
Effects of Noncompliance on the Success of Alternative Designs of Marine Protected-Area Networks for Conservation and Fisheries Management

JACOB P. KRITZER*

Department of Biological Sciences, University of Windsor, 401 Sunset Avenue, Windsor, ON N9B 3P4 Canada

Abstract: *Studies examining the efficacy of marine protected areas (MPAs) rarely consider the potential for noncompliance. Violation of MPAs will typically occur near boundaries, so perimeter-to-area ratios will be important determinants of actual protection, suggesting that MPAs should be larger and likely fewer. If larval dispersal is highly localized, however, MPAs will need to be more numerous, widespread, and likely smaller in order to replenish many fished areas. Thus, there is a discord between the MPA network that would best achieve external replenishment and that which would maximize compliance. I investigated these competing criteria with a spatially structured model of a hypothetical marine fishery exploiting a sedentary reef-dwelling organism. With full compliance, a network of several small MPAs protects a population of similar size to that in a single large MPA and produces higher fishery yield across a range of fishing mortality rates. As noncompliance increases, however, the protected population in the network of several small MPAs approaches zero, whereas the single, large MPA population declines much less. Furthermore, at high levels of fishing mortality and noncompliance, yield with the network of several small MPAs begins to mirror that with no MPAs and drops below the yield with the single large MPA. Temporal variability in both the protected population size and yield are similar between the two designs with full compliance, but the single large MPA provides much greater stability in both metrics at high fishing mortality rates as noncompliance increases. My results highlight the important effects of noncompliance in realized MPA benefits and can explain why observed and expected effects might differ. Moreover, my results support a call for increased attention to rates of noncompliance and their ecological effects and greater collaboration among natural scientists, social scientists, managers, and stakeholders in understanding and altering illegal behavior.*

Efectos del Incumplimiento sobre el Éxito de Diseños Alternativos de Redes de Áreas Marinas Protegidas para Conservación y Gestión de Pesquerías

Resumen: *Los estudios que examinan la eficacia de áreas marinas protegidas (AMP) raramente consideran el potencial de incumplimiento. La violación de AMP típicamente ocurrirá cerca de los límites, por lo que las relaciones perímetro:área serán importantes en la determinación de la conservación actual, lo que sugiere que las AMP deben ser más grandes y posiblemente menos en número. Sin embargo, si la dispersión larvaria está muy localizada, las AMP deberán ser más numerosas, más dispersas y posiblemente más pequeñas para reestablecer muchas áreas pescadas. Por tanto, hay una discordancia entre la red de AMP que mejor logre el reestablecimiento externo y que maximice el cumplimiento. Investigué estos criterios en competencia con el modelo estructurado espacialmente de una pesquería marina hipotética que explota a un organismo arrecifal sedentario. Con cumplimiento total, una red de varias AMP pequeñas protege una población de tamaño similar al de una sola AMP grande y tiene mayor rendimiento pesquero en un rango de tasas de mortalidad por pesca. Sin embargo, a medida que aumenta el incumplimiento, la población protegida en la red de varias*

*Current address: Environmental Defense, 257 Park Avenue South, New York, NY 10010, U.S.A., email jkritzer@environmentaldefense.org
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AMP pequeñas se acerca a cero, mientras que la declinación de la población en la única AMP grande es mucho menor. Más aún, en niveles altos de mortalidad por pesca y de incumplimiento, la producción en la red de varias AMP pequeñas comienza a ser similar a la de sin AMP y cae debajo de la producción con la única AMP grande. La variabilidad temporal tanto del tamaño como la producción de la población protegida es similar en los dos diseños con cumplimiento total, pero la única AMP grande proporciona mucha más estabilidad en ambas medidas en tasas de mortalidad por pesca altas a medida que aumenta el incumplimiento. Mis resultados resaltan los efectos importantes del incumplimiento sobre los beneficios de AMP y pueden explicar porque pueden diferir los efectos observados y esperados. Más aún, mis resultados son un llamado para mayor atención a las tasas de incumplimiento y sus efectos ecológicos y para una mayor colaboración entre científicos naturales, sociales, administradores y público para entender y alterar la conducta ilegal.

Introduction

Marine protected areas (MPAs) are receiving increasing attention in the conservation and fisheries literature as a management strategy that can achieve multiple objectives, particularly for reef-dwelling fishes and invertebrates (reviewed by Roberts & Polunin 1991; Dugan & Davis 1993; Guenette et al. 1998; Roberts 2000; Roberts et al. 2001; Russ 2002). Marine protected areas can provide conservation benefits by protecting population and community structure from anthropogenic effects in some parts of a larger system. These benefits have been well documented, with numerous studies demonstrating higher densities and larger body sizes of exploited species and greater overall biodiversity within MPAs. Such benefits are often achieved quickly and generally are not dependent upon MPA size (Coté et al. 2001; Halpern & Warner 2002). Marine protected areas also have the potential to provide fisheries benefits through export of adults or larvae to fished areas following build-up of biomass (Roberts et al. 2001), although proving this benefit has been difficult (Russ 2002). Most reef-dwelling species are largely sedentary after settlement, so yield in these systems is unlikely to be greatly enhanced by movement of adults (Polachek 1990; Demartini 1993). Dispersal of pelagic larvae, on the other hand, can be more widespread and can be a more effective mechanism by which MPAs supplement harvested populations.

Replenishment of fished areas through the higher reproductive output of MPAs is a theoretical possibility (MPA models are reviewed by Guenette et al. 1998; Gerber et al. 2003). However, achieving effective transport of offspring from MPAs to fished areas in practice is hampered by a general dearth of information on larval dispersal pathways and the resultant demographic connectivity of marine populations (Russ 2002; Sale 2002; Kritzer & Sale 2004). This information is crucial for determining the number and distribution of MPAs required to seed the majority of harvested populations (Roberts et al. 2001). If marine larvae disperse broadly, then only a few large MPAs are needed because their reproductive output will be spread widely. In contrast, if larvae disperse over smaller distances and self-recruitment is high, MPAs will need to be numerous and well distributed to replenish

as many fished areas as possible. Given this uncertainty, larval dispersal is an increasing focus of contemporary marine research, particularly with respect to coral reef fishes.

