

BACKGROUND PAPER 2**BIOLOGICAL AND ECOLOGICAL CONSIDERATIONS IN THE DESIGN, IMPLEMENTATION AND SUCCESS OF MPAs<sup>1</sup>**

by

*Louis W. Botsford, Fiorenza Micheli and Ana M. Parma<sup>2</sup>***Summary points**

- 1) While Marine Protected Areas (MPAs) have a long history, there has recently been increasing interest in implementing them as a tool for fishery management. This interest is driven in large measure by the observation that some 25 percent of world fisheries are over-exploited or recovering from over-exploitation. To aid decision makers in deciding whether implementing MPAs will improve their fisheries and marine ecosystems, and in selecting the best MPA designs, we review what is known about their ecological performance from empirical observations and modelling studies.
- 2) The answer to the question of whether species will benefit inside reserves is reasonably well known. Empirical evidence from 70 existing marine reserves indicates that 63 percent of them have higher densities inside them than outside, 90 percent have higher biomass, 80 percent have a larger mean size of individual fish, and 59 percent have greater taxonomic diversity. The higher biomasses are primarily in fished species, and the effect is stronger for species at higher trophic levels and for species with greater body size.
- 3) The answer to the question of how reserves will contribute to the fisheries outside reserve is less well understood. The species that attain higher biomass or abundance inside reserves could contribute to fisheries outside through larvae produced in reserves being transported out of them. However, there is little empirical evidence regarding the magnitude and extent of the contribution of larvae produced within reserves to recruitment outside reserves.
- 4) Fish whose juvenile and adult stages are highly mobile could also contribute to fisheries outside reserves by juvenile and adult movement to outside the MPAs. However, individuals spending a large amount of time outside reserves will be exposed to fishing outside the reserves, hence more mobile species will be less well protected by marine reserves. Although empirical comparisons among species with varying adult mobility show that less mobile species increase more in abundance inside reserves, in other cases such comparisons are confounded by the stronger influences of fishing intensity.
- 5) Empirical evidence indicates that catch and CPUE of mobile species can be higher near marine reserves than far away from them, but few studies have assessed the net gain in catch and CPUE due to marine reserves when the loss of fishing area to reserves is accounted for. These few studies yielded conflicting results on whether increased CPUE around MPAs compensates losses associated with closure of fishing grounds.

---

<sup>1</sup> This paper was produced for the FAO Expert Workshop on Marine Protected Areas and Fisheries Management: Review of Issues and Considerations (12–14 June, 2006).

<sup>2</sup> The views expressed in this paper are solely those of the authors, Louis W. Botsford, Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA 95616 United States, Fiorenza Micheli, Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950, United States, and Ana M. Parma, Centro Nacional Patagonico (CENPAT), 9120 Puerto Madryn, Argentina.

- 6) There are no empirical comparisons of increases in catch with reserves to the increases possible through a reduction in fishing effort. Modelling studies indicate that the yield possible through management by marine reserves is approximately equal to the yield possible through conventional management. This implies that reserve implementation will increase yield only for heavily fished species (empirical evidence in Bullet 2). Exceptions to this approximate equivalence include species with pre-dispersal density-dependence, species with ontogenetic migration (e.g. specific spawning areas) and species with a distinct source/sink structure. For species with pre-dispersal density dependence, models suggest that yield may be less with reserves than with conventional management, whereas the opposite is predicted for species with distinct source/sink structure, if MPAs can be designed to protect sources.
- 7) The question of how to choose the size and spacing of MPAs currently depends on modelling results because there is no empirical information available regarding the dependence of yield and sustainability on size and spacing of marine reserves. Modelling studies of the level of sustainability brought about by different size and spacing of reserves indicate that, when there is intense fishing: (1) single reserves will sustain species with larval dispersal distances less or equal to the linear dimension of the reserve, and (2) systems of many marine reserves will sustain species with larvae dispersing any distance, when the fraction of area covered in reserves is greater than the minimum fraction of lifetime egg production needed for replacement. The latter is a network effect. The reserve area required for sustainability is less when there is less fishing outside reserves.
- 8) Management by MPAs depends on different uncertainties than conventional fishery management. The significant uncertainties relevant to the design of marine reserves are the limited knowledge of larval dispersal patterns, a poor understanding of the minimal individual replacement (i.e. minimum Lifetime Egg Production or Spawning Potential Ratio) required for population sustainability, and indirect effects of protection in reserves through species interactions. Conventional fishery management shares a critical dependence on the last two elements, and has, in addition, considerable implementation uncertainty.
- 9) The decision as to whether to employ marine reserves for fishery management may be approached differently depending on the amount of ecological and socio-economic data available. For data-rich management environments, the ecological aspects of design and implementation of reserves can be approached through a modelling framework. Uncertainties can be identified and explored and performance of different reserve designs combined with other conventional management tactics can be compared under different scenarios that represent the existing uncertainty. Even in data-rich situations, major uncertainties remain (see bullets 3 and 8) and it is important that learning through monitoring is included in the implementation plans.
- 10) For data-poor management environments, rules of thumb from the modelling studies may be useful. The influences of management costs, practicality of implementation and enforcement, and uncertainties (bullet 8) on the decision of whether to implement reserves or conventional quota or effort management differ from the data-rich case. Reserves, probably in combination with some form of effort limitation, tend to be more advisable than catch quotas when many species are taken by the same gear and when the resource has a persistent spatial structure due to low mobility of the individuals (see bullet 4).

## 1. INTRODUCTION

Over the past several decades a substantial number of marine protected areas (MPAs) have been implemented throughout the world, and the creation of more has been recommended. MPAs have been created and are recommended both to improve fishery management as well as to preserve biodiversity. The former is motivated by the observation that some 24 percent of world fisheries are overfished, depleted or recovering (e.g. Garcia and Grainger 2005). As their use increases there is a need to

establish guidelines for their design, implementation and evaluation. Here we provide the ecological/biological aspects of the scientific background required for those guidelines.

Design, implementation and evaluation of MPAs all rely on an understanding of how MPA performance depends on both MPA configuration and species life history characteristics. Because the use of MPAs is a form of spatial management, the important life history characteristics are the various kinds of movement over space, i.e. in the larval stage, as well as the juvenile and adult stages. Although spatial aspects of population dynamics have been addressed in some analyses of conventional fisheries (e.g. Beverton and Holt 1957), the fundamental dynamics are different enough that the intuition of a typical fishery analyst or manager may be inadequate to address the design of MPAs. Also, because performance in spatial management depends on different processes than conventional fisheries management, management with MPAs will need to deal with different sources of uncertainty.

The major components of performance of interest in this investigation of the use of MPAs in fishery management are persistence (or sustainability) and yield. These are the same two issues that form the central focus of the Food and Agriculture Organization of the United Nations' (FAO) guidelines for conventional fishery management, with population persistence typically associated with Limit Reference Points (LRPs) and yield typically involved in Target Reference Points (TRPs) (FAO 1995). MPAs created for the preservation of biodiversity also involve persistence as a goal, while possible resulting reductions in yield are treated as a cost. Persistence and yield are population level characteristics, while MPAs are typically viewed as a tool for ecosystem management. However, population persistence is important to ecosystem management also, since ecosystems cannot exist without persistent populations. We also address here, the way in which MPAs affect species differently, as well as how MPAs will affect community interactions between species.

To describe how performance depends on MPA configuration and location we first turn to direct empirical evidence. We describe several examples of observed performance of MPAs, as well as the existing major meta-analyses of MPA performance. Unfortunately, the lessons for MPA design and implementation from empirical evidence are limited. The difficult task of monitoring MPAs to compare the responses of yield and sustainability to MPA configuration and location over a range of species and life history characteristics is seldom undertaken. Information is usually limited to a comparison of biomass or abundance inside vs. outside the MPAs for a limited number of species. Therefore, after reviewing the existing empirical information, we also review the information available from modelling studies of how fished populations respond to the implementation of MPAs. In most cases the models involve an extension of conventional fishery modelling to add explicit movement and spatially heterogeneous fishing rates. Although these models extend the dynamics beyond what is supported by typical observations of MPAs, they increase our understanding of the spatial dynamics, and can increase our ability to focus on the important empirical gaps in our knowledge.

Both the empirical evidence regarding performance of MPAs and the population modelling results can be put in an accessible context by briefly reviewing what might be expected to occur when an MPA is implemented. Focusing on a single species initially and assuming that fishing effort is reduced to zero within the MPA, the initial effect inside the MPA would be a "filling-in" of the age or size structure, which would have been truncated by fishing. This would tend to increase abundance and biomass in the MPA, and the amount of that increase would be greater the more intense the fishing had been. The new value of fishing mortality rate  $F$  with the MPA would depend on the mobility of the fish occurring in the MPA, essentially on how much time they spent outside of the MPA. For species with little juvenile and adult movement,  $F$  would be close to zero. For mobile species, as the time spent outside the reserve increased, there would tend to be less protection in the reserve (greater  $F$ ), but there could also be greater yield outside the reserve. The fishing mortality rate outside the reserve would also depend on the response of fishermen to the reserve, i.e. whether they continued to fish and simply shifted their effort outside the reserve (Smith and Wilen 2005).

An important, but more complex question would be whether we would expect recruitment to increase, both inside and outside the MPAs. We know that for fished populations that are assumed to be well-mixed over space, the equilibrium recruitment to a population is determined by a single stock-recruitment relationship (actually the (total egg)-recruitment relationship). The equilibrium recruitment is at the intersection of that curve with a straight line through the origin with slope  $1/LEP$ , where LEP is lifetime egg production (Sissenwine and Shepherd 1987) (Fig. 1). From that relationship, we know that for moderate to low abundance, as LEP declines, recruitment declines and vice versa. The population ceases to persist (i.e. the equilibrium level is zero) when LEP is small enough that the slope of the straight line exceeds the slope of the egg-recruit function at the origin. This result is important because it means that for population sustainability we do not necessarily need to know the stock-recruitment relationship, we only need to know the point at which the LEP drops below a certain value. This aspect of this density-dependent population dynamics is similar to the lifetime reproduction,  $R_0$ , in density-independent population dynamics. Fisheries analysts have examined the question of how much spawning biomass per recruit is enough to sustain populations using conventional stock-recruitment relationships and have concluded that the fraction of LEP (FLEP) at which the population ceases to persist can be reasonably bounded, at least over taxa of similar species (Myers *et al.* 1999, 2002). A value of FLEP of 35-40 percent was originally proposed as a safe management target for maximizing productivity (Mace and Sissenwine 1993; Clark 1990). That value has been determined to be too small for some species (e.g. Ralston 2002).

The essential question when we shift from persistence of a single well-mixed population to a population distributed over space is how to interpret LEP in a spatial context, especially when an MPA is implemented. Since LEP is essentially a measure of the degree to which individuals are tending to replace themselves through reproduction, we need to reinterpret that replacement in a spatial context. In conventional fishery management we assume that the LEP of all eggs or larvae, that is their capacity to replace themselves, is independent of where they settle. But when MPAs are present, larvae may settle either inside or outside of an MPA. Those that settle inside will survive longer and produce more eggs in their lifetime than those that settle outside. To describe replacement in the case with MPAs then, for each location we need to know the fraction of larvae produced there that will settle in MPAs, and the fraction settling outside, and the LEP associated with each location. In addition, because we are concerned with replacement, we need to know the larval return produced at each settlement site (see Botsford and Hastings 2006 and Hastings and Botsford 2006 for further details). This modified concept of replacement suggests that we should expect abundance to tend to be greater when MPAs are larger or closer together. Furthermore, if the distance over which larvae disperse is shorter, we would expect recruitment to tend to be greater in the MPAs because fewer larvae will settle outside the MPAs thus leading to greater replacement.

This brief, qualitative description gives us some idea of what to expect from MPAs, but it also underscores some of the difficulties in attempting to understand the performance of MPAs solely from empirical evidence. Essentially, many mechanisms will tend to increase or decrease abundance in MPAs, hence any single observation of an MPA tells us little about the operative processes. Understanding enough about MPAs to design them on the basis of empirical information alone would require well-planned experimental design and extensive meta-analysis. The description above also points out the opportunities (needs) for a better quantitative understanding of the various processes involved. For the time being at least, those questions are being addressed through modelling.

Before reviewing what is known about the performance of MPAs, it is useful to summarize what we would want to know to design and implement them, as well as to monitor their performance. Much of the effort in the literature associated with MPAs has been focused on obtaining a *strategic* view of their performance, e.g. asking questions such as, how frequently does abundance increase when an MPA is implemented? As we see in the following sections, the answer is that abundance within a reserve increases in a large fraction of cases studied. Unfortunately the answer to that strategic question does not help us to design effective MPAs. An agency designing and implementing an MPA would want to maximize the chances that the MPA had a positive effect on the population or fishery or ecosystem of interest. Hence they would want to know which aspects of MPA design or species life

history have determined whether they increase, and by how much. Thus, for the design and implementation of MPAs, there is a need to develop a *tactical* approach to marine reserve performance to complement the strategic results.

When the purpose of the MPAs is fishery management, the primary design goal is not just an increase in abundance inside the reserves, but rather an increase in the catch or sustainability of a fishery. The primary decisions to be made are what should the size and spacing of the MPAs be, where should they be located, and how should the management of the fishery outside the MPAs be changed. We therefore would like to know how the size, shape and location of MPAs, and the level of fishing outside MPAs would affect sustainability and yield of the fishery. Furthermore, the effect of the MPAs on fisheries is relevant even when the overall goal is just to conserve biodiversity. In that case sustainability (persistence) is the primary issue, and the effect on fishery yield may be a cost of MPA implementation.

## 2. EMPIRICAL OBSERVATIONS

This section reviews what is known about the effects of MPAs on populations, communities, and fisheries productivity, based on previous syntheses and individual case studies. Examination of empirical evidence will highlight: (1) general responses from protection in reserves; (2) reserve attributes, environmental characteristics, and life history correlates of differential responses among locations, ecosystem types, and species; and (3) remaining uncertainties about the types, magnitude, and directions of effects.

### 2.1 Population and community responses to protection in MPAs

A majority of empirical studies of marine reserves has compared populations or community measures before/after the establishment of reserves, or between reserves and adjacent locations with similar habitat characteristics. Review of 89 studies, including data from 70 reserves, showed that in a majority of studies (Fig. 2) no-take reserves host greater densities (63 percent of reserves), biomass (90 percent), mean sizes of organisms (80 percent), and taxonomic diversity (as species richness; 59 percent) compared to reference conditions (Halpern 2003). Only a minority of reserves had lower values for these biological variables, compared to reference conditions: 7 percent of reserves had lower densities, 2 percent had smaller organisms, and 10 percent had lower species diversity compared to reference conditions, whereas in no instances did reserves have lower biomass (Halpern 2003). Synthesis of quantitative results from 69 of these studies revealed that, on average, values of density, biomass, organism size, and species diversity were 91, 192, 31, and 23 percent greater in reserves, respectively (Fig. 3). While these studies include a variety of levels of replication and most frequently consist of spatial comparisons between reserves and adjacent fished areas, rather than before-after control-impact designs, the consistency of results across systems and types of study design suggests that results are robust. Although a systematic analysis of how results of each study may be influenced by the specific design and level of replication has not been conducted, meta-analytical techniques are designed to give greater weight to studies with higher and more balanced replication (e.g. lower sampling variance), thereby partly accounting for such heterogeneity in the dataset.

Other meta-analyses, similarly utilizing comparisons between no-take reserves and reference conditions also highlighted differential responses to protection among taxonomic and functional groups. Mosquera *et al.* (2000) conducted a meta-analysis of species-level data extracted from 12 studies, for a total of 346 fish species from 56 families. Overall, fish abundances were over three times greater within reserves, however there was high between-species variability in responses, with a subset of fish families (7 of 19) showing significantly greater abundances in reserves, and thereby driving the overall density increase. In contrast, no statistically significant difference was detected in 11 families, and one (Gobiidae, small-bodied, omnivorous benthic fishes typically not targeted by fishers) had significantly lower densities within reserves (Mosquera *et al.* 2000). Additional analyses indicated that much of this variation could be attributed to the fishery status of species, with only species targeted by fishing outside reserves showing significantly greater densities within the reserves, and no significant

differences for non-target species. Moreover, the species' body size was also an important factor in determining variation in responses to protection, with species characterized by large maximum body sizes showing the strongest positive responses (reaching densities up to 33 times greater in reserves than in adjacent fished areas), and the magnitude of effects increasing with increasing body size (Mosquera *et al.* 2000). Because maximum body size is generally correlated with life history parameters such as age at maturity, growth, and reproductive output, this variable may be a surrogate for predicting recovery rates (Jennings *et al.* 1999; Jennings 2001).

