THE ROYAL SOCIETY

Received 10 October 2002
Accepted 19 March 2003
Published online 17 July 2003

Review Paper

Matching marine reserve design to reserve objectives

Benjamin S. Halpern* **and Robert R. Warner**

Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA

Recent interest in using marine reserves for marine resource management and conservation has largely been driven by the hope that reserves might counteract declines in fish populations and protect the biodiversity of the seas. However, the creation of reserves has led to dissension from some interested groups, such as fishermen, who fear that reserves will do more harm than good. These perceived differences in the effect of marine reserves on various stakeholder interests has led to a contentious debate over their merit. We argue here that recent findings in marine ecology suggest that this debate is largely unnecessary, and that a single general design of a network of reserves of moderate size and variable spacing can meet the needs and goals of most stakeholders interested in marine resources.

Given the high fecundity of most marine organisms and recent evidence for limited distance of larval dispersal, it is likely that reserves can both maintain their own biodiversity and service nearby non-reserve areas. In particular, spillover of larger organisms and dispersal of larvae to areas outside reserves can lead to reserves sustaining or even increasing local fisheries. Ultimately, the success of any reserve network requires attention to the uncertainty and variability in dispersal patterns of marine organisms, clear statements of goals by all stakeholder groups and proper evaluation of reserve performance.

Keywords: marine reserve design; fisheries; resource management; biodiversity conservation; marine protected areas

1. INTRODUCTION

The past few years have seen a tremendous increase in public interest in using marine protected areas to manage marine resources, and many countries are moving towards regional and national programmes of reserve establishment. Much of this interest has arisen as a result of the dramatic success of existing reserves in increasing population sizes within reserve boundaries. However, current reserve systems were established rather haphazardly. Some areas were set aside because they happened to be located adjacent to military installations, sub-tidal anthropogenic structures (oil rigs, communication cables, etc.) or dramatic natural features (e.g. Didier 1998; Johnson *et al.* 1999). Still other reserves were established because local fisheries began to collapse (e.g. Russ & Alcala 1996; Murawski *et al.* 2000) or because scientists wanted a small patch of 'natural' area to study (e.g. Ballantine & Gordon 1979; Castilla & Durán 1985). Briefly, most reserve locations and boundaries were chosen by a political process that focused on economics, logistics or public acceptance, while largely overlooking or ignoring how the complex ecology and biology of an area might be affected by reserve protection (McArdle 1997; Roberts 2000).

Recent planning efforts indicate a dramatic shift in the way reserves are being designed, with a focus on community and scientific involvement in creating ecologically sound networks of protected areas (National Oceanic and Atmospheric Administration 1996; Airame *et al.* 2003; CAFGC 1999). However, even these efforts show that it is difficult to develop reserve designs that satisfy all stakeholder groups involved in the planning process (Suman *et al.* 1999; Nuttall *et al.* 2000). For example, the process to develop no-take reserves in the Florida Keys National Marine Sanctuary led to 'overwhelming opposition' from the commercial fishermen in the area (Suman *et al.* 1999).

Although there exist a growing number of cases where fishermen have spoken out in support of reserves as a management tool (Roberts & Hawkins 2000; Roberts *et al.* 2001), many fishermen remain strongly opposed to including anything but the smallest amount of no-take reserves in management plans (Suman *et al.* 1999; Haskell 1999; Nuttall *et al.* 2000; Bustamante *et al.* 2001). We believe these difficulties in gaining full stakeholder support for reserve design efforts stem from: (i) a general lack of understanding of how existing marine reserves have performed; (ii) ignorance of what the questions are that remain to be addressed and answered; and (iii) a poorly articulated explanation of how stakeholder goals can be met using marine reserves. Reasonable goals, appropriate design criteria and the success of marine reserves can only be achieved if all stakeholders are armed with information about reserve performance *relative to their needs*.

To help address these information needs, it is useful to assess what is known about how reserves actually function relative to how current theory suggests they might function. More importantly, can this empirical evidence and existing theory then be put into practice to provide practical guidelines for marine reserve design?

The answers to these questions depend critically on the intended function of marine protected areas, and as often happens the perceived function depends on who is asked (Dayton *et al.* 2000). Groups interested in marine conservation or ecotourism view reserves as wilderness areas where all species and whole ecosystems can persist without extractive or destructive human activity. For these

*Author for correspondence (halpern@lifesci.ucsb.edu).

DOI 10.1098/rspb.2003.2405

groups, reserves need to support and protect, within their boundaries, genetically diverse populations of the full suite of local and regional species. By contrast, other groups view reserves as a resource management tool, intended to export a dependable supply of some resource to other areas where it can be taken for human consumption. Economically viable increases, or at a minimum no decreases, in the total catch of organisms after the creation of a reserve is therefore the goal of these groups of people. These two sets of goals require reserves to provide fundamentally different functions. As we will show, however, the different goals of conservation and exploitation are not necessarily incompatible with one another.

2. STAKEHOLDER CRITERIA: CAN A SINGLE RESERVE NETWORK DESIGN MEET THEM ALL?

All stakeholder groups have the common goal of sustainability at the lowest cost (or maximum benefit), although exactly what they want to sustain differs dramatically between the groups.

