Ecology Letters, (2001) **4**: 144–150

REPORT

Dependence of sustainability on the configuration of marine reserves and larval dispersal distance

Louis W. Botsford,[1],* Alan Hastings[2] and Steven D. Gaines[3]
[1]Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA 95616, USA
[2]Department of Environmental Sciences and Policy, University of California, Davis, CA 95616, USA
[3]Department of Ecology, Evolution and Marine Biology, Marine Science Institute, University of California, Santa Barbara, CA 93106, USA
**Correspondence: E-mail: lwbotsford@ucdavis.edu*

Abstract

Marine reserves hold promise for maintaining biodiversity and sustainable fishery management, but studies supporting them have not addressed a crucial aspect of sustainability: the reduction in viability of populations with planktonic larvae dispersing along a coastal habitat with noncontiguous marine reserves. We show how sustainability depends on the fraction of natural larval settlement (FNLS) remaining after reserves are implemented, which in turn depends on reserve configuration and larval dispersal distance. Sustainability requires FNLS to be greater than an empirically determined minimum. Maintaining an adequate value for all species requires either a large, unlikely fraction ($> 35\%$) of coastline in reserves, or reserves that are larger than the mean larval dispersal distance of the target species. FNLS is greater for species dispersing shorter distances, which implies reserves can lead to: (1) changes in community composition and (2) genetic selection for shorter dispersal distance. Dependence of sustainability on dispersal distance is a new source of uncertainty.

Keywords

Marine reserves, dispersal, sustainability, fisheries, uncertainty.

Ecology Letters (2001) 4: 144–150

INTRODUCTION

Calls for greater use of marine reserves note improved protection of marine biodiversity and more sustainable management of fisheries as the potential benefits (e.g. Murray *et al.* 1999). Most analyses of the benefits have been in a fisheries context, and they have argued that: (1) marine reserves can increase catch (Quinn *et al.* 1994; Attwood & Bennett 1995; Holland & Brazee 1996; Sladek Nowlis & Roberts 1999) and (2) marine reserves reduce uncertainty in fisheries management (Clark 1996; Lauck *et al.* 1998; Mangel 2000a; Mangel 2000b). The latter is as important as the former since uncertainty in future projections of potential deleterious effects of fishing or other uses of the sea is a key factor leading to overexploitation (Ludwig *et al.* 1993; Botsford *et al.* 1997). Most of these assessments of marine reserves have depicted the larval stage as a common larval pool, with larvae evenly redistributed over the population (termed the LPER assumption, larval pool with even redistribution; exceptions include Quinn *et al.* 1994; Attwood & Bennett 1995). There have been some efforts to describe the connectivity between reserves provided by dispersing larval stages (e.g. Roberts 1997), but no systematic investigation of how that connectivity affects sustainability. Thus, the way in which fragmentation of the juvenile and adult habitat by a system of marine reserves will affect the persistence of populations with specific dispersal characteristics remains an unanswered, but important, question. Design principles for reserves for terrestrial populations (e.g. Gilpin & Diamond 1980; Higgs & Usher 1980; Pressey *et al.* 1993) are not directly applicable because most marine populations receive larval propagules through ocean dispersal from hundreds of kilometres away (Roughgarden *et al.* 1988; Botsford *et al.* 1994; Allison *et al.* 1998).

Here, we show that the persistence of populations in marine reserves depends on the fraction of natural larval settlement (FNLS) remaining after the implementation of reserves, a quantity that depends on reserve configuration and larval dispersal distance. We determine conditions on FNLS for sustainability of populations in marine reserves, whether they are designed for fishery management or maintenance of biodiversity. The results provide answers to questions such as what fraction of coastline is needed for sustainability and how big reserves should be, and also identify new concerns, regarding uncertainty, community species composition and genetic selection, that must be accounted for in future studies and implementations of marine reserves.

METHODS

Models of persistence of fragmented meroplanktonic populations

We initially consider a population distributed along a linear coastline of infinite length. We assume that adults are sedentary, and that density-dependence occurs after larval dispersal and depends only on the density of the dispersers metamorphosing to a juvenile stage at that location. This is appropriate for structure-dwelling benthic invertebrates (Caddy 1986; Wahle & Steneck 1991) and many reef fishes (Caley *et al.* 1996), but not for some soft bottom invertebrates (Olafsson *et al.* 1994).

