

Population Connectivity and Spatial Management of Marine Fisheries

BY MICHAEL J. FOGARTY AND LOUIS W. BOTSFORD

Understanding dispersal pathways and population connectivity is an essential prerequisite for devising effective fishery management strategies in at least two critical ways. The first concerns the delineation of appropriate spatial scales for management, while the second involves specification of subareas that are to be protected from exploitation and that are nested within broader management units. An understanding of dispersal patterns at all life-history stages is crucial to meeting both objectives. Spatial management units are typically defined on the basis of genetic structure, differences in morphological and demographic characteristics, fishing patterns, and/or movement and dispersal patterns of individual species (Cadrin et al., 2004). Classical models employed in single-species management typically assume that the population is well mixed throughout the manage-

ment area. Today, our enhanced ability to resolve finer-scale population structure and patterns of connectivity with refined monitoring programs and advances in genetic techniques, elemental fingerprinting, and other tools (see Hedgecock et al., this issue; Thorrold et al., this issue) reveals the need to adopt a metapopulation perspective in which subpopulations linked through dispersal at one or more points in the life cycle comprise the management unit (Kritzer and Sale, 2006).

Spatially explicit harvesting strategies that involve both seasonal and long-term closures of fishing grounds, and whose objectives are to protect nursery areas or spawning aggregations and enhance yield, have an extensive history and remain widely employed in marine fishery management (Kruse et al., 2002). Moreover, increasing concern over the status of marine resources and ecosys-

tems under escalating anthropogenic stress has led to calls for a more holistic strategy for ocean management that incorporates broader ecosystem principles (e.g., U.S. Commission on Ocean Policy, 2004). The use of networks of Marine Protected Areas (MPAs)—areas of the ocean protected from one or more forms of human disturbance—is strongly advocated as a tactical management tool in this context (NRC, 2001). Particular interest centers on the potential utility of no-take marine reserves (a form of MPA) in which all extractive activities are prohibited. Here, the objective is to preserve ecosystem structure and function. The reserve concept therefore extends the traditional form of fishery closures to encompass wider objectives, more inclusive protection, and in many cases, broader time horizons (Fogarty et al., 2000).



For MPAs to provide fishery benefits, at least one of two conditions must hold: (1) there must be an increase in reproductive capacity and biomass within the reserve, and (2) the consequent export of eggs and/or larvae and/or movement of juveniles and adults to areas open to fishing (“spillover”) must be adequate to increase yield or at least sustainability (e.g., Murawski et al., 2005). Exchange between reserve and nonreserve areas also has the potential to enhance resilience in the open areas by supplying a population subsidy. Here, we explore the central role of dispersal and connectivity in the dynamics of exploited marine systems. Our principal focus is on the critical importance of understanding dispersal processes that control both larval export and movement of later life-history stages in order to specify effective spatial management strategies, with an emphasis on no-take marine reserves.

LARVAL EXPORT AND DISPERSAL PATTERNS

Substantial evidence has now accrued that biomass is significantly enhanced within MPAs. Halpern (2003) noted that in 37% of marine reserves, biomass within reserves has been shown to be greater than outside, while in 4% it is the same. These increases signal a considerable build-up in reproductive capacity through larger mean size of individuals within reserves and, in many cases, increases in population abundance. The fecundity of most marine organisms increases with the cube of length and therefore reproductive output of the population potentially can be dramatically increased (Bohnsack, 1996). The total impact at the population level will,

of course, depend on the fraction of the population protected.

The second condition, that enough of this increase in reproductive output and biomass is exported outside the reserve, has been accorded less attention, and the empirical evidence is less clear. In contrast to the body of evidence showing increases in population fecundity, far less information is available on egg and larval dispersal pathways because of the difficulty in tracking the early life-history stages of marine organisms. The lack of quantitative information on dispersal and connectivity at these stages is, in fact, the greatest source of uncertainty in understanding the potential efficacy of marine reserves in actual management settings (Fogarty et al., 2000; Botsford et al., 2003).

Some studies inferring larval dispersal from biogeochemical and other markers (e.g., Thorrold et al., this issue) or applications of numerical hydrodynamic

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models (e.g., Cowen et al., 2000, 2006; see Box 1) to estimate exchange rates are available and the prospects for rapid advances in this area are encouraging, as contributions to this special issue demonstrate (Werner et al., this issue). However, the relative paucity of currently available information on egg and

larval dispersal has required the use of models incorporating simplified patterns of exchange. Many such models assume sedentary adult populations, a common larval pool, and uniform dispersal of propagules, while others assume simple idealized dispersal patterns (e.g., Laplacian distributions) and explore the spatial scales of dispersal. Many important qualitative insights have emerged from these theoretical treatments. In the following section, we concentrate on their heuristic value while recognizing that more detailed models will ultimately be required to evaluate the design and performance of actual MPAs.