There is currently no consensus on the scale of dispersal in reef systems (Mora & Sale 2002), nor should we expect one given the clear dependence on geographic context. Several recent studies of reef fishes, however, provide evidence of relatively short-distance transport, with >50% of offspring recruiting near their natal reef (Jones et al. 1999; Swearer et al. 1999; Cowen et al. 2000). This suggests that, for a given proportion of area to be protected, marine fisheries management should opt for a network of small and well-distributed MPAs. Smaller and more widely distributed MPAs should also provide a benefit in buffering against environmental uncertainties. Marine-protected-area networks of any design will suffer the effects of large-scale perturbations such as climate change. However, smaller-scale events such as localized oil spills will have greater effects if all protected populations and habitat are confined to a single MPA. Furthermore, many marine populations experience wide interannual fluctuations in recruitment (Myers 2002). If these fluctuations are independent among local areas (e.g., Doherty 1987), then widely distributed MPAs will minimize the risk of all protected populations experiencing contemporaneous recruitment failure (Bascompte et al. 2002).

Smaller MPAs do entail at least one cost that is rarely addressed. Most models assume complete displacement of fishing effort into open areas after implementation of the MPA (e.g., Polachek 1990; Demartini 1993; Guenette & Pitcher 1999; Sladek Nowlis & Roberts 1999; Crowder et al. 2000; Pezzey et al. 2000; Sanchirico & Wilen 2001; Gerber et al. 2002; Lockwood et al. 2002). However, noncompliance will undoubtedly result in some fishing inside MPA boundaries, which can reduce the potential benefits of the MPA for both conservation and fisheries management (Roberts 2000). Illegal fishing within MPAs will most likely occur near the periphery, as a result of accidental straying across the boundary, ease of access from external locations, or violators risking entering a closed area up to a distance from which they feel they can quickly exit (Peres & Terborgh 1995; Gribble & Robertson 1998).

Boundary effects result in ecological changes generated at the perimeter of reserves. These include shifts from natural to anthropogenically modified habitats (e.g., Schonewald-Cox & Bayless 1986) and gradients of density and body size of exploited species (e.g., Chapman & Kramer 1999). The magnitude of boundary effects will be lessened in larger MPAs as a result of a lower ratio of perimeter to area. In other words, larger MPAs will have a greater amount of well-protected and largely unaffected area relative to the amount of peripheral area affected by noncompliant behavior. Therefore, if larval dispersal is a relatively small-scale process, then there is a discord between the MPA network design that will best achieve replenishment of fished areas and that which will provide the greatest degree of protection from illegal fishing and edge effects.

On the surface, considering the potential conflict between dispersal ecology and noncompliance appears to place MPA design issues in the context of the SLOSS (single large or several small) debate that occupied terrestrial conservation biology in the 1970s and early 1980s. However, SLOSS deals primarily with protection of biodiversity and seeks the reserve-network design that will house the greatest number of species (Soulé & Simberloff 1986; Simberloff 1988). In contrast, and despite my use of the SLOSS terms “single large” and “several small,” I examined the effects of network design on the population dynamics of a single species. Thus, I adopted a more autecological perspective more closely aligned with population viability analysis, which largely superceded SLOSS (Soulé & Simberloff 1986; Simberloff 1988). I examined how reserve size, number, and arrangement interact with dispersal patterns and extrinsic influences (fishing and stochastic variability in recruitment) to determine population dynamics.

I used a spatially structured model of a hypothetical marine population and fishery to examine the replenishment benefits of several small MPAs, assuming localized dispersal, as they contrasted with the enforcement benefits of a single large MPA, assuming that illegal fishing occurs primarily near MPA boundaries. I adopted an approach similar to that of Sanchirico and Wilen (2001) and Gerber et al. (2002) and examined the effects of alternative network designs in terms of conservation benefits, measured as the mean annual population size within MPAs, and fisheries benefits, measured as the mean annual yield. Furthermore, I examined the effects of different MPA network designs on the temporal variability in both population size within MPAs and yield.

Methods

Population Structure and Dynamics

The hypothetical population I modeled was composed of distinct breeding groups, each within one of 64 cells

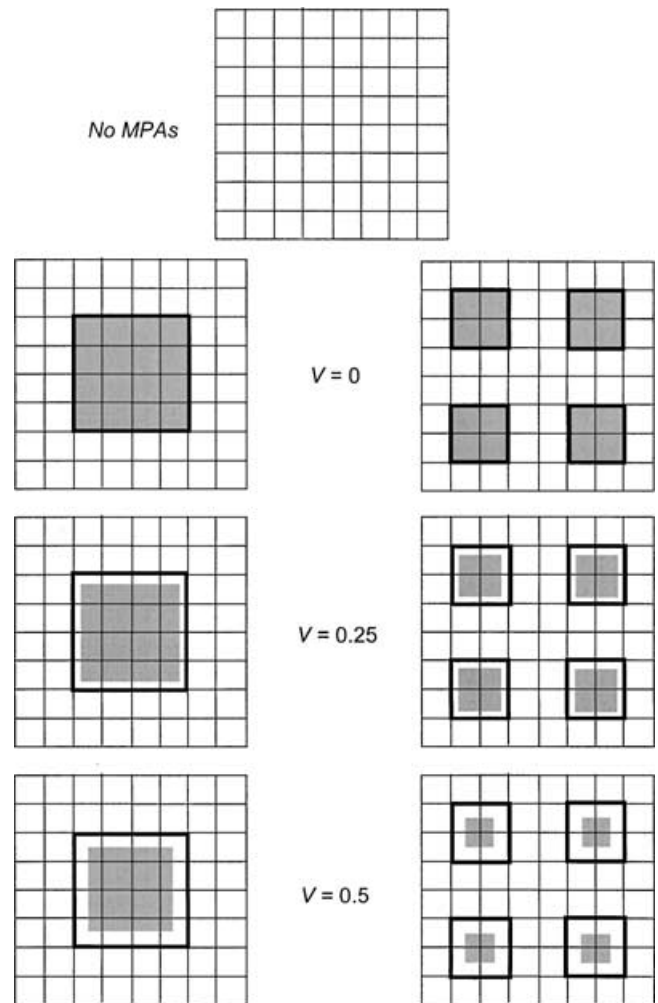


Figure 1. Model of the 8 × 8 cell geographic range of the hypothetical fish population (top). The lower three pairs of grids illustrate the area effectively protected (shaded) by the single large (left side) and several small (right side) marine protected area (MPA) network designs under different values of the violation distance parameter, V (expressed as a proportion of cell width). Thick lines represent the MPA boundaries.