To elucidate general principles, we consider the effects of dividing the coastline into a number of evenly spaced reserves of width w and spacing s (Fig. 1a), and initially ignore larval production outside reserves. Fragmenting the coast in this way reduces the number of dispersing larvae reaching any point. We assume the fraction of dispersers (p) released at point x that successfully travels to and metamophoses at point y has a Laplacian form, centred at the origin (Van Kirk & Lewis 1997)

$$p(x,y) = \frac{a}{2} e^{-a|x-y|} \tag{1}$$

with mean dispersal distance $1/a$. This expression is obviously a simplification of a real dispersal pattern, but it allows us to assess the effects of dispersal distance. Use of more complex expressions would be situation-specific and severely limited by the fact that dispersal paths for all species except those dispersing less than 100 m are unknown (Allison *et al.* 1998).

We take two independent approaches to determining conditions for a sustainable population, one an *ad hoc* approach, and the other based on existing theory for semelparous populations distributed over space. For the former, we assume recruitment depends linearly on settlement up to a value of settlement of D_{sat}, beyond which the habitat is saturated, and recruitment is constant at a level that produces K potential settlers per year. To determine the amount of successful settlement required for persistence, we assume all points receive sufficient settlement to saturate the habitat, hence produce the maximum number of larvae possible each year, then solve for the level of settlement required to accomplish saturation, and therefore persistence. The lowest settlement in each reserve will occur at the edges because that is where the maximum amount (one-half) must originate outside the reserve. We conservatively assess the amount of dispersal from the total area in reserves along the coast that successfully settles at the left hand edge of a reserve in Fig. 1(a). To do this we first integrate the larval contribution, Eq. (1), from all reserves to the right of that point, numbering reserves (k) from zero,

$$k\sum_{k=0}^{\infty} a \int_{ks}^{ks+w} e^{-ax}\mathrm{d}x = K(1 - e^{aw})\sum_{k=0}^{\infty} e^{-ka}$$

$$= K\frac{(1 - e^{-aw})}{(1 - e^{-as})} \tag{2}$$

Integrating the contribution from all reserves to the left, numbering reserves from 1, gives

$$k\sum_{k=1}^{\infty} a \int_{ks-w}^{ks} e^{-ax}\mathrm{d}x = K(e^{-aw} - 1)\sum_{k=1}^{\infty} e^{-aks}$$

$$= K\frac{(e^{-aw} - 1)e^{-as}}{(1 - e^{-as})} \tag{3}$$

The sum of half of each of these is total settlement, which must be greater than the level that saturates the postsettlement habitat for persistence to occur,

$$\frac{1}{2}\left[\frac{(1 - e^{-wa}) + (1 - e^{-sa})e^{-sa}}{1 - e^{-sa}}\right] > \frac{D_{\text{sat}}}{K} \tag{4}$$

The approach from existing theory is based on analyses by Van Kirk & Lewis (1997). Their eq. (52) describes the dynamics of nonlinear, semelparous populations distributed over heterogeneous habitat. Their key step is approximating the population by its spatial average of abundance, in their description of density-dependence. For an infinite number of patches, their expression for population dynamics becomes the limit

$$\overline{N_{\text{appr}}} = f(\overline{N_{\text{appr}}})\left[\frac{\sum_k \int_\Omega s_k(x)\mathrm{d}x}{V_\Omega}\right] \tag{5}$$

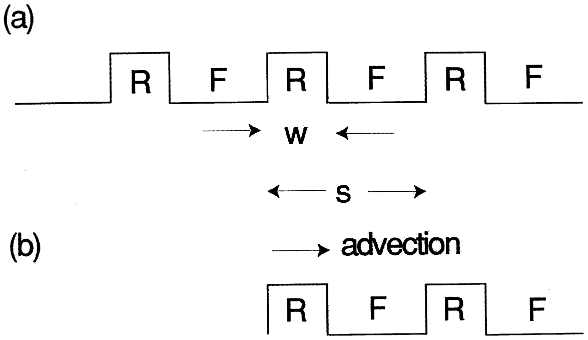

Figure 1 The assumed configurations of marine reserves (R) and fished (F) areas of width, w, and spacing, s (a) along an infinite coastline and (b) along a semi-infinite coastline with net larval advection in the indicated direction.

