

Marine protected areas and the value of spatially optimized fishery management

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There is a growing focus around the world on marine spatial planning, including spatial fisheries management. Some spatial management approaches are quite blunt, as when marine protected areas (MPAs) are established to restrict fishing in specific locations. Other management tools, such as zoning or spatial user rights, will affect the distribution of fishing effort in a more nuanced manner. Considerable research has focused on the ability of MPAs to increase fishery returns, but the potential for the broader class of spatial management approaches to outperform MPAs has received far less attention. We use bioeconomic models of seven nearshore fisheries in Southern California to explore the value of optimized spatial management in which the distribution of fishing is chosen to maximize profits. We show that fully optimized spatial management can substantially increase fishery profits relative to optimal nonspatial management but that the magnitude of this increase depends on characteristics of the fishing fleet and target species. Strategically placed MPAs can also increase profits substantially compared with nonspatial management, particularly if fishing costs are low, although profit increases available through optimal MPA-based management are roughly half those from fully optimized spatial management. However, if the same total area is protected by randomly placing MPAs, starkly contrasting results emerge: most random MPA designs reduce expected profits. The high value of spatial management estimated here supports continued interest in spatially explicit fisheries regulations but emphasizes that predicted increases in profits can only be achieved if the fishery is well understood and the regulations are strategically designed.

ecological modeling | reserve network design | spatial ecology

Spatially explicit fisheries management has garnered considerable attention in recent years, and this trend is likely to increase as more focus is placed on marine spatial planning (1, 2). Some forms of spatial management simply prohibit fishing in certain locations, using tools such as no-take marine protected areas (MPAs). In other cases, regulations may have a more nuanced effect on the spatial pattern of fishing. Examples of these more flexible approaches include spatial zoning of fleet access (3), spatially localized gear restrictions (4, 5), and spatially explicit catch quotas (6). In addition to regulation-based approaches, spatial user rights can also affect the distribution of fishing effort (7). These varied tools have all been suggested to improve fisheries outcomes by changing the spatial pattern of harvesting. Such spatial management can take advantage of heterogeneity in the seascape by protecting populations that are key sources of larvae (8) or by tuning harvest regulations in response to local life-history parameters (9).

Spatial management is not without its challenges. Spatial approaches often require or at least benefit from spatially explicit data about the environment, biology, and fishery (e.g., ref. 10). Furthermore, fishermen often oppose limits on where they can fish (11, 12), and it may be more difficult or costly to enforce spatially complex regulations. Faced with these hurdles, it is important to assess the value of spatially explicit management of marine systems and to determine under what conditions it is advantageous to pursue such management. Knowledge of the

potential gains will indicate whether resources should be devoted toward these approaches. In cases where expected gains in profit or yield are substantial, this information may also reduce social resistance to new regulations.

A number of recent theoretical studies have looked at the potential for MPAs to increase fishery yields or profits (13–15), but these have focused on no-take MPAs and give us little indication of how a more flexible form of spatial management would impact profitability. A few studies have addressed the generalized form of spatial management in which effort levels in each location can be set to maximize total profits. However, they have focused on determining whether MPAs are part of the optimal fishing distribution (e.g., refs. 16 and 17) and have not quantified the value of this approach, much less its value relative to simpler forms of spatial management. Costello and Kaffine (18) explore the role of MPAs in a spatial property rights fishery and show that MPAs increase total profits if fishing outside of the MPAs is not coordinated but decrease profits if fishing is cooperative.

Thus, previous work has left several important questions unanswered: Can optimal spatial fisheries management, in which fishing pressure is regulated at a fine spatial scale, increase profits substantially compared with nonspatial management? How do these increases depend on the biological and economic characteristics of a fishery? In addition, can a strategically designed MPA network capture most of the benefits available from more complex spatial management?

Here we develop a bioeconomic model uniquely suited for addressing these open questions. This spatially explicit model represents seven fisheries in southern California that span a range of life-history characteristics (*Methods*). The model benefits from the unusually high-quality spatial data available in Southern California. Comprehensive maps of the seafloor allow us to accurately describe the distribution of habitat for each species, and sophisticated models of ocean currents provide the most detailed estimates of point-to-point dispersal probabilities ever produced (Fig. 1). A modeling approach to our questions is necessary for two reasons. First, although the conservation benefits of spatial fishery management can be studied empirically (19, 20), the effect of such management on fishery yields or profits has proven harder to measure directly, particularly at the larger scales relevant to most fisheries (21, 22). Second, fully optimized spatial management of the type considered here is an experiment that has not yet been implemented in any fishery to our knowledge.