Effects on Fishery Yield

Models incorporating the simplifying assumptions described above show that marine reserves can potentially confer a significant degree of resilience to harvesting in exploited systems (e.g., Hastings and Botsford, 1999;

Hart, 2006). Levels of fishing mortality that would cause population collapse in the absence of reserves can be maintained if sufficiently large reserves are established (although yield may remain suboptimal under these conditions, depending on the type of protection afforded [Figure 1]). These general con-

clusions hold when these assumptions are relaxed and directional dispersal patterns are allowed at different life stages from prerecruit to adult (e.g., Quinn, et al., 1993; Holland and Brazee, 1996; Tuck and Possingham, 2000; Apostolaki et al., 2002) or when harvesting affects both population size and habitat quality (Fogarty, 2005).

For these simple models, the equivalence of marine reserves and alternative management strategies, such as control of fishing mortality, can be demonstrated under a range of different assumptions and model structures. Hastings and Botsford (1999) show that the question of how much area to place in reserves is mathematically identical

to the conventional management question of how high to set the harvest rate when considering the numerical yield (catch in numbers). Mangel (1998) further demonstrates that it is possible to provide the same yield by specifying different combinations of fishing mortality rate and area open to fishing. In light of these results, we take the maximum

BOX 1. SEA SCALLOPS ON GEORGES BANK: A CASE STUDY

Georges Bank, a broad shallow plateau located off the New England coast, has been recognized as an extremely productive fishing ground for over three centuries (Fogarty and Murawski, 1998). On the crest of the bank, the water column is well mixed throughout the year, with associated high levels of primary productivity. Strong rotary tidal currents are a dominant feature of the oceanography of the region. The tides and topography result in a well-established anticyclonic gyre on the bank

with important implications for retention of planktonic organisms, particularly during the stratified season when the mean retention time exceeds five months. At the close of 1994, large-scale closed areas were established on the bank and in adjacent areas for purposes of groundfish management. These areas are closed to all forms of mobile-gear fisheries, including scallop dredging (which involves incidental catches of groundfish species). Some forms of stationary gear (e.g., lobster-traps) are permitted. Collectively, over 17,000 km² have been placed in year-round closures, and there are additional seasonal closures. The two closed areas on Georges Bank proper comprise approximately one-third of the U.S. portion of the Bank (see Figure A-1).

The Atlantic sea scallop *Placopecten magellanicus* currently supports one of the most lucrative commercial fisheries in the northeastern United States. Prior to the implementation of more restrictive management starting in 1994, the fishery followed a classical boom-bust cycle under open access and inadequate controls on fishing mortality (Murawski et al., 2000; Hart and Rago, 2006). In 1994, a moratorium on new scallop permits and restrictions on gear and crew size were implemented. A constraint on allowable days at sea for each vessel was also added.

Although the closures were not specifically established with the objective of enhancing scallop yield, they have exerted profound effects on the scallop population. Scallops are highly fecund (up to three million eggs for large females) and the duration of the larval stage is on the order of 40 days. Sea scallop dispersal is largely confined to the egg and larval stages although some limited

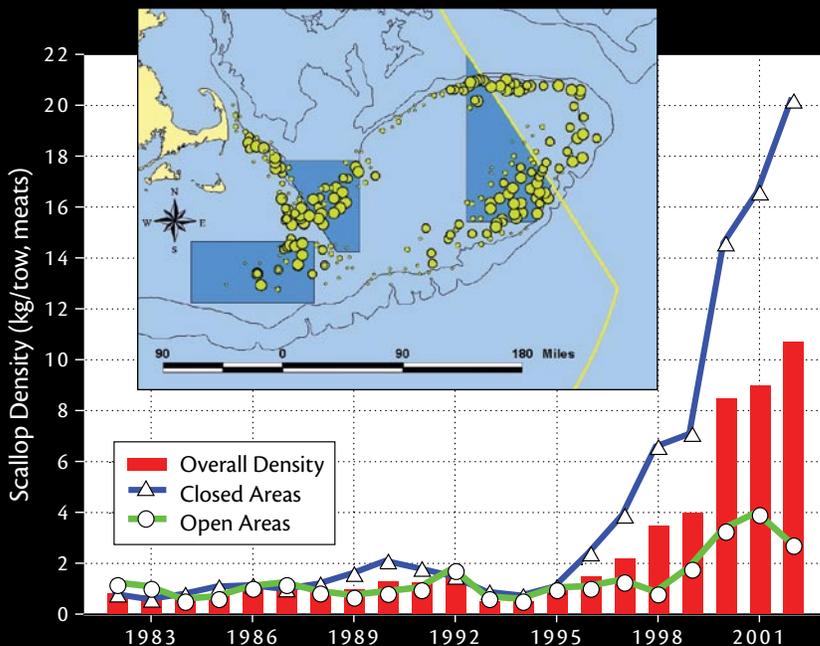


Figure A-1. Trends in sea scallop population density (kg/tow) derived from Northeast Fishery Science Center surveys on Georges Bank for open and closed areas and for the overall area. The inset shows the distribution of sea scallops in the 2003 survey. Closed areas were implemented at the end of 1994.

yield possible from conventional management as a benchmark against which to assess the performance of reserves (Botsford et al., 2003). We note that cases where strong source/sink relationships exist or where dependence of recruitment on postdispersal adult density is important (Gaylord et al., 2005) can lead to greater yields when reserves

are implemented. Conversely, predispersal density dependence can lead to lower yield with reserves (Parrish, 1998; Gardmark et al., 2006).