as $V_{\Omega} \rightarrow \infty$, where $s_k(x)$ is the number of larvae arriving at x from reserve k, $f(N)$ is the number of recruits at adult density N, and V_{Ω} is in this case the length of the coastline, making the quantity in brackets the sum over all reserves of the larvae arriving in a reserve. Equation (5) implies that the term in brackets be greater than $1/f(0)$ for persistence, where $f(0)$ is the number of recruits per spawner at low abundance. To obtain the term in brackets, we first write for the number of larvae arriving from all reserves outside the destination,

$$s_k(x) = \frac{a}{2}\int_0^w e^{-a(x-y)}\mathrm{d}y = \frac{e^{-ax}}{2}[e^{aw} - 1]. \tag{6}$$

The term in brackets in Eq. (5) is then the integral over all outside sources,

$$(e^{aw} - 1)\sum_{k=1}^{\infty}\int_k^{k+w} e^{-ax}\mathrm{d}x = \frac{(e^{aw} - 1)(e^{-aw} - 1)}{wa}$$

$$\sum_{k=1}^{\infty} e^{-ak} = \left[\frac{(e^{aw} - 1)(1 - e^{-aw})e^{-as}}{wa(1 - e^{-as})}\right] \tag{7}$$

plus the contribution of the same reserve,

$$w\left[1 - \frac{1 - e^{-aw}}{aw}\right]$$

from Eq. (7) in Van Kirk & Lewis (1997), which results in

$$\left[\frac{(e^{aw} - 1)(1 - e^{-aw})e^{-as}}{wa(1 - e^{-as})}\right] + \left[1 - \frac{1 - e^{-aw}}{aw}\right] > \frac{1}{f'(0)}, \tag{8}$$

The right hand sides of Eqs (4) and (8) are essentially the same quantity, the inverse of the number of larvae produced per settler in their lifetime, at low density (i.e. the slope at the origin of the settler/recruit relationship). Survival through the larval phase, the number of settlers per larvae, is the left hand side of each, which must be greater than (or equal to) this quantity for persistence. In Eq. (8), since recruitment and spawners are written in the same units, sustainability requires $f(0) > 1$, so $1/f(0)$ is the fraction of natural reproduction required for a sustainable population. Similarly, in Eq. (4), K/D_{sat} is the slope of the relationship between larvae produced and settlement.

To assess the effects of various assumptions, such as a lack of net alongshore advection of larvae, less fishing between reserves, and different assumed requirements for sustainability, we also derived an expression for a semi-infinite coastline. A semi-infinite coastline (Fig. 1b) represents a faunal break due to lack of postsettlement habitat, the situation in which the effects of alongshore advection are most detrimental. Expression (4) becomes

$$\left(\frac{1 - e^{-wa}}{1 - e^{-sa}}\right) + L_F\left(\frac{e^{-wa} - e^{-sa}}{1 - e^{-sa}}\right) - (1 - e^{-\delta a}) > \frac{D_{\mathrm{sat}}}{K} \tag{9}$$

where L_F is the fraction of unfished lifetime larval production in the fished parts of the population, and δ is the distance the dispersal pattern is shifted (this simple expression holds only for small values of δ, $\delta < w$). The first two terms in Eq. (9) reflect the contributions from reserves and fished areas, respectively, on a semi-infinite coastline. The first term is the same as the first term above, and the second is the same as the second term above with s–w substituted for w. The third term is the consequence of substituting a new expression for the diminished settlement in the leftmost reserve $(1–e^{-(w-\delta)a})$ for the original term $(1–e^{-aw})$.

The two independent approaches [Eqs (4) and (8)] lead to similar requirements for persistence of the population – that the fraction of natural postlarval recruitment remaining after the institution of reserves must be greater than a minimum value [D_{sat}/K and $1/f(0)$, respectively]. Because that fraction accounts for the effect of habitat fragmentation on successful completion of the larval stage, we refer to it as the fraction of natural larval settlement (FNLS) of a reserve configuration. Populations require a certain degree of connection between generations, i.e. successful reproduction, for sustainability. In meroplanktonic marine populations, this connection involves a dispersing larval stage. The strength of this connection is reduced by allowing only those larvae that settle in marine reserves to reproduce, and FNLS reflects the fraction by which this is reduced.

