showing persistent dips in density just outside the reserve boundary.

Linking fish density and fishing effort: an analysis of empirical patterns and model predictions across a temperate marine-reserve boundary

Numerous studies have explored how different species respond differentially to marine reserves (Halpern et al. 2004, Micheli et al. 2004, Gaylord et al. 2005). Much of the focus has considered the roles of species interactions and the history of fishing prior to reserve establishment. The above theoretical model suggests that species may also differ predictably in their spatial distribution within and near marine reserves. Few empirical studies have documented the spatial distribution of multiple fished species inside and out of marine reserves (Rakitin and Kramer 1996, Chapman and Kramer 1999, Tupper and Rudd 2002, Kaunda-Arara and Rose 2004, Abesamis et al. 2006) at spatial scales that are relevant to fish movement (e.g., see discussions in Kramer and Chapman 1999 and Palumbi 2004). Moreover, none of these studies examines how the spatial pattern evolves when fishing is

present vs. absent. In this section we present a case study of fish densities along a spatial gradient during fishing and non-fishing seasons to illustrate how fishing effort distributions may substantially alter density gradient patterns, as suggested by the modeling section.

The empirical study investigating two fishery species at the Catalina Marine Science Center Marine Life Refuge (CMLR), California, USA, by I. Tetreault is well suited to examine model predictions. Densities of kelp bass (*Paralabrax clathratus*) and California sheephead (*Semicossyphus pulcher*) were measured using visual underwater techniques across the southeastern boundary of CMLR (see Appendix B for detailed methods and results). Established as a no-take MPA in 1988, CMLR encompasses 0.13 km² and is located off the northwest coast of Santa Catalina Island in southern California. The reserve's southeastern boundary (Blue Cavern) bisects a region of preferred habitat: rock substratum and giant kelp (*Macrocystis pyrifera*) (see Lowe et al. [2003]: Fig. 5 for habitat map). Acoustic tracking and tagging studies of sheephead both within and outside of the CMLR indicate that this species crosses the marine-reserve boundary (Topping et al. 2005: Fig. 2C; I. Tetreault, *unpublished data*). Furthermore, fishing-the-line behavior has been observed near this CMLR boundary. For example, during the summer and fall of 2002, 56% of the sampled fishing effort within 1000 m of the reserve occurred within the first 200 m ($n = 25$ anglers; I. Tetreault, *personal observation*). Finally, kelp bass and California sheephead commonly co-occur in southern California kelp forests, possess traits that predict different relative mobility, and have important fisheries. As such, we expect these species to be differentially impacted by the no-take marine reserve on Catalina Island.

Three lines of evidence suggest that kelp bass may have a greater impact on the FTL ratio than California sheephead. First, kelp bass are more abundant than sheephead both inside and outside the reserve (roughly twice as abundant). Second, regional landings show that roughly four times as many kelp bass are caught as sheephead (Appendix C). Part of this difference is likely due to their higher abundance, but these patterns also suggest kelp bass have a higher catchability (q) for the same fishing effort. Third, although direct comparisons of mobility of these two species are rare, and some results are inconsistent, it appears that kelp bass are more likely to make long-distance movements and home range relocations than California sheephead. Both species exhibit site fidelity (Johnson et al. 1994, Lowe et al. 2003, Topping et al. 2005). The direct comparison by Johnson et al. (1994) suggests that California sheephead exhibit greater site fidelity than kelp bass. In contrast, Lowe et al. (2003) and Topping et al. (2005) reported larger home range sizes for California sheephead than for kelp bass. However, Lowe et al. (2003) and others (Collyer and Young 1953, Limbaugh 1955, Young 1963, Quast 1968, Love 1996) report that kelp

bass are much more likely to make directed long-range movements with home range relocations (e.g., 20% moved >1 km, up to 450 km) that will certainly lead to crossing reserve boundaries. Because the majority of kelp bass and California sheephead tagged by Lowe et al. (2003) and Topping et al. (2005) remained within the CMLR reserve boundaries, these longer distance movements by kelp bass may be a more important indication of spillover and susceptibility to fishing mortality. Studies detailed here and others for California sheephead show little long-distance movement (Davis and Anderson 1989) and a high rate of recapture at the tagging site (71%; see DeMartini et al. 1994). (See Appendix D for a more detailed summary of movement studies on these species.) One potential driver for differences in movement may be diet. Kelp bass are piscivorous (a secondary carnivore), with greater resource requirements than California sheephead (a primary carnivore), and thus kelp bass are more likely to leave a crowded or resource-limited environment and establish a new home range than California sheephead.

