Integrating marine protected areas with catch regulation

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Abstract: Previous models of marine protected areas (MPAs) have generally assumed that there were no existing regulations on catch and have frequently shown that MPAs, by themselves, can be used to maintain both sustainable fish stocks and sustainable harvests. We explore the impact of implementing an MPA in a spatially structured model of a single-species fish stock that is regulated by total allowable catch (TAC). We find that when a stock is managed at maximum sustainable yield, or is overfished, implementation of an MPA will require a reduction in TAC to avoid increased fishing pressure on the stock outside the MPA. In both cases, catches will be lower as a result of overlaying an MPA on existing fisheries management. Only when the stock is so overfished that it is headed towards extinction does an MPA not lead to lower catches. In a TAC-regulated fishery, even if the stock is overfished, MPA implementation may not improve overall stock abundance or increase harvest unless catch is simultaneously reduced in the areas outside the MPA. Models that consider differential adult and larval dispersal need to be explored to see if these results are found with the more complex biology of a two-stage model.

Résumé : Les modèles antérieurs de zones de protection marine (« MPA ») présupposent généralement qu'il n'y a pas de règlements actuels sur les captures et ils ont souvent démontré que les MPA, par elles-mêmes, peuvent servir à maintenir tant des stocks soutenables de poisson que des récoltes soutenables. Nous examinons l'impact de l'établissement d'une MPA dans un modèle structuré en fonction de l'espace d'un stock monospécifique de poissons qui est contrôlé par la capture totale permise (« TAC »). Lorsqu'un stock est géré à un rendement maximum soutenable ou qu'il est surexploité, l'établissement d'une MPA exige la réduction de TAC pour éviter une pression accrue de la pêche sur le stock à l'extérieur de la MPA. Dans les deux cas, les captures vont diminuer puisque la MPA se surajoute à la gestion actuelle de la pêche. C'est seulement lorsque le stock est tellement surexploité qu'il risque l'extinction que la MPA ne cause pas de réduction des captures. Dans une pêche commerciale réglementée par TAC, même lorsque le stock est surexploité, l'établissement d'une MPA peut ne pas améliorer l'abondance globale du stock, ni augmenter la récolte, à moins que la capture ne soit simultanément réduite dans les zones extérieures à la MPA. Il faudra explorer les modèles qui tiennent compte de la dispersion différente des adultes et des larves afin de voir si les mêmes résultats sont obtenus d'un modèle à deux niveaux avec une biologie plus complexe.

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Introduction

In recent years considerable attention has been paid to the implementation of networks of marine protected areas (MPAs) as a method to protect marine biodiversity and help manage fisheries (Allison et al. 1998). Although less than 1% of coastal marine environments are currently protected in MPAs (Roberts and Hawkins 2000), numbers of newly established MPAs have been increasing rapidly, and the implementation of more extensive reserve networks is underway in several nations (e.g., the Great Barrier Reef (Australia), the Channel Islands (California, USA), and the Bahamas; Airamé et al. 2003).

MPA establishment is frequently associated with increased abundance, biomass, and sizes of focal species, increased total abundance, biomass, and diversity of all species, and changes in the structure of species assemblages (Palumbi 2001; Halpern and Warner 2002; Micheli et al. 2004). In addition to enhancing populations and assemblages within the protected area, MPA establishment can increase catch-per-unit-effort (CPUE) in adjacent areas through export of juveniles and adults (Yamasaki and Kawahara 1990; Russ and Alcala 1996; Roberts et al. 2001). However, empirical evidence of increased fishery catches following reserve establishment is still controversial. In particular, increased catches may not be sufficient to compensate for the decreased extent of the fishing grounds to produce greater total yields, at least in the short term (e.g., McClanahan and Mangi 2000). Because of the difficulty of documenting MPA effects on fishery yields, questions about the effective-

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ness of MPAs for fisheries management have been addressed largely through modeling (reviewed by Guenette et al. 1998; Botsford et al. 2003; Gerber et al. 2003).