Population Sustainability

Estimates of the level of reproductive output required to ensure replacement of the adult population play a critical

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movement of post-settlement individuals occurs. Following the establishment of the closed areas, the overall biomass of scallops in the U.S. sector of the Bank increased 18-fold (Figure A-1). This biomass increase has largely occurred in the closed areas where a 25-fold increase has been observed and where dramatic increases in mean size of individuals has occurred. More limited increases in the areas open to fishing have also been observed (Figure A-1).

To assess the role of larval export in both seeding areas outside the closures and replacement within the closed areas, potential transport pathways have been explored using numerical hydrodynamic models. A finite element Lagrangian particle tracking model was employed to trace movement of sea scallop larvae from the two closed areas (Craig V. Lewis, Advance Study, La Spezia, Italy, *pers. comm.*). Sea scallop larvae spawned in Closed Area II are predicted to provide settlers to areas open to fishing along the periphery of the bank and to contribute to the replenishment of both closed areas I and II (Figure A-2 upper). Closed Area II is predicted to be self-seeding and to contribute settlers along the southwestern periphery of the closure in areas open to fishing (Figure A-2 lower). The predicted settlement patterns are consistent with observed distribution of sea scallops on the bank with concentrations along the periphery, indicating that the main features of the transport processes are correctly captured (c.f. inset in Figure A-1). Despite the large buildup in biomass in the closed areas and associated increase in reproductive capacity, no significant increases in recruitment have been observed in either the open or closed areas (Hart and Rago, 2006), implying that given the high population fecundity of sea scallops and the predicted retention on the bank, there is a settlement saturation effect. The increase in biomass in the open areas is principally attributable to reductions in fishing mortality and minimum size limits.

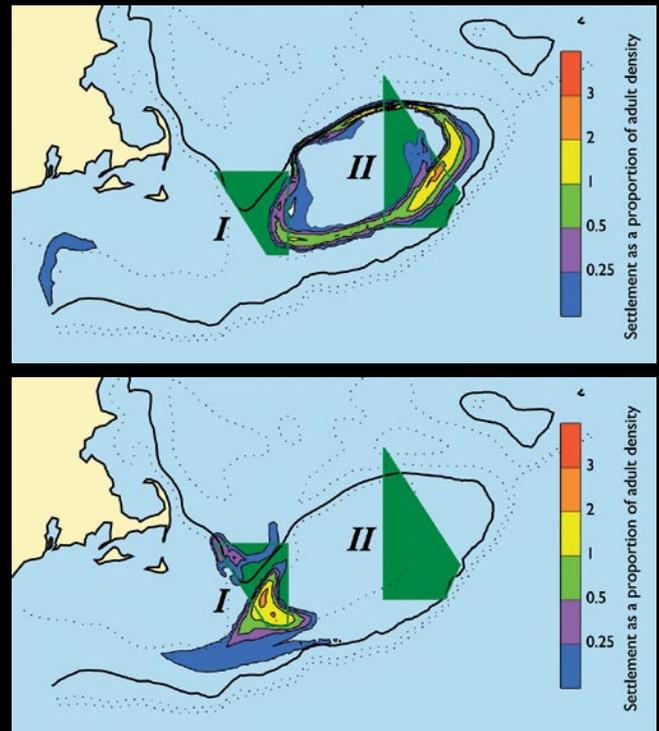


Figure A-2. Predicted settlement locations for sea scallop larvae spawned in Closed Area I (upper) and Closed Area II (lower) as determined by a finite element Lagrangian particle tracking simulator (C.V. Lewis, Advance Study, La Spezia, Italy, *pers. comm.*). Figure provided by Partnership for Interdisciplinary Studies in Coastal Oceanography (PISCO)