Meta-analysis of additional studies (20 studies, from 31 different temperate and tropical locations) also found that only fished species exhibited significantly greater abundances in no-take reserves, whereas non-target species had similar abundances between reserves and reference fished areas (Micheli *et al.* 2004). These analyses indicated that different overall population increases in no-take reserves occurred for different levels and types of exploitation (Fig. 4): species that are primary fisheries targets, that are caught occasionally or as bycatch, and species targeted by the aquarium trade all showed significantly greater abundances in reserves, with similar average magnitudes of the effect of protection across these three exploitation groups (Micheli *et al.* 2004). Although all trophic groups except the omnivores had significantly greater abundances in no-take reserves, the largest increases were observed in species at the top of food webs (piscivores, with trophic levels >3.5) (Fig. 5). Piscivores accounted for 10-43 percent (av. 24.5 percent, N=10) of total fish biomass, as compared to 5-24 percent (av. 15.5 percent, N=10) outside reserves. A finer categorization of species into functional groups taking into account not only a species' trophic level, but also its maximum size and mobility showed that in addition to abundances and biomass increasing disproportionately for some trophic groups, protection in reserves results in overall greater functional diversity, with specific combinations of trophic levels, size and mobility represented only within protected areas, and not in the presence of fishing (Micheli and Halpern 2005).

Piscivorous fish were also the only group to show a significant, positive relationship with the duration of protection within no-take reserves, with magnitudes of responses increasing since time of establishment across different reserves (Micheli *et al.* 2004). Thus, in addition to fisheries status of species, a species trophic level and the age of reserves interacted in determining responses to protection, with evidence for a gradual build up of top predators biomass within reserves over decadal time frames (Micheli *et al.* 2004).

Trends from these spatial comparisons corroborated results of both spatial comparisons and long-term monitoring from specific locations. These case studies showed that large-bodied, long-lived top predators respond slowly to protection, and frequently do not show a levelling off of abundance and biomass even after decades of protection in no-take reserves (Russ 2002). Monitoring of Serranidae (grouper), Lethrinidae (emperors) and Lutjanidae (snapper) at both fished and unfished coral reef locations within Apo and Sumilon islands, in the southern Philippines, revealed significantly greater biomass within reserves after four years of protection (Russ *et al.* 2005). Over 18-year long monitoring of these locations, the relationship between predator biomass and duration of protection was exponential within reserves, and linear outside. Rates of biomass buildup were similar between these temporal monitoring and spatial comparisons among 15 reserves with varying durations of protection (Russ *et al.* 2005), except that significantly greater biomass within reserves was evident after a slightly longer duration of protection (six years) compared to results from long-term monitoring (four years).

Species other than top predators can also show lags in recovery, either because of slow population turnover or through indirect effects mediated through species interactions. For example, establishment of the Mombasa Marine National Park in Kenya was followed by increases in a sea-urchin predator, the wrasse *Chelinus trilobatus*, during the first three years (McClanahan 2000). However, sea urchin declines and recovery of benthic corals occurred after more than ten years, and coincided with later recovery of the triggerfish *Balistapus undulatus*, also a predator of sea urchins. Data from five fully protected Kenyan MPAs indicate that populations of *B. undulatus* showed positive trends in their abundances after over 30 years of protection (McClanahan 2000).

Rapid buildup of abundances and biomass documented at specific locations, (e.g. Caribbean coral reefs, Roberts 1995) and in meta-analyses of marine reserve studies (Halpern and Warner 2002), where significant increases occurred within 1-3 years of protection, appear to be driven by rapid responses of fished species with short generation times. Documented slower recovery of long-lived species and lags in responses through indirect effects (e.g. predator-prey and competitive interactions, or habitat recovery) lead to temporal changes in community composition and relative dominance by different species and trophic groups, with reserves moving through a series of transient states (e.g. McClanahan 2000; Shears and Babcock 2003; Micheli *et al.* 2004).

For long-lived species, a key mechanism in allowing for population recovery and possible contribution to adjacent fisheries is the effect of protection on age and size structure, in particular the increased survivorship of larger individuals. Because in most fish and invertebrates fecundity increases approximately cubically with length, older, larger individuals contribute disproportionately to reproductive output from the populations, producing quantities of gametes orders of magnitude greater than small reproductive individuals (Sadovy 1996 and Bohnsack 1998 describe the impact of this well known fact on marine reserves). Shifts in age and size structure towards larger size classes and older individuals have been commonly documented in marine reserves across multiple fish and invertebrate species and in different ecosystem types (e.g. Polunin and Roberts 1993; McClanahan and Kaunda-Aurara 1996; Russ and Alcala 1996; Wallace 1999; Paddock and Estes 2000; Mumby *et al.* 2006). Based on size-fecundity relationships, reproductive output has been estimated to be up to four times greater following reserve establishment (e.g. for Nassau grouper in the Exuma Cays Land and Sea Park, Bahamas, Sluka *et al.* 1997; or abalone in British Columbia, Wallace 1999; and for rockfish in central California, Paddock and Estes 2000).

As discussed earlier, a life history trait that is expected to influence species responses to protection in marine reserves is a species' mobility. A species with high mobility relative to reserve size would receive less protection than a more sedentary species. Empirical support of this prediction is scarce and contradictory. Fisher and Frank (2002) examined changes in community composition from a 31-year time series of abundances of over 70 fish species within a fishery closure and an adjacent reference area on the Scotian Shelf, Canada. A preliminary review of life history attributes for 16 species in this dataset indicated that different trajectories may be related to dispersal ability of the species. Species with benthic eggs, ovoviviparity, and small body size (i.e. species likely to have limited dispersal in the larval, juvenile or adult stages), tended to benefit from the fishery closure more than those with pelagic eggs or larger body sizes, (i.e. potentially greater dispersal abilities and home ranges, Fisher and Frank 2002).

In contrast, meta-analysis of responses to protection in species assigned to different adult mobility classes (sedentary or territorial, mobile, and highly mobile or migratory), failed to detect any overall differences in responses in relation to mobility (Micheli *et al.* 2004). In these analyses, the lack of an effect of species mobility on their responses to protection may be explained by the strong positive correlation between mobility and exploitation level among the species in this dataset ( $r=0.38$ ,  $P=0.0001$ ,  $N=920$ ). Thus, mobile species tend to be subject to intense fishing pressure and the expected dependence of effects of protection on species mobility may be obscured by the counteracting dependence on exploitation level.

Larger reserves are expected to support higher population densities and more diverse communities. However, differences in densities (in terms of biomass and numbers), mean organism sizes, and species diversity were not correlated to reserve sizes across reserves ranging from 0.002 to 846 km<sup>2</sup> in surface areas (Halpern 2003). Micheli *et al.* (2004) also found that the magnitude of responses of different trophic groups to protection in reserves was uncorrelated to reserve size. Though not generally supported by these synthetic analyses, the prediction that effectiveness of reserves is size dependent is supported by a specific case study. Among four Tasmanian coastal reserves, the largest reserve (7 km<sup>2</sup>) contained overall greater fish, abalone and lobster sizes, densities of large fish, macroalgal cover, and species diversity of algae, fish and invertebrates compared to adjacent fished sites (Edgar and Barrett 1999). In contrast, in three smaller reserves (~0.6 km<sup>2</sup>), significant differences

were found only for density and diversity of large fish in one reserve, and for macroalgal cover in another (Edgar and Barrett 1999). However, observations from the large reserve are unreplicated, the three smaller reserves have a total surface area of less than 2 km<sup>2</sup>, and even the larger reserve is fairly small. This is also an issue with the meta-analyses discussed above, where half of the reserves in the dataset ranged 1-10 km<sup>2</sup> in size, and the median reserve size was 4 km<sup>2</sup> (e.g. Halpern 2003).

These results show that even small reserves lead to some biological responses. But data over a broad range of reserve sizes or local, replicated comparisons of reserves of varying sizes are not available to allow for empirical tests of the effects of reserve sizes and spacing on reserve effectiveness. To our knowledge, no empirical studies have disentangled a possible effect of reserve size from the local confounding of how species characterized by different mobility and habitat use may be affected by reserves of different sizes. Therefore, the result that the magnitude of responses to protection by individual species and sets of species is uncorrelated to reserve size (Halpern 2003; Micheli *et al.* 2004) should be interpreted with caution.

From this brief review of empirical reserve studies, some general trends emerge. Much information has been gathered on how frequently increases in some biological variables occur. These include abundances, biomass, sizes, and diversity. Although several reviews have highlighted that marine reserve studies frequently suffer from problems with experimental design, particularly a dearth of replicated, long-term before-after/control impact studies (e.g. Russ 2002; Sale *et al.* 2005; Willis *et al.* 2003) the consistency in the direction of responses observed across multiple studies (Halpern 2003; Mosquera *et al.* 2000; Micheli *et al.* 2004), and documentation of positive effects in studies using BACI designs (Halpern and Warner 2002; Willis *et al.* 2003) indicate that documentation of benefits inside reserves is robust. In contrast, fewer studies have focused on recruitment, mortality and growth rates, and spatial distribution of individuals, e.g. variables that are key to understanding how reserve establishment influences population dynamics both within and outside reserves. For example, large-scale comparisons of recruitment and post-settlement mortality of seabreams (*Diplodus* spp.) across Spanish, French and Italian marine reserves did not find increased or decreased recruitment and mortality rates within reserves (Macpherson *et al.* 1997). However, more studies are needed before general conclusions can be drawn. Also, relationships with potential correlates of responses, including some life history traits of species (e.g. life span, body size, and trophic level), and some characteristics of reserves (e.g. duration of protection and reserve size) have been examined. In contrast, no systematic analyses have been conducted of how other life-history traits (larval durations and dispersal potential, growth rates, recruitment periodicity) influence species responses.

Moreover, the basic questions of how many reserves should be established, how big they should be, and how they should be arranged relative to each other to re-build populations, restore communities, and sustain fisheries are still largely unanswered in the empirical literature. Detailed process-based studies are difficult and costly. Also, few opportunities to investigate the effects of networks of reserves exist, and most studies have been conducted on one or few reserves. The recent or proposed establishment of reserve networks (e.g. the re-zoning and expansion of the Great Barrier Reef Marine Park, to include 33 percent of coral reefs in no-take reserves; the protection of 19 percent of the Channel Islands National Marine Sanctuary state waters in multiple reserves; the proposed establishment of a network of up to 40 reserves in the Bahamas; and the ongoing designation of a reserve network in coastal California through the Marine Life Protection Act) will provide invaluable opportunities for such empirical assessments (see Channel Islands Marine Protected Area Monitoring Plan, [http://www.dfg.ca.gov/mrd/channel\\_islands/monitoring.html](http://www.dfg.ca.gov/mrd/channel_islands/monitoring.html)).

## **2.2 Habitat quality and configuration in marine seascapes**

An additional question in MPA design relates to where reserves should be established, and specifically what habitat or oceanographic features they should include. Habitat characteristics are key considerations in reserve design. While most reserve planning to date has proceeded in an ad hoc fashion (Pressey *et al.* 1993; Stewart *et al.* 2003), more systematic approaches to reserve design and conservation planning have been advanced recently in terrestrial systems and are being applied to

marine systems. Networks of MPAs are currently being designed in a variety of marine settings (e.g. the Great Barrier Reef, Australia, GBRMPA 2004; the Channel Islands, California, Airame *et al.* 2003; and Baja California, Mexico, Sala *et al.* 2002) based on the objective of maximizing representation of habitat and species per unit of area protected within the network (Possingham *et al.* 2000). It is assumed that protection of representative components of the biodiversity of a region will maintain or restore the ecological functioning of the ecosystem as whole (Possingham *et al.* 2000). Under the principle of representativeness, an MPA network is designed so that it includes at least a minimum portion of each conservation target (e.g. habitats or populations) within the network. This translates to a goal of including at least one example or a minimum percentage of the available area of each habitat, community or population in the reserve network, under the constraint of minimizing the total area or cost of the network (Pressey *et al.* 1993).

A variety of computer-based mathematical algorithms that apply the above criteria to spatial data on the distribution of biological features have been developed for the selection of alternative networks of MPAs (Ferrier *et al.* 2000; Possingham *et al.* 2000). Such models often formulate this as a minimum representation problem and attempt to select the minimum area that will meet the conservation target (e.g. represent 35 percent of every habitat type) (Kirkpatrick 1983; Pressey *et al.* 1993; Leslie *et al.* 2003). Minimizing area (and/or boundary length) while maximizing representation is assumed to minimize opportunity costs (e.g. lost opportunities for fishing or other extraction within reserved areas) and costs associated with implementing, enforcing and monitoring the MPA network (Possingham *et al.* 2000).

Surprisingly, few empirical studies have explicitly addressed how habitat quality and heterogeneity influence the performance of established reserves. Habitat is known to affect productivity of fish and invertebrate stocks, and thus to be fundamentally important to fisheries production (Dayton *et al.* 1995). Mumby *et al.* (2004) showed that in Caribbean coral reefs, biomass of several species, including fisheries species, is more than doubled when reef habitat is adjacent to mangroves, and that the parrotfish *Scarus guacamaia*, the largest herbivorous fish in the Caribbean, is present only on reefs that are adjacent to mangroves. Thus, inclusion or proximity to nursery habitats may be a key determinant of the performance of reserves in maintaining populations and contributing to fisheries production. Although no direct tests of this hypothesis exist, empirical evidence from case studies indicates that: (1) habitat composition within reserves can be a good predictor of what species are positively affected through protection; (2) declining habitat quality within reserves can result in population declines despite protection from fishing; and (3) habitat composition and heterogeneity around reserves may influence rates of spillover from the reserve to adjacent areas.

In the San Diego-La Jolla ecological reserve, one the oldest marine reserve on the United States west coast (established in 1971), higher densities of large individuals of green abalone (*Haliotis fulgens*), red sea urchins (*Strongylocentrotus franciscanus*), vermillion rockfish (*Sebastes miniatus*), and sheephead (*Semicossyphus pulcher*) were in boulder-reef, kelp and submarine canyon habitats respectively, compared to similar habitat types outside the reserve (Parnell *et al.* 2005). For vermillion rockfish, the only large individuals in the La Jolla area were likely to be found in the canyon within the reserve, highlighting how inclusion of a diversity of habitat types is key to maintaining source populations of species with specific habitat requirements. Thus, protection in the reserve affected densities of multiple species associated with specific habitat types, even though only 0.8 percent of the kelp habitat and 11 percent of the boulder-reef habitat in the La Jolla area are included in the reserve. However, it is important to note that several fished species did not exhibit any response to the reserve, and in fact in most cases declined in the reserve, with the exception of a few sedentary species, suggesting that the reserve might be too small (~2.16 km<sup>2</sup>) to protect populations with intermediate or high mobility (Parnell *et al.* 2005).

A combination of bleaching, increased sedimentation from terrestrial run-off, and outbreaks of the coral predator *Acanthaster planci*, the crown-of-thorn starfish, caused coral decline between 1996-2003 from an average 66 percent to less than 7 percent live coral cover in four marine reserves in Papua New Guinea (Jones *et al.* 2004). Coinciding with habitat degradation, 75 percent of fish species

declined in abundance, and 50 percent to half of their original abundance, despite continued protection in reserves. The occurrence and magnitude of decline was correlated to the dependence of a species' juveniles on coral as recruitment substrate, thereby linking habitat quality to population declines (Jones *et al.* 2004). In contrast with these results of continued habitat degradation despite protection in reserves, other studies comparing biogenic habitat between fisheries closures and fished areas indicated that cessation of fishing significantly influenced biogenic habitat. In a comparison of seafloor characteristics between one of the Georges Bank closures and an adjacent fished area, Lindholm *et al.* (2004) found that the abundance of two biogenic microhabitat types, shell fragments and sponges, was greater within the closure than in the fished area, after 4.5 years of protection. In the same area, Collie *et al.* (1997) had similarly documented that biogenic habitat was more abundant in areas undisturbed from fishing compared to disturbed sites. Undisturbed sites were characterized by an abundance of epifaunal taxa (bryozoans, hydroids, worm tubes) that provide a complex habitat for shrimps, polychaetes, brittle stars, mussels and small fish (Collie *et al.* 1997). Thus, in systems where habitat features are dynamic, such as on soft sediments, habitat recovery in reserves may occur rapidly (few years).

Finally, spillover of reef-associated fishery species from Mediterranean MPAs is influenced by habitat configuration around reserves. In particular, fish densities decline significantly within tens of meters from the reserve boundaries on sandy bottoms, whereas gradual declines occur over ~ 2 km, indicative of greater spillover, over rocky bottom and mixtures of rocky outcrops and sand (P. Guidetti, *in preparation*). Thus, the function of structural habitat as 'corridors' connecting different areas, which has been demonstrated for vegetated habitats in estuarine environments (e.g. Micheli and Peterson 1999), appears to have the potential to influence spillover from reserves as well.

### 2.3 Effects on fisheries production

In contrast to the plethora of studies of effects of protection on populations and communities within reserves, fisheries effects of reserves have been addressed primarily through models (Section 3), and through studies conducted at specific locations. Here, we will review empirical evidence from these case studies.