Models of MPAs have shown that effects on yield depend on dispersal in the larval, juvenile, and adult stages, size and configuration of reserves, and status of the fishery. Over the past decade, models of MPAs have produced three generalizations about effects on fishery yields. First, MPA establishment is expected to increase yields when fishing effort cannot be controlled and populations would otherwise be overfished, but it is unlikely to improve yields of lightly fished fisheries (Holland and Brazee 1996; Sladek-Nowlis and Roberts 1999; Gerber et al. 2003). Second, for MPAs to be effective, rates of adult fish movement cannot be too high. As adult movement rates increase, larger MPAs are needed to achieve gains (Polacheck 1990). Species with low movement rates receive the greatest benefits from MPAs in terms of increased reproductive potential, but these benefits rarely move out of the reserve to contribute to the fishery. Thus, fishery gains are expected to be greatest for species with intermediate rates of movement (DeMartini 1993; Botsford et al. 2003). Finally, MPAs reduce variability in catches in the face of stochastic events such as recruitment failures (Sumaila 1998; Sladek-Nowlis and Roberts 1999) and make fisheries less sensitive to uncertainty in fishing mortalities (Lauck et al. 1998; Mangel 2000).

Much of the traditional analysis focuses on how MPAs compare with conventional fishery management using size limits, effort control, or regulation of total catch (TAC). Models addressing this question indicate that the effect of reserves on yields is similar to increasing the age of first capture or to reducing effort (Botsford et al. 2003). In their classic analysis, Beverton and Holt (1957) examined the effects of using reserves as a management tool by assuming that after reserve establishment, fishing effort would become concentrated in a smaller area and that movement between unfished and fished areas is in proportion to abundances in the source area. As the extent of the unfished area increases, the shape of the relationship between yield per recruit and fishing mortality changes in a similar way to what results from assuming greater age limits (Beverton and Holt 1957; Guenette et al. 1998). As noted above, both large unfished areas and high age limits maintain high yields when the population is overfished. Several models have indicated that the establishment of MPAs is equivalent to a reduction in fishing mortality rate in a nonspatial management context (Quinn et al. 1993; Holland and Brazee 1996; Hastings and Botsford 1999). In particular, Hastings and Botsford (1999) showed that for species with sedentary adults, dispersal through a larval pool, and postdispersal density dependence, the selection of optimal MPA size is mathematically identical to the determination of optimal fishing mortality rate.

In most developed countries where large-scale MPA networks are being proposed, existing fisheries management systems are in place, which include gear, effort, and often TAC limitation. Thus, in practice, MPAs will not be established as alternatives to existing fisheries management, but as additions to it. Accordingly, models have either removed fishing effort as a function of reserve size or have increased fishing mortality outside MPAs (e.g., Beverton and Holt 1957; Holland and Brazee 1996). Spatial analyses of fishermen redistribution among patchy resources indicate that fishermen behavior needs to be integrated within models (e.g., Sancherico and Wilen 1999; Stefansson and Rosenberg 2005). Stefansson and Rosenberg (2005) explored regulatory structures that mixed effort controls, total catch controls, and closed areas and concluded that a mix of these three approaches provided the best combination of economic yield and buffering against uncertainty. Rodwell and Roberts (2004) explored the consequences of reserves under constant harvest rate TACs but assumed that the TAC depended only on the population outside the reserve, thus there was implicitly a TAC reduction at the time of TAC implementation. Thus MPA establishment also implied TAC reduction. To our knowledge, no study has examined the effects of establishing MPAs within an existing management system when the spatial dynamics of target populations, fishing fleet, and regulated catches are included.

The purpose of this paper is to explore the consequences of imposing a system of MPAs on top of an existing fisheries management system that limits catches by setting an annual TAC. We specifically test the hypotheses that establishment of MPAs will increase both population abundance and fisheries yields. To do this we use the spatially explicit model described below.

Materials and methods

Our model assumes a linear array of 100 areas such as might occur along a coastline. The underlying assumptions are logistic growth in each area, with movement each year distributing individuals to other areas as a decreasing function of distance to those areas. A list of symbols used in the equations is provided in Table 1.

The basic model equations for each area before movement are logistic growth with harvesting:

$$(1) \qquad N'_{i,t+1} = \left(N_{i,t} + N_{i,t}\, r \left(1 - \frac{N_{i,t}}{k} \right) - u_{i,t}\, N_{i,t} \right)$$

The fish are then moved according to a movement probability matrix:

$$(2) \qquad N_{i,t+1} = \sum_{j=1}^{n} N'_{j,t+1}\, p_{j,i}$$

The movement matrix is calculated by assuming that the movement probability has a normal shape centered on the area of origin:

$$(3) \qquad p'_{j,i} = \exp\left(-\frac{(i-j)^2}{2m^2} \right)$$

which is normalized to sum to one for each donor area:

$$(4) \qquad p_{j,i} = \frac{p'_{j,i}}{\sum_i p'_{j,i}}$$

This model is highly simplistic in that there is no spatial heterogeneity and no stochasticity in the dispersal process.