in an 8 × 8 cell geographic range (Fig. 1). Individuals were sedentary within a cell after completing the pelagic larval stage, so all intercell exchange occurred during the larval stage. Larval dispersal was short-distance with high local retention, and export was only to adjacent cells. Minor dispersal beyond adjacent cells was not considered because my focus was on localized dispersal scenarios, and infrequent extreme transport events have little effect on population dynamics or MPA benefits (Lockwood et al. 2002). Proportional supply to adjacent cells is constant across all cells, so a portion of the larvae produced by cells on the periphery were lost to the system (Crowder et al. 2000).

The model was structured by age. Survivorship during the first year of life in each cell is a density-dependent function of initial cohort size:

$$N_1 = \frac{N_0 \cdot S_{0-1}}{1 + \frac{S_{0-1}}{K_{0-1}} \cdot N_0},$$

where N_0 is cohort size at settlement, N_1 is cohort size at age 1, S_{0-1} is the maximum annual survivorship of new settlers (i.e., slope of the function at the origin), and K_{0-1} is the carrying capacity of new settlers (Doherty 2002). After the first year of life, annual survivorship, S_{1+} , was constant up to the maximum age, t_{\max} . Production of larvae that survive to settlement, L , was directly proportional to the number of individuals within a cell greater than or equal to the age at maturity, t_{mat} .

Environmental stochasticity was introduced by modifying larval supply to each cell. Each cell was initially allocated a random variate from a log-normal distribution (Doherty 2002) with a mean of 1 and coefficient of variation, CV_L ($= SD \times 100$ when mean = 1), of 150%. However, because variability in larval supply is likely to be more similar among neighboring populations than distant ones, the final value used to modify larval supply to each cell was the mean of its own initial random variate and those of all adjacent cells. This produced unique modifiers for each cell that were correlated with other cells as a function of distance (c.f. modeling of spatially correlated fire outbreaks by McCarthy and Lindemeyer 1999).

Parameter values are given in Table 1. Empirical data for coral reef fishes were used to select S_{0-1} (reviewed by Doherty 2002), S_{1+} , t_{mat} , and t_{\max} (e.g., Sheaves 1995; Hart & Russ 1996; Kritzer 2002). The carrying capacity of new settlers was arbitrary and essentially scaled population size. When population size was small, the per capita rate of production of settling larvae ($=6$ fish) yielded approximately 2.25 new age-2 spawners after 1 year of mortality as a new settler and 1 year of mortality as a subadult. This conforms to the finding of Myers et al. (1999) that the per capita rate of production of new recruits at small population sizes is between 2 and 3 for many marine fishes. The value of CV_L ($=150\%$) produced time series of recruitment to the spawning population that had CVs between 50% and 100%. This falls within the range of most values for CV of recruitment reported for marine fishes (Myers 2002). Larval transport parameters simulated localized dispersal. The analysis compared two levels of self-recruitment, p_{self} , at 20% and 50% (e.g., Jones et al. 1999), and associated levels of export to adjacent cells, p_{adj} .

Fishing Mortality and MPA Designation

In the absence of MPAs, fishing effort was applied equally to all cells. The instantaneous fishing mortality rate, F , of age classes 2 and up was assumed to be directly proportional to effort and ranged from 0 to 1.0 per year (Table 1). Catchability was assumed to be knife-edged at t_{mat} . When

Table 1. Parameter values used in a spatially structured model of a marine population and fishery.

Parameter	Value(s)
Per capita production of settling larvae, L	6 fish
Proportion of larval retention, p_{self}	0.5, 0.2
Proportion of larvae dispersed to adjacent cells, p_{adj} *	0.0625, 0.1
Coefficient of variation in larval supply, CV_L	150%
Maximum survivorship of new settlers, S_{0-1}	50% per year
Carrying capacity of new settlers, K_{0-1}	1000 fish per cell
Maximum age, t_{\max}	15 years
Post-settler survivorship (ages 1+), S_{1+}	76% per year
Age at maturity, t_{mat}	2 years
Age at first capture, t_c	2 years
Instantaneous fishing mortality rate, F	0–1.0 per year
Distance fished into a reserve cell, V	0, 0.25, 0.5 cell width

* Calculated as $(1 - p_{\text{self}})/8$.

MPAs were implemented and there was full compliance, the fishing effort that would have been applied to cells in MPAs was redistributed equally among all open cells. When there was violation of MPA closures, only a proportion of the effort that would be applied in the absence of MPA designation was redistributed, whereas the remaining effort was applied within the MPA cell.

The proportion of effort that was redistributed was equivalent to the area of the cell that was beyond the limits of illegal fishing (Fig. 1). This was a function of a parameter for the distance into an MPA that violation will occur, V , and the position of a cell in the MPA. The proportion of effort redistributed from corner cells was $1 - 2V + V^2$ (i.e., the area of a “safe” square with sides of $1 - V$), and the proportion redistributed from edge cells was $1 - V$ (i.e., the area of a “safe” rectangle with sides of 1 and $1 - V$) (Fig. 1). Central cells experienced no illegal fishing (Fig. 1). The proportion of effort redistributed would be 0 for all $V \geq 1$, but $V > 0.5$ progressively replicated the no-MPA situation and were not considered herein (Table 1). In all simulations, cell-specific fishing mortality was held constant over the time series, which was undoubtedly a simplification of real fishing behavior. There is evidence, however, that fishers are more likely to fish areas they have fished in the past, even when presented with information on potentially more productive sites, so fishing patterns by individuals can show considerable stasis over short to medium temporal scales (Holland & Sutinen 2000).