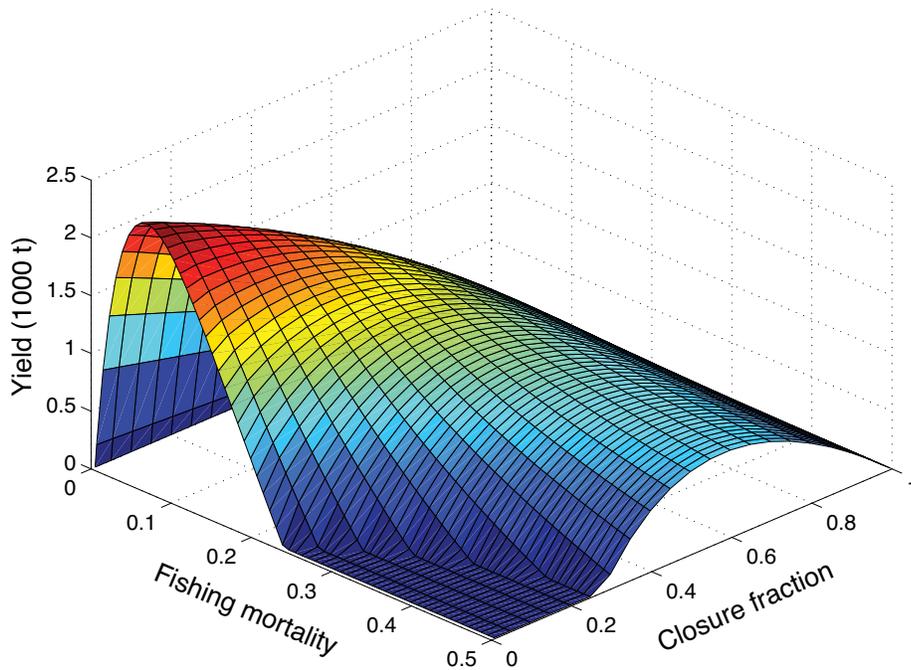


Figure 1. Yield as a function of the instantaneous rate of fishing mortality and the area closed to fishing activity for Canary rockfish (*Sebastes pinniger*) from an age-structured population model with a common larval pool and sedentary adult population (Hart, 2006).

role in setting biological reference points for sustainability in conventional fisheries management with single-population, nonspatial models. Although the fraction of the potential lifetime reproductive output required varies considerably as a function of the species' life history, compilations for a broad spectrum of marine taxa show that at least 35% of the unfished potential should be maintained (Clark, 1991; Mace and Sissenwine, 1993; Ralston, 2002). For species characterized by delayed maturation and low reproductive output, the required fraction may be considerably higher. In the following, we will employ the 35% level as a generic reference point.

We can apply this basic concept to a spatial model to ask what combinations of reserve width and area set aside for reserves will be required to meet a specified replacement fraction con-

straint. Replacement in this spatial context involves replacement through all potential dispersal paths (Hastings and Botsford, 2006). Botsford et al. (2001) provide two key results for such a system when dispersal is characterized by an exponential decay in both directions from the origin with a specified spatial scale, and fishing is assumed to remove all individuals between reserves. For a specified replacement fraction of 35%, (1) replacement is greater than the threshold level of 0.35 when the ratio of reserve width becomes greater than one dispersal unit (indicating that single reserves will sustain species with dispersal distances on the order of the width of the reserves), and (2) replacement is greater than the threshold when the fraction of coastline in reserves is greater than 0.35 regardless of individual reserve size and the species mean dispersal distance.

If all fish are not caught in the open areas between reserves, the range over which replacement will be greater than the threshold level increases, indicating smaller individual reserves and a lower fraction in reserves will sustain populations as fishing declines. Adding effects of alongshore advection to the dispersal kernel substantially diminishes the range of parameter values over which the population will persist (see also Kaplan et al., 2006). For symmetric dispersal, without advection in one direction, sustainability conditions do not depend on the shape of the dispersal pattern, but rather only on the (one-sided) mean dispersal from the origin (Lockwood et al., 2002).

We can use this understanding of the conditions for sustainability to determine the effect on catch of dispersal distance and reserve area and placement. Botsford et al. (2004) examine the case

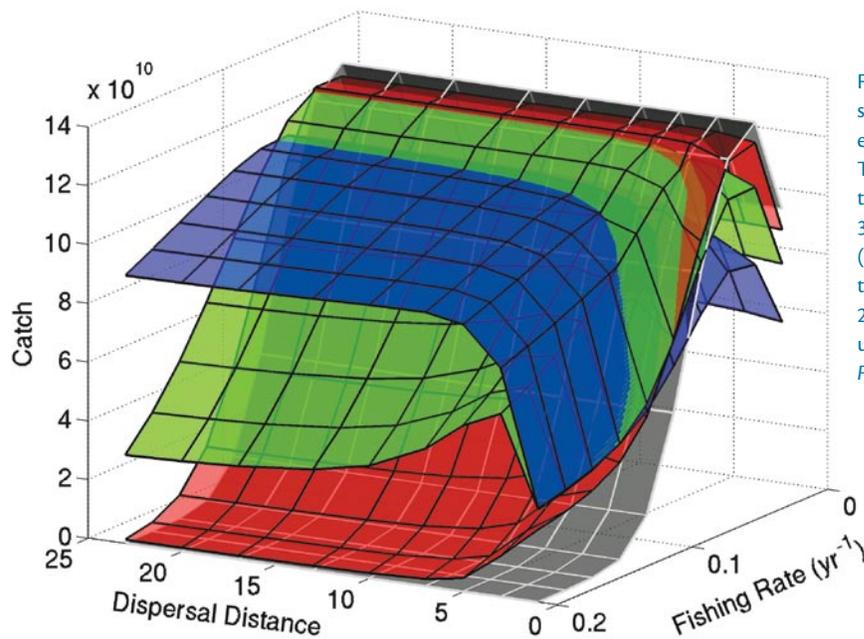


Figure 2. Catch from a simulated age-structured population with reserves every 25 spatial units along a coastline. The replacement required for persistence of the simulated population is 35%. Reserve sizes are 0 spatial units (gray), 2 spatial units covering 8% of the coast (red), 5 spatial units covering 25% of the coast (green), and 10 spatial units covering 40% of the coast (blue). From Botsford et al., 2004