We assume that the population initially is at some fraction of its carrying capacity:

Table 1. List of symbols.

Symbol	Definition
A	Number of areas in the reserve
B	Total number of boats in the entire model
$B'_{i,t}$	Intermediate variable that is the relative number of boats in an area
$B_{i,t}$	Number of boats in area i at time t
c	Parameter that determines how boats aggregate in areas of the most abundance
d	Initial population size as a fraction of carrying capacity
I	Intercept of the catch vs. stock size relationship
K	Carrying capacity in each area
m	Movement distance parameter
$\tilde{N}$	Maximum abundance of fish outside the reserve
$N'_{i,t}$	Number of individuals in area i at time t before movement
$N_{i,t}$	Number of individuals in area i at time t after movement
$p_{i,j}$	Probability of an individual moving from area i to area j
q	Fraction of the stock in an area harvested by each boat
r	Intrinsic rate of increase in each area
s	Slope of the catch vs. stock size relationship
TAC_t	Total allowable catch over all areas in year t
$u_{i,t}$	Fraction harvested in area i at time t
z	Proportional reduction in fishing effort in all areas required to make total catch equal to the TAC

$$(5)\qquad N_{i,1} = dK_i$$

Reserve implementation and harvest

A total of a areas are set aside in a reserve, in the middle of the total linear array of areas. The year of first establishment of the MPA is adjustable.

Boats are allocated to areas based on the abundance of fish in the areas outside the reserve, no vessels fish inside the reserve. Let $\tilde{N}$ be the maximum abundance outside the marine reserve in any given year; the following two-step process allocates boats along the fishery (subscripts for time have been dropped for simplification):

$$(6)\qquad \begin{cases} B'_i = \exp\left[-c\left(1-\dfrac{N_i}{\tilde{N}}\right)\right] & \text{if area } i \text{ is not in a reserve} \\ B'_i = 0 & \text{if area } i \text{ is in a reserve} \end{cases}$$

$$B_i = B\frac{B'_i}{\sum_i B'_i}$$

These equations cause boats to concentrate in places of highest fish abundance. Therefore as the value of c increases, the concentration of boats also increases.

The fraction harvested in each area is determined by the number of boats, the efficiency of boats (q), and a scaling factor when regulations reduce the allowable catch (z).

$$(7)\qquad u_{i,t} = B_{i,t}\,q\,z$$

Regulations

Each year, the fishing vessels are allowed to operate until the overall catch equals the annual limit, namely the TAC. The TAC can be set through a flexible rule (Hilborn and Walters 1992) that can represent a constant harvest rate, a fixed escapement, a constant catch, and many intermediate policies, that is

$$(8)\qquad \mathrm{TAC}_t = \left[I + s\sum_A N_{i,t}\right]$$

where I is the intercept and s is the slope of a relationship between TAC and total number of fish summed over all areas inside and outside the MPA. If I is set to 0, then s represents a constant harvest rate. For instance, TAC can be computed by setting the harvesting rate to the value s that would guarantee the maximum sustainable yield (MSY) in an homogeneous population with the same demographic parameters (reproductive rate and carrying capacity) but no spatial dynamics of the larvae and (or) fishes and of the fleet and no restriction to the fishing areas.

If the catch that would occur without regulation is less than the TAC, then the regulations have no effect. If the catch that would occur without regulation is greater than the TAC, then the catch in each area is reduced proportionally so that the total catch is equal to the TAC by adjusting the scaling factor z.

$$(9)\qquad z = \frac{\mathrm{TAC}_t}{\sum_i qB_{i,t}N_{i,t}}$$

As a consequence, the total effective harvest in any given year is computed as follows:

$$\text{Total harvest}_t = \sum_i u_{i,t}N_{i,t}$$

$$= \begin{cases} \sum_i qB_{i,t}N_{i,t} & \text{if } \sum_i qB_{i,t}N_{i,t} < \mathrm{TAC}_t \\ \mathrm{TAC}_t & \text{if } \sum_i qB_{i,t}N_{i,t} \geq \mathrm{TAC}_t \end{cases}$$

Fig. 1. Temporal pattern in catch (thick solid line), total fish abundance (thin solid line), and fish abundance outside of reserve (broken line) for scenario 1, where stock was headed towards extinction until a marine protected area was implemented.