We use the model to estimate the maximum fishery profit that could be obtained under management scenarios that span a range of spatial complexity: (i) “nonspatial management,” in which a manager can set the total amount of effort but has no control over how that effort is spatially allocated, (ii) “fully optimized spatial management,” in which a manager can set the fishing effort applied in each location, (iii) “strategic MPA-based

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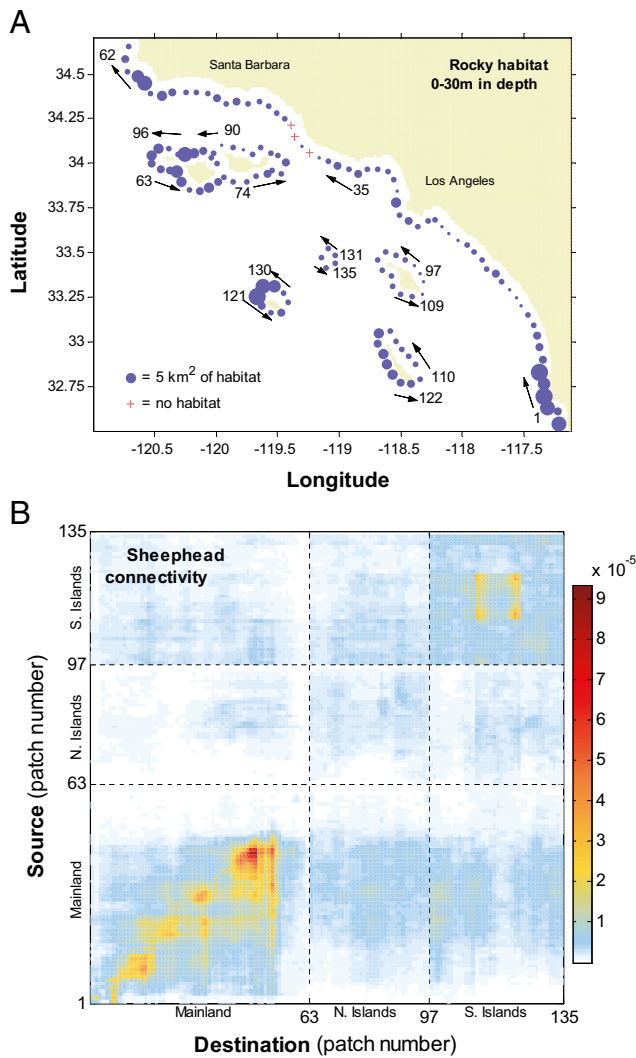


Fig. 1. (A) Map of the Southern California region, with circle sizes representing the amount of sheephead habitat in each patch, and numbers and arrows indicating patch indexing. (B) Example connectivity matrix for sheephead showing the relative probability of larval transport from each source patch to each potential destination. Indexing for the connectivity matrix follows the patch numbers in A.

management,” in which a manager can set total effort and designate some locations as no-take MPAs but cannot control how fishing outside of MPAs is distributed, and (iv) “nonstrategic MPA-based management,” in which a manager starts with arbitrarily placed MPAs and then optimizes the total effort outside to maximize profits. Within the limits of each management scenario, we optimize the fishing regulations to maximize total profits. By comparing the best outcome that is possible using each of these approaches, we illustrate how the choice of management system affects the potential value of the fishery. We highlight the value of fully optimized spatial management, which represents the extreme end of a spectrum of complexity of spatial management and thus indicates the upper bound of returns possible with these approaches. We also identify scenarios in which MPAs are likely to realize a large fraction of this value, as well as cases in which MPAs are likely to be ineffective or even reduce fishery profits.

Results

Value of Spatial Management. We used our bioeconomic models to estimate the maximum profit attainable under each management

scenario for seven species over a range of assumptions about the strength of density dependence (expressed as the compensation ratio, CR) and the cost per unit effort of fishing (denoted θ). The value of spatial management, calculated as the percentage by which the value of fully optimized spatial management (scenario 2) exceeds the value under optimal nonspatial management (scenario 1), is generally high but varies across the seven species considered here. If the population is sensitive to harvest (small CR) and fishing costs are low (small θ), spatial management can increase fishery profits between 14% and 81% relative to nonspatial management (CR = 4, $\theta = 0.01$; Fig. 2A). However, if the population is robust to harvest or expensive to fish, the value of spatial management is typically considerably lower (Fig. 2B and C and Fig. S1).

