

IMPACTS OF DISPERSAL, ECOLOGICAL INTERACTIONS, AND FISHING EFFORT DYNAMICS ON EFFICACY OF MARINE PROTECTED AREAS: HOW LARGE SHOULD PROTECTED AREAS BE?

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ABSTRACT

Management for sustainable fisheries requires effective tactics for limiting exploitation rates. Limitation based on annual stock assessments and total allowable catches calculated from these assessments can be very dangerous, and marine protected areas (MPAs) are one means by which to limit exploitation rate directly even when total stock size is highly uncertain. This application of MPAs would probably require much larger areas than are now envisioned for limited objectives related to protection of seed spawning stock and local biodiversity. It might in fact cause a basic shift in thinking—from regarding MPAs as exceptional areas to regarding fishing areas as the exception (as is now the practice in, e.g., salmon and herring fisheries). The present paper describes the use of ECOSPACE, a new modeling tool based on ecosystem simulations, for preliminary determination of how large MPAs need to be; ECOSPACE models suggest that dispersal, trophic responses (prey depletion, increased dispersal of predators in response to competition), and spatial fishing-effort responses (concentration of fishing near MPA boundaries) are all likely to reduce the effectiveness of small MPAs. The models suggest we should see not simple high-low density differences across MPA boundaries but rather spatial gradients from low density in exploited areas to high density near the centers of larger MPAs. Such spatial density gradients should be accompanied by spatially organized ‘trophic cascade’ patterns if trophic interactions are important determinants of abundance. MPA design can work with or against spatial variation in fishing effort caused by economic cost and risk factors; ECOSPACE can help to demonstrate ecological consequences of alternative design strategies, but the most important uncertainties are about socioeconomic responses (cooperation or competition) rather than ecological ones. Design of experimental policies and monitoring programs for evaluation of MPAs should proceed from careful modeling to define likely spatial, temporal, and trophic scales for both ecological and fishing responses.

A revolution is underway in thinking about how to design safe and sustainable policies for fisheries harvesting. Sad case studies (e.g., Walters and Maguire, 1996) and policy failures are beginning to teach us that very few natural populations can be adequately managed on the assumption of the old unit stock concepts—a well-mixed pool of fish with a stable production or recruitment relationship that produces a set of alternative stable population sizes dependent on harvest rates and some single level that produces the highest average yield. Instead, we generally see complex spatial stock structure that can erode over time under fishery development, production relationships that vary on long time scales with changes in environmental and trophic conditions, and harvest rates that can vary in pathological ways over time (e.g., depensatory effects) because of inadequate assessment systems and incomplete control of fishing activities. Our thinking about how to deal more effectively and safely with these complexities is resulting in a variety of controversial recommendations, ranging from large marine protected areas (Walters, 1998) to fixed-exploitation-rate strategies (Walters and Parma, 1996) to ecosystem accounting

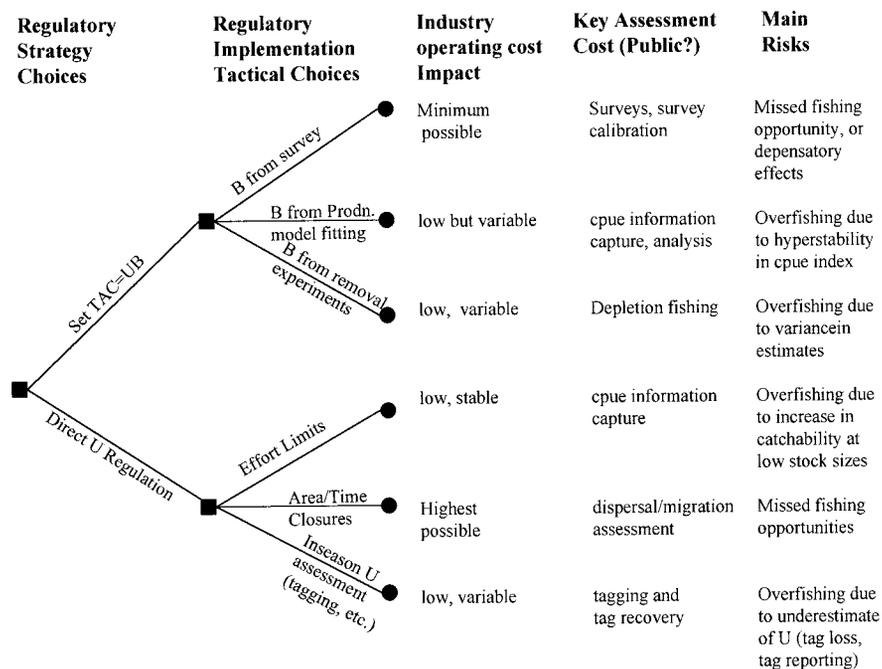


Figure 1. Options for attempting to achieve a target annual exploitation rate U (from Perry et al., 1999).