(a) *Conservation and ecotourism: within-reserve responses to protection*

Some of the primary stakeholder groups espousing marine reserves are conservation/biodiversity preservation organizations and the people they represent, and those who profit from non-extractive human activity in the area (e.g. diving, ecotourism organizations). For these groups, marine reserves need to preserve and enhance biological resources inside reserves, and ensure them against future degradation. An even larger community may benefit from the 'ecosystem services' provided by intact marine communities, such as wave buffering and biological filtering of contaminants (Snelgrove 1999).

There is abundant evidence that marine species within reserve boundaries respond strongly and quickly to reserve establishment. Most of this evidence has been evaluated in a recent comprehensive review of empirical studies of more than 100 studies of reserves around the world (Halpern 2003). This review showed substantially higher values of organism density, biomass, average size and diversity inside reserves relative to appropriate reference areas. These results were independent of reserve size or age, and the higher values inside reserves accrued rapidly, reaching mean values within 1–3 years after protection (Halpern & Warner 2002; Halpern 2003). Thus, the overall pattern of response to marine reserve protection is one of rapid, dramatic and persistent increases of within-reserve biological measures. From a conservation perspective, therefore, no-take reserves successfully achieve the goal of increasing and maintaining abundance and diversity within reserves.

Conservationists also want systems of reserves that encompass a representative sample of the local and regional biodiversity. An extensive literature has developed on how such a goal can be achieved in terrestrial systems (see review by Margules & Pressey (2000)), and much of this work is now being modified for and applied to marine conservation efforts (Zacharias & Roff 2000; Carr *et al.* 2003). Although these ideas have recently been applied to the design of marine reserves (Zacharias & Roff 2001; Airame *et al.* 2003), few existing reserves were created with biological representation in mind. Since future systems will certainly include existing reserves, designers should make efforts to account for biodiversity not yet represented within marine reserves.

Furthermore, for reserves to fully achieve conservation goals, they should also enclose genetically diverse populations (Botsford *et al.* 2001). To provide this function, reserves should be connected to one another through dispersal to allow genetic mixing of populations. Therefore, dispersal distance is a critical input parameter for designing reserves that successfully provide within-reserve functions. We discuss below the implications for stakeholders of various species-dispersal patterns on marine reserve design.

To meet the criteria of biodiversity representation and sustainable populations within reserves, network designs will probably require that marine reserves be larger than those currently in existence. In most of the world, reserves make up less than 1% of the coastal ocean (Roberts & Hawkins 2000). While small reserves can be effective in increasing the diversity and abundance of many species (Halpern 2003), species–area models and existing evidence indicate that larger reserves will provide protection to more species than smaller reserves (MacArthur & Wilson 1967; McClanahan & Mangi 2000; McClanahan & Arthur 2001; Neigel 2003). Furthermore, reserves would need to be very extensive to maintain large, self-sustaining populations of all species. Such a reserve design, with large single reserves in each biogeographic region, is likely to be contentious with fishermen because it could force them to travel greater distances to reach fishable waters, although this design would serve conservation interests. Fortunately, reviews of existing research on risk minimization suggest that conservation goals for most species can be met with reserves covering 30–50% of the total stock area (Turpie *et al.* 2000; National Research Council 2001; Airame *et al.* 2003), and evidence suggests that networks of reserves of moderate size (10–100 km^2) and variable spacing should adequately protect and maintain the density and biodiversity of a large proportion of benthically associated organisms (Murray *et al.* 1999; National Research Council 2001; Roberts *et al.* 2001, 2003; Allison *et al.* 2003). The exact placement of individual reserves would need to account for: (i) biodiversity representation within the reserve network; and (ii) dispersal patterns (location of retention eddies, etc.) that would affect the self-sustainability of individual reserves and the connectivity within the network of reserves (Roberts *et al.* 2003).

While the overall results of biological responses inside reserves are encouraging, some important points of caution emerge. First, responses to reserve establishment can be highly variable, depending on the intensity of exploitation of the species before protection (e.g. the cessation of fishing in an area not being fished will obviously have little if any impact on that area), or the particular life history or trophic level of a species (Polacheck 1990; Carr & Reed 1993; Rowley 1994; Russ & Alcala 1998*b*; Jennings *et al.* 1999*a*,*b*). For example, large, long-lived species that require many years to reach maturity are likely to respond much less quickly than small, fast-growing species, and perceived impacts of reserve protection will depend on which species are measured (Russ 2002).

Second, the increases in abundance and diversity after reserve establishment do not necessarily represent a return to 'pristine' conditions (Dayton *et al.* 1998; Jackson *et al.* 2001). For example, there are many large species that have been effectively extirpated from coastal ecosystems over the past few hundred years (Jackson *et al.* 2001). Because of the rarity and large home range size of these large species, reserves may be ineffective in restoring these species to their former abundance in any local area.

Finally, reserves are effective in reducing habitat destruction and direct human-induced mortality on some species within reserves, but these are not the only sources of disruption in coastal ecosystems. Pollution, excess nutrients and alteration of pelagic communities outside reserves can have profound effects on species and community structure within protected areas (Allison *et al.* 1998), and any policy establishing reserves must take these distant factors into account. These three cautionary comments are important for setting appropriate goals for marine reserves and in the last case may modify decisions of where individual reserves are placed.