We find that in some cases strategic management with MPAs also increases profits substantially relative to nonspatial management. If the population is sensitive to harvest and fishing costs are low, strategically placed MPAs can increase profits between 8% and 52% relative to optimal nonspatial management (CR = 4, $\theta = 0.01$; Fig. 2D). As with full spatial management, however, this value is lower if the target species is robust to fishing or fishing costs are high (Fig. 2E and F and Fig. S1).

For each species and parameter set, fully optimized spatial management outperforms MPA-based management, as would be expected given that any fishing distribution created by the latter system is also possible under the former (Fig. 3). Fully optimized management can improve profits by 8–15% even in scenarios whereby MPA-based management has no effect (as evidenced by

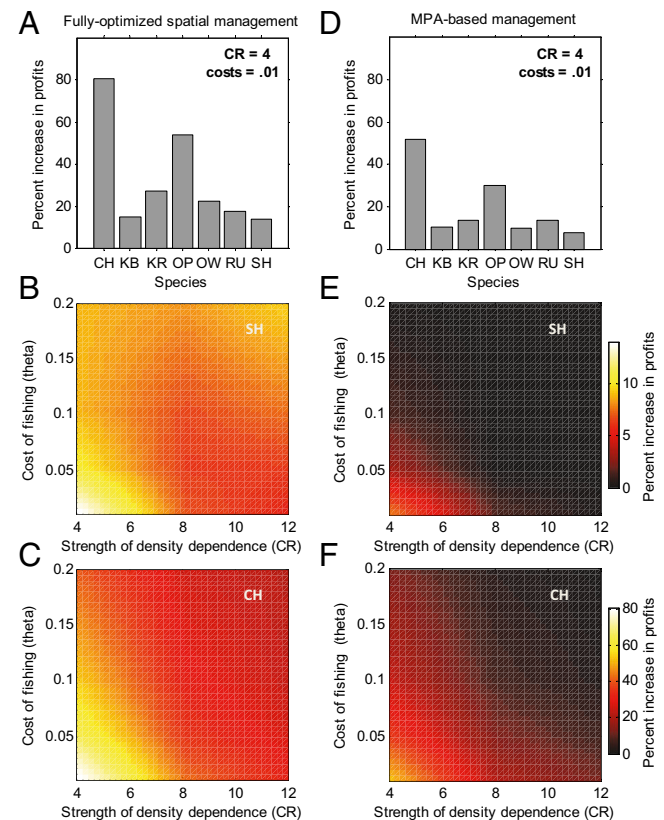


Fig. 2. (A–C) Value of fully optimized spatial management relative to optimal nonspatial management for (A) all seven species when CR = 4, $\theta = 0.01$ (species abbreviations in Table 1); (B) sheephead over a range of density dependence and cost values; (C) California halibut over a range of density dependence and cost values. (D–F) Value of strategic MPA-based management relative to optimal nonspatial management for (D) all seven species when CR = 4, $\theta = 0.01$; (E) sheephead over a range of density dependence and costs; (F) California halibut over a range of density dependence and costs.

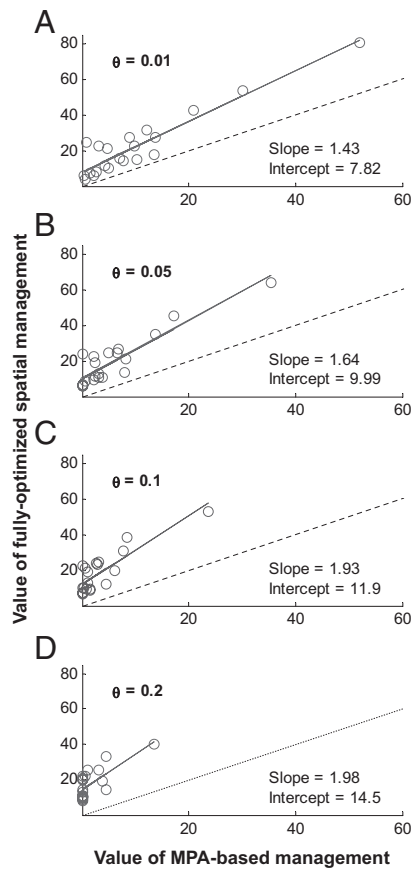


Fig. 3. Correlations between the value of strategic MPA-based management and the value of fully optimized spatial management for all seven species, with CR values of 4, 8, and 12 and (A) low cost of fishing ($\theta = 0.01$), (B) moderate cost of fishing ($\theta = 0.05$), (C) high cost of fishing ($\theta = 0.1$), and (D) very high cost of fishing ($\theta = 0.2$).