Marine-protected-area scenarios included no MPAs and two MPA network designs. Each housed the same total proportion of habitat area (16 cells = 25%): a single large 4×4 cell MPA (SL) and four smaller 2×2 cell MPAs (SS) (Fig. 1). The SS design positioned each fished cell in contact with at least one MPA cell, but the overall perimeter-to-area ratio was 2:1. The SL design had a perimeter-to-area ratio of only 1:1, but all peripheral cells were not in direct contact with any MPA cells and relied

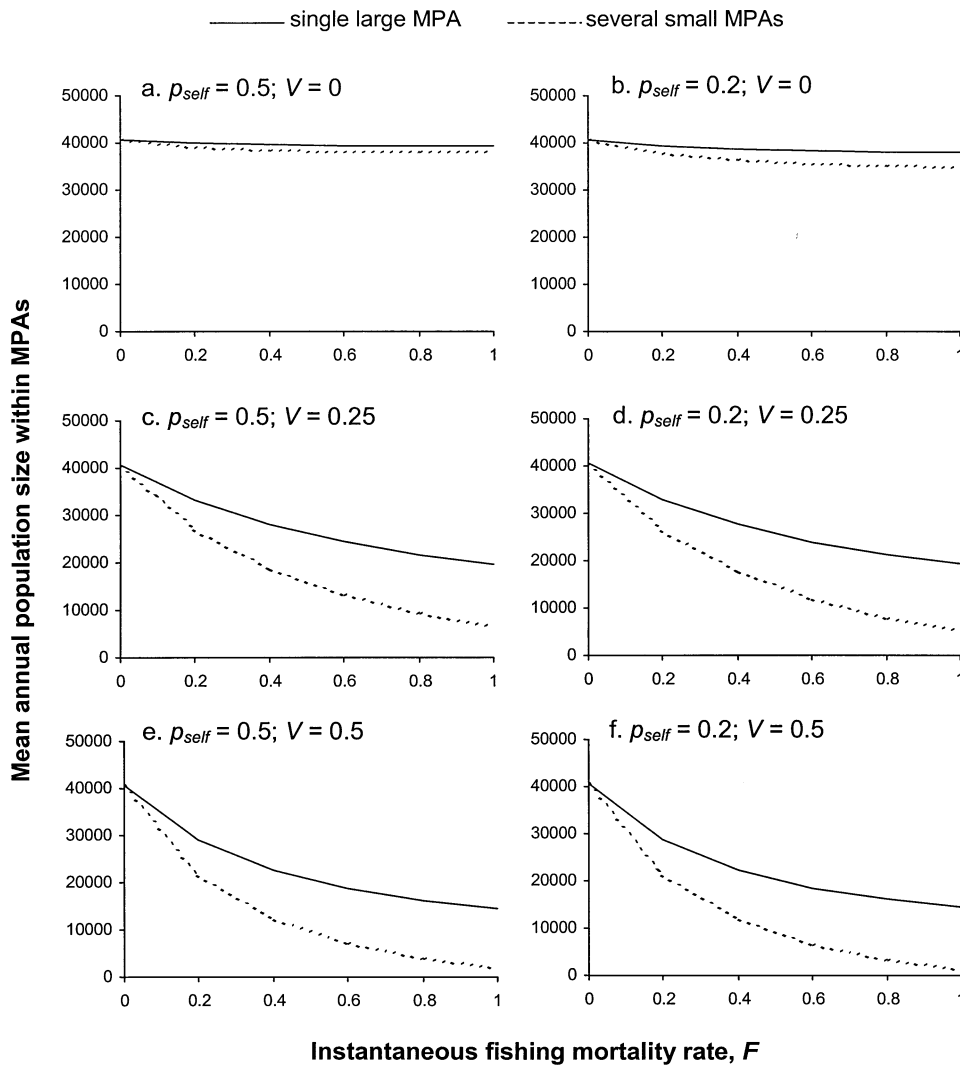


Figure 2. Mean annual size of the total fish population housed within marine protected areas (MPAs) over the final 20 years among 100 replicate simulations against instantaneous fishing mortality rate with either a single large MPA or several small MPAs at two levels of proportional self-recruitment, p_{self} , and three levels of violation distance, V .

solely on other fished cells for replenishment beyond self-recruitment.

Modeling Approach

The model was initialized with 500 new settlers per cell and then run without human impacts for 20 years to fill all age classes. Thereafter, the model was run for an additional 30 years incorporating fishing mortality, MPA designation, and illegal harvest. Two response variables were recorded over the final 20 years of each time series: the average annual size of the total population contained within MPA boundaries, as an index of conservation benefits, and the average annual yield, as an index of fishery benefits. Also, the CVs of the two metrics over the final 20 years were recorded.

I report the average of each response variable and their CVs over 100 replicate time series for each combination of p_{self} , V , and F with each of the three MPA scenarios. The focus was on p_{self} , V , and F because these are the most topical parameters in the context of the objectives of this study. To assess the generality of the results, however, I

ran additional simulations that used alternative values of the biological parameters reported in Table 1.

Results

Conservation Benefits

When no MPAs were established, all animals were exposed to fishing (assuming no natural refuges). Therefore, the conservation objective of protecting some components of the population from direct fishing mortality was not achieved. When MPAs were implemented and there was perfect compliance, the SL and SS designs protected populations of comparable size (Fig. 2a & 2b). Furthermore, the size of the protected populations changed little from the natural state (i.e., with $F = 0$) over the range of F considered (Fig. 2a & 2b). This suggests that self-recruitment combined with replenishment from the three neighboring MPA cells in the SS design was sufficient to maintain nearly the largest population possible in an MPA cell under either pattern of larval dispersal considered.