Increased catch-per-unit-effort (CPUE), and in some cases, total catches around reserves has been documented in small no-take reserves established in coral reefs, temperate rocky reefs, and lagoonal or estuarine environments. In addition, extensive analyses of abundance and catch gradients across and away from reserve boundaries have recently been conducted around large (over 20 000 km<sup>2</sup> in total) fishery closures on Georges Bank (Murawski *et al.* 2004, 2005). These studies typically show fairly localized effects, with increased catches within hundreds of meters to a few kilometres from reserve boundaries, and variable results on whether increased CPUE around reserves or closures compensate losses associated with closure of fishing grounds. Examinations of trends for multiple species indicate that only a few exhibit patterns consistent with spillover, likely depending on species mobility, habitat preferences, and fishing patterns. Finally, the mechanisms underlying reserves' contribution to adjacent fisheries include juvenile or adult movements, as evidenced by examination of density gradients and tagging studies (reviewed by Gell and Roberts 2003). A few studies of species with sedentary adults also support the hypothesis of larval seeding from reserves into fished areas (Stoner *et al.* 1998; Gell and Roberts 2003), but empirical evidence for a larval contribution of reserves is more limited.

CPUE around coral reef reserves in Kenya increased by ~50 percent in a seven-year study of the fishery effects of a coral reef park in Kenya. Spillover was most pronounced for moderately mobile species in the families Lethrinidae (emperors), Acanthuridae (surgeonfish) and Siganidae (rabbitfish). However, this increase did not compensate for the reduced size of these coastal fishing grounds (~50 percent), and total catches were reduced by 30 percent following the establishment of the park (McClanahan and Kaunda-Arara 1996; McClanahan and Mangi 2000). By combining these field data and models, the authors concluded that the optimal reserve size for achieving an adequate balance between protection and spillover in coral reef fisheries dominated by species with moderate mobility

should be 10-15 percent of the total area. However, the size of the optimal protected area may increase if larval export from the reserve is significant and if slow recovery of large-bodied species (see above) will contribute to larval, juvenile, and adult export over longer time frames (McClanahan and Mangi 2000).

Densities and biomass of large predators increased within 500 m from reserve boundaries in Apo Island, Philippines (covering ~10 percent of the coral reef fishing area of this island) during the first 11 years of establishment (Russ and Alcala 1996). Continued monitoring showed linear increase in biomass outside this and the Sumilon Island reserve boundaries over 18 years (Russ *et al.* 2005). Interviews with local fishermen indicated that fishery yields had increased following reserve establishment (Russ and Alcala 1996). Comparisons of fish yields from the early 1980s with roving creel surveys conducted between 1997-2001 at Apo Island confirmed increased CPUE from hook and line fisheries of nearly an order of magnitude between 1980-81 and 1997-2001, whereas total annual fish yields remained stable between 1980-2001 (Maypa *et al.* 2002), despite the reduced extent of the fishing area. The authors speculate that the islands setting relative to currents and large contributions to fish production by planktivores and their predators may contribute to supporting high and stable catches.

Additional examples are reviewed by Gell and Roberts (2003). These include fish trap CPUE increases between 46-90 percent five years after the establishment of coral reef reserves in St Lucia (Caribbean), more variable lobster catches close to the Leigh Marine reserve (New Zealand) boundaries than from areas far from the reserve, more common large catches, and 66 percent increases in trammel net CPUE of snappers groupers and emperors five years after the establishment of a network of five no-take reserves in the Egyptian Red Sea. Evidence of spillover also comes from studies of movements of individuals from protected to fished areas (crabs in the Sea of Japan, lobster in Newfoundland and New Zealand, sea breams in New Zealand and South Africa; see Gell and Roberts 2003). In addition, tagging studies have documented movements in the Nassau grouper from the Exuma Cays Land and Sea Park, Bahamas (Dahlgren 2004) and in lingcod from closures in south east Alaska (Starr *et al.* 2004). While temperate rocky reef studies typically documented spillover over scales of hundreds of meters to a few km from reserve boundaries, spillover can reach 10s or 100s km for more mobile species (e.g. tagged Nassau grouper migrating 100s km from the park, to spawning aggregations, Dahlgren 2004) and in estuarine and shelf habitats (e.g. Gell and Roberts 2003).

Murawski *et al.* (2005) documented local concentration of effort within 0-5 km from the boundaries of large fishery closures established in 1994 on Georges Bank. Average revenue per hour trawled (\$pue) is currently greatest within 1 km from the boundary (averaging USD 470/hr), declining to USD 273/hr at distances between 10-50 km. Overall, \$pue was approximately double within 4 km of closures compared to more distant locations, though catches near closure boundaries were more variable. Extensive analyses of density and catch gradients away from closure boundaries for 51 species/closed area combinations showed that only three species, haddock, yellow-tail flounder and winter flounder, showed significant density and catch declines with distance from closure boundaries, with haddock showing the strongest and most consistent patterns (Murawski *et al.* 2004, 2005). Aggregate measures also showing significant negative slopes (e.g. all species catch, groundfish catch, and \$pue) were driven by catches of one or more of these species (Murawski *et al.* 2005). The authors stressed the possible roles of degree and patterns of movements of species (e.g. random dispersal vs. directional seasonal movements associated with spawning), the patterns of fishing effort distribution around closures, and habitat preferences of different species in influencing the occurrence and patterns of spillover (Murawski *et al.* 2005).

Although most studies have documented spillover through movements of adults from the reserves to fished areas, only a few studies support the prediction of a contribution from the reserve to adjacent fisheries through larval spillover. This paucity of clear indications of recruitment effects is not surprising given the high variability in recruitment and the difficulties involved in ascertaining the source of recruits. On Georges Bank, legal-sized scallop densities were 9-14 times greater within the closures than outside after only five years from their establishment (Murawski *et al.* 2000). Areas of

high fishing effort, based on remote monitoring of scallop fishing vessels, corresponded to the locations on the Bank where biophysical models of passive larval dispersal predicted increased recruitment through larval export from closed areas (Murawski *et al.* 2000, and references in Gell and Roberts 2003). Protection of 24-ha area of seagrass and mud flat to rebuild clam (*Anadara* sp.) stocks in Fiji resulted in increased abundances and sizes within the fishery closure and increased clam recruitment to adjacent fisheries (Gell and Roberts 2003). After three and a half years of protection, clam densities had increased 13 times within closures and 5 times outside, with significant increases in abundances within the smaller size classes both inside and outside closures, indicative of increased recruitment. Sampling of larval queen conch (*Strombus gigas*) within and around the Exuma Cays Land and Sea Park, a large Bahamian park protecting as no-take reserve 409 km<sup>2</sup> of marine habitat since 1986, documented increased larval production within the park, and larval export through the Exuma Cays (Stoner *et al.* 1998).

Review of these case studies indicates that increased CPUE commonly occurs, particularly close to reserve boundaries. Increased total catches, and thus evidence that reserves contribute to maintaining or enhancing overall fishery yields, are documented only in a few instances. Meta-analysis of results from nine studies of temporal change in catches coinciding with the establishment of reserves or fishery closures showed an average 306 percent increase in CPUE and 120 percent increase in total catches following reserve establishment (Worm *et al.* in press). Unweighted averages of effect sizes from these studies were significantly greater than 0, indicating significant overall enhancement associated with reserves, for CPUE but not for total catches. However, averages weighted by sampling sizes available in different studies resulted in both measures showing a positive effect of reserves, suggesting that the better replicated studies, driving patterns when weighting was applied, showed significant increases in total catches (Worm *et al.* in press).

Taken together, case studies indicate that fisheries benefits are likely to be context dependent (e.g. depending on the siting of reserves relative to oceanographic patterns, habitats included and adjacent to reserves, and patterns of fishing) and highly variable among species (e.g. influenced by movement patterns and habitat preferences of fisheries species). Thus, empirical studies of effects of marine reserves and fishery closure on fisheries production indicate that key considerations in the design of MPAs as tools for sustaining and re-building fisheries include the patterns of movement and dispersal in the larval, adult and juvenile phases, habitat configuration in the region and habitat use by focal species, and patterns of fishing and expected redistribution of effort. In addition, monitoring schemes with sufficient power to detect possible effects of reserves on fisheries yields need to be developed and implemented.

#### **2.4 Community-wide effects through cascading interactions**

Empirical studies of MPA effects within and outside their boundaries tend to show high among-species variation in responses, associated primarily with the species fishery status, life history characteristics, and trophic level. Often, responses to protection are driven by a subset of species. In cases where such a subset includes species that are strong interactors in the ecosystem, and are capable of controlling population abundances of prey or competitors, protection can result in broader community changes through cascading interactions. Indirect effects of protection through predator-prey or competitive interactions may affect pairs of interacting species or multiple trophic levels. Thus, in addition to community-wide change from differential species responses, build-up of strongly interacting species within reserves can influence whole community through trophic cascades.

Cascading trophic interactions influencing the structure and dynamics of whole communities within reserves have been documented in rocky intertidal ecosystems (e.g. Chile, southern California), coral reefs (Kenya, Caribbean), and temperate kelp beds and rocky reefs (in California, Alaska, New Zealand, Maine, and the Mediterranean Sea) (reviewed by Pinnegar *et al.* 2000). In these cases, cascades reversed community changes associated with predators' removal through fishing. For example, recovery of lobster and predatory fishes within temperate reserves in New Zealand, the Channel Islands, and the Medes Islands, Spain, coincided with decreased abundances of sea urchins,

decreased grazing rates and recovery of macroalgae, and a shift from sea-urchin dominated barrens to higher-diversity macroalgal and kelp beds (reviewed by Pinnegar *et al.* 2000). Most examples highlight indirect effects of predator increases on specific species, most commonly benthic, relatively sedentary species such as herbivorous molluscs and sea urchins (Pinnegar *et al.* 2000).

No evidence of cascading effects on whole trophic levels has been detected by meta-analyses of empirical studies (Halpern 2003; Micheli *et al.* 2004). However, significant decreases within reserves were detected for an average of 19 percent of species across 31 locations examined by Micheli *et al.* (2004), suggesting that indirect effects on species, particularly small, relatively sedentary fish species not targeted by fishing, are relatively common. Negative correlations between time series of abundance indices for species linked through predator-prey or competitive interactions have also been documented at larger spatial scales in groundfish fisheries from the west coast of the United States (Mangel and Levin 2005) and the NE Atlantic Shelf (Worm and Myers 2003). Therefore, indirect effects of increases of strongly interacting species may be expected at both local and regional scales. In cases where MPA establishment results in increased mortality for species of commercial or conservation significance, responses may pose trade-offs between managing for population persistence or recovery of alternative species. Such potential trade-offs need to be addressed as considerations in reserve design, and the possible losses anticipated.

Few studies have addressed these trade-offs empirically. The re-colonization of central California by sea otters (*Enhydra lutris*) in the mid 1960s led to high predation rates and dramatic decreases in abalone (*Haliotis* spp.) abundances (Estes and VanBlaricom 1985; Wendell 1994). Recent comparisons of red abalone densities and size structure at sites within or outside the current range of sea otters in California showed that in the presence of sea otters, abalone have lower densities, smaller sizes, and tend to be restricted to cryptic microhabitats (Fanshawe *et al.* 2003). In the areas currently occupied by sea otters, fishing mortality of benthic invertebrates removed through the establishment of no-take marine reserves or the implementation of fishery closures may be replaced by high mortality from sea otter predation, with no apparent recovery of abalone and sea urchin abundances and mean sizes (e.g. Fanshawe *et al.* 2003). However, sea otter recovery has also likely allowed for kelp recovery from over-grazing by sea urchins (Estes and Duggins 1995). Thus, recovery of this predator may be accompanied by potential gains for other fisheries (e.g. rockfish, through recovery of kelp habitat). A systematic analysis of gains and losses with respect to multiple objectives in this and other ecosystems has not been conducted.

In addition, cascading effects of predator recovery in reserves may be more complex than the simple prediction of increased predators/decreased prey. Size structured species interactions, combined with species and size specific fishing mortality outside reserves can result in no change or even net increases in prey biomass following increased predator biomass. Mumby *et al.* (2006) compared the negative impacts of enhanced predation with the positive impacts of reduced fishing mortality on parrotfishes inside the Exuma Cays Land and Sea Park (ECLSP), Bahamas. Since the mass mortality of the urchin *Diadema antillarum* in 1983, parrotfishes have become the dominant grazer on Caribbean coral reefs. The grazing capacity of these fishes could be impaired by the documented six-fold increase in the biomass of their main predator, the Nassau grouper *Epinephelus striatus* inside the park. However, because large-bodied parrotfishes escape the risk of predation from Nassau grouper, the predation effect only reduces grazing by 4-8 percent. This impact is overwhelmed by the increase in density of large parrotfishes, which are caught in fish traps outside the park, resulting in a net doubling of grazing inside the park. Increased grazing caused a four-fold reduction in the cover of macroalgae, the principal competitors of corals, highlighting the potential importance of reserves for coral reef resilience.

An understanding of the patterns and strengths of species interactions in fished and unfished communities, and systematic analyses of possible indirect effects and trade-offs associated with alterations of community interactions through marine reserves are crucially important for including multiple fisheries, as well as other economic (e.g. from increased tourism revenues, in the case of sea otters and kelp forests) and ecological (restoration of processes allowing for habitat recovery, e.g.

increased grazing and decreased macroalgal cover in coral reef reserves) benefits as considerations for the design of reserves that may pose trade-offs for species recovery.

### 3. POPULATION DYNAMICS

The empirical results in the previous section give us some information on what to expect when an MPA is implemented, but they do not answer some of the basic questions we would have in designing MPAs: e.g. how many, how large and how far apart? Broadly speaking, observations of MPAs have thus far focused on strategic questions such as "How frequently do abundance, biodiversity, size, etc. increase inside reserves?" at the expense of the more difficult tactical questions of "*Why* do abundance, biodiversity, size, etc. increase inside reserves?" and "When do catch and CPUE outside reserves increase?" Unfortunately, while it is comforting to know how often certain attributes change inside reserves, to design reserves that increase abundance and fishery yield we need the answer to the questions "Why?" and "What happens outside?"

There are several reasons why the observations of MPAs are limited. One is that the processes we wish to observe, especially recruitment, display high random variability. A second is that MPAs are typically not designed with experimental design or adaptive management in mind. Because many characteristics can lead to a difference in abundance between reserves, observations of a few reserves without specific experimental design will allow some effects to be occluded by others. For example, recall that in the empirical observations in Section 2, the effects of different movement patterns were obscured by the differences in level of fishing.

Because we do not have a broad empirical basis on which to design and implement MPAs, we need to use models to examine the consequences of both the empirical information we do have and the information we do not have (i.e. the different sources of uncertainty). Examples of the former include individual growth rates, mortality rates and fecundities, as well as their dependence on size or age. These models will depend on many parameters and processes from conventional fishery management, but they will also include processes we have not had to describe explicitly in conventional management. Examples include larval dispersal and spatial patterns of movement of juveniles and adults. Because these processes are not well studied, they may introduce uncertainty into the application of MPAs.

#### 3.1 Persistence (or sustainability)

To design marine reserves or predict how well they will protect a certain species, we need to know how characteristics of MPAs (e.g. size and spacing) and life histories combine to produce sustainable or persistent populations. For example, we know intuitively that a 1 km by 1 km MPA will not sustain a population of a highly mobile species such as tuna, but we don't necessarily have a ready answer for the question of the minimum size MPA that would be necessary. Persistence of populations in MPAs depends on movement through the larval phase as well as swimming of juveniles and adults. We begin with the former.

##### 3.1.1 Larval dispersal

Beginning with the simple case of a species with a dispersing larval stage but sedentary juveniles and adults, we wish to know how the size and spacing of the MPAs we are designing will affect persistence or sustainability in the MPAs. Our understanding of sustainability is based on modelling studies (Botsford *et al.* 2001; Kaplan and Botsford 2004; Lockwood *et al.* 2002). The results of these can be understood by examining two cases, a single MPA and a system of several MPAs distributed along a coastline. For a single MPA, species will persist if their mean dispersal distance is less than the linear spatial dimension of the MPA. In terms of the replacement interpretation described in Section 1.0, a population will persist in a reserve if a high enough fraction of the larvae released from that reserve return to the same reserve. Similar to the single, non-spatial population, that fraction is the fraction of natural, unfished LEP (e.g. 35 percent). In the second case, a system of reserves, a

population with larvae that disperse any distance will persist in a system of reserves (of any size) that covers a certain fraction of the coastline. The replacement interpretation of this result is essentially the same: a population will persist if a certain fraction of the larvae released by the population return to the population. To understand this case consider a population at a location in a reserve to be dispersing larvae all along the coast, and assume that fishing removes all individuals between reserves before they reproduce. The fraction of reproduction that will be successful for long-distance dispersers will be the fraction of the coastline covered in reserves. From the single, well-mixed population results we know that a certain fraction of LEP is needed, hence the fraction of the coastline needed in the spatially distributed population is the same. This effect by which many reserves provide for the sustainability of a population when one MPA alone would not is referred to as a *network effect*. While the explanation is posed in terms of complete removal by the fishery outside reserves, it stands to reason that a lower fraction of the coastline in reserves is required as fishing is reduced and the FLEP outside reserves is greater.