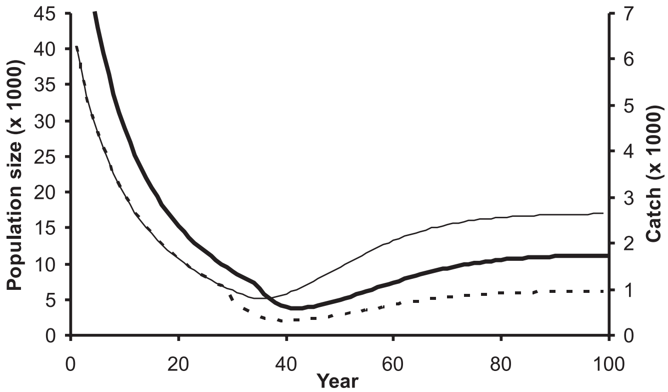
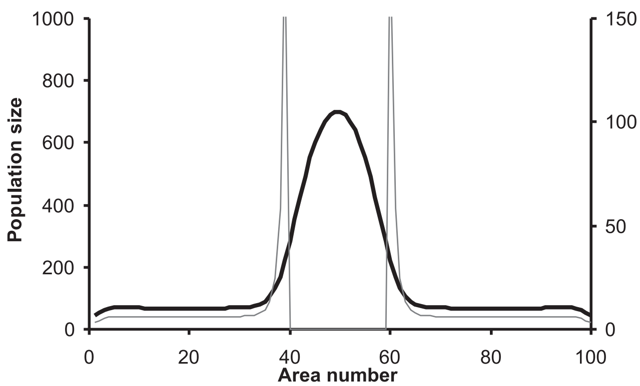


Fig. 2. Distribution of boats and fish after 100 years in scenario 1. Thick line is the abundance of fish, the thin line is the number of boats.



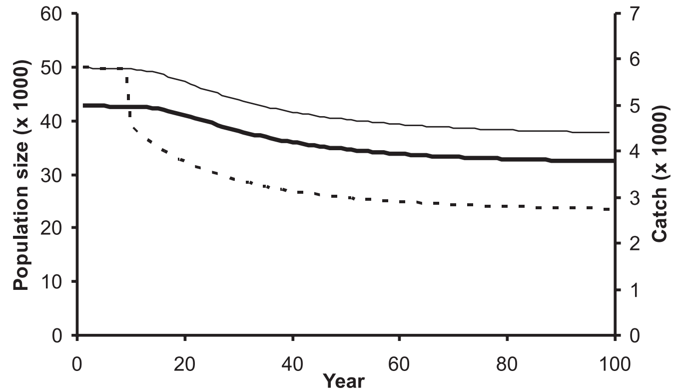
Further assumptions

In all scenarios, we have assumed that one MPA of size 20 is implemented in the middle of the 100-unit area, corresponding to 20% of the area in MPAs. The stock always has an intrinsic rate of increase of 0.2 and a carrying capacity in each area of 1000. Under these assumptions, it follows that harvest rate that guarantees the MSY, namely s_{MSY}, is equal to 10%, whereas the corresponding population size at equilibrium and catch over the coastline are 50 000 and 5000 fishes, respectively. Harvesting rates equal to, or exceeding, 20% would lead to population extinction.

In these simulations, the total number of fishing boats B is 1000 and q is 0.3, which means that if evenly spread across 100 areas, the exploitation rate in each area would be 30%, which is sufficient to drive the population in each area to extinction. As a consequence, in the absence of a TAC regulation or an MPA, the population would be driven to extinction.

The fleet aggregation parameter c has been set to 5 so that fishing effort is mainly clustered along the edges of reserves where fish density is higher. The fish movement rate m is set to 3, which allows significant spillover from a reserve. To test the sensitivity of our results to values for c and m, we ran further simulations using values that range from 1 to 5 for c and from 1 to 10 for m. A value of $c = 1$ means that the fleet is reasonably uniformly distributed outside the reserve. Increasing values of c provide for increasing concentration of fishing effort at the locations of highest fish abundance. A value of $m = 1$ means that the population is almost sedentary, with little spillover outside the reserve. A value of $m = 10$ means that the stock is highly mobile and there is little effect on the reserve.

Fig. 3. Temporal pattern in catch (thick solid line), total fish abundance (thin solid line), and fish abundance outside of reserve (broken line) for scenario 2, where stock was at maximum sustainable yield before marine protected area implementation.