The density gradient study of kelp bass and sheephead by I. Tetreault lends itself to a unique analysis, because fishing effort near the CMLR has a strong seasonal component, which may help us gain a better understanding of fish mobility and the impacts of fishing behavior. In the context of our model, this fishery represents a competitive fishery, because individuals operate independently. Harvesting of kelp bass and California sheephead consists mainly of recreational angling and also a nominal commercial live-trap fishery for California sheephead. Kelp bass are more likely to be targeted, because they are the more abundant species and highly sought after by fishermen (Love 1996). The area around the CMLR is a popular recreational destination in the summer. Landings of these two common nearshore game species in the vicinity of Santa Catalina Island are highest in spring and summer. In 2001, 70% of kelp bass recreational landings were caught from May through August, while landings of commercial and recreational California sheephead had a less defined peak from March through September (Appendix C). Thus, any effects of fishing would be most evident in fall at the end of the intense fishing period.

A comparison of temporal and spatial patterns of kelp bass and California sheephead densities *inside and outside* the CMLR suggests that fishing is impacting this system. Mean densities of legal-sized kelp bass and California sheephead were depressed near the CMLR boundary in fall 2001, shortly after the peak fishing season (Fig. 5C, D). If the low densities outside the reserve were due simply to habitat differences, then a similar density pattern would be expected during the off-fishing season (winter 2002). However, the mean densities of both species shift substantially when fishing declines (Fig. 5E, F). There is a significant interaction between the effects of reserve and fishing ($df = 1, 435, F = 4.236, P = 0.040$, see Appendix B: Fig. B2). Moreover,

fish were significantly more abundant inside than outside the CMLR at the end of the peak fishing season ($df = 1, 435, F = 45.160, P < 0.001$), but there were no significant differences in abundance inside vs. outside the reserve during the off-fishing season ($df = 1, 435, F = 1.536, P = 0.216$).

The temporal and spatial patterns of California sheephead densities *outside* the reserve suggest that fishing the line is also operating in this system. At the end of the fishing season there was a complete absence of legal-sized California sheephead within the first 100-m section outside the CMLR (Fig. 5). Densities differed significantly among the five 100-m sections outside the CMLR ($df = 4, 58, F = 2.558, P = 0.048$), with mean fish density significantly lower in the 100 m adjacent to the reserve boundary than in the four more distant sample regions ($df = 1, 58, F = 5.666, P = 0.021$). Using only these data from the peak fishing season, there is no way to separate the contributions of fishing the line from spatial variation in sheephead habitat as a source of these density patterns. However, the greatest rebound in sheephead density during the off-season occurred immediately adjacent to the reserve (from 0 to 2.67 ± 0.84 per 180 m^3). Since sheephead densities were near their peak just outside the reserve when fishing was reduced, poor quality habitat is unlikely to be a major cause of the absence of sheephead near the reserve boundary when fishing is more intense. Rather, a causal role for fishing the line is supported by the temporal changes in fish density immediately outside the marine reserve.

Comparison of these empirical data to the spatial patterns that arise in the multispecies fishery model are consistent with the prediction that fishing effort in the vicinity of CMLR is allocated primarily to spatially homogenize CPUE of kelp bass. Densities of kelp bass outside the marine reserve shortly after the fishing season (fall 2001) is relatively uniform compared to the dip at the reserve boundary observed in sheephead. This prediction that kelp bass play a disproportionate role in setting spatial patterns of fishing intensity is further supported by the facts that kelp bass are nearly twice as abundant as sheephead near CMLR and regionally recreational and commercial landings of kelp bass (214280 Mg [where 1 Mg = 1 metric ton]) were almost four times that of California sheephead in 2001 (53955 Mg; see Appendix C). Additionally, the spatial density pattern shortly after the peak summer fishing season suggests an edge effect for both species within the CMLR. The zone of depressed fish densities within the reserve extends 500 m for kelp bass vs. only 300 m for California sheephead. These density patterns within the CMLR in combination with the theoretical model predictions infer that the catchable flux of kelp bass across the southeastern reserve boundary is greater than that of California sheephead.