Both the single reserve effect and the network effect can be seen in Fig. 6. For all three levels of Fraction of Lifetime Egg Production (FLEP) resulting from fishing outside reserves, the short distance dispersers (1 km and 5 km) persist in almost all of the reserves, even the smallest ones. The longer distance dispersers persist over areas where a larger fraction of the coastline is in reserves, and the area over which they persist is greater for less fishing (i.e. higher FLEP).

While we have presented these results in terms of heuristic explanations, they are supported by specific mathematical results, and it is important to know the specific assumptions on which they depend. The initial attempt to answer this question through modelling was to calculate the conditions for persistence of a population in a system of identical MPAs with uniform spacing and complete removal by the fishing that occurred between them (Botsford *et al.* 2001). The density-dependence in the population occurred between larval settlers at a location and those that were actually recruited, and it was assumed to be a Beverton-Holt relationship. Larval dispersal was assumed to decline exponentially in each direction from its origin, with mean dispersal distance a parameter to be varied, and total larval production each year was held constant, independent of dispersal distance.

The basic persistence result was originally described for the situation in which there was no reproductive contribution from outside reserves, i.e. complete removal fishing, but the sensitivity to less fishing outside reserves was also presented graphically (Botsford *et al.* 2001). Allowing less fishing led to a slightly more complex condition for persistence which indicated that, as would be expected, for any given size of MPA, less fishing outside reserves meant that species that disperse longer distances would be allowed to persist, and the fraction of coastline in MPAs required for persistence of a system of reserves was less (Kaplan *et al.* in press). An important aspect of these results is that the level of fishing outside of MPAs affects persistence only through the value of FLEP outside the MPAs.

Subsequent studies showed that as long as the dispersal pattern was symmetrical, the details of the shape of the larval dispersal pattern did not affect the results, rather they depended primarily on the mean distance dispersed (Lockwood *et al.* 2002). Sustainability or persistence was quickly reduced when advection (displacement of the symmetrical dispersal pattern) was introduced (Botsford *et al.* 2001).

These results indicate that a single MPA or a network of MPAs will provide for persistence of species that disperse up to a certain mean distance, AND all those dispersing shorter distances. The alternative view, that a variety of spacings among reserves was necessary in a system of MPAs to account for the variety of dispersal distances (e.g. Palumbi 2003) was tested by computing the persistence of randomly distributed MPAs (Kaplan and Botsford 2004). A random distribution of MPAs made little difference in population persistence, except in the rare cases where populations were marginally sustainable and the randomness fortuitously created a region of higher fraction of coastline covered by MPAs, leading to local persistent population (at the expense of persistence elsewhere along the coast).

While these results are useful in understanding the strategic question of why empirical observations of abundance and biomass increased or decreased inside (and outside) the MPAs reviewed in Section 2, to design MPAs we also need similar tactical tools that will allow projection of whether specific designs are likely to increase or decrease recruitment. Such tools are being developed and used in reserve designs based on direct extensions of the mathematical methods used in the studies described here (i.e. the two methods used in Botsford *et al.* 2001) (Hastings and Botsford 2006; Kaplan *et al.* 2006). The former provides an analytical method for determining the equivalent of lifetime reproduction ( $R_0$ ) for spatially distributed populations, and emphasizes the importance of replacement loops over space. The latter describes a numerical method for computing the area over which a population will persist given a specific distribution of habitat and reserves, and a level of fishing outside reserves. These methods can be structured as one-dimensional models (i.e. along a coastline) or two-dimensional models. A one-dimensional model is shown here because it illustrates the effects of reserve size and spacing on persistence, and the way that the level of fishing outside the MPAs affects those relationships (Fig. 6). A two-dimensional model also demonstrates the effects of size and spacing on species dispersing different distances (Fig. 7). These models allow MPA designers to see how size and spacing interact with fishery management outside MPAs, as well as the distribution of habitat inside and outside MPAs.

### 3.1.2 Juvenile and adult movement

We can extend the view gained from these modelling results that consider larval dispersal only, to include the effects of juvenile and adult swimming. Because the results for persistence depend on the LEP of a population at a specific location, we can interpret the effects of swimming behaviour in terms of its effect on LEP. Generally, species with greater movement (e.g. larger home range) would be expected to spend a greater amount of time outside of the MPA, where they would be more susceptible to fishing. The consequent higher fishing mortality rate would lead to a lower LEP, hence lower expected recruitment in the MPA and a less sustainable population.

Several existing studies quantify these relationships. These have their origin in the special case of marine reserves in Beverton and Holt (1957) (see Guenette *et al.* 1998 for further description). They divided an area into reserve and fished portions, then examined the effect of having various fractions of the area in reserve. Movement between the areas was described in terms of specified transfer rates. Results were expressed in terms of eggs-per-recruit (EPR) and yield-per-recruit (YPR). For our purposes here, EPR can be considered the same as LEP, thus reducing EPR has the same effect on equilibrium recruitment as the effect of reducing LEP described above. This approach was extended by Polacheck (1990) and applied to species with different scales of movement by DeMartini (1993).

DeMartini (1993) computed the effects on EPR of various combinations of fishing mortality rate  $F$  and the fraction of habitat in MPAs for two species, one of which had a movement rate 25 times that of the other (Fig. 8). The major result is indicated by the difference in the slopes of the lines of constant EPR between Fig. 8A and Fig. 8B. From them it is clear that MPAs have much less of an effect on a species with greater movement in and out of the MPAs (i.e. slopes of constant EPR are steeper in Fig. 8A than Fig. 8B). Results indicated for a species with little movement (Fig. 8A), EPR increased approximately linearly with the fraction placed in reserves at high fishing mortality rate, but was virtually independent of fishing mortality rate. For low fishing mortality rates ( $0.5 \text{ y}^{-1}$  to  $1.0 \text{ y}^{-1}$ ), EPR depended on both fishing mortality rate and fraction in reserves (Fig. 8A). For the species with greater movement (Fig. 8B) at high fishing mortality rates, EPR increased with fraction in reserves and decreased with increasing fishing mortality rate. For low fishing mortality rate, EPR was more dependent on fishing mortality rate, with little dependence on fraction in reserves (Fig. 8B). In summary, MPAs appear to have a greater affect on EPR when fishing mortality rates are high for both species, and reserves have a greater effect on EPR for the species with less movement.

## 3.2 Fishery yield

To design MPAs that are being implemented for the purpose of fishery management, we would be concerned that it provide maximal, or at least adequate yield, or that it provide greater yield than the current conventional management. We have seen from the review of empirical results that there are several examples where the implementation of marine reserves appears to increase CPUE, and a few cases of increase in fishery yield, but there are not enough examples to determine empirically the characteristics of reserves that lead to greater catch, or to predict how a given MPA will affect yield. Mathematical modelling can be used to project the way that yield will depend on MPA design (i.e. spacing, size and location).

A useful way of assessing the consequences of implementing an MPA or a system of MPAs is to compare the fishery yield with the MPAs in place, to yield under conventional management. Following that approach, if we were to implement MPAs in an area, it would reduce the amount of area available for fishing. For yield to be the same as under conventional management, catch in the area outside MPAs would have to increase to the point that it could compensate for the decline in area fished.

An increase in catch in the area outside of reserves would consist of two components: (1) an increase in recruitment outside of reserves and (2) an increase in the number of fish swimming out of the newly protected area. The former term would be controlled by the dynamics of recruitment described above under persistence. The resulting recruitment at each location would depend on the LEP at all other locations nearby, as well as larval dispersal rates between those locations and the location of interest. It would require an increase in LEP inside the reserve area, minimal decrease in LEP outside the MPA area (due to displacement of effort from formerly fished MPA area), and that the dispersal pattern of the species be broad enough to reach that point. The latter term would be the same as YPR dependence on size limits and fishing mortality rate in single, non-spatial populations, except that the fishing mortality rate would depend on how the combination of the spatial configuration of marine reserves combined with the movement behaviour of juveniles and adults to change the effective  $F$ . Recall that in conventional management YPR will either increase monotonically with fishing mortality rate or increase rapidly to a maximum then decline monotonically (Beverton and Holt 1957). The latter term would depend in a complex way on how recruitment changed inside MPAs and how the change in effective fishing mortality rate inside the MPAs changed with the implementation of the MPA. This would affect both the yield due to fish moving out of the reserves, and the EPR in the MPA in an inverse way. Calculating or estimating these changes is complex and involves uncertain parameters as well as details of the specific MPA implementation.

### 3.2.1 Larval dispersal

For the case in which larval dispersal is the only source of movement over space (i.e. no juvenile or adult movement) a valuable benchmark allows us to avoid having to make extensive calculations to compare fishery performance in MPAs to conventional fishery performance. For a simple age structured model with post-dispersal density-dependent recruitment of the Beverton-Holt (1957) type, and larval pool dispersal, the problem of maximizing yield in a system with MPAs is mathematically exactly the same as the problem of maximizing yield in conventional management by setting fishing mortality rate (Hastings and Botsford 1999). This means that the yields possible with MPAs and conventional management are the same for this case. The possible difference for at least some other cases can be judged intuitively. For example, if there is pre-dispersal density-dependence, conventional management is likely to produce higher yield because MPAs are likely to increase pre-dispersal density to high levels.

An important consequence of this result is that if a population is being managed by conventional management to obtain the highest possible yield, changing to management by MPAs will not achieve higher yields. To phrase this in terms of the empirical results reviewed above, we should expect to see the greatest improvements in yield with implementation of MPAs in situations in which fisheries are

recruitment overfished. This result can be seen in a number of simulation studies of MPAs (e.g. Quinn *et al.* 1993; Holland and Brazee 1996) (Fig. 9), and this question has also been addressed more specifically by Hart (2006).

The approximate equivalence of fisheries yield from MPAs and conventional management was also contained in a result indicating that for populations represented by a logistic model and implicit larval pool dispersal, yield depended only on the product of fishing mortality and area not in MPAs, and did not depend on the value of each factor (Mangel 1998, 2000).

There are several exceptions to this benchmark rule that yield from MPAs is approximately the same as yield from conventional management, and these may be important in some instances. Possibly the most important exceptions occur in situations with substantial source/sink structure in larval dispersal. For example, in a case in which a single self-persistent source population sustained three others, protecting the source population provided greater yield than conventional harvesting of all at the same fishing mortality rate (Morgan and Botsford 2001). An important constraint, however, was that the source/sink structure had to be known in order to take advantage of it. If it were not, yield with MPAs was not greater than with conventional management at maximum sustainable yield (MSY). In general, larval dispersal patterns are not well known. A similar exception is a case in which dispersal among populations along a coastline involved substantial advection in different alongshore directions each year (Gaines *et al.* 2003). In this case also, the dispersal patterns created a source/sink pattern. Gaylord *et al.* (2005) obtained higher fishery yields through marine reserves using a stage-structured model with spatial pattern in adult densities and larval dispersal. Hilborn *et al.* (2006) formulated a model with logistic populations and fisher movement, and obtained greater catches through reserves only when the fishing level would lead to extinction outside reserves.

A second area of exceptions to this rule involves the effects of density-dependence on the population in reserves; strong density-dependence leads to poorer performance of reserves in comparison to conventional management (Botsford *et al.* 2003). Parrish (1999) showed in a modelling study that the presence of over-compensatory density-dependence diminished yields obtained through use of reserves. Gardmark *et al.* (2006) used a model with density-dependent growth to show that it could lead to conventional fishery management having greater yields than management by reserves.

Equivalence in yield should not be equated with equivalence in performance: costs associated with extracting the same yield would be higher with MPAs than with conventional management. Under spatial management, the population outside the reserve would be exploited harder and therefore would be more depleted than when effort is spread over the entire spatial expanse of the fishery. Fishers would thus experience much lower densities and catch rates when a substantial fraction of the biomass that sustains the productivity is placed in a reserve (NRC 2001).

### 3.2.2 *Juvenile and adult movement*

Adding the possibility of juvenile and adult swimming behaviour to our assessment of the effects of movement on yield provides an important exception to the rough equivalence between MPAs and conventional management: the case involving ontogenetic, rather than inter-population movement. When there is substantial ontogenetic movement, protection of spawning and juvenile rearing areas can often provide greater catch than fishing all areas (Apostolaki *et al.* 2002).

While it is becoming widely appreciated that MPAs will be less effective for species whose juveniles and adults move frequently over large distances, there are few examples comparing the effects of different patterns of movement. However, we can gain some insight from the fact that recruitment at a location depends on LEP. As movement frequency and distances increase, fish spend greater amounts of time outside of MPAs subject to fishing. As noted above, one consequence of the greater catch is a reduction in LEP, which will likely decrease recruitment in the MPA. On the other hand an increase in yield is possible if the increase in YPR outweighs the decline in recruitment.

We can get some idea of the possibilities from the examples in DeMartini (1993), who plotted the lines of constant YPR and EPR as a function of fishing mortality  $F$  and proportion of area within reserves, for two species of different mobility (Fig. 8). The important characteristic of these plots is that the lines of constant YPR are essentially parallel to the lines of constant EPR. This represents a trade-off between EPR and YPR, but it runs in opposite ways for these species because they have different dependencies on  $F$ , even with no MPAs. For the species with low movement (Fig. 8A), note that with no MPAs YPR increases monotonically with  $F$ . As the fraction in reserves increases, this sign of this dependence remains the same, but the values of YPR decline. For the more mobile species (Fig. 8B), with no MPAs, YPR peaks at a low value of  $F$ , then declines. As the fraction in MPAs increases, the dependence of YPR on  $F$  again remains the same, but the values of YPR are lower. For the species with low movement this implies an inverse relationship between YPR and EPR. For the species with greater movement, the opposite is true, primarily because that is the relationship with no reserves (i.e. this is not necessarily a characteristic of greater movement).

### 3.3 Combining yield and persistence

Few studies have explicitly addressed the combined effects of MPAs on persistence and yield (though most simulations that assess yield do so with models that remain persistent). One study addressed the question of whether the spatial configuration of reserves should differ for the different goals of MPAs for fishery management or general conservation of biodiversity (Hastings and Botsford 2003). That study considered species with sedentary adults and larval dispersal as the only movement. The important conclusion of that study is that while cost considerations may dictate that for the biodiversity goal large reserves should be used (rather than covering a certain fraction of the coast), for fishery management a system of small reserves covering the minimal fraction of the coast required for persistence is the best. The basic reason for this is that the higher number of MPA edges provides greater larval spillover. This result would likely change if juvenile and adult movement were considered.

Another example was a simulation of a size structured model with dispersal exponentially from its origin and MPAs that were spaced 25 units apart with size varied from 0 to 10 units. Results show the combined effects for a species with no juvenile or adult movement, in a population for which individuals cease to replace themselves when  $F$  is greater than  $1.1 \text{ y}^{-1}$  (Fig. 10). With no reserves, as  $F$  increases catch at first increases, then collapses at  $F=1.1 \text{ y}^{-1}$ , with no dependence on dispersal distance. When 8 percent of the coastline is in reserves, catch is slightly greater at high  $F$  for species that disperse short distances. As the fraction of coastline in reserves increases to 40 percent, catch remains high at all dispersal distances except short distances, in spite of high  $F$ .

## 4. EMPIRICAL RESULTS, MODELLING EXTENSIONS AND UNCERTAINTY

The empirical results available for marine reserves indicate that removing fishing pressure frequently does have the expected effect of allowing an increase in abundance, biomass and mean size inside reserves, but they provide little in the way of guidance regarding how to design MPAs to assure they produce these increases, as well as producing an increase in fishery yield or sustainability. The most common type of study is a comparison of conditions inside reserves with conditions outside, and there are fewer examples that follow a reserve over time from implementation. Trends useful for design of reserves include the tendencies for harvested species, species with greater body size, and species at higher trophic levels to be more likely to increase in reserves. There is also one study that indicates species with less potential for larval and adult movement were more likely to increase than species with greater potential for movement (Parnell *et al.* 2005). There appear to be few differences due to the size of reserves, and no attempts to assess the effects of spatial configuration. While habitat type is often accounted for in the design of reserves, there have been few attempts to address the effect of habitat quality and heterogeneity.