Results

To illustrate the basic functioning of the model, scenario 1 assumes that the stock begins at $K/2$, but the fishery is poorly regulated and the overall harvest rate is 0.2, so it is headed towards extinction (Fig. 1). In year 30, the MPA is implemented, allowing the stock to rebuild inside the MPA and providing spillover to areas outside the MPA, which in turn leads to a rebuilding of total abundance and catch. The distribution of boats and fish in year 100 of this scenario are illustrated (Fig. 2) with the boats accumulating on the edge of the MPA, and the fish abundance high in the center of the MPA but declining towards its edges. This is a classic illustration of how an MPA can provide increases in yield in an overfished system and prevent population extinction. However, total population size and harvest from this system (50 000 and 5000, respectively) is far less than at MSY. In scenario 2 (Fig. 3), all parameters are the same except that the stock is harvested at s_{MSY} (10% per year), holding the stock at the MSY from before implementation of the MPA. When the marine reserve is implemented, management rules still require the annual TAC to be computed as 10% of the overall stock, namely the sum of individuals inside and outside the MPA. The result of the MPA is to cause both the stock size and the catch to decline slightly. In fact, before MPA implementation, the exploitation rate is exactly optimal for MSY management. After the MPA, the fleet can operate only outside the MPA but keeps fishing until the TAC is removed: as a consequence, the harvest rate outside the MPA is higher than s_{MSY}, and thus the stock declines.

In scenario 3 (Fig. 4), all parameters are the same again except that before MPA implementation, the stock is just at one-tenth of its carrying capacity K, i.e., quite overfished, and the TAC is computed by setting the harvest rate s (eq. 8) at 15% per year, a level that will allow the stock to rebuild

Table 2. Comparison of results for a range of movement rates and fleet aggregation parameters when the exploitation rate is 10% and provides maximum sustainable yield.

	Fleet aggregation parameter (*c*)				
Movement rate (*m*)	1	2	3	4	5
1	0.08, 0.37	0.07, 0.36	0.08, 0.36	0.11, 0.38	0.17, 0.41
2	0.17, 0.34	0.18, 0.32	0.22, 0.34	0.27, 0.37	0.32, 0.40
3	0.55, 0.54	0.67, 0.66	0.72, 0.72	0.75, 0.75	0.77, 0.77
4	0.77, 0.77	0.82, 0.82	0.85, 0.85	0.87, 0.87	0.88, 0.88
5	0.85, 0.85	0.89, 0.89	0.90, 0.90	0.92, 0.92	0.92, 0.92
6	0.90, 0.90	0.92, 0.92	0.93, 0.93	0.94, 0.94	0.95, 0.95
7	0.93, 0.93	0.94, 0.94	0.95, 0.95	0.96, 0.96	0.96, 0.96
8	0.94, 0.94	0.95, 0.95	0.96, 0.96	0.96, 0.96	0.97, 0.97
9	0.95, 0.95	0.96, 0.96	0.97, 0.97	0.97, 0.97	0.97, 0.97
10	0.96, 0.96	0.97, 0.97	0.97, 0.97	0.97, 0.97	0.98, 0.98

Note: The first number in each cell is the ratio of catch with a reserve to catch without a reserve. The second number is the ratio of total population with a reserve to total population without a reserve.

Fig. 4. Temporal pattern in catch (thick solid line), total fish abundance (thin solid line), and fish abundance outside of reserve (broken line) for scenario 3, where stock was rebuilding from overexploitation before marine protected area implementation.