DISCUSSION

Using a spatially explicit model, we have shown that the optimal distribution of fishing effort near marine-

reserve boundaries is likely to include a strong fishing-the-line component irrespective of the harvester strategy (coordinated, competitive, and multispecies). When fishing effort in a multispecies fishery is allocated to maximize CPUE of the more mobile species, the intensity of effort located near the reserve boundary can generate sharp depressions of density for less mobile species. This was demonstrated as a likely mechanism driving the spatial patterns of kelp bass and California sheephead across the boundary of a protected area in southern California and is one example of the compromises that are likely to occur when we look beyond single-species responses to marine-reserve establishment.

Literally hundreds of studies address the effects of marine reserves by comparing patterns inside the reserve with those outside in comparable habitat (Halpern 2003, Willis et al. 2003). The vast majority of these studies compares a small number of random quadrats or transects inside vs. outside the reserve, without specific consideration of the location of the sampling points relative to the boundary of the reserve. Our model results suggest that such spatially vague sampling may have unexpectedly large effects on the magnitude of measured reserve impacts. The effect size in a reserve evaluation should vary predictably with sample location. For all but the most sedentary species, comparisons of sites outside the reserve with sites inside but close to the boundary of the reserve should suggest smaller reserve benefits than comparisons done with reserve sites sampled toward the center of the reserve. Moreover, the magnitude of this difference should vary predictably among species based upon their scales of movement. If the model is capturing the critical spatial dynamics, the locations of sites within the reserve are especially critical, since densities outside should be more homogenized. To illustrate the potential consequences of ignoring sampling location, consider the spatial data from Catalina. Considering all sample locations, the densities inside the reserve were three (kelp bass) to five (California sheephead) times as high inside the reserve as outside. These values are consistent with typical aggregate species patterns found in Halpern's (2003) synthesis. Without such spatially extensive sampling, however, the ratio of densities inside vs. outside could have varied enormously. Considering the variation in densities within the reserve in the observed sampling, the ratios could have been as large as 30 (both species) or as small as 0.15, depending on where sample transects were sited. The reserve effect size varies by two orders of magnitude, depending upon where density was measured (especially inside the reserve). The scale of species' movement rates and the scale of the fishery are both likely to play large roles in this variation, and their impacts warrant far more attention.

Studies that explicitly examine spatial gradients in abundance across reserves and adjacent areas are extremely limited (reviewed in Kellner 2004; see also Murawski et al. 2004, 2005, Goñi et al. 2006). In addition, nearly all studies with spatially explicit data

sample at a scale that is coarse relative to the scales of fish movement. In the empirical data presented here, sampling resolution was on the order of hundreds of meters, corresponding to the reported short-term linear distances traveled by kelp bass and sheephead (Lowe et al. 2003, Topping et al. 2005). These empirical data were not collected as a test of the model predictions. Nonetheless, the patterns are qualitatively consistent with several key model predictions (e.g., gradients in abundance inside the reserve near the boundary, "halo" effect with very low abundance outside the reserve for one species, greater homogeneity of fish abundance outside the reserve than inside). Moreover, all of these patterns disappear seasonally when fishing intensity drops, suggesting a strong causal role for fishing. Some of these spatial features of abundance can also be seen in the work of Murawski et al. (2004, 2005) and Goñi et al. (2006) across larger spatial scales for more highly mobile species. For example, Goñi et al. (2006) found that CPUE of spiny lobster near a western Mediterranean marine reserve declined with distance from the reserve center, exhibited a depression at the boundary, and plateaued outside the reserve. The dip in density adjacent to the reserve boundary was attributed to intense fishing-the-line behavior: 75% of fishing sets were deployed within 1 km of the marine protected area. Murawski et al. (2004, 2005) found that haddock, yellowtail flounder, and winter flounder had increased abundances within reserves and significantly decreasing densities as a function of distance from closed areas in New England waters off the northeastern United States. The majority of catches for these species were concentrated within 10 km of reserve boundaries. In contrast, witch flounder, white hake, and monkfish catches exhibited positive density-distance catch relationships away from reserve boundaries, a pattern that may be attributable to depth preferences of these deepwater species. The diverse spatial patterns observed in these two locales highlight the need to distinguish the effects of spatial variation in habitat from spatial variation in fishing intensity to interpret the multispecies patterns associated with marine reserves.