With regard to fishery performance, increased CPUE, and in some cases, total catches around reserves have been documented in small no-take reserves established in coral reefs, temperate rocky reefs,

lagoonal or estuarine environments, as well as larger scale fishery closures. In most cases, increased CPUE is apparent within hundreds of meters to a few kilometres from reserve boundaries, and increases are driven by a few species. Movement patterns, habitat preferences and fishing patterns likely influence changes in fishery yield by different species. Effects on total catches are more variable, with overall increased or stable fishery yields documented only in few cases. In most documented cases, adult fish movements across the reserve or closure boundaries appear to underlie MPA contribution to adjacent fisheries. A few studies of species with sedentary adults also support the hypothesis of larval seeding from reserves into fished areas, but empirical evidence for a larval contribution of reserves is more limited.

Modelling studies extend our understanding of how populations respond to size and spacing of reserves beyond the direct empirical results by allowing examination of both known life history characteristics of fish, such as growth, mortality and fecundity, as well as poorly known characteristics, such as larval dispersal patterns and adult/juvenile mobility. Model results indicate that for sedentary species with dispersing larvae: (1) single reserves will allow for persistence of species dispersing mean distances on the order of the linear dimension of the reserve; (2) systems of reserves that cover a certain fraction of the coastline will allow for persistence of species dispersing a broad range of mean distances; and (3) a good benchmark estimate of the yield to be expected from reserves is that the maximum yield from reserves will be roughly equal to the maximum yield from conventional management controlling catch or effort. As juvenile/adult mobility increases, the sustainability of species in reserves will decline, but yield may increase.

#### 4.1 Uncertainty

The significant uncertainties that affect the design and implementation of reserves involve movement rates of both juvenile/adult and larvae and productivity at low population size (i.e. the replacement threshold). The latter is also present in conventional management. Because the potential fisheries benefits derived from reserves of different sizes will depend on our ability to control Fs outside the reserves, we include a description of the implementation uncertainty associated with conventional management.

##### 4.1.1 Reserves

We described in Section 3 how modelling has indicated that both sustainability and yield depend on larval dispersal patterns and juvenile/adult movement of the species of interest. While information on larval dispersal is available from several sources (reviewed in Shanks *et al.* 2003 and Kinlan and Gaines 2003), larval dispersal patterns are known only for the few species whose larvae disperse hundreds of meters or less. It is interesting that there is little empirical evidence for the effect of dispersal distance on persistence in reserves. There are several possible reasons for this lack: since dispersal distances are poorly known the analysis is difficult, the effect of dispersal distance diminishes as the impact of fishing on LEP outside reserves declines and it is possible that most species have short mean dispersal distances.

Adult and juvenile movement in marine species is better known than larval dispersal, and there are several examples of studies in the context of marine reserves (Section 2). The relative paucity of evidence for the effect of juvenile adult mobility on sustainability of implemented reserves could also be due to the fact that reserves have been implemented in areas where FLEP is still relatively high, but the confounding effect of variable exploitation rates across studies noted in Section 2 is another possibility.

##### 4.1.2 Reserves and conventional management

The dependence of sustainability of different levels of protection (i.e. reserve sizes or fractions of habitat within reserves) on the minimum value of FLEP that achieves population replacement is common to conventional, single population management and management by reserves, thus linking

the two management tools. In fisheries management this uncertain parameter is commonly associated with reference points or control rules. It plays a fundamental role in management, defining how hard a population can be fished before it collapses, whether managed spatially through MPAs, or by limiting catch or effort.

#### 4.1.3 *Implementation uncertainty in conventional management*

The equivalence between conventional management and MPAs discussed above was established in terms of the fraction of area protected and the level of fishing mortality that would produce the same yield for sedentary species. In reality, the rate of fishing mortality  $F$  is only controlled through catch quotas and/or effort restrictions, the effects of which are very uncertain. In the case of quota-based management, the uncertainty in the estimates of stock biomass used to set quotas translates directly into uncertain  $F$ s. Likewise, the relationship between effort limitations and  $F$  depends on highly uncertain predictions about catchability. Worse, assessment errors tend to be correlated from year to year, specially in cases of model misspecification, with the result that  $F$ s can be consistently above (or below) target for several years in a row. So, while in theory conventional management may be equivalent to MPAs for some systems, in practice the consequences of implementing either form of harvest controls are so uncertain that it would be impossible to determine the actual regulatory tactics that would result in similar yields.

Indeed, one of the main arguments for advocating the use of MPAs has been as a buffer against errors in the implementation of conventional management (Lauck *et al.* 1998). While the effectiveness of MPAs themselves depends on very uncertain dynamic processes, the kinds of uncertainties that affect the two types of management are for the most part different and independent of each other (with the exception of the minimum replacement required for persistence). Thus, a combination of harvest controls involving catch and/or effort quotas and reserves may outperform either type of management when implementation uncertainty is substantial. Stefansson and Rosenberg (2005) illustrated this point using a simulation model inspired by the Icelandic cod fishery. They found that combining catch quotas with a large closed area was an effective system for reducing the risk of stock collapse and maintaining economic performance. In their model, which was based on the assumption that implementation errors were independent from year to year, best economic performance was still achieved by setting low target  $F$ s. Another example is environmentally driven shifts in the spatial distributions of fished populations, which could affect MPA performance, but may not affect the effectiveness of quota management.

## 5. RECOMMENDATIONS FOR GUIDELINES AND TOPICS FOR THE WORKSHOP

The state of knowledge described in reviews and summaries of empirical observations and modelling results suggest guidelines for the design and implementation of MPAs. We presume that the guidelines to be provided will be a central topic for discussion at the anticipated workshop. First, we note that our ability to recommend guidelines here is somewhat limited by the fact that we have focused on the effects of ecological factors, whereas decisions regarding the design and implementation of marine reserves frequently involve tradeoffs among ecological, social, economic and other factors, which are case-specific. Here we provide the ecological perspective on potential guidelines, and point out additional required information.

In addition the guidelines most appropriate in each specific situation will depend on the amount of data available. Accordingly, our recommendations span the range from data rich to data poor.

### 5.1 Data-rich situations

For a data-rich situation, with the resources and infrastructure for technical planning through a decision framework, modelling through some of the techniques shown here (e.g. Hastings and Botsford; Kaplan *et al.*) can be used to evaluate the robustness of alternative reserve designs and fishing controls to achieve management goals, such as persistent populations and good associated

yields. For example, plots such as those in Fig. 6 could be examined for each proposed spatial design to determine how well they provided for persistence of species over a range of dispersal distances. The effect of fishery management outside reserves could be accounted for by choosing the plot with the appropriate value of LEP (Fig. 6 a, b, or c). Values of FLEP can be taken from values of spawning potential ratio (SPR) for species for which a stock assessment has been done, or they can be estimated by methods that are less data intensive (e.g. O'Farrell and Botsford 2005). For example, estimation of FLEP for several species of rockfish on the west coast of the United States, this method indicated values at levels as low as 0.2 (O'Farrell and Botsford 2006). Values of FLEP estimated from assessments may need to be modified to account for the effects of increased fishing mortality outside the reserves associated with displacement of fishing effort from the closed areas, and of course to reflect any possible modifications in the management outside the reserves, if those are considered. Once the areas of persistence are determined, the expected distributions of yield along the coastline can be computed from them, as in Kaplan *et al.* (in press). Proposed combinations of reserve configuration and fishery management outside reserves can then be chosen.

While these equilibrium methods offer valuable and computationally efficient means to evaluate the interaction between reserve size and spacing, fishing outside reserves and dispersal distance, they still depend on uncertain parameters and processes. To incorporate the effects of dispersal distance, even though dispersal patterns are very poorly known, they assume an exponential decay from the origin with a specified mean distance. Effective replacement, through lifetimes and over space, are ultimately compared to a threshold that is unknown, just as it is in conventional fishery management. Both of these sources of uncertainty require specific evaluation of their effects on the management decision processes. This would involve sensitivity assessments and application of a precautionary approach. The aim should be to find combinations of reserve designs and other management controls that appear to work well (i.e. are robust) for a range of scenarios considered likely, and not on the determination of an optimal solution for any single scenario.

In addition to uncertainty about key processes in the population dynamics, the relative merits of different regulatory schemes involving reserves and conventional harvest controls (e.g. catch and effort quotas) will depend on our ability to implement the desired harvest targets, as discussed in Section 4.1.3. The so-called implementation uncertainty needs to be considered as well in the decision framework.

Beyond the equilibrium approaches outlined in Section 3.1.1, more complex simulation models could be used to evaluate management performance in data-rich situations, if specific scenarios about fish movement, fleet behaviour and/or implementation uncertainty were to be examined. Examples of this type of spatially-structured models are the models used by Steffanson and Rosenberg (2005) for Icelandic cod or by Little *et al.* (2005) for common coral trout on the Great Barrier Reef. The downside of these approaches, of course, is a steep increase in complexity and computing time.

## 5.2 Data-poor situations

The decision as to whether to implement reserves for fishery management will depend to some degree on the anticipated yield for different management schemes. In conventional management, different proxies for MSY have been proposed to guide decisions in data-poor situations. Some of the same guidelines may be applicable to the design of MPAs by taking advantage of the rough equivalence between MSY with reserves and MSY with conventional management. While there are exceptions to this equivalence, the processes involved can frequently be accounted for (e.g. pre-dispersal density dependence) or they have to be ignored because their use to improve reserve design would require more information than is possible to obtain (e.g. estimating reserves provide greater catch because of source sink structure). Yields possible through implementation of marine reserves would be compared with yields through a change in conventional management, and the costs of management by each method. For example, if a fishery involves multiple species with the same gear, and the species are poorly known, it may be advisable to manage with reserves, provided they can be enforced at reasonable costs.

In the design of the spatial configurations of reserves, to obtain higher yields, a number of smaller reserves would be preferable over fewer large reserves, to maximize larval spillover. For species with greater juvenile/adult mobility, yield would likely be greater than for sedentary species. However, for species with greater mobility, eventually the effect of reserves could tend to zero so that the reserves would provide no increase in sustainability, but would also not diminish catch.

In data-poor situations, different assumptions about the type and level of uncertainty associated with implementation of different regulatory schemes would change the anticipated effectiveness of alternative combined rules. In the extreme, quota-based management may simply be impractical in many situations due to one or more of the following conditions: (i) insufficient information to conduct quantitative stock assessments on which to base quotas; (ii) unenforceability of quotas; and (iii) inappropriateness of global controls in the case of populations with persistent spatial structure. It is not uncommon that these conditions are all true simultaneously. Typically, this is the case of many small-scale artisanal fisheries based on spatially-structured stocks, in which data-poorness has some structural correlates that also lead to lack of compliance with fishing regulations and makes conventional fisheries assumptions untenable (Parma *et al.* 2003). Interestingly, in some of these artisanal fisheries, marine reserves, combined with effort controls or at least restrictions to fleet size/capacity, may provide a more feasible system for the control of harvest rates than catch quotas. Indeed, MPAs have met with success in some artisanal reef fisheries, especially when fishing communities have been involved in the process and have seen the benefits derived from their implementation (White *et al.* 2006).

### **5.3 No evaluation**

It is also worthwhile to provide guidelines regarding the risks and potential benefits of simply implementing marine reserves without evaluation of ecological effects based on the premise that they will improve fishery yield or sustainability. If the species of interest in the implementation of a reserve does not have high juvenile or adult mobility (e.g. large home ranges that would take them outside the reserve frequently), it is likely that biomass will increase in the reserve. In addition, if the larval dispersal distance is substantial but not greater than the linear dimension of the reserve, the species is likely to remain persistent inside the reserve and provide increased replacement paths for parts of the population near the reserve. The question then is whether the increased larval input to fished areas and juvenile/adult movement outside reserves are large enough to increase yield by an amount that compensates for: (1) the effects of removing the reserve area from the fishable area and (2) the effects of additional effort in the fished area that has been displaced from the reserve area.

### **5.4 Importance of monitoring.**

An important guideline is the recommendation of monitoring to accompany the implementation of a marine reserve. Monitoring of reserves is commonly recommended as a means to demonstrate that a system of reserves is achieving its goals, and that rationale often draws greater attention when reserves are implemented with the goal of improving fishery management. That one should monitor any resource management project to determine whether it is accomplishing goals is now well accepted, whether on the basis of demonstrating that it was a justified expenditure or the appeal of the optimality of adaptive management. However, in the case of marine reserves, because their wide-spread use is in a nascent phase, there are broader reasons for monitoring that go beyond individual implementations themselves. As indicated by the reviews of empirical information and modelling results, the performance of marine reserves depends on design attributes (e.g. location, size, spacing) and life history characteristics in a way that is not well understood. There is a general need for improvement in our ability to design and implement marine reserves, that can be met through more careful monitoring.

To date monitoring reserves has typically consisted of post hoc comparison of abundance, biomass, mean size and diversity inside reserves in relation to outside. However, there is increasing awareness that before/after comparisons at the same location are superior, and a broader range of attributes are

being monitored. The information presented here provides the motivation for including size and spacing as well as the level of fishing outside reserves as "treatments" in whatever experimental design might be involved in monitoring. As noted in Section 2, we have little empirical information on whether we should be using large or small reserves, and what level of persistence we can expect as fishing increases outside the reserves currently being designed. Such information is needed to improve our design, and reduce the uncertainty in our projections of reserve performance.

## 5.5 Context-recommendations by others

As a final section we add a comparative note of the fact that others have made similar suggestions for the future path of research and implementation of marine reserves. For the most part recommendations are similar in calling for steps toward a better understanding of the dependence of performance on spatial design, but there are some differences.

The conclusions of Hilborn *et al.* (2004) are similar to ours (which is not surprising since two of us were also co-authors of that study). That study addresses the general conditions under which the use of reserves or MPAs is advisable for fisheries, while we focus here on the ecological aspects. The authors note that marine reserves are likely to be a useful tool for management of fisheries on more sedentary stocks (consistent with our description of the dependence of yield and sustainability on juvenile adult movement) and fisheries that are multi-species (consistent with Section 5.2). They recommend careful planning and management so that in the future we will know what aspects of our design worked and why.

Sale *et al.* (2005) present another view of the state of knowledge of the functioning of marine reserves. They review some of the same modelling results described here, to identify gaps in the science underlying the performance of marine reserves. The gaps identified are: (1) our understanding of larval dispersal, (2) limited understanding of juvenile and adult movement, (3) limited knowledge of ecosystem aspects of reserves, (4) poor understanding of coastal circulation and (5) "remarkably few well designed studies of no-take reserves that can rigorously demonstrate that they have sustained or enhanced fishery yield in the surrounding region." Their conclusions are, for the most part, consistent with ours, though we would include arguments associated with the network effect described in Section 3.1.1 as a way of justifying a specific fraction of the coast as reserve (see Box 1 of Sale, *et al.* 2005). As shown in Fig. 6, persistence of longer distance dispersers depends on the fraction of coast in reserve, which declines as FLEP outside reserves increases.

## REFERENCES

- Airamé, S.; Dugan, J.E.; Lafferty, K.D.; Leslie, H.M.; McArdle, D.A. & Warner, R.R. 2003. Applying ecological criteria to marine reserve design: a case study from the California Channel Islands. *Ecological Applications* 13: S170-S184.
- Apostolaki, P.; Milner-Gulland, E.J.; McAllister, M.K. & Kirkwood, G.P. 2002. Modelling the effects of establishing a marine reserve for mobile fish species. *Can. J. Fish. Aquat. Sci.* 59: 405-415.
- Beverton, R.J.H. & Holt, S.J. 1957. On the dynamics of exploited fish populations. *Fisheries Investigations*, London (Series II) 19:1-533.
- Bohnsack, J.A. 1998. Application of marine reserves to reef fisheries management. *Australian Journal of Ecology* 3: 298-304.
- Botsford, L.W. & Hastings, A. 2006. Conservation dynamics of marine metapopulations with dispersing larvae. Pp. 411-429 and Ch 12 in *Marine Metapopulations*, edited by P. Sale and J. Kritzer.
- Botsford, L.W.; Hastings, A. & Gaines, S.D. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distances. *Ecology Letters* 4: 144-150.