(b) *Sport fishers and artisanal fishermen: export of large fishes*

Small-scale fishermen also represent some of the major stakeholders, in terms of revenue generated and numbers of participants, affected by reserve establishment. If marine reserves are to benefit these fishermen, enough fishes must leave the reserve, where they can be caught, to compensate for the amount of fishes 'lost' to reserve closures. Research is just now beginning to show strong evidence for spillover rates high enough to sustain (and even increase) catches from local artisanal and small-scale fisheries (Attwood & Bennett 1994; Russ & Alcala 1998*a*; McClanahan & Mangi 2000; Roberts *et al.* 2001; Gell & Roberts 2002). A recent review of the evidence for spillover, in fact, suggests that spillover of fishes from reserves can be significant (Gell & Roberts 2002). Further evidence for spillover comes from studies showing how recreational fishermen often 'fish the edge' of a reserve for both greater catches and trophy-sized specimens (Johnson *et al.* 1999; Roberts *et al.* 2001). For example, between 1986 and 1990, eight world-record fishes were taken in the vicinity of the Merritt Island National Wildlife Refuge in Florida, where tagging studies have documented the movement of large adult fishes out of the reserve (Johnson *et al.* 1999; Roberts *et al.* 2001).

Theoretical modelling of reserve design has shown how body size, behaviour and movement patterns of particular species will affect their potential rate of spillover (e.g. Polacheck 1990; DeMartini 1993; Kramer & Chapman 1999). Optimal levels of spillover require that many organisms leave the reserve but that a sustainable number also remain within the reserve; excessive spillover negates the value of a reserve. Kramer & Chapman (1999) point out that spillover can be reduced by creating larger reserves that encompass the potential home ranges of species. Consequently, the degree to which spillover can compensate local fishermen for area (or stock) lost to reserve closures depends, mainly, on the mobility and home range of a given species, with mobile species having higher rates of spillover (Kramer & Chapman 1999; Cole *et al.* 2000; Gell & Roberts 2002). Local fishermen are more likely to benefit from spillover than regional fishermen since the export of large individuals tends to be concentrated near the edges of reserves (Chapman & Kramer 1999; McClanahan & Mangi 2000; Murawski *et al.* 2000).

Given that reserves must supply large organisms through spillover to meet the criteria of sport and artisanal fishermen, these stakeholders will benefit most with ready access to as much reserve edge as possible. The ideal reserve design for these stakeholders, then, may be one that includes many small reserves. However, if fishing pressure outside small reserves is particularly intense, highly mobile species may cross the boundaries often enough to be depleted despite reserve establishment (Kramer & Chapman 1999; Bohnsack 2000). Large reserves also have extensive boundaries, of course, and have the added benefit that continued protection in the centre of such reserves buffers the loss at the edges. Furthermore, the shape of these larger reserves can be modified to increase the edge-to-area ratio. Again, a network of reserves of moderate size and variable spacing should serve the needs of these stakeholder groups while allowing some protection from depletion.

(c) *Commercial fishermen: larval export*

Some of the most important stakeholders in ocean resources, and often the most vocally opposed to the creation of marine reserves, are commercial fishermen and those regulating the fishing fleets. Many from this group feel that the removal of any fishing area simply means fewer fishes to catch. To meet the needs of these stakeholders, marine reserves must supply enough larvae and adults to non-reserve areas to compensate for the area lost to fishing.

Models of successful networks of fisheries reserves require that sufficient numbers of larvae be exported outside the protected areas (Hastings & Botsford 1999; Mangel 2000), and suggest that marine reserves can provide this function as long as they constitute a significant portion (model estimates generally range between 20% and 50% set asides) of the total stock area (Roberts & Hawkins 2000; National Research Council 2001). Reserves larger than these levels will be less effective because of the extensive loss of area where extraction is allowed. We have performed quantitative analyses of the potential effects of marine reserves on larval export and have shown that reserves can export a sufficient amount of larvae to compensate for reserve closures of up to at least 50% of the total area used by a population (B. S. Halpern, S. D. Gaines and R. R. Warner, unpublished data). Of course, the larval replenishment function of reserves is most effective for those fisheries that are most depleted, and so the implementation of reserves may have little effect on fisheries that are not overfished and could have no effect, or even a detrimental effect, on well-regulated fisheries (Hastings & Botsford 1999; National Research Council 2001).

Unfortunately, empirical support for the ability of reserves to replenish fished areas through larval dispersal is limited. There exist very few marine reserves of sufficient size relative to the management unit that would allow for a proper evaluation of model predictions. One exception is the large area (*ca.* 17 000 km^2) set aside in 1994 for groundfish protection on Georges Bank and southern New England; this represents between 17% and

29% of the area occupied by the stocks (Murawski *et al.* 2000). Although groundfish densities are increasing in the reserves, it is the faster-growing sea scallops (also protected by the closure) that have shown the most rapid response; biomass increased 14-fold over 4 years. Significantly, scallop recruitment to areas outside the reserve has increased and become more dependable, sustaining an active fishery. Scallop landings from the Georges Bank in 1998 were over twice the level in 1994, whereas landings in the Middle Atlantic Bight (without reserves) declined by *ca*. 50% over the same period (Murawski *et al.* 2000). Therefore, the evidence suggests that a network of reserves covering a significant portion of the management area could ensure adequate larval export of species for fisheries, as well as the conservation and sustainability of those species within the reserve network.