and management approaches that attempt to account for much more than the direct effects of fishing. Public support has been considerable for innovative policy approaches to fisheries conservation and restoration, at least as adaptive-management experiments, despite the lack of good data and modeling tools with which to justify these approaches. That support could evaporate as the harsh social and economic impacts of effective regulation become apparent, unless we can begin to demonstrate clearly that long-term gains will outweigh such impacts.

Simulations of long-term management of populations in variable physical and trophic environments (long-term regime changes) suggest that a very simple, basic strategy should provide nearly optimum long-term yields: maintain a fixed exploitation rate (catch/stock), at a relatively small fraction (0.5–0.8) of the natural mortality rate (Walters and Parma, 1996; Walters and Pearse, 1996). A key issue is how to achieve this strategy. The two general approaches are shown in Figure 1 (Perry et al., 1999): (1) do annual stock assessments and set total allowable catches (or quotas) at a constant fraction of estimated abundance and (2) directly regulate exploitation rate by limiting the proportion of fish exposed to risk of harvest, by having large protected areas. A few success stories in fisheries management have apparently been due to a major reversal in thinking (Fig. 2), in which we have come to view the ocean as generally protected from fishing and have treated fishing areas as the small, local exceptions (Walters, 1998).

If fisheries managers are going to advocate the use of large protected areas as a basic tool for limiting exploitation rates, they obviously need better modeling tools—models that can at least define minimum protected-area requirements in the face of ecological dispersal, effects on trophic interactions, and behavior of fishers. That is, we can expect protected areas to generate a variety of ecological effects and changes in distribution of

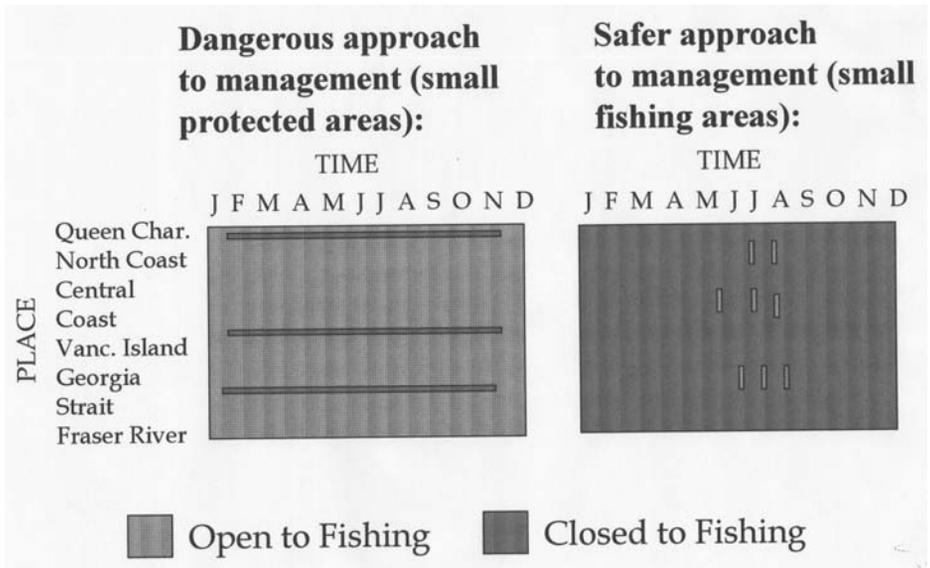


Figure 2. Sustainable fisheries management may eventually require a reversal of perspective, from thinking about protected areas as exceptional to thinking about fishing areas as exceptional. This perspective is already the norm in a few fisheries, such as commercial salmon and herring net fisheries along the British Columbia coast (from Walters, 1998).

fishing that cannot be represented simply by construction of spatial single-species models. Generally our knowledge of these factors is not sufficient to allow detailed quantitative predictions, but we should at least be able to provide models to 'screen' policy alternatives so as to provide clear alternative hypotheses about likely responses, eliminate options that could not possibly be effective (e.g., reserves that are too small), and help in design of monitoring programs for experimental policy evaluation (recommend where to look for effects, possible magnitudes).