the intercepts in the linear relationships in Fig. 3). In cases in which MPAs do increase profits, fully optimized spatial management further increases profits an additional 43–98% (shown by the slopes in Fig. 3). The linear relationship between the values of the two management approaches holds across species and assumptions about density dependence but is sensitive to the cost of fishing. If fishing costs are low, optimal MPA-based management can achieve up to 70% of the results possible with fully optimized spatial management, but if fishing costs are high MPAs capture a smaller fraction of that maximum value.

Patterns of Fishing Under Alternative Management Approaches. Although optimized MPA-based management can be seen as a simplified form of fully optimized spatial management, very different patterns of fishing are obtained under the two approaches. For example, for sheephead (CR = 4, $\theta = 0.01$; Figs. S2 and S3), the correlation between the amount of effort in each patch under the two approaches is only 0.69. Fewer patches are fished under MPA-based management, but fishing in open patches may be quite intense, ranging up to 0.6, a level of effort that removes 45% of the fish within that patch in a year (Fig. S3A). Under full spatial management, by contrast, fewer patches are closed to fishing, and fishing effort is relatively modest everywhere, with an effort of less than 0.45 in even the most intensely fished patch (equivalent to removing 35% of the fish in that patch in a year). The fact that more fishing is required under MPA-based management likely explains why MPAs are less useful when fishing is expensive; increases in yields due to MPAs are offset by the high costs of fishing a few locations intensely.

These patterns are consistent across species and scenarios, with correlations between fishing effort under the two management approaches ranging from 0.12 to 0.91 (Table S1). In each case the amount of habitat that is unfished and the effort in the most intensely fished location are both higher under MPA-based management (Figs. S3–S5).

Contrasting Effects of Strategic and Random MPA Placement. Although MPAs have considerable potential to increase fishery profit, this is only true if they are strategically placed to take advantage of spatial heterogeneity in habitat and larval dispersal. By contrast, if MPAs are placed randomly such increases are not possible. This is true even if the area of habitat protected by the random MPA scenarios is the same as that protected by the equivalent strategically designed MPA network. In fact, the vast majority of random MPA networks reduce fishery profits relative to optimal nonspatial management (e.g., Fig. 4A). In almost every case the expected value of the fishery with randomly placed MPAs is lower than it would be under nonspatial management (Table 1). The one exception in our results is halibut, with weak density dependence and low fishing costs. The potential for spatial management to improve halibut yields is so great that even random MPAs can increase profits, but at a rate much lower than achieved with strategically placed MPAs (Fig. 4B). Between the poles of random and optimal MPA placement there is a range of intermediate network designs with strategic but imperfect MPA placement. When some MPAs are selected from the optimal network and the rest are randomly placed, we found that typically greater than 50% of MPAs had to be drawn from the optimal network before these intermediate networks outperform nonspatial management (Table 1).

Discussion

We demonstrate that fully optimized spatial management has great potential to increase nearshore fishery profits relative to those obtained with nonspatial management, with the magnitude of these increases varying across species. The most dramatic outlier was California halibut, for which spatial management was almost twice as valuable as for any other species. Halibut likely stands out because it was the only soft bottom species modeled; its habitat is relatively broadly distributed throughout southern California, providing more opportunity for spatial management to protect source populations than is possible with a more patchily distributed species. Additional variation across species results from differences in basic life-history characteristics such as growth, spawning season, and pelagic larval duration. Despite variability across species, we observe very strong concordance between the increase in profits from fully optimized spatial