- Botsford, L.W.; Micheli, F. & Hastings, A.** 2003. Principles for the design of marine reserves. *Ecological Applications* 13: S25-S31.
- Clark, W.G.** 1990. Groundfish exploitation rates based on life history parameters. *Canadian Journal of Fisheries and Aquatic Science* 48:734-750.
- Collie, J.S.; Escanero, G.A. & Valentine, P.C.** 1997. Effects of bottom fishing on the benthic megafauna of Georges Bank. *Mar. Ecol. Prog. Ser.* 155: 159-172.
- Dahlgren, C.P.** 2004. Bahamian marine reserves – past experience and future plans. Pages 268-286 in J. A. Sobel and C.P Dahlgren, eds. *Marine reserves – A guide to science design and use.* Island Press, Washington, DC, USA.
- Dayton, P.K.; Thrush, S.F.; Agardy, M.T. & Hofman, R.J.** 1995. Environmental effects of marine fishing. *Aquatic Conservation in Marine and Freshwater Ecosystems* 5; 202-232.
- DeMartini, E.E.** 1993. Modelling the potential for fishery reserves for managing Pacific coral reef fishes. *Fishery Bulletin* 91(3):414-427.
- Edgar, G. & Barrett, N.** 1999. Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *Journal of Experimental Marine Biology and Ecology* 242:107-144.
- Estes, J.A. & VanBlaricom, G.R.** 1985. Sea otters and shellfisheries. In: *Conflicts between marine mammals and fisheries.* Beverton, R. H., D. Lavigne, and J.D. Beddington (eds), Allen And Unwin, London. Pp. 187-25.
- FAO.** 1995. Code of Conduct or Responsible Fisheries. 41pp.
- Fanshawe, S.; VanBlaricom, G.R. & Shelly, A.A.** 2003. Restored top carnivores as detriments to the performance of marine protected areas intended for fishery sustainability: a case study with red abalones and sea otters. *Cons. Biol.* 17: 273-283.
- Ferrier, S.** 2002. Mapping spatial pattern in biodiversity for regional conservation planning: Where to from here? *Systematic Biology* 51:331-363.
- Fisher, J.A.D. & Frank, K.T.** 2002. Changes in finfish community structure associated with an offshore fishery closed area on the Scotian Shelf. *Marine Ecology Progress Series* 240: 249-265.
- Gaines, S.D.; Gaylord, B. & Largier, J.L.** 2003. Avoiding current oversights in marine reserve design. *Ecological Applications*, 13: S32-S46
- Garcia, S.M. & Grainger, R.J.R.** 2005. Gloom and doom? The future of marine capture fisheries. *Philosophical Transactions of the Royal Society B* 360, 21-46.
- Gardmark, A.; Jonzen, N. & Mangel, M.** 2006. Density-dependent body growth reduces the potential of marine reserves to enhance yields. *J. Applied Ecology* 43: 61-69.
- Gaylord, B; Gaines, S.D.; Siegel, D.A. & Carr, M.H.** 2005. Marine reserves exploit population structure and life history in potentially improving fishery yields. *Ecological Applications* 15: 2180-2191.
- GBRMPA.** 2004. *Great Barrier Reef Marine Park zoning plan 2003.* Great Barrier Reef Marine Park Authority, Townsville, Australia [WWW document].  
URL [http://www.gbrmpa.gov.au/corp\\_site/management/zoning/index.html](http://www.gbrmpa.gov.au/corp_site/management/zoning/index.html)
- Gell, F.R. & Roberts, C.M.** 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Tr. Ecol. Evol.* 18: 448-455.
- Guenette, S.; Lauck T. & Clark, C.** 1998. Marine reserves: from Beverton and Holt to the present. *Reviews in Fish Biology and Fishes*, 8: 251-272.
- Halpern, B.** 2003. The impact of marine reserves: do they work and does reserve size matter? *Ecological Applications*, 13: S117-137.

- Halpern, B.S. & Warner, R.R.** 2002. Marine reserves have rapid and lasting effects. *Ecology Letters*, 5: 361-366.
- Halpern, B.S.; Gaines, S.D. & Warner, R.R.** 2004. Confounding effects of the export of production and the displacement of effort from marine reserves. *Ecological Applications*, 14: 1248-1256.
- Hart, D.R.** 2006. When do marine reserves increase fishery yield? *Can. J. Fish. Aquat. Sci.*, 63:1443-1449.
- Hastings, A. & Botsford, L.W.** 1999. Equivalence in yield from marine reserves and traditional fisheries management. *Science*, 284:1537-1538.
- Hastings, A. & Botsford, L.W.** 2003. Are marine reserves for fisheries and biodiversity compatible? *Ecological Applications* 13: S65-S70.
- Hastings, A. & Botsford, L.W.** 2006. Persistence of spatial populations depends on returning. *Proceedings of the National Academy of Sciences*, 103:6067-6072.
- Hilborn, R.; Micheli, F. & De Leo, G.A.** 2006. Integrating marine protected areas with catch regulation. *Can. J. Fish. Aquat. Sci.*, 63: 642-649.
- Hilborn, R.; Kevin Stokes, K.; Maguire, J.-J.; Smith, T.; Botsford, L.W.; Mangel, M.; Orensanz, J.; Parma, A.M.; Rice, J.; Bell, J.; Cochrane, K.L.; Garcia, S.; Hall, S.J.; Kirkwood, G.P.; Sainsbury, K.; Stefansson, G. & Walters, C.** 2004. When can marine reserves improve fisheries management? *Ocean Coastal Manage.*, 47, 197–205.
- Holland, D.S. & Brazee, R.J.** 1996. Marine reserves for fishery management. *Marine Resource Economics*, 11: 157-171.
- Jennings, S.** 2001. Patterns and prediction of population recovery in marine reserves. *Reviews in Fish Biology and Fisheries*, 10: 209-231.
- Jennings, S.; Reynolds, J.D. & Polunin, N.V.C.** 1999. Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. *Conservation Biology*, 6: 1466-1475.
- Jones, G.P.; McCormick, M.I.; Srinivasan, M. & Eagle, J.V.** 2004. Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Science*, 101:8251-8253.
- Kaplan, D.M. & Botsford, L.W.** 2005. Effects of variability in spacing of coastal marine reserves on fisheries yield and sustainability. *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 905-912.
- Kaplan, D.M.; Botsford, L.W. & Jorgensen, S.** 2006. Dispersal per recruit: an efficient method for assessing sustainability in marine reserve networks. *Ecological Applications* (in press)
- Kinlan, B.P. & Gaines, S.D.** 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology*, 84: 2007-2020.
- Kirkpatrick, J.B.** 1983. An iterative method for establishing priorities for the selection of nature reserves an example from Tasmania Australia. *Biological Conservation*, 25:127-134.
- Lauck, T.; Clark, C.W.; Mangel, M. & Munro, G.R.** 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications*, 8: S72-S78.
- Leslie, H.; Ruckelshaus, M.; Ball, I.R.; Andelman, S. & Possingham, H.P.** 2003. Using siting algorithms in the design of marine reserves. *Ecological Applications*, 13: S185-S198.
- Lindholm, J.; Auster, P. & Valentine, P.** 2004. Role of a large marine protected area for conserving landscape attributes of sand habitats on Georges Bank (NW Atlantic). *Mar. Ecol. Prog. Ser.*, 269: 61-68.
- Lipcius, R.N.; Stockhausen, W.T. & Eggleston, D.B.** 2001. Marine reserves for Caribbean spiny lobster: empirical evaluation and theoretical metapopulation recruitment dynamics. *Marine and Freshwater Research*, 52: 1589-98.

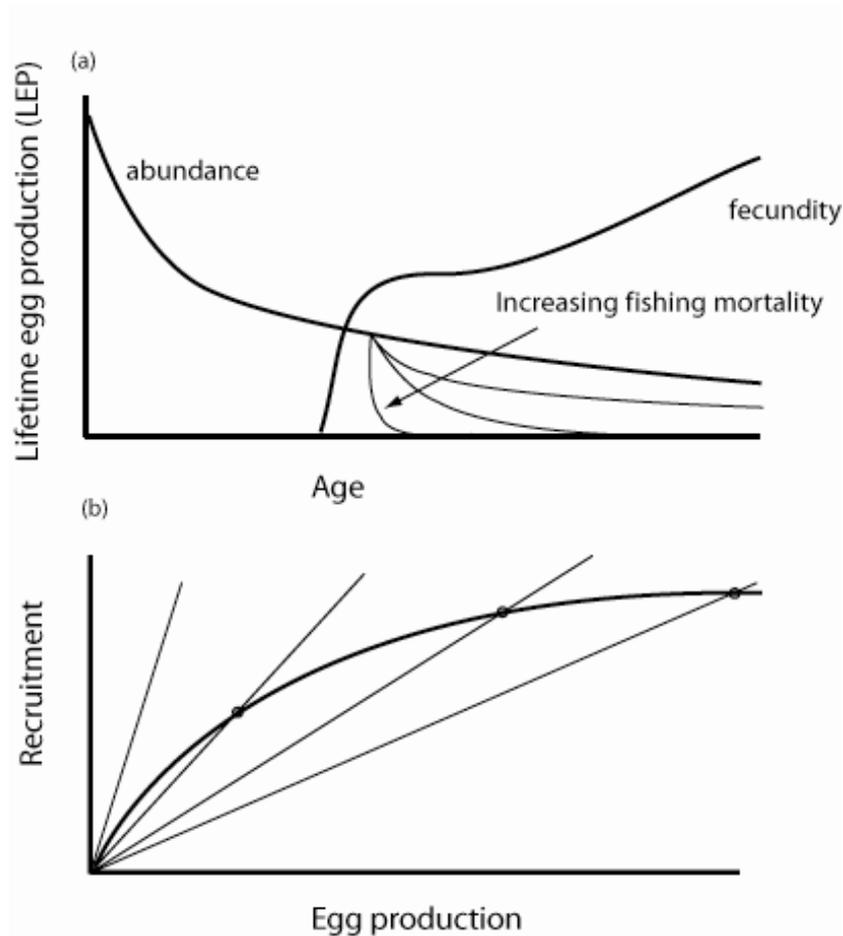
- Little, L.R.; Mapstone, B.D.; Smith, A.D.M.; Pantus, F.; Punt, A.E.; Davies, C.R. & McDonald, A.D.** 2005. Evaluating the potential implications of the “Larval Subsidy Effect” for management of reef fish populations on the Great Barrier Reef, Australia. In Zenger, A. and Argent, R.M. (eds) *MODSIM 2005 International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand*, December 2005, pp. 170-176. ISBN: 0-9758400-2-9. [http://www.mssanz.org.au/modsim05/papers/ascough\\_1.pdf](http://www.mssanz.org.au/modsim05/papers/ascough_1.pdf)
- Lockwood, D.R.** 2002. The effects of larval dispersal and spatial heterogeneity on the design of marine reserves. Ph. D. Thesis, Population Biology, University of California, Davis.
- Lockwood, D.R.; Hastings A. & Botsford, L.W.** 2002. The effects of dispersal patterns on marine reserves: does the tail wag the dog? *Theoretical Population Biology*, 61: 297-309.
- Lubchenco, J.; Palumbi, S.R.; Gaines, S.D. & Andelman, S.** 2003. Plugging a hole in the ocean: the emerging science of marine reserves. *Ecological Applications*, 13: S3-S7.
- Mace, P.M. & Sissenwine, M.P.** 1993. How much spawning per recruit is enough? In Smith, SJ, JJ Hunt, and D Rivard (eds.), Risk evaluation and biological reference points for fisheries management. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 120:101-118.
- Macpherson, E.; Biagi, F.; Francour, P.; Garcia-Rubies, A.; Harmelin, J.; Harmelin-Vivien, M.; Jouvenel, J.Y.; Planes, S.; Vigliola, L. & Tunesi, L.** 1997. Mortality of juvenile fishes of the genus *Diplodus* in protected and unprotected areas in the western Mediterranean Sea. *Mar. Ecol. Prog. Ser.*, 160: 135-147.
- Mangel, M.** 1998. No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. *Ecology Letters*, 1: 87-90.
- Mangel, M.** 2000. On the fraction of habitat allocated to marine reserves. *Ecological Letters*, 3: 15-22.
- Mangel, M. & Levin, P.S.** 2005. Regime, phase and paradigm shifts: making community ecology the basic science for fisheries. *Phil. Trans. R. Soc. B*, 360: 95-105.
- Maypa, A.P.; Russ, G.R.; Alcala, A.C. & Calumpong, H.P.** 2002. Long-term trends in yield and catch rates of the coral reef fishery at Apo Island, central Philippines. *Mar. Freshw. Res.*, 53: 207-213.
- McClanahan, T.R.** 2000. Recovery of a coral reef keystone predator, *Balistapus undulatus*, In East African marine parks. *Biological Conservation*, 94: 191-198.
- McClanahan, T.R. & Kaunda-Auarara, B.** 1996. Fishery recovery in a coral reef marine park and its effects on the adjacent fishery. *Conservation Biology*, 10: 1187-1199.
- McClanahan, T.R. & Mangi, S.** 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecological Applications*, 10: 1792-1805.
- Micheli, F. & Halpern, B.S.** 2005. Low functional redundancy in coastal marine assemblages. *Ecology Letters*, 8: 391-400.
- Micheli, F. & Peterson, C.H.** 1999. Estuarine vegetated habitats as corridors for predator movements. *Conservation Biology*, 13: 869-881.
- Micheli, F.; Halpern, B.S.; Botsford, L.W. & Warner, R.R.** 2004. Trajectories and correlates of community change in no-take marine reserves. *Ecological Applications*, 14: 1709-1723.
- Morgan, L.E. & Botsford, L.W.** 2001. Managing with reserves: modelling uncertainty in larval dispersal for a sea urchin fishery. Pp. 667-684 in *Spatial Processes and Management of Marine Populations*, Alaska Sea Grant College Program. AK-SG-01-02.
- Mosquera, I.; Côté, I.M.; Jennings, S. & Reynolds, J.D.** 2000. Conservation benefits of marine reserves for fish populations. *Animal Conservation*, 4: 321-332.

- Mumby, P.J.; Edwards, A.J.; Arias-Gonzalez, J.E.; Lindeman, K.C.; Blackwell, P.G.; Gall, A.; Gorczynska, M.I.; Harborne, A.R.; Pescod, C.L.; Renken, H.; Wabnitz, C.C.C. & Llewellyn, G.** 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*, 427:533-536.
- Mumby, P.J.; Dahlgren, C.P.; Harborne, A.R.; Kappel, C.V.; Micheli, F.; Brumbaugh, D.R.; Holmes, K.E.; Mendes, J.M.; Broad, K.; Sanchirico, J.N.; Buch, K.; Box, S.; Stoffle, R.W. & Gill, A.B.** 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, 311: 98-101.
- Murawski, S.A.; Brown, R.; Lai, H.L.; Rago, P.J. & Hendrickson, L.** 2000. Large-scale closed areas as a fishery-management tool in temperate marine systems: the Georges Bank experience. *Bull. Mar. Sci.*, 66: 775-798.
- Murawski, S.A.; Rago, P.J. & Fogarty, M.J.** 2004. Spillover effects from temperate marine protected areas. *Am. Fish. Soc. Symp.*, 42: 167-184.
- Murawski, S.A.; Wigley, S.E.; Fogarty, M.J.; Rago, P.J. & Mountain, D.G.** 2005. Effort distribution and catch patterns adjacent to temperate MPAs. *ICES J. of Mar. Sci.*, 62: 1150-1167.
- Murray, S.N.; Ambrose, R.F.; Bohnsack, J.A.; Botsford, L.W.; Carr, M.H.; Davis, G.E.; Dayton, P.K.; Gotshall, D.; Gunderson, D.R.; Hixon, M.A.; Lubchenco, J.; Mangel, M.; MacCall, A.; McArdle, D.A.; Ogden, J.C.; Roughgarden, J.; Starr, R.M.; Tegner, M.J. & Yoklavich, M.M.** 1999. No-take reserve networks: sustaining fishery populations and marine ecosystems. *Fisheries*, 24: 11-25.
- Myers, R.A.; Bowen, K.G. & Barrowman, N.J.** 1999. Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.*, 56: 2404-2419.
- Myers, R.A.; Barrowman, N.J.; Hilborn, R. & Kehler, D.G.** 2002. Inferring Bayesian priors with limited direct data: applications to risk analysis. *North American Journal of Fisheries Management*, 22: 351-364.
- National Research Council, USA (NRC).** 2001. Marine Protected Areas. Tools for Sustaining Ocean Ecosystems. National Academy Press, Washington, 272 pp.
- O'Farrell, M.R. & Botsford, L.W.** 2005. Estimation of change in lifetime egg production from length frequency data. *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 1626-1639.
- O'Farrell, M.R. & Botsford, L.W.** 2006. Estimating the status of nearshore rockfish (*Sebastes spp.*) with length frequency data. *Ecological Applications* (in press).
- Paddack, M.J. & Estes, J.A.** 2000. Kelp forest fish populations in marine reserves and adjacent exploited areas of central California. *Ecological Applications*, 10: 855-870.
- Palumbi, S.R.** 2002. Marine reserves: a tool for ecosystem management and conservation. Pew Oceans Commission. Arlington, Virginia.
- Parma, A.M.; Orensanz, J.M.; Elías, I. & Jerez, G.** 2003. Diving for shellfish- and data: incentives for the participation of fishers in the monitoring and management of artisanal fisheries around southern South America. In Newman, S.J., Gaughan, D.J., Jackson, G., Mackie, M.C., Molony, B., St John, J. & Kaiola, P. (Eds.) *Towards sustainability of data-limited multi-sector fisheries*, Australian Society for Fish Biology Workshop Proceedings, Bunbury, Australia. 23-24 September 2001, Department of Fisheries, Perth.
- Parnell, P.E.; Lennert-Cody, C.E.; Geelen, L.; Stanley, L.D & Dayton, P.K.** 2005. Effectiveness of a small marine reserve in southern California. *Marine Ecology Progress Series*, 296: 39-52.
- Parrish, R.** 1999. Marine reserves for fisheries management: why not? Symposium of the CalCOFI Conference: a continuing dialogue on no-take reserves for resource management, Asilomar, CA, USA; 4 November 1998. California Cooperative Oceanic Fisheries Investigations Report 1999;40: 77-86.