My coworkers and I are developing an interactive 'gaming' simulation called "ECOSPACE" that is intended to provide an initial screening capability for protected-area options (Walters et al., 1999). The present paper provides an overview of how ECOSPACE works and reviews some of the disturbing findings that we have made in the first few months of playing with it. Preliminary versions of the model are available for download as part of the "ECOPATH with ECOSIM" software system for trophic mass-balance analysis (<http://www.ecopath.org>).

ECOSPACE METHODS

Recently there has been considerable growth in the use of ECOPATH methods (Polovina, 1984; Christensen and Pauly, 1992) to estimate trophic mass-balance relationships (biomasses and biomass fluxes in ecosystems) and to provide broad assessments of fishing impact on trophic structure of exploited ecosystems (Pauly et al., 1998), but ECOPATH provides only static snapshots of trophic structure. To provide a crude dynamic simulation capability, we developed a biomass-dynamics model called "ECOSIM" as a differential equation system that expresses biomass flux rates among ecosystem biomass pools (or 'compartments') as time-varying functions of biomass and of time-varying harvest

rates applied to one or more of the biomass pools (Walters et al., 1997). A key concept used in the design of ECOSIM is that predator-prey (resource-consumer) interactions can be moderated by prey behaviors that limit exposure to predation, so trophic flow patterns can exhibit either 'bottom-up' or 'top-down' (trophic cascade) control depending on how effective various prey behavioral tactics are at preventing increases in mortality rate with changes in predator abundance. ECOSIM has provided useful insights about the role of top predators in structuring marine food webs (Kitchell et al., in press) and about effects of fishing at intermediate trophic levels (Mackinson et al., 1997). We have recently extended ECOSIM to include age-structure and trophic ontogeny effects for selected species by representing such species as separate juvenile and adult numbers-biomass pools, using delay-difference modeling methods (Walters et al., 2000).

The essential idea in ECOSPACE is to replicate the ECOSIM biomass-dynamics equation system over a spatial grid of small, relatively homogeneous cells, while the spatial cells are linked through two processes: (1) dispersal of organisms and (2) spatial movement of fishing effort in response to changes in profitability of fishing (often a multispecies combined profitability) and creation of protected areas. The ECOSPACE model 'inherits' parameter estimates for trophic relationships (feeding and predation rates, diet compositions, primary production rates, detritus fates) from the ECOSIM dynamic model for a 'typical' spatial cell, which in turn is parameterized from an ECOPATH mass-balance assessment. The ECOSPACE user adds three types of information not needed for ECOPATH/ECOSIM: (1) estimates of spatial dispersal rates for each ECOPATH biomass pool, measured by mean annual movement distance of the organisms in that pool; (2) a spatial map (sketched over the cells with a computer mouse) defining land and water areas and hence constraints on movement patterns; and (3) a map (again sketched by mouse) defining areas closed to fishing. Model users can sketch three additional types of maps for more realistic simulations of spatial patterns: (1) spatial patterns of fishing costs so that modeled fishing effort will be reduced in high cost-cells, (2) relative primary productivity (e.g., upwelling and other nutrient-loading zones), and (3) arbitrary habitat-type codes. Biomass pools can be designated to 'prefer' certain habitat type(s); that is, organisms in nonpreferred cells can be assigned higher emigration rates, lower feeding rates, and higher vulnerability to predation. At present, dispersal is considered to be random in direction except for coastline constraints and higher likelihoods of movement toward nearby suitable habitats by organisms that are in unsuitable cells; we are attempting to develop methods to represent organized migration patterns (e.g., seasonal onshore and offshore movements) but have so far been unable to find efficient enough computational methods to simulate such patterns quickly in gaming contexts.

A factor that made ECOSPACE possible was discovery of a very efficient computational algorithm for quickly solving large systems of differential equations linked in space by movement 'fluxes' proportional to biomasses in source cells. For high movement rates, such equations are usually 'stiff' and can only be solved over very short time steps (a huge computational problem as shown, for example, by Ault et al., 1999; for general definitions and discussion of stiff equations, see Press et al., 1992: 727; Fletcher, 1991: 246). Our algorithm is based on the idea of treating the differential equation system as a forced linear system over short time steps; such linear systems move toward an equilibrium point that can be computed efficiently, and we found that the cumulative, nonlinear dynamic responses can be approximated as a series of such linear moves with nonlinear variation between moves in the equation forcing terms. The algorithm allows us to repre-

sent crudely the speed with which various biomass pools should change when marine protected areas are introduced and to calculate long-term (steady-state, mass-balanced) spatial biomass equilibria efficiently. The algorithm fails in some circumstances, in particular when local (single-cell) biomass dynamics are predicted to be naturally cyclic because of factors like cannibalism, but even in these cases the solution method provides useful perspectives about how quickly and over what spatial extent we should expect to see responses to protected area policies.