(d) *All stakeholders: lowest cost for maximum benefit*

The establishment of marine reserves will displace some fishermen. To be successful from the perspective of sport, artisanal and commercial fishermen, then, reserves must not only increase the value of the catch outside the reserves (through either larger or more numerous fishes), but also increase catch value enough to compensate for the lost fishing grounds. As mentioned above, many fishery models of reserves suggest that this compensation can occur with a moderate proportion of the total area set aside in a network of reserves. Impacts can also be lessened by placing reserves away from fishing ports, and to leave space between individual reserves so that no group of local fishermen is disproportionately affected by reserve implementation. By contrast, the easiest way to minimize enforcement costs (therefore meeting conservationists' goals) would be to create fewer larger reserves, although reserve designs composed of smaller reserves with clearly defined and easy-to-identify boundaries should help minimize these costs.

Several cases illustrate that all groups can benefit from a single reserve design, such that fish populations within reserve boundaries increase in size and biomass while at the same time local sport and commercial fishermen actually have higher net value of catch as a result of reserve implementation (Russ & Alcala 1998*a*; Murawski *et al.* 2000; Leeworthy 2001; Roberts *et al.* 2001; Gell & Roberts 2002). For example, in the Florida Keys National Marine Sanctuary all fishermen saw a net increase in catch value after the creation of the Sambos reserve, but the net increase in catch value was 44% higher for fishermen who fished near the reserve relative to fishermen who fished elsewhere in the Sanctuary (Leeworthy 2001). Everyone appeared to benefit from the reserve; those people fishing closest to the reserve benefited the most.

3. ASSESSING WHAT WE DO NOT KNOW

Given that some reserve functions appear to 'work' on a small scale, the fundamental remaining questions for reserve design are how big to make reserves—how big should individual reserves be and how much of a total management area should be set aside in reserves—and how far apart from each other should reserves be placed. Answers to these questions depend largely on issues of dispersal and so are difficult to address, but there is a growing body of evidence that can inform the process of designing reserve networks.

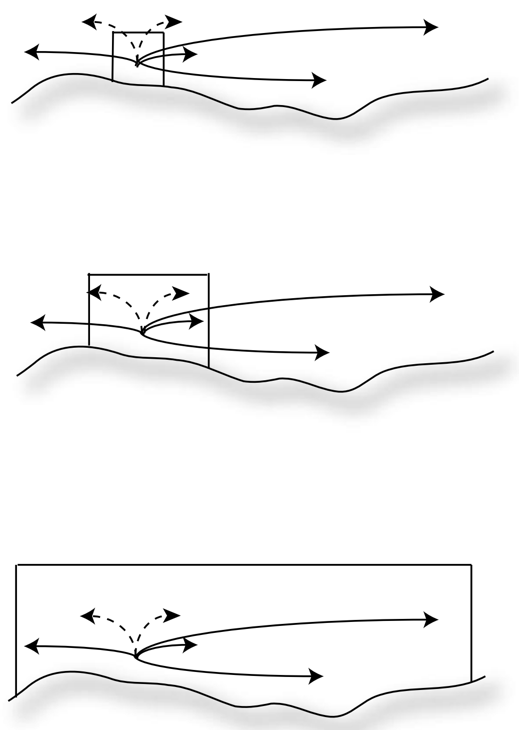
(a) *Reserve size*

(i) *Individual reserve size*

Reserves of all sizes can have positive impacts on biological measures within the reserve (see above), but this may not be sufficient to sustain an entire population. The primary factor determining optimal reserve size is dispersal, both adult and larval (figure 1). If reserves are too small, most if not all of the adults and larvae will leave the reserve, making within-reserve populations unable to sustain themselves. On the other hand, if reserves are too large, too few adults leave the reserves to make the reserve design palatable to fishermen, although such a design would be ideal for conservationists. Unfortunately, dispersal distance is notoriously difficult to measure and is therefore not known for most marine species. However, some estimates of adult movement have been made (see above), and Shanks *et al.* (2003) review dispersal patterns for 32 taxa and suggest that reserves should be able to capture most short-dispersing species if they are *ca*. 4–6 km across, and that appropriate spacing of these reserves (see below) can help capture the long-dispersing species.

Designing an optimal network of reserves for a particular species with known dispersal distances would be a relatively simple task. However, reserves are intended to serve community and ecosystem functions, and these functions involve species with many different dispersal patterns, most of which are not currently known. Such variation makes it difficult to prescribe an exact network design of given reserve size and spacing. However, given the uncertainty in sources and destination of recruits for most marine species, a consensus is emerging that networks of intermediate-sized reserves (10–100 km^2) will be more effective than fewer large reserves, particularly if the networks include a variety of representative habitats (National Research Council 2001).

The question of the efficacy of a single large or several small (SLOSS) reserves has been fully addressed for terrestrial reserve design (see Shafer 1990 for review). Although it is tempting to turn to this literature for guidance on how to design networks of marine reserves, many fundamental differences exist between terrestrial and marine systems, making it difficult to transfer lessons learned from one ecosystem to the other (Carr *et al.* 2003). These differences include: (i) the enormous potential role of dispersal in marine systems in transferring production between locations and 'blurring' boundaries; (ii) the ability for organisms to live between the reserves (unless those areas are being completely exploited); and (iii) the dramatic role of fishing in controlling population sizes (the SLOSS debate for terrestrial systems focuses more on habitat loss than direct take of target species). Because fishermen are likely to be strong advocates for smaller reserves and because dispersal of larvae will help connect and support reserves separated from one another, it is likely that a design of several smaller reserves (instead of one large reserve) will function well while also garnering the most stakeholder support.