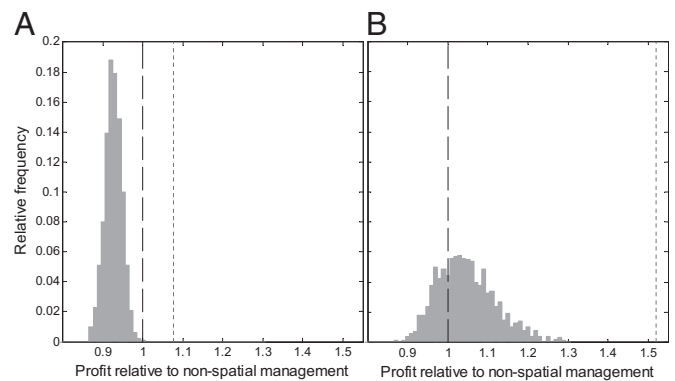


Fig. 4. Maximum profit available when randomly generated MPA networks are imposed relative to optimal nonspatial management for (A) sheephead (CR = 4 and $\theta = 0.01$) and (B) halibut (CR = 4 and $\theta = 0.01$). In each graph the vertical dotted line to the right represents the profit available given the best (strategically designed) MPA network; the dashed line indicates the profit available under nonspatial management.

Table 1. The results of randomized MPA placement

Strength of density dependence (CR)	Cost of fishing (θ)	California halibut (CH)			Kelp bass (KB)			Kelp rockfish (KR)			Opaleye (OP)			Ocean whitefish (OW)			Red sea urchin (RU)			Sheephead (SH)		
		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
		4	0.01	1.05	74	0	0.94	1	45	0.89	0	59	0.98	32	15	0.86	0	68	0.95	4	33	0.93
4	0.05	1.01	51	0	0.79	0	89	0.86	0	77	0.96	17	35	0.82	0	76	0.93	0	53	0.93	0	72
4	0.1	0.96	23	23	0.89	0	91	0.85	0	89	0.94	9	52	0.78	0	84	0.92	0	69	0.94	0	83
4	0.2	0.85	0	65	0.91	0	99	0.85	0	100	0.93	4	69	0.69	0	94	0.93	0	64	0.96	0	97
8	0.01	0.95	11	24	0.91	0	84	0.87	0	72	0.92	1	60	0.78	0	92	0.98	5	31	0.85	0	93
8	0.05	0.84	0	66	0.93	0	97	0.87	0	86	0.92	0	67	0.67	0	96	0.98	4	51	0.78	0	100
8	0.1	0.68	0	88	0.92	0	99	0.84	0	95	0.93	0	73	0.66	0	99	0.95	0	89	0.88	0	100
8	0.2	0.52	0	100	0.88	0	100	0.85	0	100	0.9	0	94	0.81	0	100	0.9	0	100	0.76	0	100
12	0.01	0.9	0	54	0.93	0	90	0.9	0	75	0.9	0	72	0.74	0	97	0.99	13	25	0.87	0	98
12	0.05	0.77	0	82	0.91	0	99	0.89	0	85	0.9	0	83	0.62	0	98	0.99	2	63	0.96	0	100
12	0.1	0.6	0	96	0.92	0	96	0.87	0	97	0.91	0	90	0.49	0	100	0.99	23	80	0.69	0	100
12	0.2	0.47	0	100	0.87	0	100	0.82	0	100	0.86	0	99	0.36	0	100	0.99	0	100	0.54	0	100

For each species and parameter set: A, expected profit with a randomly designed MPA network relative to optimal nonspatial management; B, percentage of random networks that outperform optimal nonspatial management; C, percentage of random MPAs that would need to be replaced with optimally placed MPAs for the network to outperform nonspatial management.

management and the increase in profits from strategically designed MPAs, suggesting the characteristics that make a species appropriate for one type of spatial management approach also apply to the other.

In addition to the inherent variation from species to species, we find that the value of spatial fishery management is also affected by the strength of density dependence and the cost of fishing. Spatial management is more valuable for species with weak density dependence; in these scenarios protecting key populations leads to higher recruitment in fished locations. By contrast, when density dependence is strong the increase in larval supply resulting from spatially targeted reductions in fishing has little effect on recruitment in fished locations, so spatial management has little potential for increasing profits. This result is consistent with previous theoretical work that has shown that postsettlement density dependence makes MPAs less effective (23). A high cost of fishing also reduces the utility of spatial management. Because spatial management involves reducing fishing in certain areas and increasing it in others, this shift is typically less profitable when the cost of fishing is high, aligning with previous MPA-focused theory (24).