Another feature of ECOSPACE is use of a 'gravity model' (Caddy, 1975; Walters and Bonfil, 1999) for prediction of spatial effort distribution over the map cells. The basic idea in this case is to allocate a known (or policy) total effort over the cells such that each cell receives a fraction of the total proportional to an attraction weight for the cell. This weight is set to zero for cells that are protected from harvesting and otherwise to a value proportional to profitability of fishing (sum over biomass pools of prices times pool-specific cpue, less relative fishing cost for the cell). The gravity-model derivation is based on a proposition that the animals within each cell can be in two behavioral or microdistributional 'states', vulnerable and safe, and that exchange of individuals between these states is relatively rapid (Walters and Bonfil, 1999); such behavioral differentiation is probably typical for line fisheries (e.g., Zeller and Russ, 1998), and we argue (Walters and Bonfil, 1999) that it applies for trawling as well.

PREDICTIONS ABOUT IMPACTS OF MOVEMENT AND TROPHIC INTERACTION

ECOSPACE models are currently under development for a variety of coastal and pelagic ecosystems where trophic analyses had already been done by ECOPATH methods. For example, (1) L. Hernandez (Fisheries Centre, UBC) is drawing upon results from several ECOPATH analyses in the Gulf of Mexico region to construct a single ECOSPACE model for the entire Gulf, (2) C. Boggs (NMFS, Honolulu) and J. Kitchell (Univ. Wisconsin) are modeling the central Pacific pelagic region near Hawaii, and (3) T. Okey (Fisheries Centre, UBC) is examining oil-spill and fishery impacts on Prince William Sound, Alaska. We are also searching for situations in which to test the biomass predictions against spatial survey data gathered well after establishment of deliberate or accidental protected areas; for example, we are examining survey data gathered off the coast of Brunei, where oil-field development created a large area free from trawling.

Several general predictions of ECOSPACE can be illustrated with a simple hypothetical example, showing spatial variation in steady-state biomass along a transect through a marine protected area (Fig. 3). Figure 4 shows the simulated effect of adding successive complications to the prediction of steady-state biomass for a top predator fish along this transect.

First, if we omit spatial movement and consider only trophic effects of the MPA, the general prediction is that a spatial trophic cascade should become evident along the transect (Fig. 4, 2nd panel): increases in top predator biomass in the MPA should result in local depression of prey abundances, which in more complex ECOPATH trophic arrangements will in turn result in abundance at still lower trophic levels (not illustrated). That is, if trophic cascade effects are as important in marine ecosystems as they have been found to be in freshwater systems (Carpenter and Kitchell, 1993), then we should see such effects exhibited as spatial patterns in and surrounding MPAs. Such effects would not be ob-