of individual reserves with collective areas ranging from 8% to 40% of the coast, a broad range of dispersal capabilities, and a minimum replacement level of 35% (Figure 2). Comparison with the case of no reserves (grey surface in Figure 2) again demonstrates the resilience conferred by reserves. At very high fishing mortality rates, as the area in reserve increases, yield increases and the effect of dispersal distance changes. For the case of 8% reserve coverage at high fishing mortality rates, the catch of shorter-distance dispersers is enhanced relative to the baseline case of no reserves (red surface in Figure 2). In this case, the shorter-distance dispersers meet the replacement criterion, but longer-distance dispersers do not. As the size of reserves increases further (holding reserve spacing constant), longer-distance dispersers meet the replacement

criterion, and their catch exceeds that of the shorter-distance dispersers because of the greater area of spillover (see green and blue surfaces in Figure 2).

For the case of heterogeneous larval production and dispersal patterns, spatial management strategies can result in enhanced yield relative to uniform harvesting over all locations (Morgan and Botsford, 2001). For example, in the case of a single-source population and three sink populations, catch obtained by placing the source population in a reserve is greater than that obtained if the source is fished at the same rate as the others. However, the average catch obtained by randomly choosing the patch to place in reserve reveals an important practical aspect of this result—it is necessary to know which patch is the source population to take advantage of the potential for greater catch. When populations

along a coastline are subjected to inter-annual variation in advection patterns, under certain conditions the use of reserves can result in larger catches than would be possible with spatially uniform harvesting (Gaines et al., 2003).

Analyses tailored to specific proposed spatial configurations of fishing and reserve placement are now being developed to complement and extend the more general analyses described above. An example is a recent assessment of proposed reserve configurations done for the implementation of MPAs mandated by California's Marine Life Protection Act. It entailed evaluation of dispersal resulting from the current distribution of recruits for proposed spatial distributions of reserves and habitat along a bathymetrically defined strip of the California coast to provide estimates of dispersal-per-recruit (DPR)

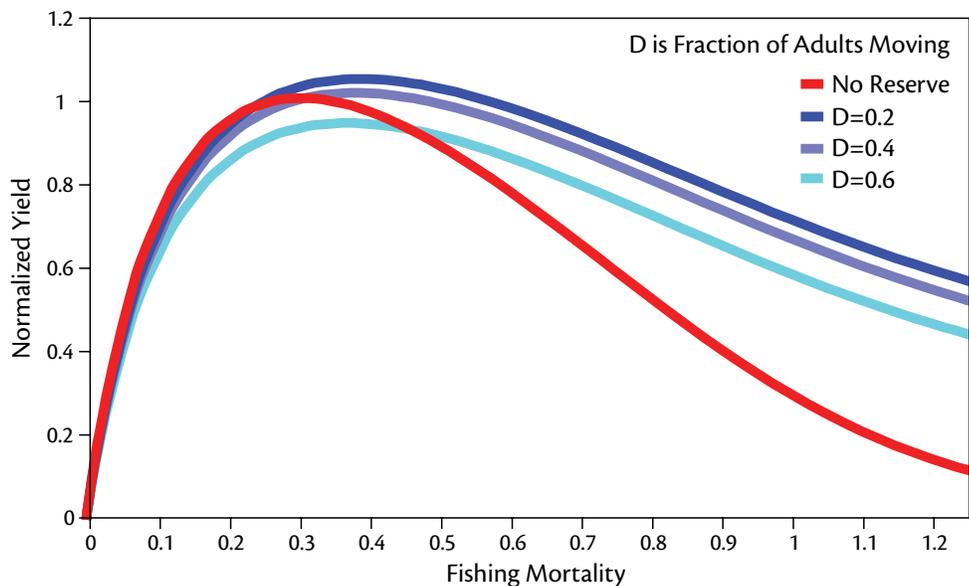


Figure 3. Yield (normalized to the maximum yield with no reserves) as a function of the instantaneous rate of fishing mortality for a simple age-structured population model comprising new recruits and fully recruited individuals. Recruitment is taken to be the age at maturity. One-third of the population is protected by the reserve in this analysis, and 20% of the recruitment is exported outside the reserve. Three levels of movement of fully recruited individuals are considered (20%, 40%, and 60%).

(Kaplan et al., 2006). Under the simplifying assumption of a one-dimensional coastal management unit, iterative solutions to the DPR problem were possible. This approach will be more difficult for more complex two-dimensional models with multiple management objectives. In this case, a single DPR calculation may be useful as a proxy for the full iterative model, or a spatial Biological Reference Point. The single DPR calculation also does not require knowing (or assuming) the nonlinear settler/recruit relationship.

SPILLOVER FROM JUVENILE/ADULT MOVEMENT

Again, in contrast to now well-documented within-reserve effects, substantially less information is available on the prevalence of spillover benefits to fisheries. Evidence from tropical and subtropical systems that demonstrate significant spillover effects is accruing (e.g., McClanahan and Mangi,

2000; Zeller et al., 2003; Russ et al., 2003; Roberts et al., 2001; Gell and Roberts, 2003) while more variable species-specific patterns are emerging for temperate systems (e.g., Horwood et al., 1998; Frank et al., 2000; Murawski et al., 2004, 2005).