	conservation	small fishery	commercial fishery	overall
(a)	reserve not self-sustaining; most species lost	high periph-to-area ratio but unsustainable	small effect on recruitment	too much loss out of reserve; minimal effect on fisheries
(b)	reserve moderately self-sustaining; some species lost	adequate periph-to-area ratio, with some individuals retained	significant source of recruits to fished areas; moderate reduction of fishing grounds	good balance of benefits for all stake-holders
(c)	reserve completely self-sustaining; all species retained	low periph-to-area ratio; relatively small amounts of spillover	little recruitment outside reserve; severe reduction of fishing grounds	little export function

Figure 1. Possible individual reserve sizes assuming adult and larval dispersal distances for a relatively sedentary species with an extended larval phase. Three possible reserve sizes (boxes) are drawn along a hypothetical coastline over dispersal distances for larvae (solid arrows) and large fishes (dashed arrows) for the stock area of a species. The ability of each reserve size to meet stakeholder goals is indicated next to each design. Small reserves export all fishes (larvae and/or large fishes), and are unable to sustain themselves (*a*). This option is unable to meet any stakeholder goals. Large reserves (*c*) capture all fishes, making the reserves suitable for conservation goals but useless for fishing interests. Reserves that are of moderate size (Shanks *et al.* 2003) suggest 4–6 km across; (*b*) retain many large fishes and some dispersing larvae but export all others. This design allows the reserve to be self-sustaining for some species while exporting enough larvae and large fishes into non-reserve areas to sustain fisheries. However, this reserve size (*b*) may not capture enough dispersing larvae and retain larger fishes for other species, and needs to be replicated in a network to preserve the entire biodiversity of an area (see figure 2).

(ii) *Total area set aside*

As outlined above, most recommendations for minimizing risk (for conservation of biodiversity) or maximizing yield (for fishery management) suggest that a minimum of 20% and an optimum of 30–50% of the total management area be set aside in reserves (National Research Council 2001; Roberts *et al.* 2002; Airame *et al.* 2003). This aggregate reserve size allows populations to remain large enough to produce sufficient offspring for maintaining themselves and to supply fisheries, while simultaneously leaving enough area open for fishermen to have sustainable catches. Unfortunately, actual reserve planning areas are often much smaller than that encompassing a stock management unit, and this can compromise the ability to detect a reserve effect. Ideally, many independent reserve networks that cover 30–50% of different management areas should be established to test their effectiveness empirically. Short of this, currently available models can only effectively guide reserve establishment if dispersal out of the reserve is confined mainly to the remaining planning area. If dispersal is much greater than this, then the reserve will represent a relatively small proportion of the area to be serviced, and models suggest that enhanced recruitment will be slight and difficult to detect in a monitoring programme. This is an important point to remember when evaluating the success of reserve networks.

(**b**) ***Reserve spacing***

Determining the optimal spacing of reserves within a network requires knowledge of how far larvae regularly disperse and how close reserves can be to each other and still be acceptable to fishermen. Shanks *et al.* (2003) estimate that reserves spaced *ca.* 20 km apart should allow long-dispersing species to encounter reserves frequently enough to ensure sustainability of populations and stocks. However, even these distances are not likely to encompass the dispersal distances of all species, and so a reserve network that incorporates a wide range of between-reserve distances is more likely to be successful than one that has uniform spacing (Carr *et al.* 2003; Kinlan & Gaines 2003; Palumbi 2003; Shanks *et al.* 2003; figure 2). Such a design should be acceptable to fishermen because it maintains accessibility to large areas of local fishing grounds.

4. NEEDS AND CAVEATS FOR FUTURE PLANNING

Clearly, the estimated dispersal distance of target species is an important parameter in planning effective marine