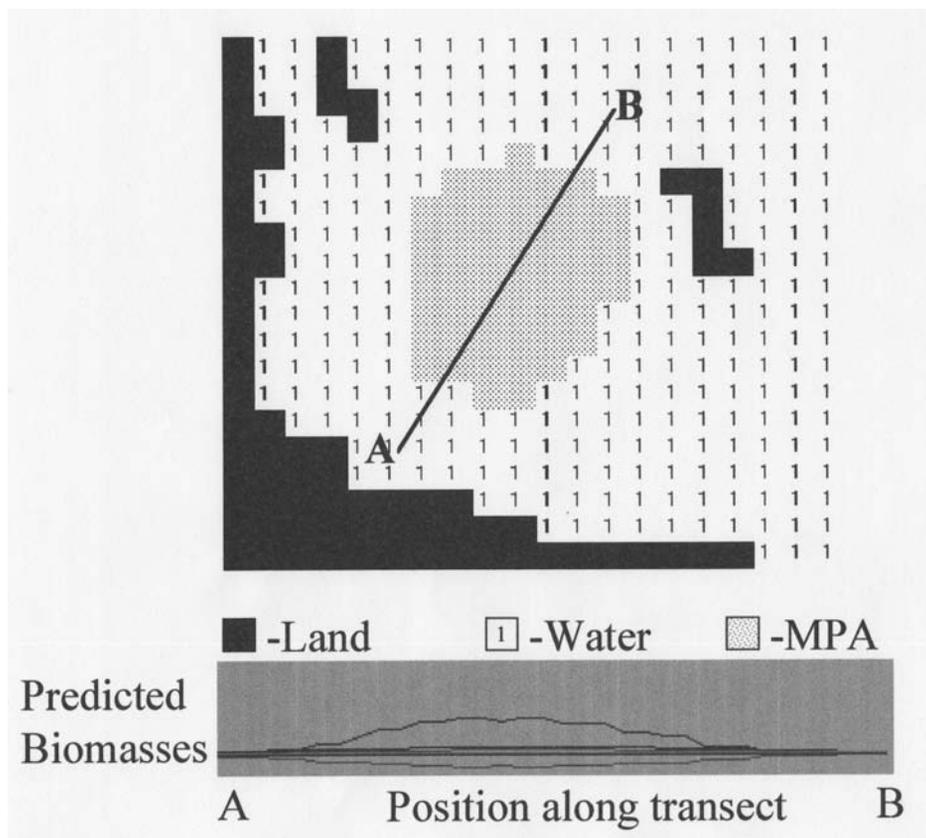


Figure 3. A hypothetical coastline and marine protected area sketched with the ECOSPACE user interface. Simulated biomass patterns along the A-B transect line are shown in the bottom panel. From Walters et al. (1999).

served if the donor control of trophic flows is strong (Menge, 1992; Strong, 1992) or if the effects are badly 'smeared' by dispersal.

Addition of spatial dispersal to the predictions, even over relatively small distances (mean dispersal distance $1-2$ cells yr^{-1}), causes a profound change in predicted biomass patterns (Fig. 4, 3rd panel). In particular, we predict that the density difference across MPA boundaries should not be a simple inside versus outside effect; rather, a density gradient or cline should develop, and effects of fishing should reach well into the MPA. This effect results from dispersal 'imbalance': as elsewhere, cells near the MPA boundary lose fish by dispersal, and these losses are not initially balanced by immigration from all surrounding cells (immigrants will be fewer, on average, from cells still open to fishing), so densities drop and cause a similar imbalance further into the MPA. This long-distance cumulative effect may well be why researchers like Zeller and Russ (1998) have been unable to detect density differences in MPAs even for species with very restricted spatial movement. Note that the development of gradient patterns rather than high-density hot spots implies not that MPAs are ineffective but rather that cumulative spatial effects should be taken into account in assessments of effectiveness of MPAs at providing seed sources for surrounding areas.