The value of spatial management results in part from capitalizing on dispersal patterns created by complex ocean currents. Recent field work has drawn attention to the link between ocean currents and patterns of fish settlement (25). Larval dispersal interacts with the patchy distribution of habitat to create a seascape in which larvae produced in some patches are distributed across many habitable destination sites, whereas larvae produced in other patches are washed offshore without the opportunity to settle, grow, or reproduce. Thus, some patches are “sources” containing populations that supply settlers throughout the region, whereas other patches are “sinks” and contribute little to the species’ regional persistence (8, 26). For the system as a whole, fish in particularly good source patches will often be worth more in the water producing offspring than on a boat headed for market.

Previous models of MPA-based management show that protecting sources can be an important conservation strategy (27), and simple models of spatial management indicate that when source–sink dynamics are strong, more heterogeneous spatial patterns of fishing are optimal (16, 17). We are able to model complex source–sink dynamics because we have access to detailed dispersal estimates produced by regional ocean modeling. Although several potentially important aspects of larval dispersal are not included in these estimates (e.g., complex larval behavior, interannual variability, resolution of surface wave-driven near-shore flows), they effectively capture the potential for larval

dispersal between sites and represent an important advance over models that assume simple diffusive or advective dispersal.

When comparing management approaches, we focus on the maximum value that could be obtained through fully optimized spatial management. Although we document considerable increases in profits, spatial management is not a silver bullet. If the spatial component of management is applied arbitrarily, it may actually decrease profits. This is emphatically demonstrated by our analysis of randomly sited MPAs. A haphazardly designed MPA network is much less effective than a strategically designed one, even when the area of habitat protected is the same. Although we focus on the contrast between fully optimized and random management, most management is likely to be strategic but imperfect, in part because of uncertainty in our understanding of the biological, physical, and economic characteristics of any fishery. We show that in most cases, MPA networks need not be perfectly designed to improve on nonspatial management, but there remains a serious question about whether uncertainty in real-world fisheries is often too great to permit strategic spatial regulations of the kind described here.

Although we find that in order for an MPA network to improve fisheries outcomes it must be designed strategically, this analysis focuses on increasing profits in a well-managed fishery. A commonly cited advantage of MPAs is that they can protect fish populations even with very little information and across a range of management contexts, a fact that has been confirmed by empirical studies (19). If we had treated the protection of fish populations as one of the goals of fishery management, randomly placed MPAs would have yielded higher value. Even if only profits are considered, randomly placed MPAs may contribute to this goal if MPAs are placed within poorly managed or open-access fisheries (28, 29). MPAs have also been proposed as insurance against accidental fishery collapse (30, 31) and may serve that purpose even if haphazardly designed.

Although fine-scale spatial management of marine systems may seem impractical to implement at first glance, it can be achieved through a variety of existing tools, such as spatially explicit limits on fishing effort or allowable catch, spatial property rights, or spatial limits on gear types or fleet access. Improvements in global positioning system and vessel monitoring technology also make enforcement of and compliance with spatial regulations cheaper and easier. Additionally, we draw a distinction between MPA-based management and fully optimized spatial management because we limit our analysis to no-take MPAs (also called marine reserves or no-take zones). However, MPAs can include a range of fishing restrictions, and a network of MPAs with different rules

could potentially be configured to approximate full spatial management. Furthermore, some of the management approaches listed above have desirable features not captured by our model. For example, spatial property rights can end the “race to fish,” allowing fishermen to harvest using the most efficient methods at the most efficient times. Of course those additional benefits might also be achieved by nonspatial reforms, such as implementation of individual transferable quotas.

Given the world’s reliance on seafood as a source of protein and the increasing pressures on the world’s oceans, identifying ways to improve the efficiency of fisheries is of immediate importance. We find that spatial management has considerable potential to increase fishery profits but that this result depends on the characteristics of the fishery, uncertainty about the system, and the degree to which spatial regulations are applied in a strategic manner. Our results should spur future research into spatial management approaches, and in particular motivate questions about the effectiveness of spatial management under realistic scenarios whereby management is applied strategically but imperfectly. In the face of real-world uncertainty, it is important to understand whether the benefits of optimized spatial management justify the costs of its implementation, or whether there are simpler, nonspatial forms of management that could achieve comparable results. Management in which fishing effort is regulated at a fine scale is currently rare but is likely to become more common in the future. For one, if terrestrial systems provide a guide to what is possible, complex spatial harvesting plans are a readily attainable goal (e.g., forest and rangeland management). Additionally, increasing trends toward privatizing ocean resources and implementing marine spatial planning for a range of competing ocean uses provide a framework for more spatially explicit fisheries management.