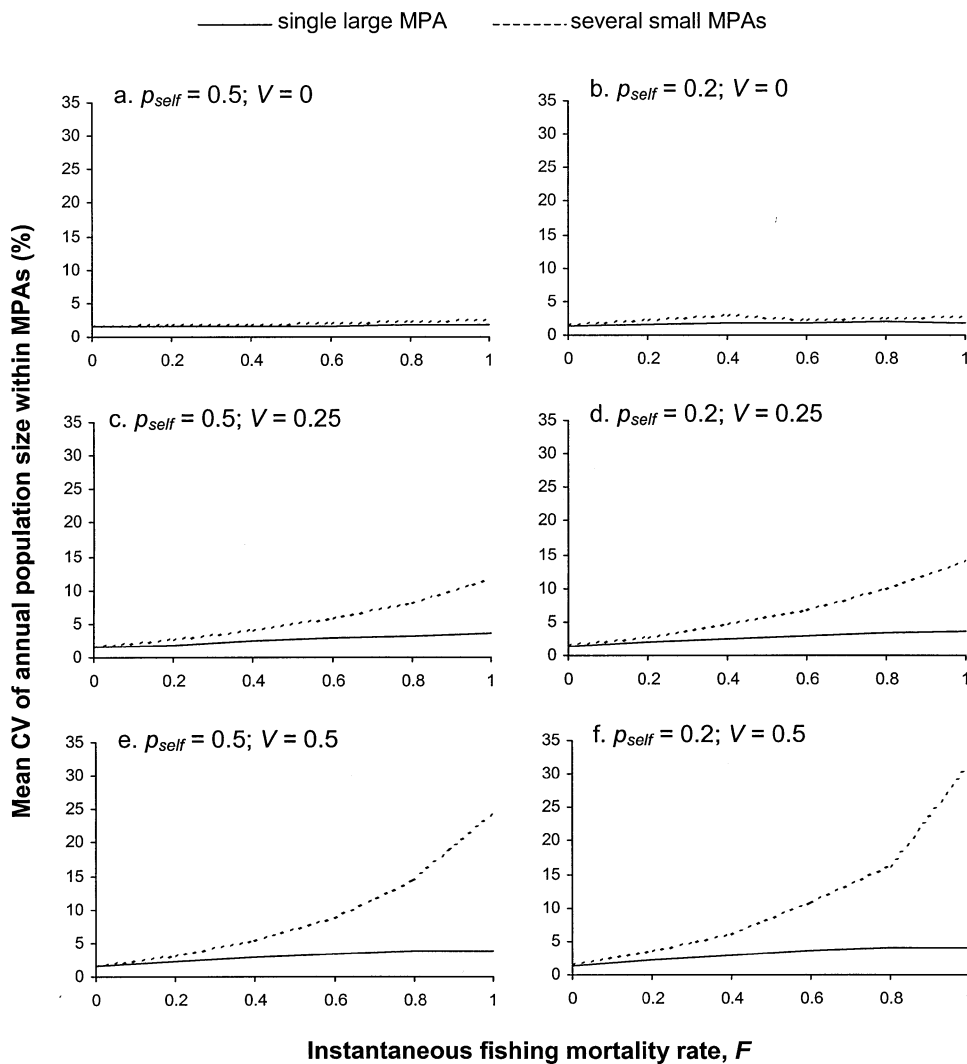


Figure 3. Mean coefficient of variation (CV) in the annual size of the total fish population housed within MPAs over the final 20 years among 100 replicate simulations against instantaneous fishing mortality rate with either a single large marine protected area (MPA) or several small MPAs at two levels of proportional self-recruitment, p_{self} , and three levels of violation distance, V .

When noncompliance was introduced, conservation benefits rapidly deteriorated (Fig. 2c-f). However, the rate of decline in the size of the protected population was much less drastic with the SL design than with the SS design. With the SL design, the proportion of virgin population size remaining at the highest F ranged from around 35% to over 50%, depending on the values of V and p_{self} (Fig. 2c-f). In contrast, the size of the protected population approached zero with the SS design when $V = 0.5$ (Fig. 2e & 2f). The extent of the decline in conservation benefits as noncompliance increased was partially dependent on dispersal patterns. For both the SL and SS designs, decreases from the values assuming full compliance were slightly greater when $p_{self} = 0.2$ than when $p_{self} = 0.5$ (Fig. 2c-f).

Temporal variability in population size within MPAs was low at all levels of F for both the SL and SS designs with full compliance, and, like the patterns for MPA population size, the degree of variability was similar between the two designs (Fig. 3a & 2b). Although population size within MPAs declined with the SL design as violation rate increased (Fig. 2), there was surprisingly little change in

temporal variability of MPA population size (Fig. 3). In contrast, with the SS design, temporal variability in population size within MPAs increased drastically as violation rate increased, with CVs in excess of 20% at $F = 1.0$ per year and $V = 0.5$ (Fig. 3). Furthermore, temporal variability became much greater as V and F increased with lower proportional self-recruitment ($p_{self} = 0.2$; Fig. 3c-f), illustrating the importance of self-recruitment in stabilizing local population dynamics in open systems.