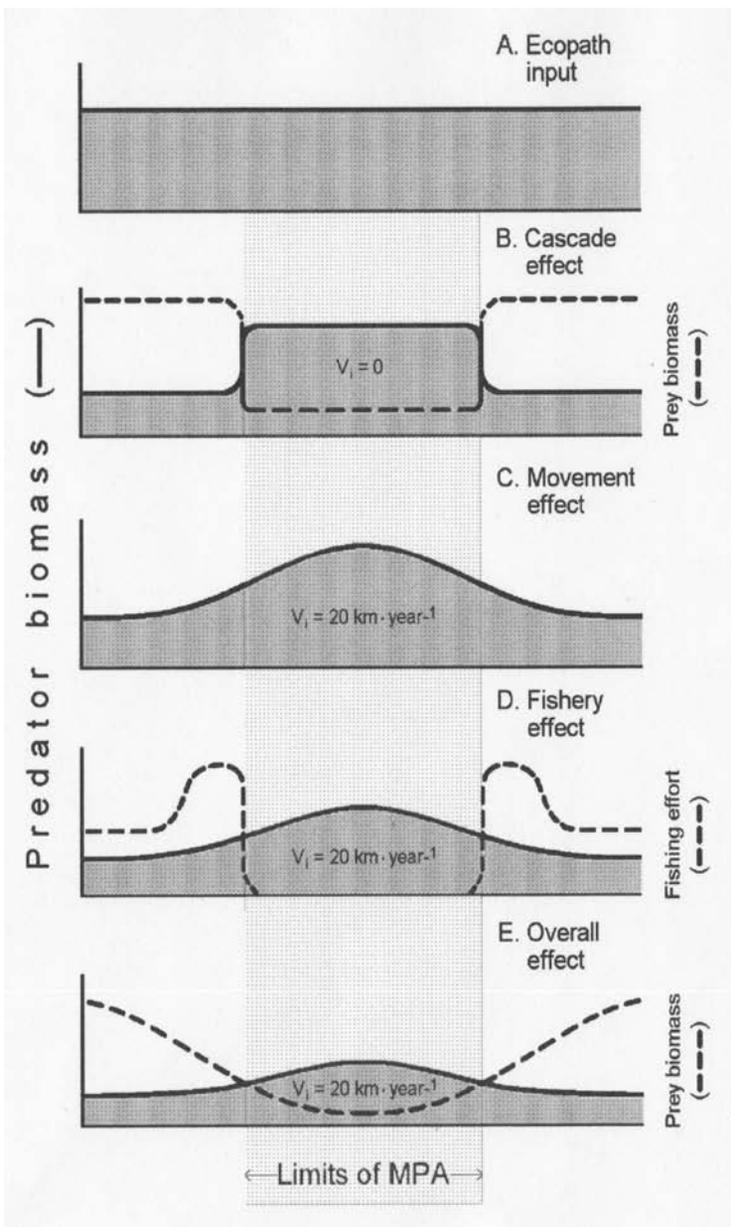


Figure 4. Idealized ECOSPACE predictions of biomass responses along the A-B transect line in Figure 3. A, density field with no fishing; B, density field with MPA but no spatial movement; C, density field with fishing and dispersal; D, density field with dispersal and concentration of fishing effort near MPA boundary; E, density field with fishing response, dispersal, and added dispersal effect of prey and predators increasing dispersal rates where ratio of predation risk to food availability is higher. From Walters et al. (1999).

If fishing effort concentrates near the MPA boundary in response to even modest increases in abundance due to dispersal across the boundary (Fig. 4, 4th panel), depression in density near the boundary should cause cumulative movement imbalance effects even

further into the MPA than would be predicted if effort were uniformly distributed over open areas. In a number of hypothetical simulations, we have found that turning on the simulated effort response causes peak densities (near MPA centers) to drop by roughly 50%, i.e., cause the predicted MPA effect to be only half as large as would be expected if effort concentration dynamics were ignored. This prediction about the interaction effect of movement and effort concentration is obviously very disturbing and hints that effective MPA design may need to include buffer zones where effort is limited, even where fishing incursions (poaching) are not a concern.

Finally, suppose that dispersal rates are even weakly dependent on trophic conditions, such that organisms move more (or are more likely to disperse) from cells that have higher predation risk and/or lower food density (μ/g risk/food behavioral response that is expected as an approximation of evolutionary optimum behavior if current size/energetic state is ignored as a factor determining optimum behavior, Werner and Gilliam, 1984). Such responses could cause increased dispersal rates out of MPAs by mobile prey organisms if/when top predator abundance starts to increase, as well as increased predator dispersal in response to initial decreases in prey density. Both of these effects act to reduce effectiveness of simulated MPAs in ECOSPACE (Fig. 4, bottom panel), but the effects are considerably reduced in simulations where we assume that predatory fish are able to detect and respond to fishing mortality risk as part of the μ in their μ/g 'assessment'. I know of no field data supporting the hypothesis that movement rates do respond to μ/g ratios, e.g., that fish can recognize safe havens from fishing, but the sensitivity of ECOSPACE predictions to assumptions about this response is large enough that I suggest it should be a key research priority.

SPATIAL BIOECONOMICS: LINKING PROTECTED-AREA DESIGN TO BEHAVIOR OF FISHERS

Although we originally designed ECOSPACE mainly as a tool for evaluating impacts of fish movement and trophic linkages, its most important applications may well be in the design of protected-area policies that work with, rather than against, the behavior of fishers. As noted above, ECOSPACE includes a simple gravity model for predicting spatial distribution of fishing effort in relation to changes in fish abundance and spatial patterns of fishing cost or risk. The immediate consequence of this representation when spatial fishing costs are ignored is to concentrate simulated fishing effort near the boundaries of MPAs, hence reducing densities and increasing the negative effects of dispersal on densities within MPAs.

If we look broadly at the spatial histories of fishery development, we see many cases where economic costs and technological limitations initially created large and effective MPAs that resulted in sustainable harvesting systems, which disappeared over time with technological innovation (Walters, 1998). The cod fishery off Newfoundland persisted for several centuries as a summer coastal activity, and the stock was not depleted until large trawlers appeared that were able to work offshore on winter spawning concentrations. In spite of development of purse-seine fishing, many tuna fisheries still have strong offshore gradients in fishing effort so that offshore pelagic zones act at least to some degree as protected areas. Along coastlines and reef systems in the developing world, fishing effort and depletion are often concentrated near villages and inshore, and more distant and riskier fishing sites are depleted only when larger and faster vessels become