Analytical treatments of this problem dating to the seminal work of Beverton and Holt (1957) indicate the central importance of juvenile and adult movement rates. In an age-structured model of the recruited component of the population (focused on the individuals vulnerable to the fishery, but without a stock-recruitment relationship), Beverton and Holt (1957) demonstrate that yield-per-recruit benefits can accrue with the use of fishery closed areas relative to nonspatial management if the dispersal rates are moderate and the stock is overfished (their Figure 18.23). Very low rates of dispersal mean that the recruited biomass is locked in the reserve and

little or no spillover occurs. Conversely, with high rates of adult movement, sufficient protection may not be afforded to individuals in the population because the within-reserve buildup of reproductive potential increases more slowly with increasing reserve size (Polacheck, 1990; DeMartini, 1993).

For models incorporating dispersal at different life stages, it can be shown that spillover effects enhance both resilience and yield if reserves are properly located. For example, Apostolaki et al. (2002) demonstrate substantial increases in resilience to fishing with the use of MPAs. These studies afford different types of protection (closure of nursery grounds or spawning grounds) and use different assumptions with respect to the redistribution of fishing effort (from closed to open fishing grounds). In cases where juvenile fish are targeted and nursery grounds are protected, the reserves not only increase resilience but

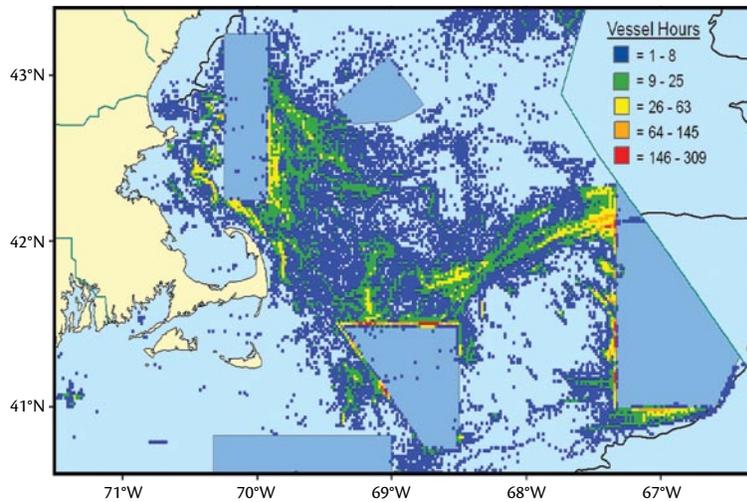


Figure 4. Distribution of fishing effort in the vicinity of fishery closed areas off the New England coast in 2003 as determined by a satellite vessel tracking system (Murawski et al., 2005). Data are filtered to include only vessels moving at speeds consistent with fishing operations (i.e., vessels moving at transit speeds are eliminated). Warmer colors indicate higher concentrations of fishing effort.

also result in enhanced yields.

In Figure 3, we illustrate the effects of MPAs on resilience to fishing with a simple age-structured model comprising new recruits and fully recruited individuals (e.g., Fogarty, 1998; Tuck and Possingham, 2000; Yakubu and Fogarty, 2006). In this example, one-third of the population is protected by a reserve. We examine the case in which a fixed fraction of prerecruit production is exported to the open area, and we consider three levels of adult export (spillover). In this illustration, we assume that fishing effort is not redistributed from the closed to the open area, although this constraint is easily removed. The expected yield in weight for the case of no reserve is used as a reference level. Note that the use of the reserve results in substantial increases in resilience to higher levels of fishing mortality due to the subsidy effect of dispersal from the closed to the open area. The level of fishing mortal-

ity resulting in maximum yield is higher when reserves are used. In addition, it is clear in this example that while relatively low (20%) adult export provides a maximum yield slightly higher than that for no reserve, higher levels of adult movement result in lower overall levels of yield (Figure 3). Similar results are reported by Apostolaki et al. (2002) in their analysis of the effects of fisheries targeting adults when spawning grounds are protected.

Understanding the likely response of fishers to the imposition of MPAs is no less important. It is well recognized that where spillover effects are anticipated by fishers, concentration of fishing effort along MPA boundaries will occur (e.g., Wilcox and Pomeroy, 2003; Murawski et al., 2004, 2005; Figure 4). “Fishing the line” can ultimately result in dissipation of potential benefits of reserve creation and spillover (Walters et al., 1999). Further, the issue of

whether fishing effort will be redistributed to the remaining open areas can substantially affect predicted yields.

In an analysis of four fishery closed areas off the New England coast, Murawski et al. (2004, 2005) found that the relative importance of spillover effects for individual species was linked to their seasonal migration patterns, diffusive and directed movements, habitat preferences, and distribution with respect to the marine protected area. A total of 22% of 279 species/area combinations examined provides evidence of density gradients consistent with spillover effects (Murawski et al., 2005). Particularly dramatic effects were evident for haddock (*Melanogrammus aeglefinus*) for which 42% of the U.S. catch was taken within 1 km of a closed area boundary and 73% taken within 5 km. Figure 5 provides an illustration of haddock catch rates at the boundary of one fishery closed area.