Unfortunately, the minimum value of FNLS required for sustainability is difficult to determine because the reproductive dynamics of marine populations at low abundance are poorly known (Myers *et al.* 1995). However, in efforts to diagnose overfishing, fishery biologists have sought methods for assessing sustainability of fished populations with limited data (Sissenwine & Shepherd 1987; Clark 1991; Mace & Sissenwine 1993; Mace 1994). The condition for persistence is essentially that the slope of the stock–recruitment curve at the origin (i.e. recruits per larva produced) must be greater than the inverse of the number of larvae produced in the lifetime of a recruit (Sissenwine & Shepherd 1987). The resulting minimum lifetime larval production, expressed as the fraction of unfished lifetime reproduction, is the minimum lifetime recruit production required for sustainability of a population, whether natural production has been reduced by removal of larvae-producing individuals, or postlarval habitat. The estimated value of that quantity varies among fished species between 20 and 70%. Fishery managers generally try to maintain a value of 35%, though there have been suggestions that a higher value may be necessary. For illustrative purposes, we used the value of 0.35 here.

RESULTS

Plots of FNLS [Eqs (4) and (8)] readily allow identification of the conditions under which a system of reserves will maintain a value greater than the required minimum of 0.35 (Fig. 2). First note that the two approaches, Eqs (4) and (8), give similar results (Fig. 2), except that Eq. (8) is more optimistic because it averages settlement over reserves instead of using settlement at the edge of a reserve. For long distance dispersers or small reserves, FNLS increases linearly with the fraction of coastline in reserves, indicating a large fraction of the coastline (equal to the fraction of unfished, lifetime reproduction required) must be in reserves. However, smaller fractions of coastline, which are more likely to be set aside, will sustain populations if the individual reserves are made large enough relative to mean dispersal distance. The option of making reserves large relative to dispersal distance, is obviously easier to accomplish for shorter distance dispersers.

Because marine reserves provide a greater FNLS, hence greater reproduction for species with shorter dispersal distances, they can (1) affect the species composition of marine communities composed of species dispersing different distances and (2) lead to genetic selection for shorter dispersal distances. We can compare the relative reproductive benefit of reserves to species with different dispersal distances by plotting FNLS [LHS of Eq. (4)] in a different way (Fig. 3). Reserves of a specified width provide adequate lifetime reproduction (0.35) for all species with mean dispersal distances less than approximately one reserve width. This result depends on our using Laplacian dispersal, but it is probably robust since this dispersal function has relatively thick tails (i.e. thinner tails would mean returns would diminish more rapidly). Furthermore, comparison of the value of FNLS due to a system of reserves to that of single reserves indicates single reserves provide most of the protection. The other reserves contribute FNLS for longer distance dispersers. The difference between contributions to FNLS by a single reserve and a network of reserves is greater as the fraction

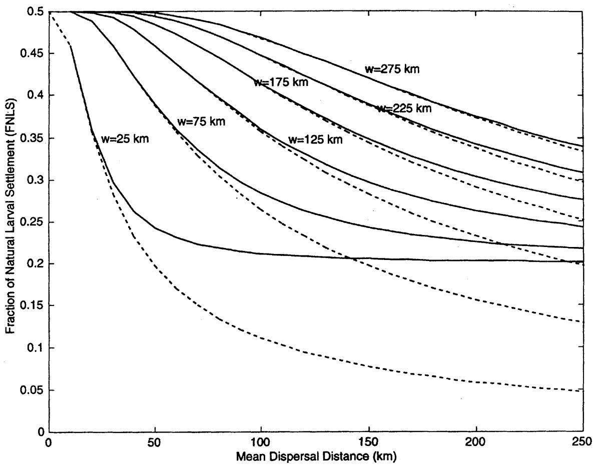

Figure 3 Fraction of natural larval settlement (FNLS) for species with various mean dispersal distances with 20% of the coastline in reserves, and reserve widths ranging from 25 km to 275 km (solid lines) [Eq. (4)]. Also shown is the connectivity that would result from a single reserve rather than a system of reserves (dotted lines).