Methods

We develop an age-structured, spatially explicit population model for the region between Point Conception, CA and the Mexican border, including both the mainland and offshore islands and all nearshore habitat less than 100 m in depth. Each run of the model simulates the dynamics of a single species at an annual timestep, dividing the seascape into 135 patches spaced approximately every 8 km along the mainland coast and around the perimeter of each island (Fig. 1A). In each patch, the model tracks the number of fish of each age, with fish dispersing between patches as larva or juveniles, experiencing density-dependent mortality during settlement, growing according to a von Bertalanffy function, and dying from both natural mortality and harvest. The model can also dynamically allocate a fixed total fishing effort based on a fleet model that assumes that each fisherman seeks to maximize their individual profits. The simulation continues until both the fish and the distribution of fishermen have reached a stable state (this eventual equilibrium is not sensitive to initial conditions, provided a nonzero initial population). The distribution of fishing effort across the system is a function of the management approach (see below), but within a patch, profits are determined by the biomass of fish, the fishing effort, and the costs of fishing. A detailed description of the biological and economic model is found in *SI Methods*.

Model Parameters. We model six fish species and one invertebrate species, chosen because they are targeted by commercial and/or recreational fishermen in Southern California: California halibut (*Paralichthys californicus*), kelp bass (*Paralabrax clathratus*), kelp rockfish (*Sebastes atrovirens*), opaleye (*Girella nigricans*), ocean whitefish (*Caulolatilus princeps*), sheephead (*Semicossyphus pulcher*), and red sea urchin (*Strongylocentrotus franciscanus*). These species cover a range of life-history, dispersal, and habitat characteristics, and each is intended to be representative of a broader group of similar species in southern California. Parameters for modeling each species follow those used in California’s Marine Life Protection Act process (Table S2; <http://www.dfg.ca.gov/mlpa>).

For each species, we calculate the area of suitable habitat in each patch in the study region based on its depth and substrate associations (Fig. 1B and Fig. S6). Habitat maps, compiled by the California Department of Fish and Game, are based mainly on sonar data, which are used to classify the substrate as hard or soft and determine the depth (seafloor.csumb.edu/csmf/csmf.html), but also use aerial surveys of giant kelp to identify shallow nearshore areas of hard substrate that can be difficult to map with sonar.

Larval dispersal patterns are determined using numerical output from a Regional Ocean Circulation Modeling System (ROMS) simulation for the Southern California Bight (32), which advects millions of Lagrangian particles, simulating the transport of fish larvae in their pelagic phase (33, 34). The resulting model synthesis provides the probability of a particle released at any one point in the study region arriving at any other location in the region (D_{ij}) for a given advection time. The validity of these dispersal probabilities has been tested using available surface drifter observations (35), and their ecological utility has been demonstrated by studies of genetic (36, 37), intertidal, and subtidal community similarity (38). Dispersal probabilities are generated for each species according to the months in which that species spawns and its pelagic larval duration (34), averaging over 7 y (1996–2002). The collection of D_{ij} values can be expressed as a matrix showing the relative probability of larvae being transported from one location to another along the coastline and islands; we treat these probabilities as determining the fraction of the larval output of each patch transferred to each other patch (Fig. 1B and Fig. S7).

Parameter Uncertainty. Some parameters in our model, such as the length-weight relationship, are relatively well known, whereas others, such as the unfished population size, are poorly known but have little effect on the model’s behavior. However, when a parameter has high uncertainty and its value has a significant effect on the results, it is necessary to analyze the model across a range of parameter space, as is the case here for the strength of density dependence and the cost of fishing.

The strength of density dependence, often expressed in the fisheries literature as the CR or the steepness of the stock–recruitment curve (39), is known to be of crucial importance for modeling fish populations. Estimates of the strength of density dependence can vary widely even for closely related species or different populations of the same species (40), and generally it is difficult to accurately estimate this parameter for species that have not been seriously overfished (41). We use a range of values that are appropriate for the long-lived benthic species we model. We start with the conservative assumption that fish are relatively sensitive to harvest (CR = 4), although some species in the region may have even lower CRs (42). We also explore values representing fish populations that are less sensitive to harvest (CR = 8 and 12) but are within the range often used when modeling similar benthic fish (e.g., ref. 29).