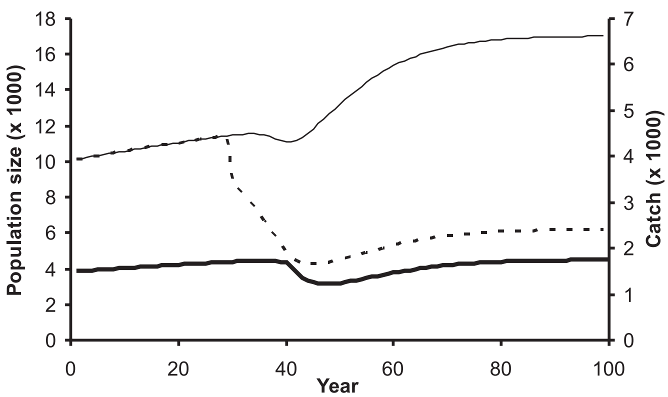
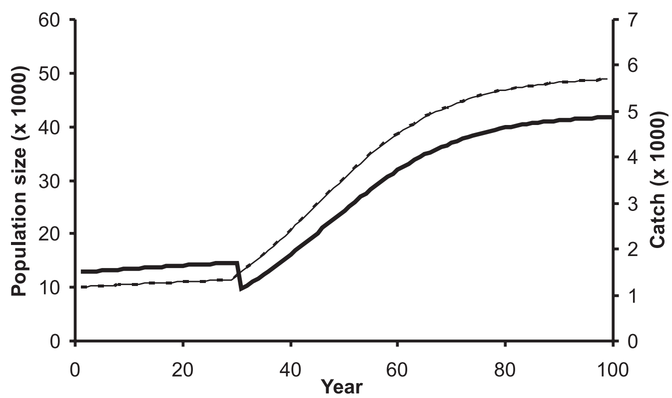


Fig. 5. Temporal pattern in catch (thick solid line), total fish abundance (thin solid line), and fish abundance outside of reserve (broken line) for scenario 4, where stock was rebuilding from overexploitation before year 30, when harvest rate is reduced to 10%. No reserve is implemented in this scenario.



but still remain overfished. The simulations show that when the MPA is implemented, both catch and stock abundance first decline, then the catch recovers to its previous level and the total stock increases significantly. At the end of 100 years, the catch is the same as it would have been without the MPA, but total abundance is higher. However, both catch and stock remain well below the level that they would have achieved by setting annual TAC at MSY (that is, $s = s_{MSY} = 10\%$) with no MPA (scenario 4). Again, when MPA is implemented, a significant portion of the total population cannot be harvested inside the MPA, so the TAC (computed as 15% of the overall stock inside and outside the MPA) can be harvested only outside the MPA; as a consequence, the actual exploitation rate outside the MPA increases substantially above 15%, and thus the population outside the reserve is strongly depleted. The increase in population abundance within the MPA in not able to compensate for the drop in abundance outside the marine reserve.

Scenario 4 (Fig. 5) is identical to scenario 3 except that no MPA is implemented. Instead, the harvest rate *s* to compute TAC is reduced to its MSY level, namely at 10%, in year 30. Both catch and biomass rebuild faster without an MPA and reach higher equilibrium levels than observed in scenario 3.

The effect of the implementation of an MPA is shown for a range of *m* and *c* values in a TAC-regulated fishery that is already at its MSY equilibrium ($s = s_{MSY} = 10\%$) (Table 2). We can see that when movement rates are high ($m > 6$), there is very little impact of the reserve, and catch and population size are almost the same with or without the reserve. However, when movement is low ($m < 3$), the impact of the reserve is remarkable. The fishes inside the reserve provide little spillover outside the reserve, while overall TAC is allocated outside the reserve, and as a consequence, stocks outside the reserve are heavily overfished. The catch is greatly diminished and the total population size is lower than without a reserve because the only fish left are found inside the reserve.

Although the impact of movement is very dramatic, the impact of the fleet aggregation parameter *c* is less so. However, when the fish movement rate is low, catch is considerably higher at higher fleet concentration values, which is when the fleet aggregates at the edge of the reserve and concentrates on the fish that do spillover.

The results of an MPA implemented in a fishery with an annual TAC of 15% of the overall stock, which leads to overexploitation but not extinction of the fish population, are reported in Table 3 as the relative performance of an MPA in

Table 3. Comparison of results for a range of movement rates and fleet aggregation parameters when the exploitation rate is 15% and the population will be overfished.

	Fleet aggregation parameter (*c*)				
Movement rate (*m*)	1	2	3	4	5
1	0.20, 1.39	0.18, 1.35	0.19, 1.34	0.26, 1.41	0.42, 1.56
2	0.41, 1.27	0.39, 1.19	0.40, 1.18	0.52, 1.29	0.71, 1.48
3	0.59, 1.12	0.55, 1.00	0.58, 0.99	0.72, 1.12	0.88, 1.29
4	0.66, 0.90	0.58, 0.73	0.59, 0.71	0.69, 0.81	0.81, 0.94
5	0.56, 0.61	0.49, 0.48	0.59, 0.59	0.66, 0.66	0.71, 0.70
6	0.61, 0.60	0.72, 0.72	0.79, 0.79	0.83, 0.82	0.85, 0.85
7	0.76, 0.75	0.83, 0.83	0.87, 0.87	0.89, 0.89	0.91, 0.91
8	0.84, 0.84	0.89, 0.89	0.91, 0.91	0.93, 0.93	0.94, 0.93
9	0.89, 0.89	0.92, 0.92	0.93, 0.93	0.94, 0.94	0.95, 0.95
10	0.91, 0.91	0.94, 0.93	0.95, 0.95	0.96, 0.95	0.96, 0.96

Note: The first number in each cell is the ratio of catch with a reserve to catch without a reserve. The second number is the ratio of total population with a reserve to total population without a reserve.