Fisheries Benefits

Introducing noncompliance was not a factor when no MPAs were in place, so fishery yield (Fig. 4) and temporal variability in yield (Fig. 5) for the no-MPA scenario were constant across V values for a given F and p_{self} . In contrast, yield to the fishery with MPAs was a function of V , F , and p_{self} (Fig. 4). For each combination of V and p_{self} , yield at the lowest levels of F considered (0.2 and 0.4 per year) was maximal or nearly so without MPAs (Fig. 4). However, with the exception of $p_{self} = 0.5$ and $V = 0$ (Fig. 4a),

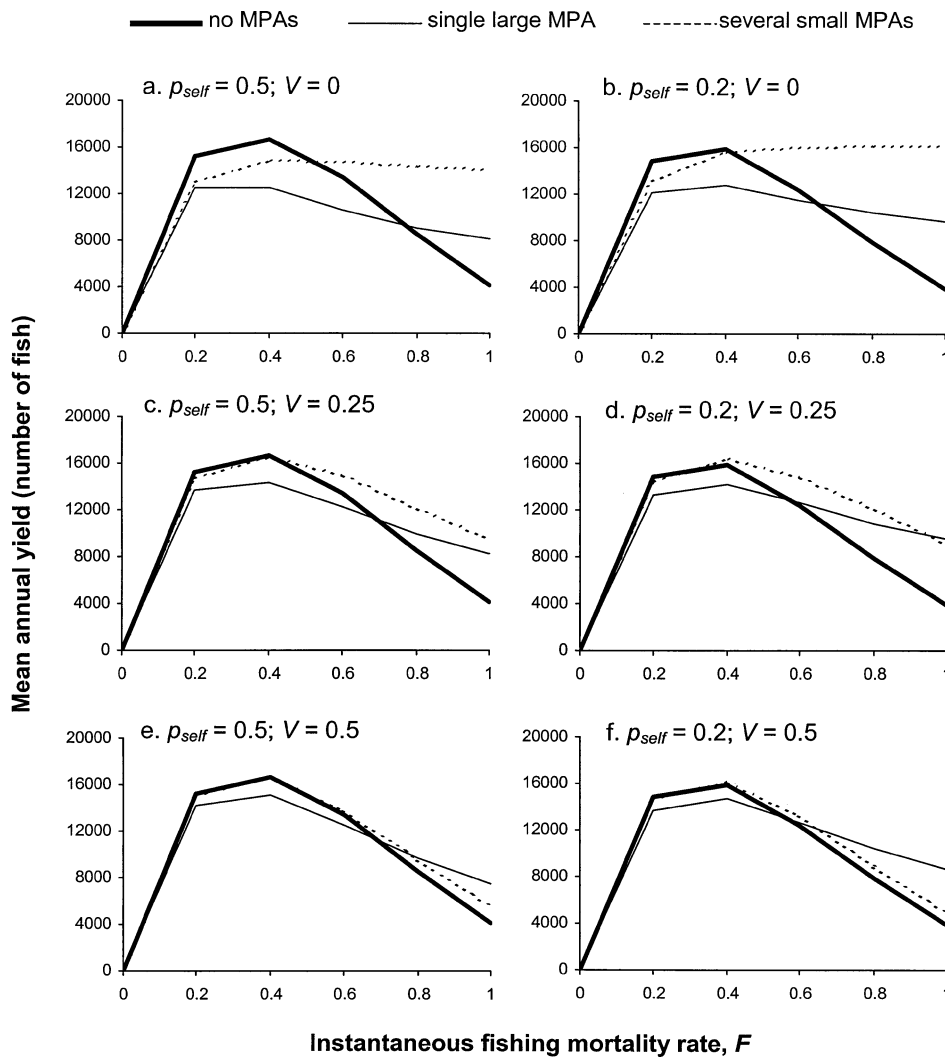


Figure 4. Mean annual yield of fish over the final 20 years among 100 replicate simulations against instantaneous fishing mortality rate with either no marine protected areas (MPAs), a single large MPA, or several small MPAs at two levels of proportional self-recruitment, p_{self} , and three levels of violation distance, V .

yield with the SS design was close to that without MPAs at $F = 0.2$ and 0.4 per year (Fig. 4b-f), so there was no significant advantage for fisheries in not implementing MPAs. However, yield was much less with the SL design at these lower levels of F (Fig. 4).

As F increased, yield in the absence of MPAs declined markedly (Fig. 4). With full compliance, yield with both the SS and SL designs remained high and declined little (Fig. 4a & 4b). In fact, when $p_{self} = 0.2$ and $V = 0$, yield with the SS design continued to increase slightly as F increased (Fig. 4b). Moreover, yield was always much higher with the SS design when $V = 0$ (Fig. 4a & 4b). When violation of MPAs was introduced, yield with the SL design changed little from the full-compliance scenario (Fig. 4). Yield with the SS design exhibited a sharp drop and progressively approximated the no MPA results (Fig. 4c-f). When $V = 0.25$ and $p_{self} = 0.5$, yield was still higher with the SS design at all F considered but was nearly equal the SL design at $F = 1.0$ per year and declined more steeply (Fig. 4c). When $V = 0.25$ and $p_{self} = 0.2$, yield with the SS design dropped below the SL design at $F = 1.0$ per year (Fig. 4d). When $F = 0.8$ per year and $V = 0.5$, yield

with the SS design fell below that with the SL design in both dispersal scenarios, but the differences were much greater when $p_{self} = 0.2$ (Fig. 4e & 4f).

Temporal variability in yield increased dramatically with increasing F in the absence of MPAs (Fig. 5). In contrast, yield was much more stable through time with either the SS or SL network at all combinations of F , V , and p_{self} (Fig. 5). Furthermore, like the results for temporal stability of the population size within MPAs (Fig. 3), temporal variability in yield was always low and changed little with the SL design, regardless of the values of other parameters (Fig. 5). Also, temporal variability in yield was actually slightly less with the SS design with full compliance (Fig. 5a & 5b). This difference might have been expected to be even more pronounced given the spatial correlation in variability in larval supply in the model and consequent risk spreading of the SS design. Variability in yield with the SS design remained close to that with the SL design up to $F = 0.6$ per year, even at the highest level of V (Fig. 5c & 5f), likely due to a trade-off between the risk-spreading benefit and the greater susceptibility to noncompliance. At $F = 0.8$ and 1.0 per year, variability in yield was still similar