We assume that for each species price is fixed (i.e., perfectly elastic over the range of harvest represented by the spatial policies examined). The cost per unit effort of fishing in patch i (θ_i) depends on distance from the nearest port (*SI Methods*, Fig. S8). These patch-specific costs are scaled to the parameter θ , which reflects the cost per unit effort of fishing in a patch at an average distance from the nearest port. Although per-trip costs (e.g., fuel, salaries, etc.) are relatively easily enumerated, the cost of catching a certain fraction of the fish in an area is more difficult to estimate. However, because both instantaneous yield and instantaneous costs are proportional to effort in this model, fishing in a patch will cease being profitable when biomass equals θ_i (i.e., instantaneous profits in a patch equals effort times biomass minus effort times θ_i). We take advantage of this relationship, expressing our cost parameter, θ , relative to the biomass in an average patch under unfished conditions. We use a range of θ values, from 0.01, which implies that in a patch an average distance from port fishing can profitably reduce populations to 1% of the average unfished population size, to 0.2, for which populations less than 20% of the average unfished population size cannot be fished profitably at that distance. At the lower bound of this range, costs are relatively unimportant; the fishing distribution that maximizes profits is similar to that which would maximize yields. At the upper bound, costs have a more substantial effect on profits, particularly when fishing has reduced population sizes (Fig. S9). In addition to exploring a range of fishing costs, we repeated our analyses under conditions whereby the cost of fishing was spatially uniform and obtained very similar results (*SI Methods*, *Alternative Fleet Model*, Tables S3 and S4, and Figs. S10–S16).

Alternative Management Approaches. To estimate the value of a fishery under different management strategies, we compare the best outcome available under nonspatial management with that obtained using spatial regulatory tools. We examine four scenarios, in each allowing a manager to optimally choose a set of management parameters $P \equiv \{P_1, P_2, \dots, P_n\}$ to maximize the value of the objective function:

$$V(P) = \sum_{i=1}^{135} \pi(P)_i, \quad [1]$$

where $\pi(P)_i$ is the annual profit generated in patch i at equilibrium, given the set, P , of management parameters, and $V(P)$ is the sum of profits in all

patches. We focus on steady-state outcomes and so implicitly assume no discounting. We also focus only on economic outcomes; the potential for spatial management to improve multiple objectives (e.g., conservation and economic objectives) simultaneously is intriguing but not addressed here. Details on optimization of each scenario are given in the *SI Methods*.

Scenario 1. The simplest form of management addressed here is “nonspatial management.” We use this as a baseline with which to compare spatial approaches. We assume that a manager can control the total fishing effort (by limiting the number of fishermen, days fished, total quota, or by other means) but that the spatial distribution of fishing effort is determined by the private decisions of individual fishermen, each seeking to maximize personal profits. For a given total amount of fishing, we implement a fleet model in which fishing effort is distributed so that at equilibrium each fished patch has the same average profit, and thus no fisher has an incentive to reallocate effort from one patch to another (Fig. S1 shows examples of how fishing effort is distributed under each scenario).

Scenario 2. The most complex form of management that we model is “fully optimized spatial management.” In this case a manager can control the fishing effort allocated to each patch (potentially including setting fishing to zero in some patches, i.e., no-take areas) and chooses a pattern of fishing that maximizes the total profits from the fishery (Fig. S1B). This represents the highest return that could be achieved by any form of spatial management.

Scenario 3. Intermediate in complexity between nonspatial and fully optimized spatial management is management that incorporates strategically

placed MPAs. Under this system a manager can set the total amount of fishing effort and can also designate certain patches as closed to fishing but cannot control how fishing effort is distributed among the unprotected patches. Fishing effort in the open patches is distributed by the fleet model as described in scenario 1 (Fig. S1C).

Scenario 4. Finally, we examine nonstrategic MPA management, whereby the locations of MPAs are randomly selected instead of being optimized. As with strategic MPA management, the manager chooses total effort to maximize profits given that particular set of MPAs. To provide a fair comparison with scenario 3, we use only MPA networks that cover the same area as the optimally chosen MPA network. Comparisons of these results with those achieved by strategic MPA management indicate the value of optimal network design. We extend this analysis by evaluating MPA networks with a mix of optimally and randomly placed MPAs. We replace MPAs from randomly designed networks with MPAs from the optimal network (for the same species and parameter set) to determine how many optimally placed MPAs are necessary on average to get higher profits than would be achieved with optimal nonspatial management.

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