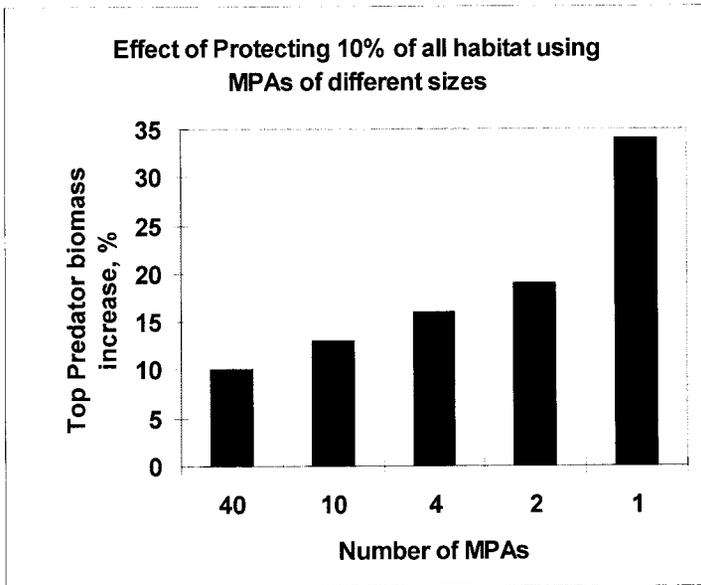


Figure 5. Predicted effect of alternative MPA sizes on long-term biomass increase in a heavily fished top predator (initial fishing rate $F = 1.0 \text{ yr}^{-1}$). Simulated predator has average movement distance of 5 km yr^{-1} , smallest MPA tested is a single $5\text{-km} \times 5\text{-km}$ cell. Effects shown are for 40 such protected cells in a total habitat area of 400 cells (10% protection), distributed spatially as 40 widely spaced single cells, 10 MPAs with 4 cells each, etc., up to a single 40-cell area. The message is simple: for relatively mobile species, single large MPAs can be much more effective than many small ones.

common (see for example various cpue-versus-effort patterns reviewed by Polunin and Roberts, 1996). In the Gulf of Carpenteria prawn fishery, fishers have asked me to help argue against further effort regulation on the basis that fishing sites far from ports are already economic protected areas, but recent growth in fishing power makes this argument suspect (Robins et al., 1998).

At least two strategies are possible for siting MPAs in relation to spatial concentrations of fishing effort associated with fishing communities, so as to prevent inequities where one or some communities are hit harder than others: (1) assume cooperative behavior—site MPAs in the most heavily fished areas close to all communities, so as to spread fishing effort, equalize economic burdens, create opportunities for nonconsumptive economic uses (e.g., diving tourism), and maximize opportunities for local cooperation in enforcement and monitoring—and (2) assume competitive behavior—work with existing economic practices by siting MPAs as far as possible from communities, where effort is already lowest and where the incentives for cheating are least because of higher fishing costs/risks. ECOSPACE simulations suggest that either of these approaches could be effective (for nonmigratory species) from an ecological perspective (Fig. 5), so the real uncertainties about these options are social and economic rather than ecological: will members of fishing communities actually work cooperatively to ensure better enforcement, and how severe will be the economic impact of forcing fishers to work further from home? Growing case experience suggests that success of the cooperative strategy depends on very clear, careful design of institutional arrangements to encourage coopera-

tion in the face of many local incentives for competitive behavior (Pinkerton, 1994; White et al., 1994; Brown, 1998).

HOW LARGE SHOULD PROTECTED AREAS BE?

ECOSPACE results to date strongly support the pessimistic assertion by Walters (1998) that we need a basic reversal in thinking about spatial protection of aquatic ecosystems: protection should be the rule, and fishing areas should be the exceptions. I originally reached that conclusion from examination of some successfully sustained fisheries and from arguments about difficulties in implementation of exploitation-rate goals caused by stock-assessment problems and regulatory failures. Almost every complication and more realistic component that we have added to ECOSPACE supports this concern: dispersal, effort concentration, and response of dispersal to changing trophic conditions should all act to make small MPAs less effective. In my judgment, it is pure wishful thinking to believe small MPAs will act as effective 'seed sources' for situations where there has apparently been large-scale recruitment overfishing (e.g., ling cod in southern British Columbia, Martell, this issue). That is not to say that small MPAs have no value; even very small protected sites may have local positive effects (Roberts and Hawkins, 1997).