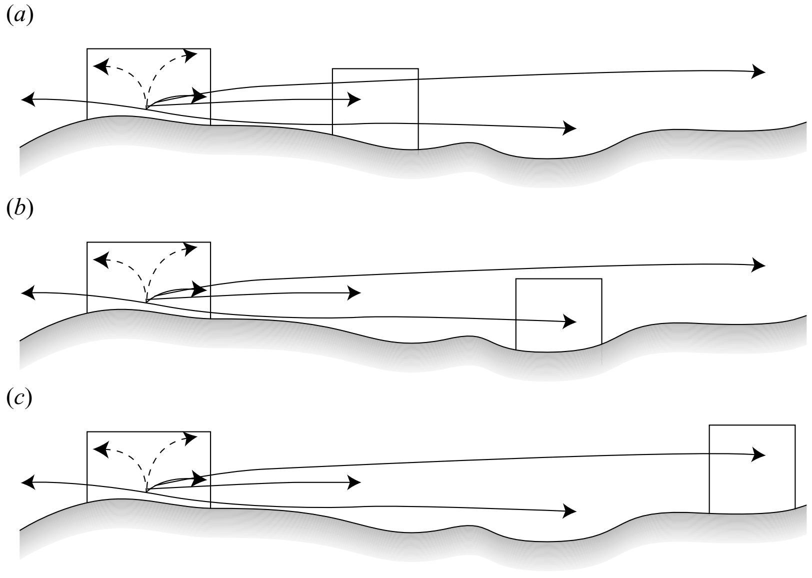


Figure 2. Possible reserve spacing within a network given a relatively sedentary species with an extended larval phase. Three possible reserve spacing options (boxes) along a hypothetical coastline are presented using option (*b*) from figure 1 for individual reserve size and assuming that large fishes (dashed arrows) disperse relatively short distances and larvae (solid arrows) can disperse varying distances for the stock area of a species. Individual reserve size can vary as long as the reserve is sufficiently large to capture enough short-dispersing individuals to make it self-sustaining (see figure 1). Reserve spacing should vary (to include options (*a–c*)) within the entire network (many reserves) to ensure that dispersers of all distances (short, medium and long dispersers for options (*a*), (*b*) and (*c*), respectively) are captured within the network of reserves. This compensates for the inability of a single reserve to capture the entire biodiversity of an area (as outlined in figure 1). This reserve network design would be self-sustaining and capture most of the biodiversity of the region (conservation goals) while exporting large fishes across reserve boundaries (artisanal/sport fishing goals) and larvae to fished areas (commercial fishing goals).

reserves. Such estimates provide an idea of how well local populations can sustain themselves as well as offering guidance for how to construct networks of reserves. Unfortunately, the spatial recruitment patterns resulting from local production are unknown for any marine species with a pelagic stage lasting longer than a few hours, although recent evidence suggests a surprising amount of local retention of production at small scales (tens of kilometres) for species with relatively long (20–50 days) pelagic larval durations (Jones *et al.* 1999; Swearer *et al.* 1999, 2002; Cowen *et al.* 2000; Warner & Cowen 2002). Given the very high fecundity of many marine organisms, it is entirely possible that a local population within a reserve could both sustain itself and provide substantial export to non-reserve areas. Estimating dispersal distances remains one of the great challenges in marine ecology.

It is important to keep in mind that our evaluations of trade-offs between reserve benefits and stakeholder requirements have focused on longer-term outcomes. Reserve effects will take at least a year or two to accrue, and decades for some species. The impacts of spatial closures on fishermen, however, will be felt immediately. To offset some of these short-term costs to fishermen from the creation of reserves, other forms of management (e.g. fleet buy-back programmes) may be necessary. In fact, many have argued that the use of marine reserves must be embedded in a larger scheme of marine management that includes a range of tools and techniques (Agardy *et al.* 2003). However, the goals of both conservation and resource exploitation focus on long-term stability of marine species, which should be achievable through the reserve design described here.

Reserve planning will be most effective if performed at the proper scale. Planning that involves only a small portion of the coastal environment (perhaps owing to limited jurisdiction) is complicated by the potential transport of organisms from outside the planning area. Of course, reserves cannot be equally effective for all the species contained within their borders, but larger planning areas allow reserve network designs that target a wider variety of species. This suggests that coordinated, large-scale programmes will have the best chance of translating marine reserve design theory into practice.

Given the relatively sparse amount of empirical data on the effectiveness of reserves for recruitment enhancement (and subsequent harvest) outside of protected areas, it is tempting to suggest that no action be taken until better information becomes available. However, the continued decline of many fisheries suggests a need to supplement traditional effort-based resource management as quickly as possible (Murray *et al.* 1999). As such, the establishment of reserves should be linked with programmes designed to gauge their effectiveness as a fishery management tool. Such an experimental approach would begin with a design based on the best scientific information available, continue with a dedicated programme to monitor reserve performance, and include a scheme to alter reserve design as performance information becomes available. To be fair and appropriate assessments of the performance of marine reserves, such pilot reserve networks should cover a significant proportion of the management area and be designed according to ecological principles (Airame *et al.* 2003; CAFGC 1999).

5. CONCLUSION

As described above, it is entirely possible that most stakeholders could be served, and served well, by a common design for a system of marine reserves. A network of marine reserves should cover a substantial portion (estimates converge on 20–50%) of the total area being managed. Individual reserves should be large enough to supply recruits to areas outside the reserve and to sustain populations inside, but small enough to allow a sufficient number of adults to 'spill' across reserve boundaries to supply opportunities to 'fish the edge'. The exact size and spacing of individual reserves within the network remain difficult to specify, but a precautionary approach of including a variety of sizes and spacing should allow for a higher likelihood of reserve success. If this design is followed, stakeholders should be able to benefit from the use of marine reserves. However, for the success of reserves to be judged fairly by all stakeholders, it remains essential that: (i) educating stakeholders about the benefits and limitations of marine reserves as a management tool be an integral part of designing reserve networks; (ii) the goals for a reserve be clearly outlined at establishment; and (iii) monitoring programmes be used to assess how well these goals are attained and to help guide modifications to the reserve system as needed. There can never be any guarantees in this process, but greater acceptance can be attained through clear expectations and continued attention to the needs of all stakeholders.

This work was conducted as part of the working group on the Science of Marine Reserves, supported by the National Center for Ecological Analysis and Synthesis, a centre funded by the US NSF (grant DEB-94-21535), the University of California—Santa Barbara, the California Resources Agency and the California Environmental Protection Agency. Support was also provided by the Partnership for the Interdisciplinary Study of Coastal Oceans (PISCO), funded by the David and Lucille Packard Foundation. S. Andelman, S. Gaines, C. Roberts and two anonymous reviewers provided valuable comments on the manuscript.

REFERENCES

Agardy, T., Bridgewater, P., Crosby, M. P., Day J., Dayton, P. K., Kenchington, R., Laffoley, D., McConney, P., Murray, P. A., Parks, J. E. & Peau, L. 2003 Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquat. Conserv.* (In the press.)

Airame, 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. *Ecol. Appl.* **13**, S170–S184.