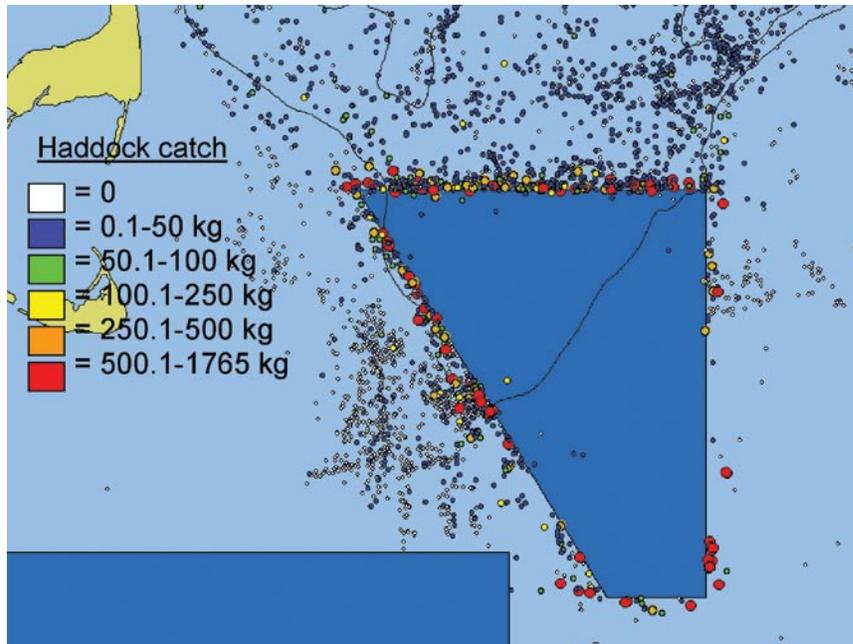


Figure 5. Distribution of haddock catch rates in the vicinity of fishery Closed Area I located off the New England Coast. See Figure 4 for exact location.

UNCERTAINTY IN CONNECTIVITY

Marine reserves have been advocated as a hedge against uncertainty. For example, in instances where the exploitation rate is uncertain or cannot be reliably controlled, implementation of a reserve can provide a buffer against implementation error in harvest policies (Lauck et al., 1998). However, the role of uncertainty in dispersal processes (including both rates of dispersal and the nature of dispersal mechanisms—e.g., whether a common larval pool exists with nondirectional dispersal or directional dispersal dominates) has been accorded much less attention (Fogarty et al., 2000) but is central to understanding the actual performance of MPAs in general.

Variation in movement patterns could result in uncertainty in the fraction of stock that would be protected by a reserve. When Fogarty et al. (2000)

extended the Lauck et al. (1998) analysis to incorporate this uncertainty, they found the mean population level to be lower under the combined effects of implementation error as considered by the Lauck study, and variability in the fraction of the population protected by the reserve. The risk to the population is accordingly greater under both types of uncertainty.

As noted above, sustainability and catch both depend on dispersal patterns (mean distance and, critically, advection). For longer-distance dispersers, the possible values of the uncertain dispersal parameters can cause wide variation in performance. For shorter-distance dispersers, sustainability will be more likely and less uncertain, but catches will be lower due to lesser area of spillover, unless all reserves are small (Figure 2) (Hastings and Botsford, 2003).

Morgan and Botsford (2001) evalu-

ated the implications of four alternative assumptions concerning dispersal patterns for a sea urchin fishery, including (1) limited distance, (2) source-sink, (3) common larval pool with equal dispersal to recipient location, and (4) “headlands” with unequal dispersal probabilities from a common larval pool. They showed that the common larval pool assumption provided the most optimistic scenario. If this assumption is incorrectly adopted, the risk to the population is potentially high, with increasing exploitation rates clearly demonstrating the importance of understanding dispersal mechanisms.

FUTURE RESEARCH DIRECTIONS

A strong commitment to understanding patterns of connectivity in marine populations will clearly be necessary to guide the practical design of networks

of marine reserves. In assessing actual management situations, the principal challenge is to go beyond simple model structures to provide more realistic representations of dispersal and connectivity linked to oceanographic conditions and to the behavior and the life-history characteristics of managed species. To date, we have primarily been forced to depend on highly stylized representations of exchange processes. Most of the model structures examined tend to provide similar qualitative insights for key elements, such as increased resilience to harvesting with the use of marine reserves in overexploited systems if properly sited and with appropriate size and spacing. However, insights into some issues, such as whether MPAs will result in an increase or decrease in yield relative to conventional management approaches, are far more model dependent. These models can be expected to be sensitive to, for example, assumptions concerning dispersal patterns at different life stages, the redistribution of fishing effort, and the protection afforded to nursery and spawning grounds. (e.g., Guenette et al., 1998; Fogarty et al., 2000; Gerber et al., 2003; Apostolaki et al., 2002; Hilborn et al., 2006).