In some jurisdictions, such as British Columbia, there is considerable public support for protecting quite large proportions of the coastal marine environment. A key issue in these settings has become how to distribute the protection in space. Decision makers appear to favor the least disruptive option of having a large number of very small protected areas, each aimed at protecting a 'unique' marine ecosystem while avoiding the 'unfair' impact on any coastal community that would result from placing a large protected area in front of it. There has been almost no discussion about the alternative, fewer but much larger areas. The basic ECOSPACE prediction about these options is very clear: unless the MPAs are intended to protect only selected sessile species, it is much better from an ecosystem perspective (many species, some with considerable movement) to have just a few large areas (Fig. 5). In fact, ECOSPACE runs with a scattering of very small MPAs, one or a few cells each in size, typically show no detectable biomass responses at all; in these cases, high ratios of edge to area result in dispersal losses that prevent any effective biomass development (and hence 'seed source' enhancement).

This point needs special emphasis: if a given total area is to be protected, dividing that total into many small MPAs is not just a somewhat less effective option than having a few larger areas; instead it may very well eliminate any beneficial result for more mobile ecosystem components. A complex ecosystem model is not needed to show why; consider how the perimeter-to-area ratio varies: it is on order 4 if the total area is in one (square) MPA, on order 8 if the area is divided into 4 MPAs, and on order 16 if the area is divided into 16 MPAs. That is, relative loss to dispersal as measured by the ratio of boundary length (exposure to movement) to biomass density (area) increases by at least fourfold for the 16 small MPA option; ECOSPACE simulations often produce even larger relative losses than these, when effects like effort concentrations near boundaries are included.

ECOSPACE also suggests that the efficacy of MPAs may depend on how they are located relative to coastal features that restrict dispersal (Fig. 6). Considerably higher biomasses usually develop in simulated bays, where dispersal and fishing edge effects are minimized. Such predictions could be partly an artifact of considering only biomass-

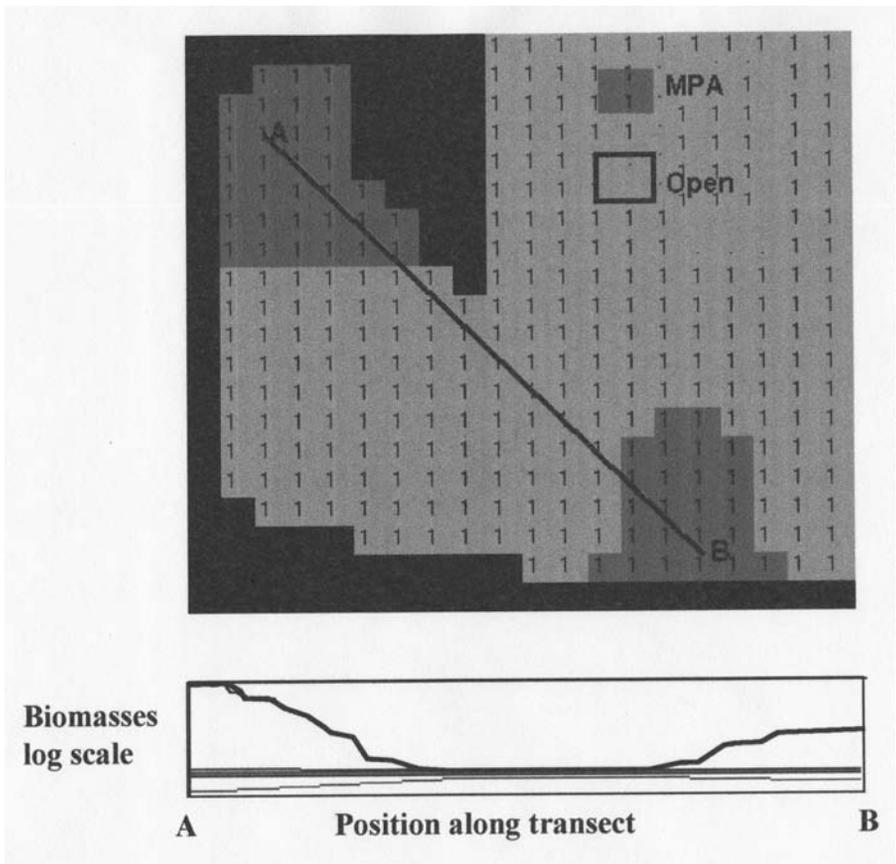


Figure 6. Predicted biomass development patterns for two MPAs, one in a bay with restricted dispersal (A) and the other along an open coastline (B). Much higher top predator biomass is achieved in the area with restricted dispersal.

dynamics responses independent of factors such as availability and transport of larvae, but they do suggest that it is at least worth testing whether coastal structure has an important impact on MPA performance and hence should be a key criterion in site selection.

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