Allison, G. W., Lubchenco, J. & Carr, M. H. 1998 Marine reserves are necessary but not sufficient for marine conservation. *Ecol. Appl.* **8**, S79–S92.

Allison, G. W., Gaines, S. D., Lubchenco, J. & Possingham, H. P. 2003 Ensuring persistence of marine reserves: catastrophes require adopting an insurance factor. *Ecol. Appl.* **13**, S8–S24.

Attwood, C. G. & Bennett, B. A. 1994 Variation in dispersal of galjoen (*Coracinus capensis*) (Teleostei: Coracinidae) from a marine reserve. *Can. J. Fish. Aquat. Sci.* **51**, 1247–1257.

Ballantine, W. J. & Gordon, D. P. 1979 New Zealand's first marine reserve, Cape Rodney to Okakari Point, Leigh. *Biol. Conserv.* **15**, 273–280.

Bohnsack, J. A. 2000 A comparison of the short-term impacts of no-take marine reserves and minimum size limits. *Bull. Mar. Sci.* **66**, 635–650.

Botsford, L. W., Hastings, A. & Gaines, S. D. 2001 Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol. Lett.* **4**, 144–150.

Bustamante, R., Wellington, J. & Troya, R. 2001 In Galápagos, clashes between fishers and managers jeopardize conservation efforts. *MPA News* **2**, 1–3.

CAFGC (California Fish and Game Code) Marine Life Protection Act 1999 Division 3, chapter 10.5, sections 2850–2863.

Carr, M. H. & Reed, D. C. 1993 Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Can. J. Fish. Aquat. Sci.* **50**, 2019–2028.

Carr, M. H., Neigel, J. E., Estes, J. A., Andelman, S. J., Warner, R. R., Largier, J. L. & Lubchenco, J. 2003 Comparing marine and terrestrial ecosystems: implications for principles of reserve design in coastal marine ecosystems. *Ecol. Appl.* **13**, S90–S107.

Castilla, J. C. & Durán, L. R. 1985 Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos* **45**, 391–399.

Chapman, M. R. & Kramer, D. L. 1999 Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. *Mar. Ecol. Progr. Ser.* **181**, 81–96.

Cole, R. G., Villouta, E. & Davidson, R. J. 2000 Direct evidence of limited dispersal of the reef fish *Parapercis colias* (Pinguipeidae) within a marine reserve and adjacent fished areas. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* **10**, 421–436.

Cowen, R. K., Lwiza, K. M. M., Sponaugle, S., Paris, C. B. & Olson, D. B. 2000 Connectivity of marine populations: open or closed? *Science* **287**, 857–859.

Dayton, P. K., Tegner, M. J., Edwards, P. B. & Riser, K. L. 1998 Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecol. Appl.* **8**, 309–322.

Dayton, P. K., Sala, E., Tegner, M. J. & Thrush, S. 2000 Marine reserves: parks, baselines, and fishery enhancement. *Bull. Mar. Sci.* **66**, 617–634.

DeMartini, E. E. 1993 Modeling the potential of fishery reserves for managing Pacific coral reef fishes. *Fish. Bull.* **91**, 414–427.

Didier Jr, A. J. 1998 Marine protected areas of Washington, Oregon, and California. Report to the Pacific Fishery Management Council, Gladston, OR.

Gell, F. R. & Roberts, C. M. 2002 *The fishery effects of marine reserves and fishery closures*. Washington: WWF-US.

Halpern, B. S. 2003 The impact of marine reserves: have reserves worked and does reserve size matter? *Ecol. Appl.* **13**, S117–S137.

Halpern, B. S. & Warner, R. R. 2002 Marine reserves have rapid and lasting effects. *Ecol. Lett.* **5**, 361–366.

Haskell, B. 1999 Tortugas working group gets consensus on reserve, is challenged by anglers. *MPA News* **1**, 1–2.

Hastings, A. & Botsford, L. W. 1999 Equivalence in yield from marine reserves and traditional fisheries management. *Science* **284**, 1537–1538.

Jackson, J. B. C. (and 18 others) 2001 Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–637.

Jennings, S., Greenstreet, S. P. R. & Reynolds, J. D. 1999*a* Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J. Anim. Ecol.* **68**, 617–627.

Jennings, S., Reynolds, J. D. & Polunin, N. V. C. 1999*b* Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. *Conserv. Biol.* **13**, 1466–1475.

Johnson, D. R., Funicelli, N. A. & Bohnsack, J. A. 1999 Effectiveness of an existing estuarine no-take fish sanctuary within the Kennedy Space Center, Florida. *N. Am. J. Fish. Mngmt* **19**, 436–453.

Jones, G. P., Milicich, M. J., Emslie, M. J. & Lunow, C. 1999 Self-recruitment in a coral reef fish population. *Nature* **402**, 802–804.

Kinlan, B. P. & Gaines, S. D. 2003 Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* **84** (In the press.)

Kramer, D. L. & Chapman, M. R. 1999 Implications of fish home range size and relocation for marine reserve function. *Environ. Biol. Fish.* **55**, 65–79.

Leeworthy, V. R. 2001 Preliminary findings from two years of monitoring the commercial fisheries: impact of no take areas. Report to NOAA, US Dept. Comm., Silver Spring, Maryland.

McArdle, D. A. 1997 *California marine protected areas*. La Jolla, CA: California Sea Grant College System.