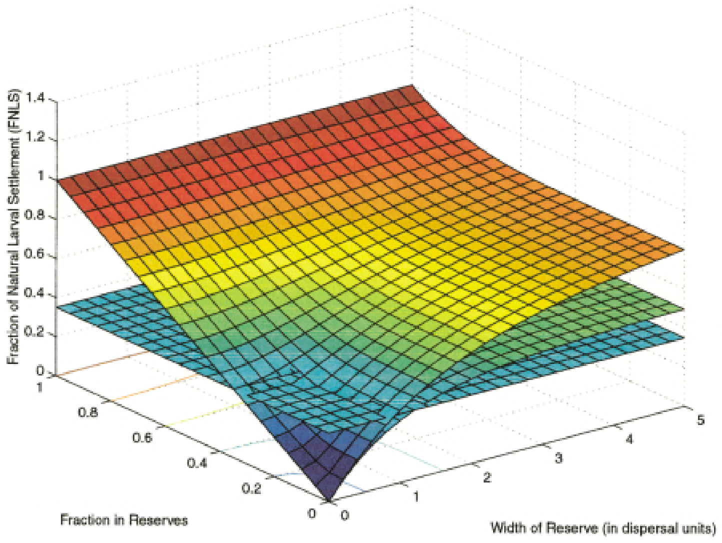

Figure 2 Fraction of natural larval settlement (FNLS) for various fractions of coastline in reserves and widths of reserves (in units of average dispersal distance, $1/a$), expressed as a fraction of natural settlement (without reserves or fishing) computed from results in Van Kirk & Lewis (1997) (top surface) and an *ad hoc* approach (second surface), compared to the minimum value required for population persistence (0.35) determined from a number of fish species (lower, constant plane). Sustainable populations are possible where the curved surface exceeds the plane.

in reserves increases (i.e. in Fig. 3, the solid lines indicating effects of a network all are greater than, and converge to the fraction of coastline in reserves, which in this case is 0.20). The effects on community composition, food web dynamics and selection for shorter distance dispersal of the differential reproductive advantage, conferred by reserves on species dispersing different distances, could be substantial, but are unknown.

Sustainability of populations in reserves is sensitive to poorly known aspects of reproduction and dispersal; hence, actual spatial requirements may be greater than computed thus far. We examine sensitivity to each of these individually. If populations actually require a minimum fraction of lifetime reproduction lower or higher in the range of 20–70%, reserve requirements will differ substantially (Fig. 4a). The suitability of coastal habitat varies and alongshore advection is common. Whether larvae are transported long distances or retained locally is currently a topic of great interest (Jones *et al.* 1999; Swearer *et al.* 1999; Cowen *et al.* 2000) and alongshore advection can have dramatic effects on population persistence in heterogeneous habitats (Gaylord & Gaines 2000). A small amount of net larval advection near a faunal boundary (Fig. 1b) dramatically increases the fraction in reserves and reserve width required for persistence (Fig. 4b). On the other hand, while these two sources of uncertainty lead to higher demands on reserve configuration than our initial calculations, accounting for egg production from the fished areas outside the reserves leads to lower demands. A nonzero contribution of propagules from fished areas reduces the fraction of coastline and the width of reserves required for a sustainable population (Fig. 4c).