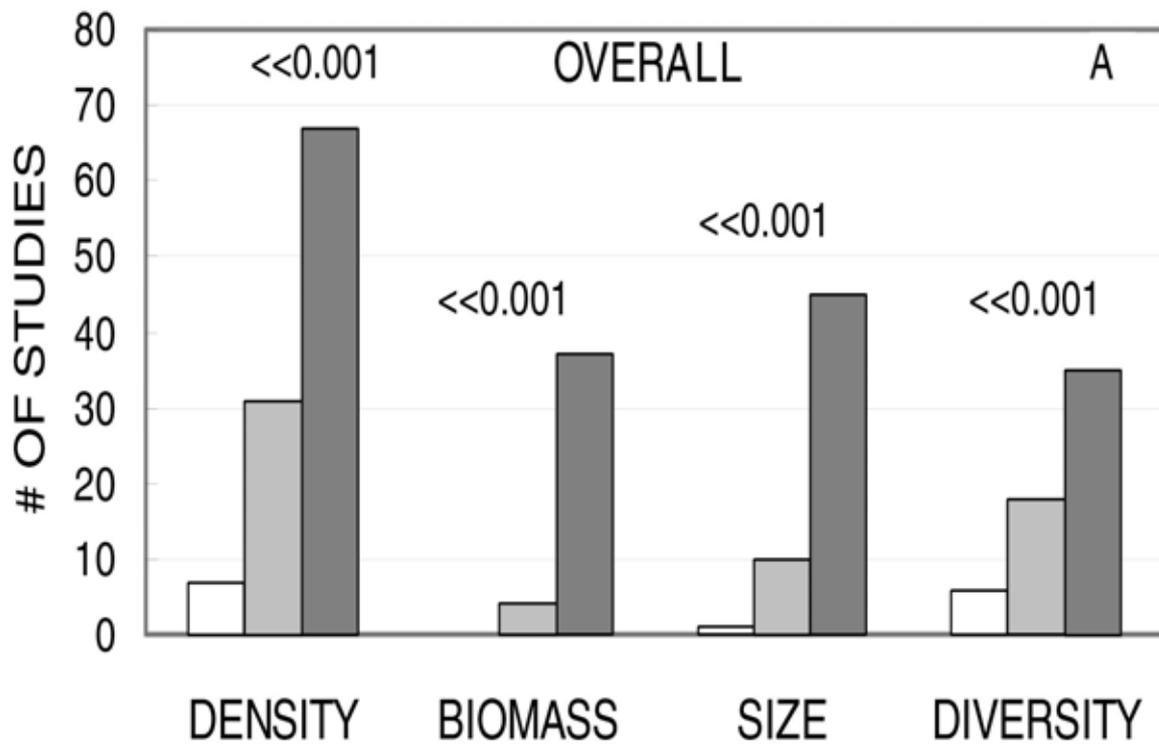
- Pinnegar, J.K.; Polunin, N.V.C.; Francour, P.; Badalamenti, F.; Chemello, R.; Harmelin-Vivien, M.L.; Hereu, B.; Milazzo, M.; Zabala, M.; D'Anna, G. & Pipitone, C.** 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Env. Cons.*, 27: 179-200.
- Polacheck, T.** 1990. Year round closed areas as a management tool. *Natural Resource Modelling*, 4(3): 327-354.
- Polunin, N.V.C. & Roberts, C. M.** 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine ecology progress series* 100:167-176.
- Possingham, H.; Ball, I. & Andelman, S.** 2000. Mathematical methods for identifying representative reserve networks. In: *Quantitative Methods in Conservation Biology* (eds. Ferson, S. & Burgman, M.). Springer, New York, pp. 291-306.
- Pressey, R.L.; Humphries, C.J.; Margules, C.R.; Vanewright, R.I. & Williams, P.H.** 1993. Beyond opportunism: Key principles for systematic reserve selection. *Trends in Ecology and Evolution*, 8:124-128.
- Quinn, J.F.; Wing, S.R. & Botsford, L.W.** 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *American Zoologist*, 33:537-550.
- Ralston, S.** 2002. West coast groundfish policy. *North American Journal of Fisheries Management*, 22: 249-250.
- Roberts, C.M.** 1995. Rapid build-up of fish biomass in a Caribbean marine reserve. *Conservation Biology*, 9: 815-826.
- Roberts, C.M.; Bohnsack, J.A.; Gell, F.; Hawkins, J.P & Goodridge, R.** 2001. Effects of marine reserves on adjacent fisheries. *Science*, 294: 1920-1923.
- Russ, G.R.** 2002. Marine reserves as reef fisheries management tools: yet another review. Pages in P. F. Sale, editor. *Ecology of fishes on coral reefs*. Academic Press, Boston, MA, USA.
- Russ, G.R. & Alcala, A.C.** 1996. Marine reserves; rates and patterns of recovery and decline of large predatory fish. *Ecological Applications*, 6: 947-961.
- Russ, G.R.; Stockwell, B. & Alcala, A.C.** 2005. Inferring versus measuring rates of recovery in no-take marine reserves. *Marine Ecology Progress Series*, 292: 1-12.
- Sadovy, Y.J.** 1996. Reproduction of reef fishery species. N.V.C. Polunin and C.M. Roberts, eds. Chapman and Hall Series in Fish Biology and Fisheries 20, Chapman and Hall, London, UK. Pp. 15-59.
- Sala, E.; Aburto-Oropeza, O.; Paredes, G.; Parra, I.; Barrera, J.C. & Dayton, P.K.** 2002. A general model for designing networks of marine reserves. *Science*, 298: 1991-1993.
- Sale, P.F.; Cowen, R.K.; Danilowicz, B.S.; Jones, G.P.; Kritzer, J.P.; Lindeman, K.C.; Planes, S.; Polunin, N.V.C.; Russ, G.R.; Sadovy, Y.J. & Steneck, R.S.** 2005. Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology and Evolution*, 20: 75-80.
- Shanks, A.L.; Grantham, B. & Carr, M.H.** 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications*, 13: S159-169.
- Shears, N.T & Babcock, R.C.** 2003. Continuing trophic cascade effects after 25 years of no-take reserve protection. *Marine Ecology Progress Series*, 246: 1-16.
- Sissenwine, M.P. & Shepherd, J.G.** 1987. An alternative perspective on recruitment overfishing and biological reference points. *Can. J. Fish. Aquat. Sci.*, 44: 913-918.
- Sluka, R. et al.** 1997. The benefits of a marine fishery reserve for Nassau grouper, *Epinephelus striatus*, in the central Bahamas. Proceedings of the 8<sup>th</sup> International Coral Reef Symposium 2: 1961-1964.

- Smith, M.D. & Wilen, J.E.** 2003. Economic impacts of marine reserves: the importance of spatial behavior. *Journal of Environmental Economics and Management*, 46: 183-206.
- Starr, R.; O'Connell, V. & Ralston, S.** 2004. Movements of lingcod (*Ophiodon elongates*) in southeast Alaska: potential for increased conservation and yield from marine reserves. *Can. J. Fish. Aquat. Sci.*, 61: 1083-1094.
- Stefansson, G. & Rosenberg, A.A.** 2005. Combining control measures for more effective management of fisheries under uncertainty: quotas, effort limitation and protected areas. *Phil. Trans. R. Soc. B*, 360: 133-146.
- Stewart, R.R.; Noyce, T. & Possingham, H.P.** 2003. Opportunity cost of ad hoc marine reserve design decisions: an example from South Australia. *Marine Ecology Progress Series*, 253:25-38.
- Stoner, A.W., et al.** 1998. Mesoscale distribution patterns of queen conch (*Strombus gigas* Linne') in the Exuma Sound, Bahamas: links in recruitment from larvae to fishery yields. *J. Shellfish Res.* 17:955-969.
- Wallace, S.** 1999. Evaluating the effects of three forms of marine reserve on northern abalone populations in British Columbia, Canada. *Conservation Biology*, 13: 882-887.
- Wendell, F.** 1994. Relationship between sea otter range expansion and red abalone abundance and size distribution in central California. *Ca Fish and Game*, 80: 45-56.
- White, A.T.; Gomez, E.; Alcalá, A.C.; Russ, G. & Vincent, A.** 2006. Evolution and lessons from fisheries and coastal management in the Philippines. In T.R. McClanahan and J.C. Castilla (eds.) *Fisheries Management: Progress Towards Sustainability*, Blackwell Publ. (in press).
- Willis, T.J.; Millar, R.B.; Babcock, R.C. & Tolimieri, N.** 2003. Burdens of evidence and the benefits of marine reserves: putting Descartes before des horses? *Environmental Conservation*, 30: 97-103.
- Worm, B.; Barbier, E.B.; Beaumont, N.; Duffy, J.E.; Folke, C.; Halpern, B.S.; Jackson, J.B.C.; Lotze, H. K.; Micheli, F.; Palumbi, S.; Sala, E.; Selkoe, K.A.; Stachowicz, J.J. & Watson, R.** *In press*. Impacts of biodiversity loss on ocean ecosystem services. *Science*.
- Worm, B. & Myers, R.A.** 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology*, 84:162-173

## ANNEX 1: FIGURES

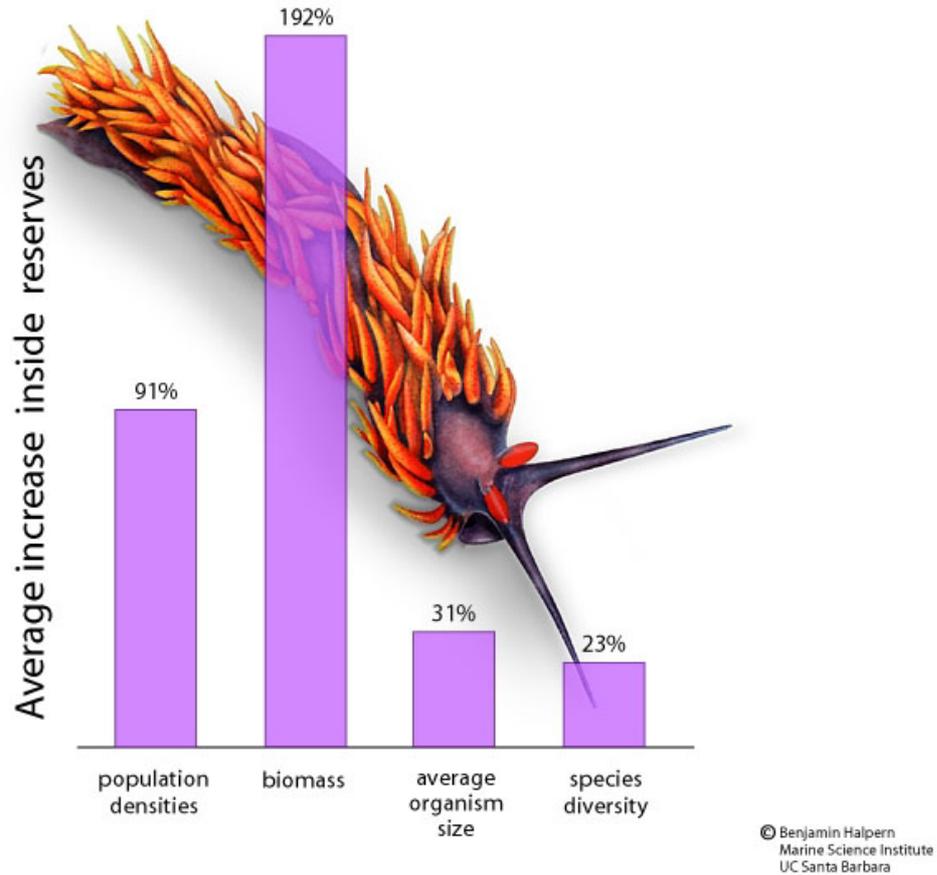


**Figure 1. The dependence of population equilibrium and collapse on Lifetime Egg Production (LEP). (a) LEP is the sum over age of the product of abundance and fecundity. As fishing increases, there are fewer old, fecund females, and LEP declines. (b) The equilibrium level of recruitment occurs at the intersection of the recruit/egg relationship and a line through the origin with slope  $1/LEP$ . As fishing increases, LEP and equilibrium recruitment decline. When  $1/LEP$  is greater than the slope of the recruit/egg relationship at the origin, the population collapses. Because that slope is poorly known, fishery biologists assume that collapse occurs when the fraction of LEP (FLEP) is below a certain value (e.g. 35 percent).**



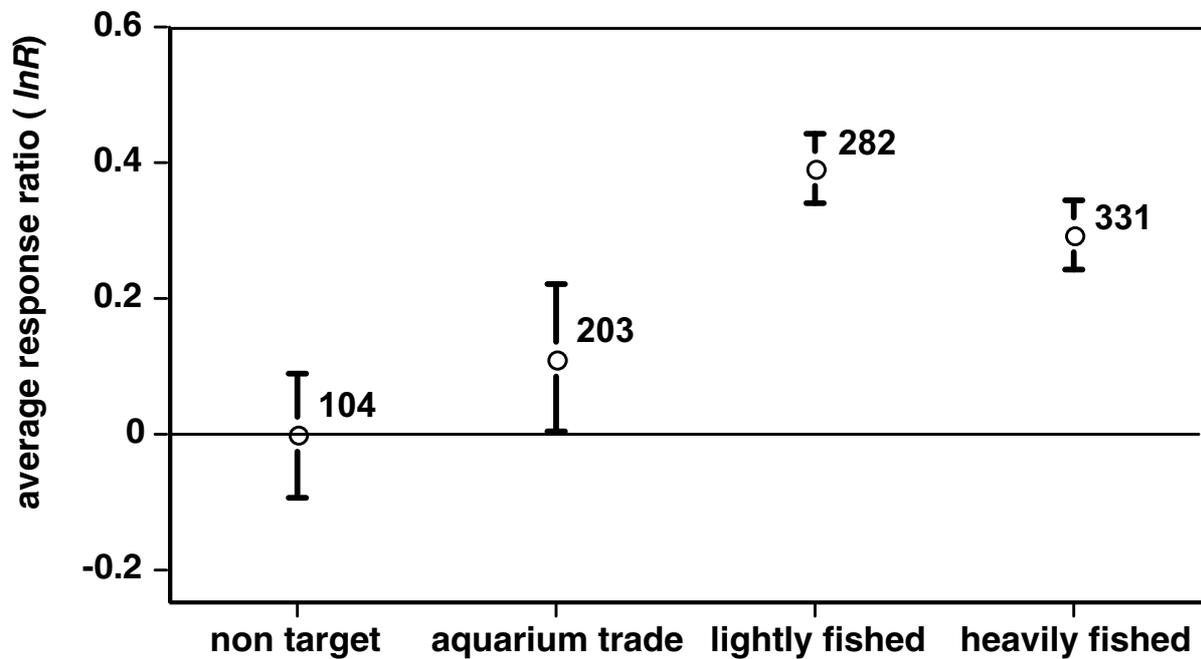
**Figure 2.** Number of independent marine reserve measurements (density, as No. individuals/area; biomass as mass/area; mean size of organisms, and diversity, as total species richness) plotted separately for each of three trends: lower values inside reserves compared to reference conditions (white bars); no difference between reserves and non-reserve areas (grey bars); and higher values inside the reserve (dark bars).

*Source: Halpern 2003*



**Figure 3. Average increases in population densities, biomass, organism size, and species diversity inside reserves. Overall averages were based on 69 studies of marine reserves from tropical and temperate coastal ecosystems.**

*Source: Halpern 2003*



**Figure 4.** Results of meta-analyses of the response ratios ( $\ln R$ , where  $R$  is the ratio between abundances inside and outside reserves, or before and after reserve establishment) for each of four exploitation levels of coastal fish populations (non-target species, and species targeted by aquarium trade, lightly fished or heavily fished). Average response ratios, weighted by sampling variances, are reported for each category. Bars represent 95 percent confidence intervals. When confidence intervals do not overlap 0, weighted averages are considered significantly different from 0. The number of comparisons within each category is reported to the right of each average.