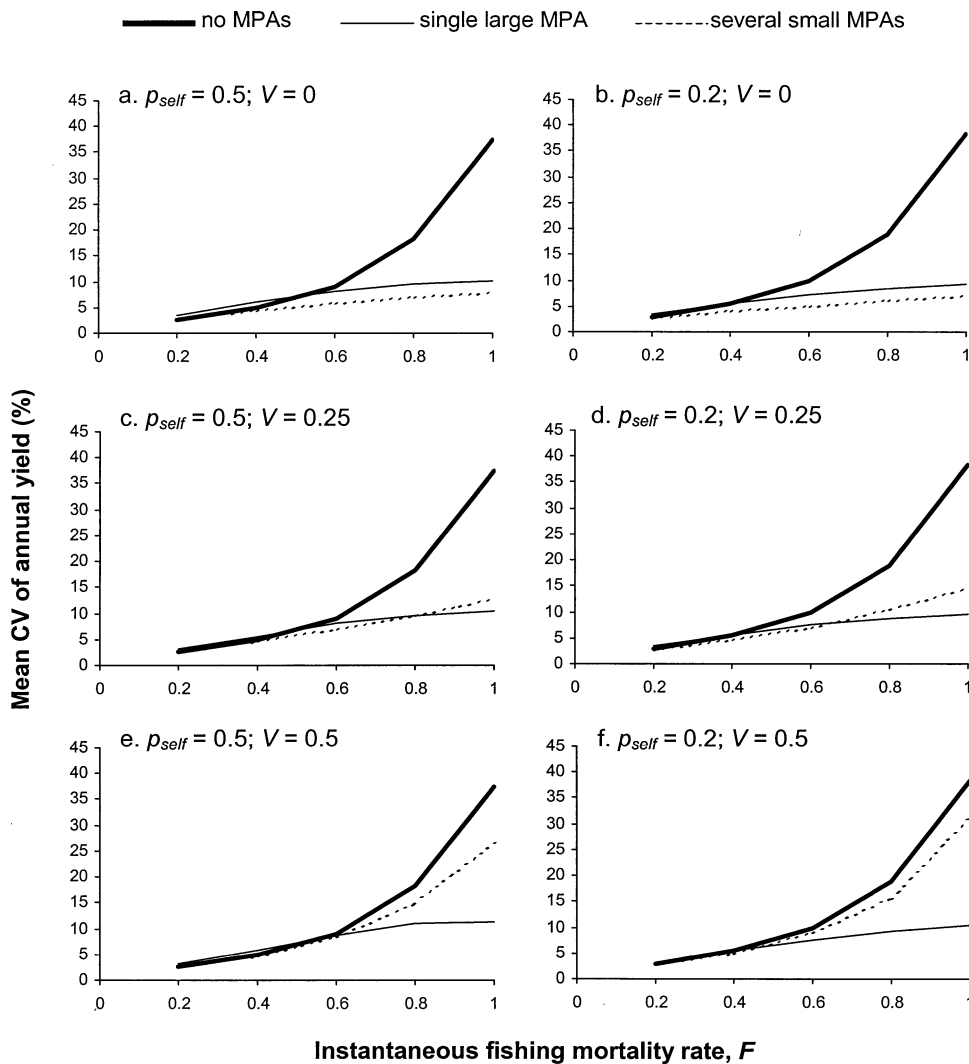


Figure 5. Mean coefficient of variation (CV) of annual yield of fish over the final 20 years among 100 replicate simulations against instantaneous fishing mortality rate with either no marine protected areas (MPAs), a single large MPA, or several small MPAs at two levels of proportional self-recruitment, p_{self} , and three levels of violation distance, V .

between the SS and SL designs when $V = 0.25$ (Fig. 5c & 5d). Differences became greater, however, when $V = 0.5$, particularly when $p_{self} = 0.2$ (Fig. 5e & 5f).

Effects of Different Biological Parameter Values

Changing the various biological parameters affected the quantitative results of the model, but in all cases the qualitative patterns were the same as those reported above. The nature of the quantitative differences were predictable from the nature of the parameter changes. Any parameter change that diminished the replenishment potential of the stock lowered the value of the protected population size and yield and raised the CV of each. Such changes included increasing t_{mat} and reducing t_{max} (and therefore increasing S_{1+}), S_{0-1} , L , and t_c . Opposite changes in these parameters had opposite effects on the response variables. These parameter changes also changed the levels of F and V , at which including MPAs produced higher yield than not including MPAs and at which the SL design performed better than the SS design in terms of both conservation and fisheries metrics. The

general trends remained the same, however: increasing F progressively made MPAs preferable to no MPAs, and increasing V progressively made the SL design preferable to the SS design.

Discussion

Inadequate enforcement is frequently implicated when MPAs fail to demonstrate expected benefits (e.g., Jennings et al. 1996; Acosta 2001; Rogers & Beets 2001). These results suggest that this implication has merit: noncompliance can erode the potentially positive effects of MPAs for both conservation and fisheries management. Gerber et al. (2003) argue for the importance of mathematical models in providing short-term guidance for MPA design in light of the large spatial and temporal scales on which the dynamics of open marine systems operate and the associated difficulties of conducting empirical research within the time frames needed to address management needs. Gerber et al. (2003) also identify six key ecological questions that future MPA modeling efforts need to

address. To their list should be added questions related to the effects of noncompliance on MPA efficacy and how these effects differ among alternative spatial configurations of MPAs. My study takes a first step toward answering those questions.

Effects of Noncompliance on Population Size and Yield

Simulated benefits of MPAs assuming full compliance conformed to expectations and previous modeling results. At low F , yield without MPAs was higher or comparable to yield with the SS design (c.f. Guenette & Pitcher 1999; Sladek Nowlis & Roberts 1999). Without MPAs, however, all components of the harvested stock were affected by fishing, so there was no conservation of natural population structure. At low to intermediate F , the difference between yield without MPAs and with the SS design was minor, and it would likely be of broader social benefit to sacrifice any small differences in yield by implementing an MPA network to achieve large gains for conservation and other nonextractive objectives (Roughgarden & Armsworth 2001). With full compliance, the SS design achieved conservation benefits comparable to those of the SL design and fisheries benefits in excess of those of the SL design and comparable to those of the no-MPA design. This supports the argument that smaller, more numerous, and more widely distributed MPAs are preferable when larval dispersal is localized.