Collectively, these findings suggest that the spatial distribution of fishing effort can have a dramatic impact on total population size, catch, and the density of fish inside and near a marine reserve. The spatial distribution of fishing effort warrants as much attention in marine-reserve design as more commonly considered issues such as habitat representation, connectivity, ontogenetic habitat shifts, and density-dependent population regulation (Sánchez Lizaso et al. 2000, Malakoff 2002, Sala et al. 2002, Roberts et al. 2003, Shanks et al. 2003, Kellner 2004, Gerber et al. 2005).

The ad hoc assumption of empirical studies is often that fish density will be highest inside the reserve and decline with distance from the reserve edge. However, this view arises from only considering part of the biological response: spillover of fish. The other biolog-

ical response is by humans and their redistribution of fishing effort. Spatial discontinuities, such as fishing the line, may play a critical role in marine-reserve effectiveness and therefore need to be more accurately accounted for in both empirical and theoretical MPA design and evaluation. Further investigations of fishing the line would benefit from a more comprehensive representation of socioeconomic factors that drive fisher behavior. Here we focused on fisher dynamics that are driven by differences in species movement rates, but one could also ask how differences in the relative value of targeted species in a multispecies fishery might influence the optimal fishing intensity near a marine-reserve boundary. Additionally, future studies of fishing-the-line behavior should explore how social and physical interactions among fishermen alter reserve impacts, e.g., when crowding of boats around reserve boundaries or limited anchorages constrain fishermen from spatially optimizing their effort distribution.

The model results are generally robust to changes in parameter values; however, there is an important caveat to this conclusion. We developed the models with several conservative assumptions that focused on the role of adult movement but ignored other features of reserves that likely enhance total population size and catch. For example, we assume that protection from fishing does not enhance habitat quality such as shelter or food availability by restricting destructive fishing practices. Such enhancements could increase the carrying capacity or the productivity of individuals inside the reserve. In addition, we assume that per capita fecundity remains constant, despite the repeated observation that stock buildup within a reserve typically includes much larger, more fecund individuals (Halpern 2003). Other models that focus on this reserve enhancement of production have shown that larval dynamics will also play an important role in marine-reserve effectiveness and the spatial distribution of fish beyond reserve boundaries (Botsford et al. 2001, Lockwood et al. 2002, Gaines et al. 2003, Gaylord et al. 2005).

Discussion of the "spillover effect" in the marine-reserve literature is often isolated from that of the larval export or recruitment effect (Russ 2002, Gaines et al. 2003, Gaylord et al. 2005). The results of this study make it clear that we need a more integrated approach to modeling reserve impacts. First, fishing the line can reduce stocks inside the marine reserve ("edge effect") even for species with limited adult mobility (Fig. 2), which in turn will affect the ability of the reserve stock to seed areas outside of its boundaries. Second, emerging evidence on the scales of larval dispersal (Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2003, Kinlan and Gaines 2003, Shanks et al. 2003, Palumbi 2004, Kinlan et al. 2005) suggest we cannot separate the two components of individual movement (larvae vs. adults) spatially. Given that both larval and adult dispersal play important and likely nonindependent roles in setting the impact of reserves on fisheries, the time is ripe for

modeling and empirical efforts to examine their interactions.

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APPENDIX A

An analysis of the optimal distribution of individual effort in a competitive fishery (*Ecological Archives* A017-037-A1).

APPENDIX B

A description of the empirical study of fish densities across a no-take marine-reserve boundary (*Ecological Archives* A017-037-A2).

APPENDIX C

A table of recreational and commercial landings for kelp bass and California sheephead near Catalina Island, California, USA, in 2001 (*Ecological Archives* A017-037-A3).

APPENDIX D

A review of research investigating movement patterns of kelp bass and California sheephead (*Ecological Archives* A017-037-A4).