Table 4. Comparison of results for a range of movement rates and fleet aggregation parameters when the exploitation rate is 20% and the population would be driven to extinction without a reserve.

	Fleet aggregation parameter (*c*)				
Movement rate (*m*)	1	2	3	4	5
1	12.3, 121	11.5, 117	11.5, 117	14.0, 120	25.3, 136
2	25.5, 110	24.1, 103	24.2, 102	29.7, 110	43.2, 128
3	36.1, 97.3	33.5, 86.2	33.9, 84.2	41.1, 94.8	52.4, 110
4	37.3, 74.2	30.9, 57.3	29.7, 53.0	34.3, 59.8	40.9, 69.9
5	23.7, 38.5	13.9, 20.5	11.4, 16.0	12.3, 17.3	14.3, 20.2
6	8.92, 12.0	3.79, 4.54	2.82, 3.24	2.88, 3.30	3.24, 3.75
7	2.91, 3.36	1.18, 1.22	0.96, 0.96	0.97, 0.97	0.97, 0.97
8	1.14, 1.17	0.97, 0.97	0.98, 0.98	0.98, 0.98	0.98, 0.98
9	0.97, 0.97	0.98, 0.98	0.98, 0.98	0.98, 0.98	0.99, 0.99
10	0.98, 0.98	0.98, 0.98	0.99, 0.99	0.99, 0.99	0.99, 0.99

Note: The first number in each cell is the ratio of catch with a reserve to catch without a reserve. The second number is the ratio of total population with a reserve to total population without a reserve.

an overharvested TAC fishery with respect to a fishery harvested at its MSY ($s = s_{MSY}$). Although implementation of an MPA might be beneficial to fish abundance (but not to catch) for lower values of *m* in the case of moderate overfishing, simulations show that the establishment of an MPA is never as effective as regulating the fishery by setting the annual TAC to its MSY (namely, by reducing *s* to s_{MSY}). We know this because at MSY (s = 10%), yield is higher than when *s* = 15%, and the implementation of MPAs with *s* = 15% never provides increased yields. In fact, by implementing an MPA in an overfished stock (*s* = 15%), the equilibrium harvest is about 40% of that achieved at MSY and the equilibrium population size is about 20% of that at MSY. As in Table 2, adding a reserve has little impact when movement rates are high and both catch and population size are about the same. When movement rates are low, again the reserve leads to considerably reduced catch but now leads to higher population sizes. With low movement rates, the populations inside the reserve build to near-virgin condition, while there are few fish outside the reserve. From a population abundance perspective, reserves provide major benefits, but there are no benefits in terms of fisheries yields.

The results for a harvest rate *s* = 20%, which leads to extinction in the long term, are shown in Table 4. In the 100 years of simulation, the population is reduced to very low numbers in the absence of a reserve. As long as movement rates are low enough (<7), both catch and population size are better with a reserve in place. This is consistent with what we observed in Fig. 1. Thus, reserves result in both population and fisheries benefits when stocks are heavily overfished.

Discussion

This simple model illustrates that the consequences of MPA implementation on both stock abundance and yield will depend on the regulations used to limit catch and that MPA implementation may even have negative consequences on abundance and catch of a TAC-regulated fishery at its MSY if harvesting strategies are not simultaneously modified and vessels allowed to remove all the TAC (computed on the overall stock) outside the MPA. Under these conditions, MPA implementation can slow down rather than increase stock-rebuilding rates (scenarios 3 and 4), and even when the stock is overexploited, we found no catch benefits from MPA establishment unless overexploitation is so intense that stocks are headed towards extinction in the absence of protection though MPA. Thus, MPA implementation may not increase fish yields if the fishery is already regulated unless the fishery is heavily overexploited. We have shown results for only a single value for the rate of increase, but because the dimensions of movement rate and rate of increase are scalable, the results should be very general.