Violation of spatial closures shifted relative success from the SS toward the SL design but caused diminished conservation benefits of the SS network before diminished fisheries benefits (i.e., at lower F). Likewise, population size within MPAs declined more precipitously with either network design as noncompliance increased relative to changes in yield. This means that, when noncompliance is having an effect, conservationists are likely to denounce the efficacy of a given network and call for increased spatial coverage or a different network design, whereas the fishing industry remains content with current "effectiveness." It will therefore be important to account for the magnitude of noncompliance and the spatial origins of harvested fish when assessing MPA success to discern whether high fishery yields are due to replenishment from MPAs or fishing within their boundaries.

Temporal Stability of Population Size and Yield

The single large MPA was robust to the effects of noncompliance. Only mean population size within MPAs showed appreciable change as violation distance increased, so conservation objectives suffered the most from noncompliance. This decline was not accompanied by large increases in temporal variability, however, and temporal variability in yield likewise showed little change with increasing F or noncompliance with the SL design. The capacity for MPAs to stabilize population size and yield has received less attention than their capacity to enhance ei-

ther, but such stabilization has important implications. Less temporal variability in yield provides fishers with more predictable annual income and allows better future planning of investment and effort (e.g., Li 1998; Holland & Sutinen 2000; but see Ward & Sutinen 1994). Extinction risk typically increases with increasing population fluctuations (Foley 1994), so dampening these fluctuations can reduce that risk. Management efforts are also complicated by high variability in stock size. Miller (1996) describes how allocation of Pacific salmon among U.S. states, Canadian provinces, and coastal tribes in both countries becomes contentious when natural and anthropogenic factors combine to increase uncertainty in year-to-year stock size. Therefore, any strategy for minimizing population variability can have tremendous benefits on multiple fronts.

The few previous modeling studies that have examined the effects of MPAs on temporal variability in population size and yield all similarly illustrate that MPAs play an important role in reducing temporal fluctuations. The bioeconomic model of Pezzey et al. (2000) showed that fluctuations actually increased at first after implementation of an MPA as a result of initial spatial shifts in fishing effort. However, fluctuations were eventually considerably dampened with an MPA compared with no MPA. Guenette and Pitcher (1999) and Sladek Nowlis and Roberts (1999) measured temporal patterns by the number of poor recruitment years and the CV of annual catch, respectively. Results from both studies showed that variability was always minimized with MPAs and that the degree of reduction increased with increasing proportional coverage of the MPA. My results corroborate these previous findings but also illustrate that fluctuations in MPA population size can be dampened to a greater degree than fluctuations in yield, further strengthening the conservation importance of MPAs. Moreover, the effects can be comparable with either SL or SS network designs, unless violation rates are high. Then, a single large MPA is much more effective at stabilizing temporal changes.

Policy Implications and Future Directions

An important aspect of convincing resource users that restrictions will be beneficial in the long term is the ability to predict benefits and then demonstrate that those benefits have accrued. Failure to achieve management objectives can weaken the perceived legitimacy of a management body in the eyes of stakeholders. Often, incongruence between expectation and reality in the management of natural resources is attributed to the ecological complexity and uncertainties inherent in exploited systems. However, noncompliance can also be an important determinant of whether predicted and realized benefits equate, and must be accounted for when MPA success is measured. Therefore, a general lesson for development of marine policy arising from my study is that noncompliance

needs far more attention than it currently receives, both in management-oriented research and in development and assessment of management strategies (Hemming & Pierce 1997). Social scientists have made important progress in understanding the causes of noncompliance. This understanding can help reduce noncompliance, thus preserving the benefits of the most ecologically advantageous MPA network design.

The expectation that illegal activity will be detected is an important determinant of the decision to commit violations (Sutinen et al. 1990; Furlong 1991; Hart 1997; Kuperan & Sutinen 1998), so more effective surveillance can reduce noncompliance. The risk of detection and the costs it will incur will be weighed against expected income from illegal fishing. Hence, the penalty structure and potential profits attainable in open and closed areas will influence the relative benefits of illegal fishing (Sutinen et al. 1990; Furlong 1991; Kuperan & Sutinen 1998). Also, an important factor in many fisheries is the perceived attitudes of managers and inspectors toward fishers, which partly determine the attitude of fishers toward regulations (Sutinen et al. 1990; Furlong 1991; Kuperan & Sutinen 1998; Honneland 2000). In addition to surveillance and punishment, therefore, education, outreach, and increased fisher participation in the management process can reduce noncompliant behavior (Jentoft & McCay 1995; Alder 1996; McCay & Jentoft 1996; Sen & Neilsen 1996).

My results and those from a limited number of other studies (Gigliotti & Taylor 1990; Die & Watson 1992) illustrate that different violation rates can dissipate the potential benefits of management regulations to varying degrees. Information on the determinants of noncompliant behavior should now be used to build behavioral models that can be integrated with ecological models, allowing noncompliant behavior to become a more dynamic process in the model and resulting in more realistic context-specific models of the overall fishery system (Liu 2001). Such models can then be used to determine whether empirical estimates of noncompliance rates (figures that are rare, but see, for example, Sutinen et al. 1990; Schill & Kline 1995) represent a significant impediment to achieving management objectives. Depending on the specific, quantitative objectives of a particular management regime, some degree of illegal fishing might still allow the objectives to be attained, and it therefore might not be worth the expense of further reducing noncompliance (Sutinen & Andersen 1985). This can only be determined by defining quantitative objectives, evaluating the ecological effects of different violation rates relative to those objectives (either through modeling or adaptive-management experiments), and estimating the current level of illegal fishing to see if additional reduction is needed. This calls for greater collaboration among ecologists, social scientists, resource managers, and stakeholders in best designing and implementing MPA networks.

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