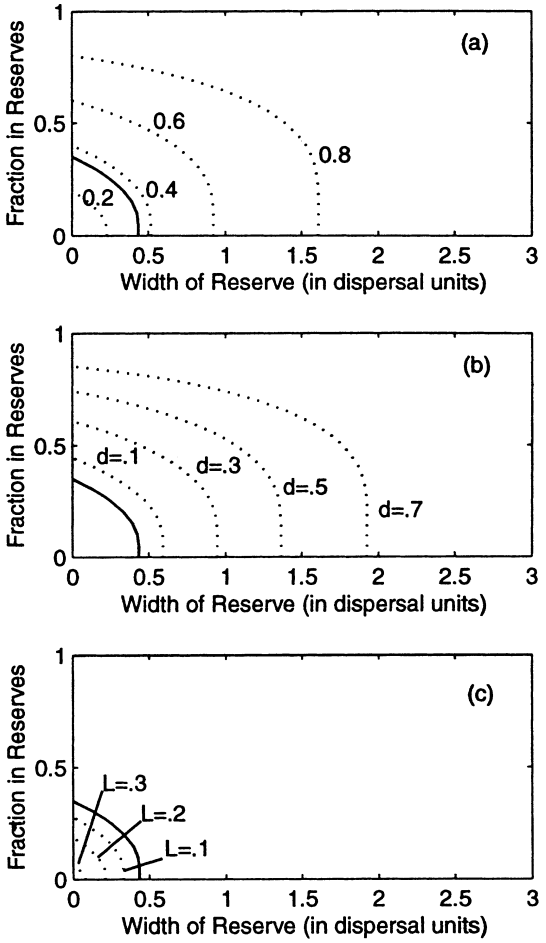

Figure 4 Sensitivity of reserve requirements to required fraction of lifetime reproduction, alongshore advection and reduced fishing outside reserves. For the case with a coastal boundary [Fig. 1b, Eq. (4)]. (a) Configurations required using minimal fractions of lifetime spawning other (dashed lines) than 0.35 (solid line). (b) Requirements using 0.35 as the fraction spawning, in the presence of various alongshore advection distances (in units of mean dispersal distance; dashed lines). (c) Requirement *s* using 0.35 as the fraction spawning, when fished areas contribute various nonzero fractions of lifetime spawning.

DISCUSSION

Although there clearly are advantages to placing some coastal area in reserves, rather than allowing it to be overfished or detrimentally impacted in other ways, the results presented here identify new problems that need to be addressed. Implementation of a marine reserve or a system of reserves will still have a positive effect on sustainability under current conditions. However, it may result in less increase in abundance than would otherwise be anticipated, and that increase will be greater in shorter distance dispersers. The real problem raised by the results obtained here will arise if reserves are depended on in the future to sustain a species, and fishing or other uses are allowed to increase outside the reserve, based on that dependence. If the effects outlined here are not accounted for, reserves may not sustain all species found in the reserve, as is currently expected.

Our results highlight a general characteristic of marine metapopulations that is crucial to sustainability, the extent to which a population provides enough successful reproduction to sustain itself. Here we focus on the reduction in this quantity due to fragmentation of the coast in marine reserves, the FNLS, but we take advantage of the fact that it is essentially the same as the reduction in egg production per recruit by fisheries. Fisheries reduce sustainability by removing individuals before they can reproduce, as reflected in the fraction of unfished reproduction per recruit (Sissenwine & Shepherd 1987; Clark 1991; Mace & Sissenwine 1993), while marine reserves increase sustainability by protecting areas from the effects of fishing and other processes affecting reproduction or survival, so that settlers can develop and reproduce. With regard to FNLS, a key feature is the way in which it is provided by varying amounts of connectivity between reserves and settlement within the same reserve, depending on the reserve configuration (e.g. Figure 3).

Although marine reserves reduce the effects of uncertainty in estimating abundance and the effects of fishing or other activities on populations (Clark 1996; Lauck *et al.* 1998; Mangel 2000a), they also introduce dependence on a new uncertainty, unknown larval dispersal distances. Both marine reserves and classical fishery management are susceptible to uncertainty in the fraction of natural reproduction required for sustainability. The sensitivity analyses above, and elsewhere (e.g. Gaylord & Gaines 2000), indicate that the effectiveness of marine reserves will depend critically on characteristics of the larval dispersal pattern, especially alongshore advection. The sensitivity of marine metapopulation behaviour to dispersal characteristics (Botsford *et al.* 1994, 1998; Gaylord & Gaines 2000) implies dispersal models should be as realistic as possible (cf. Travis & French 2000), however, given the unknown nature of dispersal, the simple model used here is a good choice in that it allows assessment of dispersal distance, without depending critically on details of the dispersal pattern.