MacArthur, R. H. & Wilson, E. O. 1967 *The theory of island biogeography*. Princeton University Press.

McClanahan, T. R. & Arthur, R. 2001 The effect of marine reserves and habitat on populations of east African coral reef fishes. *Ecol. Appl.* **11**, 559–569.

McClanahan, T. R. & Mangi, S. 2000 Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecol. Appl.* **10**, 1792–1805.

Mangel, M. 2000 On the fraction of habitat allocated to marine reserves. *Ecol. Lett.* **3**, 15–22.

Margules, C. R. & Pressey, R. L. 2000 Systematic conservation planning. *Nature* **405**, 243–253.

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.

Murray, S. N. (and 18 others) 1999 No-take reserve networks: sustaining fishery populations and marine ecosystems. *Fisheries* **24**, 11–25.

National Oceanic and Atmospheric Administration (NOAA) 1996 Florida Keys National Marine Sanctuary final management plan/environmental impact statement, vol. 1. Silver Spring, MD: NOAA, US Dept. Comm.

National Research Council (NRC) 2001 Report of the committee on the evaluation, design and monitoring of marine reserves and protected areas in the United States. Washington, DC: National Academy Press.

Neigel, J. E. 2003 Species–area relationships and marine conservation. *Ecol. Applications* **13**, S138–S145.

Nuttall, N., Braynen, M., Hixon, M. & Sealey, K. S. 2000 Bahamas to create no-take reserve network to protect fisheries, fishermen. *MPA News* **1**, 1–3.

Palumbi, S. R. 2003 *Marine reserves: a tool for ecosystem management and conservation*. Arlington, VA: Pews Ocean Commission.

Polacheck, T. 1990 Year around closed areas as a management tool. *Nat. Resource Model.* **4**, 327–353.

Roberts, C. M. 2000 Selecting marine reserve locations: optimality versus opportunism. *Bull. Mar. Sci.* **66**, 581–592.

Roberts, C. M. & Hawkins, J. P. 2000 *Fully-protected marine reserves: a guide*. Washington, DC: WWF Endangered Seas Campaign and York: Environment Department, University of York.

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.

Roberts, C. M., Halpern, B. S., Warner, R. R. & Palumbi, S. 2002 Designing marine reserve networks: why small, isolated protected areas are not enough. *Conserv. Biol. Practice* **2**, 9–17.

Roberts, C. M. (and 11 others) 2003 Application of ecological criteria in selecting marine reserves and developing reserve networks. *Ecol. Appl.* **13**, S215–S228.

Rowley, R. J. 1994 Marine reserves in fisheries management. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* **4**, 233–254.

Russ, G. R. 2002 Yet another review of marine reserves as reef fisheries management tools. In *Coral reef fishes: dynamics and diversity in a complex ecosystem* (ed. P. F. Sale), pp. 421–443. San Diego, CA: Academic Press.

Russ, G. R. & Alcala, A. C. 1996 Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecol. Appl.* **6**, 947–961.

Russ, G. R. & Alcala, A. C. 1998*a* Natural fishing experiments in marine reserves 1983–1993: community and trophic responses. *Coral Reefs* **17**, 383–397.

Russ, G. R. & Alcala, A. C. 1998*b* Natural fishing experiments in marine reserves 1983–1993: roles of life history and fishing intensity in family responses. *Coral Reefs* **17**, 399–416.

Shafer, C. L. 1990 *Nature reserves: island theory and conservation practice*. Washington, DC: Smithsonian Institution Press.

Shanks, A. L., Grantham, B. & Carr, M. H. 2003 Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. Appl.* **13**, S159–S169.

Snelgrove, P. V. R. 1999 Getting to the bottom of marine biodiversity: sedimentary habitats—ocean bottoms are the most widespread habitat on Earth and support high biodiversity and key ecosystem services. *Bioscience* **49**, 129–138.

Suman, D., Shivlani, M. & Milon, J. W. 1999 Perceptions and attitudes regarding marine reserves: a comparison of stakeholder groups in the Florida Keys National Marine Sanctuary. *Ocean Coast. Mngmt* **42**, 1019–1040.

Swearer, S. E., Caselle, J. E., Lea, D. W. & Warner, R. R. 1999 Larval retention and recruitment in an island population of a coral-reef fish. *Nature* **402**, 799–802.

Swearer, S. E., Shima, J. S., Hellberg, M. E., Thorrold, S. R., Jones, G. P., Robertson, D. R., Morgan, S. G., Selkoe, K. A., Ruiz, G. M. & Warner, R. R. 2002 Evidence of self-recruitment in demersal marine populations. *Bull. Mar. Sci.* **70**, 251–271.

Turpie, J. K., Beckley, L. E. & Katua, S. M. 2000 Biogeography and the selection of priority areas for conservation of South African coastal fishes. *Biol. Conserv.* **92**, 59–72.

Warner, R. R. & Cowen, R. K. 2002 Local retention of production in marine populations: evidence, mechanisms, and consequences. *Bull. Mar. Sci.* **70**, 245–249.

Zacharias, M. A. & Roff, J. C. 2000 A hierarchical ecological approach to conserving marine biodiversity. *Conserv. Biol.* **14**, 1327–1334.

Zacharias, M. A. & Roff, J. C. 2001 Zacharias and Roff vs. Salomon *et al.*: who adds more value to marine conservation efforts? *Conserv. Biol.* **15**, 1456–1458.