Linkage of numerical hydrodynamic models and spatially explicit population models will provide an increasingly important tool for design and performance assessment of MPAs (Werner et al., this issue). The sea scallop case history (see Box 1) illustrates how three-dimensional hydrodynamic models can be used in concert with information on larval behavior and larval-stage durations to make predictions concerning dispersal patterns and settlement in

complex oceanographic settings. This information on settlement and exchange between areas open and closed to fishing can then be used to evaluate alternative harvest strategies.

The use of MPAs for management will inherently require adoption of finer spatial resolution in population models to capture small-scale distribution and dispersal patterns. The current difficulty in taking this step stems from our limited knowledge of movement over space, both in larval dispersal and juvenile/adult movement. Information on the home ranges of exploited fish and invertebrates is the most relevant component for the latter. The advances described in this special issue will be critical in refining our understanding of processes and in estimating rates of exchange. It should

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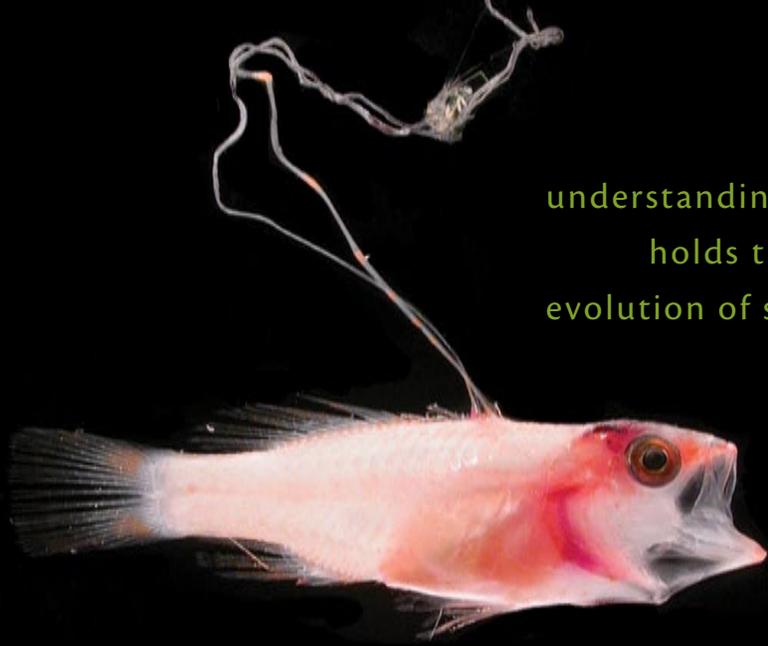
be noted that sophisticated site-selection algorithms are now being used to determine optimum locations for MPAs with information on habitat characteristics, biodiversity patterns, and dispersal characteristics of marine organisms (e.g., Sala et al., 2002; Meester et al., 2004) at relatively fine spatial scales in an increasing array of marine systems.

It is no less critical that effective mon-

itoring programs be implemented to evaluate MPA performance, in particular, the consequences of poorly known connectivity. MPAs are being advocated as ready solutions to fishery problems, but in general their actual performance has not been closely scrutinized. Meta-analyses show that reserves result most often in increases in biomass, abundance, size, and diversity (Halpern, 2003), but do not reveal the causes of the failures to produce anticipated increases. As we begin to design and assess proposed reserve systems, there is a great need for empirical information on responses inside and outside reserves to size, spacing, and siting of reserves. However, too often reserves are established without adequate pre-implementation surveys to provide baseline information and with-

out even identifying adequate reference sites for assessing reserve effects after implementation (Halpern et al., 2004).

In a broader context, MPAs can serve as critical tactical tools in the development of ecosystem approaches to management. Here, we focused on the implications of spatial structure and connectivity for a single ecosystem service—provision of fishery yield. Most models



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developed to date for evaluating MPAs in a fishery context have, in fact, focused on the single-species case. However, as we move toward more holistic management of the oceans, there is a clear need to expand the scope of these models to address community and ecosystem-level processes. MPAs are increasingly being advocated both as a solution to over-fishing (NRC, 2001) and a way to meet broader conservation objectives including preservation of biodiversity, habitat, and ecosystem structure and function (Hastings and Botsford, 2003; Fogarty, 2005; Jones et al., this issue). Few other single fishery-management tools can potentially address such a wide range of issues (Fogarty, 1999). It is within this broader setting that the potential costs and benefits of MPAs should ultimately be evaluated. It is also clear that adopting this broader perspective brings substantially increased complexity in both the scientific requirements for assessment and trade-offs in management. For example, consideration of trophic dynamics in the development of MPA models has already pointed to the fact

that not all species can benefit from the implementation of reserves (e.g., Walters et al., 1999; Micheli et al., 2004) if these interactions are strong.

Despite the wide array of outstanding research issues to be resolved, the progress evident in refining our understanding of dispersal and connectivity in this special issue holds the promise of significant advances in the evolution of spatial management strategies.

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