*Source: Micheli et al. 2004*

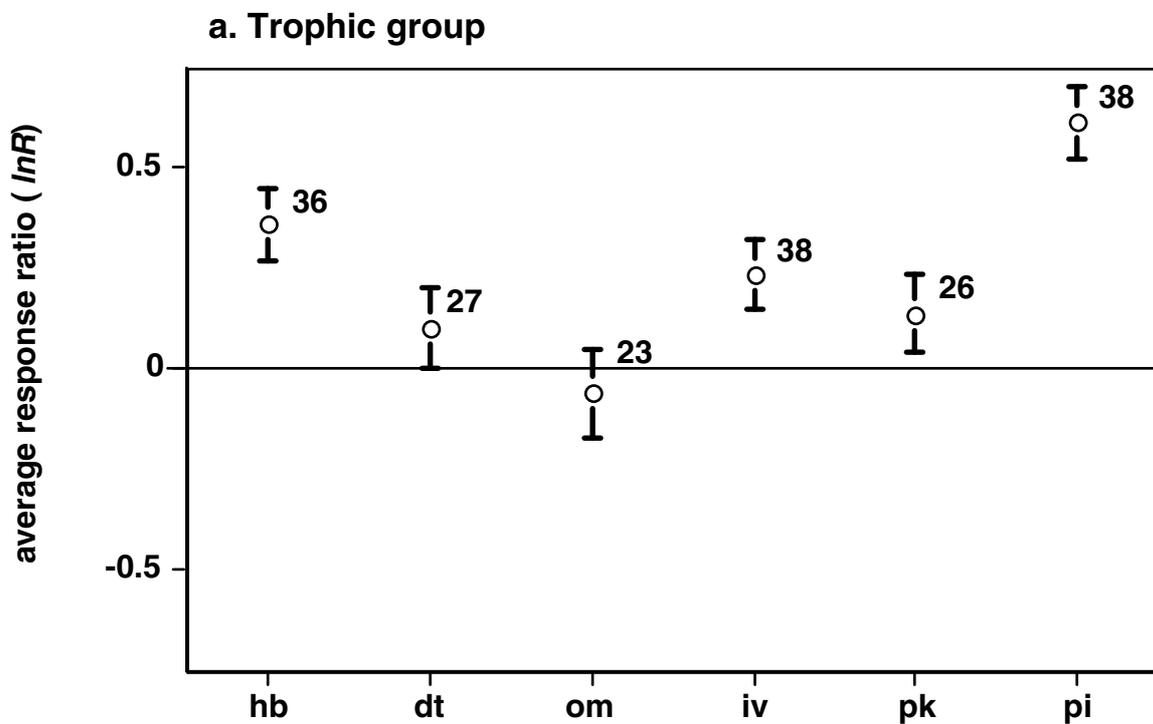
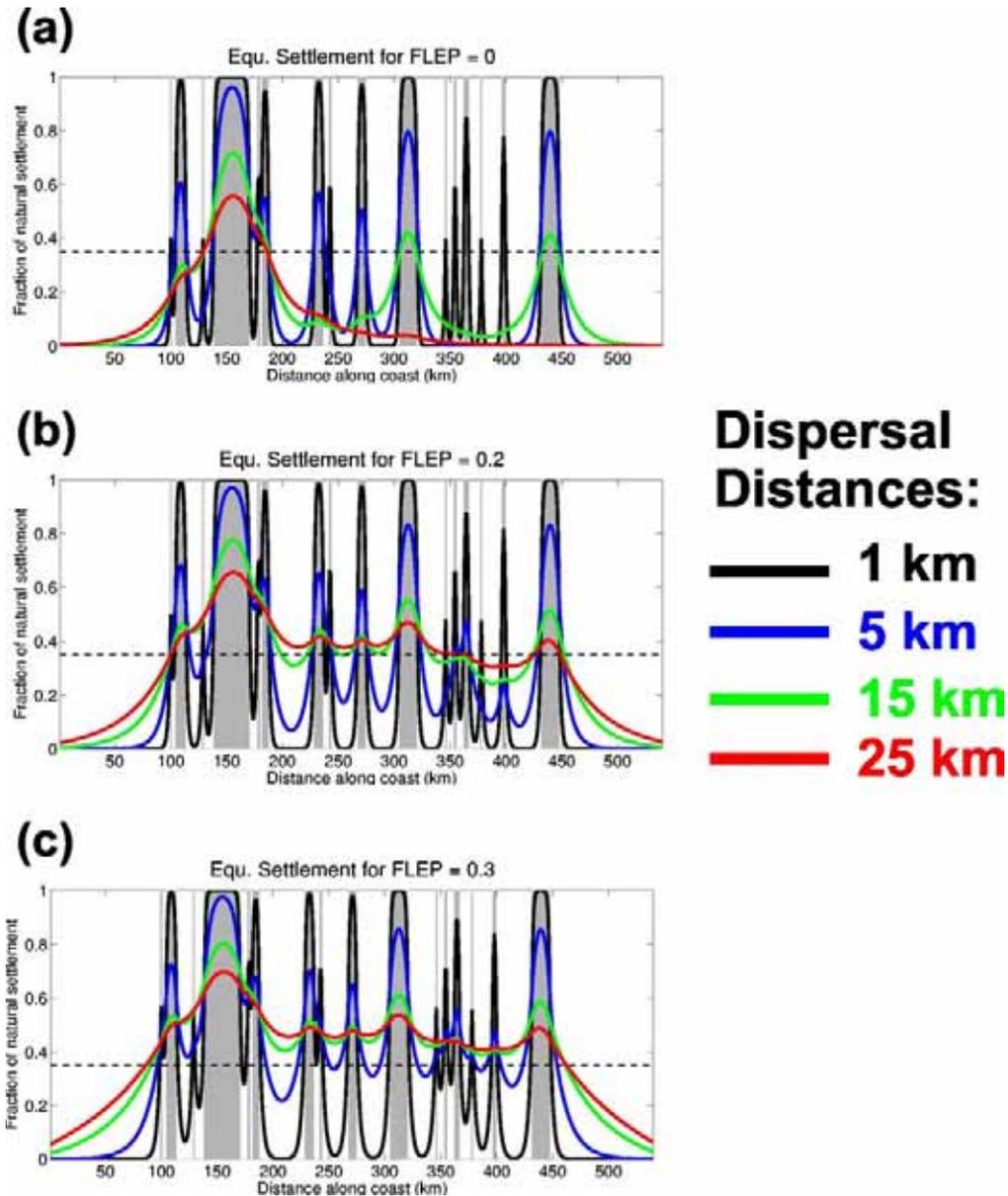
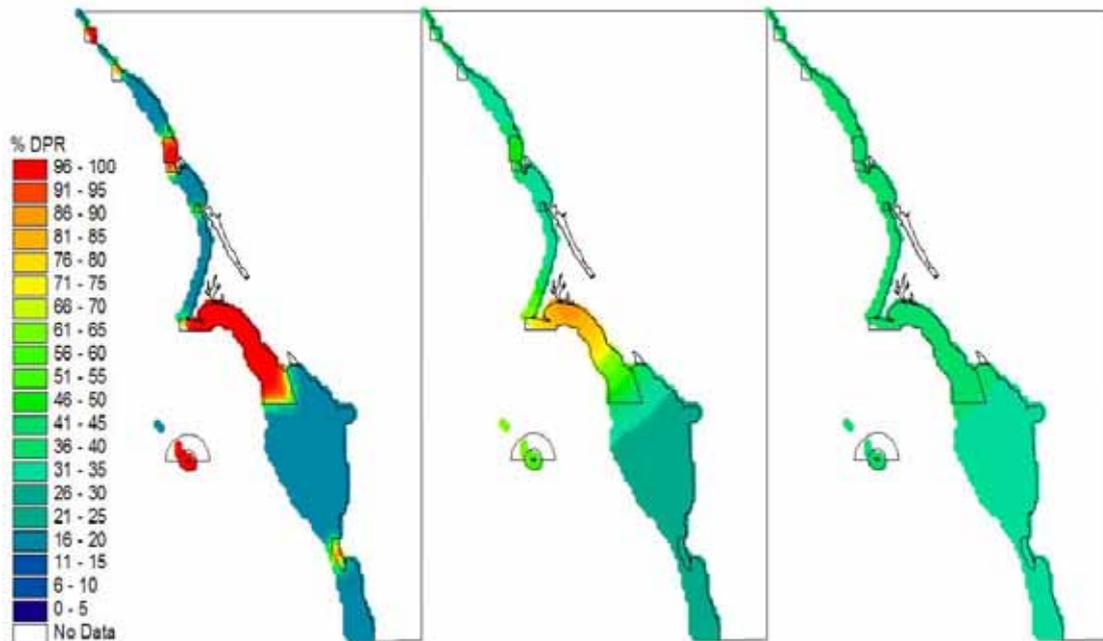


Figure 5. Results of meta-analyses of the response ratios ( $\ln R$ , where  $R$  is the ratio between abundances inside and outside reserves, or before and after reserve establishment) for each six fish trophic groups (hb=herbivores; dt=detrivores; om=omnivores; iv=invertebrate feeders; pk=planktivores; and pi=piscivores). Average response ratios, weighted by sampling variances, are reported for each category. Bars represent 95 percent confidence intervals. When confidence intervals do not overlap 0, weighted averages are considered significantly different from 0. The number of comparisons within each category is reported to the right of each average.

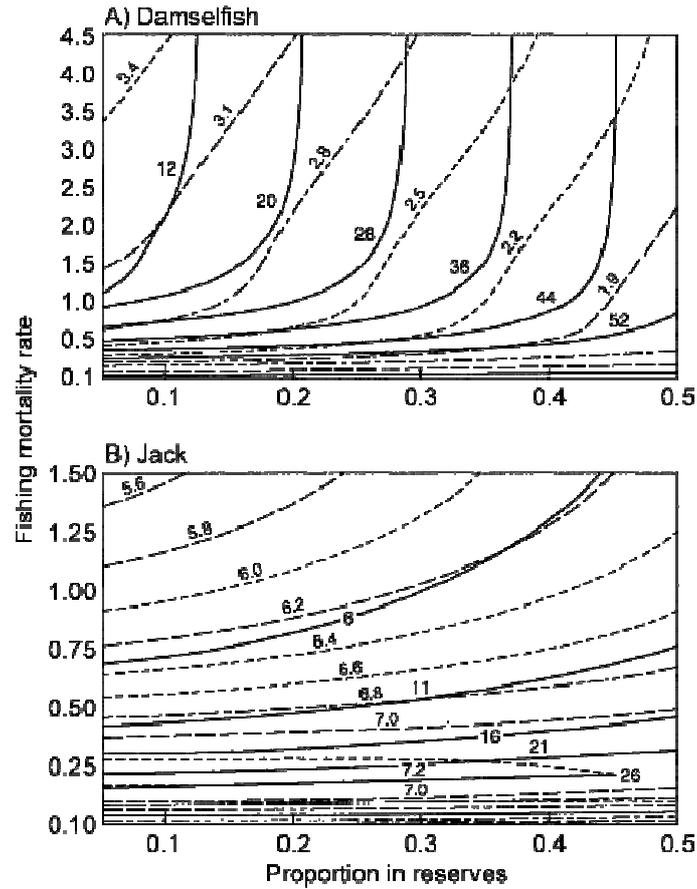
Source: Micheli et al. 2004

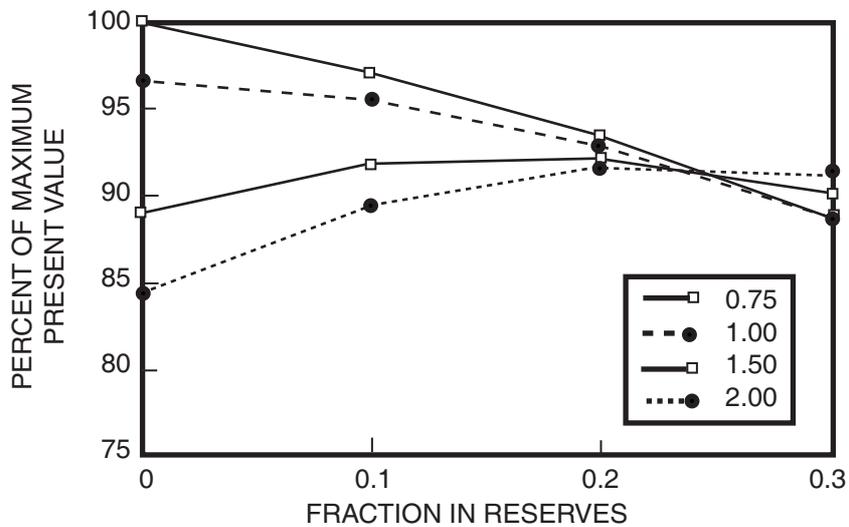


**Figure 6.** The effects of MPA width and fishing outside of MPAs on persistence. The shaded areas are MPAs of varying widths. The black, blue, green and red lines are plots of the fraction of natural settlement at each location. We can expect persistent populations wherever these lines are above the dashed line at 0.35. The level of fishing outside of the MPAs is represented the Fraction of natural, unfished Lifetime Egg Production left outside the MPA. In (a) fishing is very intense, and there is no reproductive contribution from outside the reserve, fishing in (b) has reduced FLEP to 20 percent of the natural level, an overfished state, and in (c) the populations is just barely overfished at FLEP = 0.35. With regard to the effect of MPA width, note that in (a) the narrower MPAs can support species dispersing 1 km and 5 km, but not those dispersing 15 km and 20 km. Note that in (b), where there is less fishing outside reserves, there is generally greater persistence. Species dispersing 1 km and 5 km persist in individual reserves, while there is a network effect across several MPAs for species dispersing longer distances.

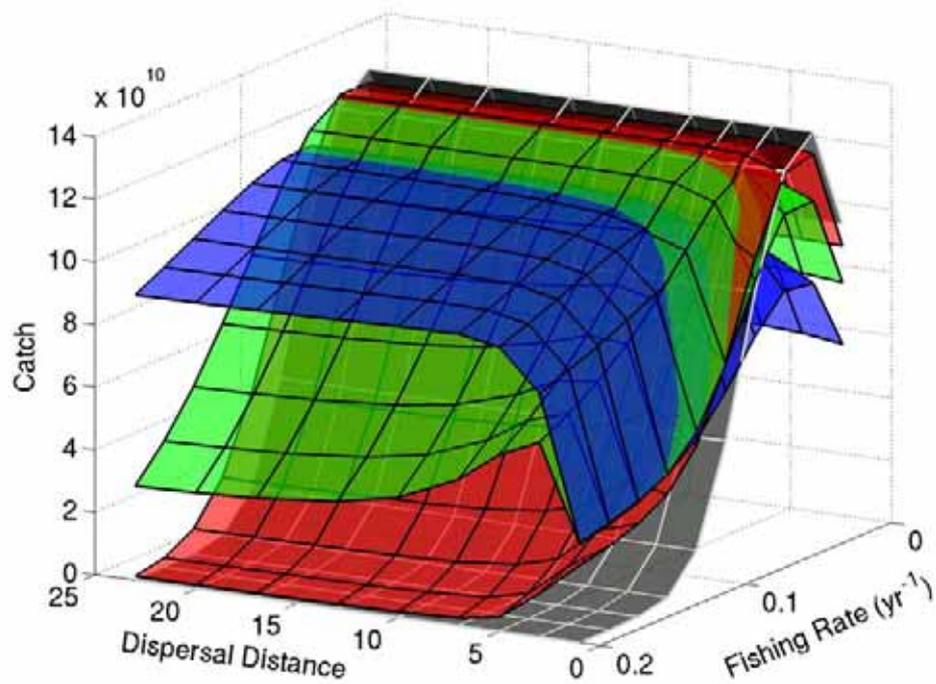


**Figure 7. A two-dimensional analysis similar to the one-dimensional analysis in Fig. 2. An example of the workshop tool used to assess and display the area over which sustainable populations would persist for proposed reserves in the Point Reyes area on the west coast of North America, north of San Francisco, California, in the United States. Dispersal distances are 1km, 10km and 100km from left to right. Sustainable populations will occur where %DPR is greater than 35 percent. This tool accounts for larval dispersal only.**





**Figure 9.** A simulation example of the rough equivalence of the effects of fishing mortality rate (legend in box) and fraction of area in reserves (MPAs) in their effect on fishery yield, expressed here as present value. If the population is heavily fished (e.g.  $F = 2.0 \text{ y}^{-1}$ ), adding reserves increases yield up to a point, while if the population is lightly fished (i.e.  $F < 1.00 \text{ y}^{-1}$ ), adding reserves decreases yield (redrawn from Holland and Brazee (1996)).



**Figure 10.** The combined effects of fishing mortality and the fraction in MPAs on species with different dispersal distances. Colours represent fraction of coastline in MPAs: grey represents no MPAs, red represents 8 percent of the coastline in MPAs, green represents 20 percent in MPAs and blue represents 40 percent in MPAs. Note that as the fraction in reserves increases, short distance dispersers are protected first, but as the area increases further, they never produce as much yield as longer distance dispersers.