This counterintuitive result is easily understood in the spatial context. The allowable harvest set by the regulatory agency on the basis of the overall stock (inside and outside the MPA) will be removed from fewer spatial areas after the MPA is implemented, leading to overexploitation outside the MPA that is not compensated for by the export of individuals from inside the MPA. For the movement rate to be low enough to provide rebuilding inside the MPA, the effect of shifting all of the allowable harvest to 80% of the total area is to provide for more intense exploitation in those areas. Although it might seem reasonable to recalculate the TAC based only on the fish outside the reserve, this will cause a decline in catch, and the joint effect of an MPA and TAC-reduction policy would need to be compared with catch reduction alone (scenario 4). In general, the results are more pronounced when fish movement is low. As movement rates are increased, the MPA has less impact overall. This is consistent with all previous MPA models. We explored a range of the fleet concentration parameter (c), and although it did affect how much of the effort was concentrated at the edge of the reserve, it did not affect the temporal pattern of total catch and stock size.

We also performed further simulations to explore the effects of implementing several smaller reserves rather than just a large one so as to increase the ratio of edge to interior of reserve. As expected, this appears to be identical to increasing the movement rate. For instance, 20% of the area divided into three reserves with the same movement rates provided almost no “reserve effect” and abundance did not increase significantly inside the reserves. Previous models of MPA impacts have not considered existing catch regulations, yet such regulations are the rule rather than the exception in Canadian and US fisheries, where the harvesting effort (as here measured by the number of fishing boats) is so high that it would rapidly deplete the stock if a limit to the allowable catch were not set. We have not considered stochastic dynamics or formalized the uncertainty in stock assessment to which MPAs should provide a buffer. Scenario 3 does have the management regulation at a level that would be considered overfishing in the US (15% harvest rate), which can be thought of as a form of management error. We recognize that the large uncertainties associated with the assessment of stock sizes, unwillingness of managers to reduce catches when stocks are overfished, and lack of compliance with regulations in many places in the world render the management of fisheries with traditional catch and effort control ineffective. Thus our analysis and results are intended to demonstrate that when catch limits are indeed effective, MPA implementation will need to be coordinated with such catch limits. In contrast, scenario 1 shows that when catch limits are ineffective and stocks are headed towards extinction, MPAs are effective in maintaining some biomass and catches. Similarly, MPAs are expected to reduce variability in catches in the face of stochastic variation in recruitment (Sumaila 1998; Sladek-Nowlis and Roberts 1999) and uncertainty in fishing mortalities (Lauck et al. 1998; Mangel 2000), which we did not include in this model.

This analysis (as in almost all previous models of MPAs) is a single-species evaluation and like most current fisheries management ignores the ecological and evolutionary consequences of harvesting marine populations in coastal ecosystems. MPAs and other spatial approaches to management are promising tools for addressing uncertainty and long-term maintenance of populations and ecosystems. Nevertheless, our model results suggest that the effectiveness of MPAs as a fisheries management tool is likely to be influenced by other regulations in place. If significant areas are placed in MPAs, existing TACs will likely need to be reduced to prevent declines in abundance of some species following MPA implementation and concentration of fishing effort outside reserves. In fact, to be effective, TACs need to be computed only on the fraction of the population that is actually harvestable and not on the overall stock inside and outside the MPA. We thus suggest that any future analysis of MPA implementation on fisheries abundance and yield needs to explicitly consider the catch regulatory structure that is in place when the MPAs are introduced.

Important research priorities include determining how including real system complexities into this simple model may influence the conclusions and developing general rules for how to integrate MPAs with existing regulations. We made no attempt to select model parameters to show specific results and thus cannot claim that any particular quantitative results are general. However, we found no combinations of parameters that had a significant MPA effect on abundance inside the reserve that did not show that catches outside the reserve would need to be reduced at the time of MPA implementation. The key message from this initial model is that MPA implementation and traditional TAC regulation may interact in unexpected ways.

A next step in model analysis is to consider models in which larvae disperse more broadly than adults. In addition to adult and juvenile movement, increased reproductive output from older, larger individuals inside MPAs and larval dispersal to adjacent fished areas are means by which MPAs are expected to increase fishery yields (Bohnsack 1992; Palumbi 2001). Including larval dispersal and possible effects of the changed age and size structures on fecundity and reproductive outputs are critical for increasing the biological realism of future models.

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