Previous assessments of the effectiveness of marine reserves focused on the effects of protecting area without accounting for reserve configurations or dispersal patterns as described here. Most studies (i.e. Holland & Brazee 1996; Hastings & Botsford 1998; Lauck *et al.* 1998; Mangel 1998, 2000a; Mangel 2000b) assumed larvae were completely mixed in a larval pool covering the entire coastline, from which larvae settled in proportion to the fraction of area in reserves (i.e. the LPER assumption). Results with this larval pool, equal redistribution (LPER) assumption would correspond to the axes in Figs 2 and 4, at which dispersal distance is infinite or reserve width is zero. To be assured of sustainability, the reserve configurations would have to involve many small reserves. These studies conclude that rather large fractions of the coastline be placed in reserves, and other independent proposals also call for fractions with a low probability of being implemented (e.g. 20%; Schmidt 1997). As we begin setting areas aside for marine reserves, in most situations we will have the advantage indicated in Fig. 4(c), that areas outside reserves will contribute to reproduction within reserves. However, there is still the danger that small, isolated reserves, by themselves may not protect long distance dispersers (Figs 2,3). Maintenance of natural communities (i.e. protection of all species) is often a promised result of marine reserves, but with the reserves areas likely to be implemented in the near future, that may not be achieved unless fishing and all other deleterious effects outside reserves are limited (Fig. 4c).

Previous analyses also did not reveal the variability in degree of sustainability with species, which depends on dispersal distance and the fraction of natural reproduction required for persistence. The use of reserves is often proposed to be better than classical fishery management because they are free of the genetic selection for younger maturity that can occur in size selective fisheries. However, as seen here, reserves can apply selective pressure for another life history trait, shorter dispersal distance. Also, from a biodiversity perspective, reserves are often described as a way to preserve natural communities. If species in a relatively small reserve have different dispersal distances, the species composition may not end up being natural because the reserve will provide a greater reproductive advantage to shorter distance dispersers.

Clearly, marine reserves will be more successful if we account for these additional factors in their design, monitoring and assessment. Most studies of the effects of marine reserves that we know of have not focused on species differences (But see McClanahan 2000). Institution of such monitoring, along with ongoing research on the nature of larval dispersal patterns will lead to more realistic expectations and better reserve designs in the future. In the long run, marine reserves are more likely to be perceived as being successful, and therefore to be more widely used, if accompanied by realistic expectations of how various configurations will function.

ACKNOWLEDGEMENTS

Supported by NSF grant OCE-9711448 and by California Sea Grant R/F 179. This is contribution 3 of the Marine Reserves Working Group at the National Center for Ecological Analysis and Synthesis, which is supported by the NSF. We thank our colleagues in that group for useful discussions, and Brian Gaylord for his comments on this manuscript.

REFERENCES

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

Attwood, C.G. & Bennett, B.A. (1995) Modeling the effect of marine reserves on the recreational shore-fishery of the south-western cape, South Africa. *S. Afr. J. Mar. Sci.*, 16, 227–240.

Botsford, L.W., Castilla, J.C. & Peterson, C.H. (1997) The management of fisheries and marine ecosystems. *Science*, 277, 509–515.

Botsford, L.W., Moloney, C.L., Hastings, A., Largier, J.L., Powell, T.M., Higgins, K. & Quinn, J.F. (1994) The influence of spatially and temporally varying oceanographic conditions on meroplanktonic metapopulations. *Deep-Sea Res.*, 41, 107–145.

Botsford, L.W., Moloney, C.L., Largier, J.L. & Hastings, A. (1998) Metapopulation dynamics of meroplanktonic invertebrates: the Dungeness crab as an example. *Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management.* (eds Jamieson, G.S., & Campbell, A.). *Can. Spec. Publ. Fish. Aquat. Sci.*, 125, 295–306.

Caddy, J.F. (1986) Modeling stock-recruitment processes in crustacea: some practical and theoretical perspectives. *Can. J. Fish. Aquat. Sci.*, 43, 2330–2344.

Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P. & Menge, B.A. (1996) Recruitment and the local dynamics of open marine populations. *Ann. Rev. Ecol. Syst.*, 27, 477–500.

Clark, W.G. (1991) Groundfish exploitation rates based on life history parameters. *Can. J. Fish. Aquat. Sci.*, 48, 734–750.

Clark, C.W. (1996) Marine reserves and the precautionary management of fisheries. *Ecol. Applications*, 6, 369–370.

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.

Gaylord, B. & Gaines, S.D. (2000) Temperature or transport? Range limits in marine species mediated solely by flow. *Am. Nat.*, 155, 769–789.

Gilpin, M.E. & Diamond, J.M. (1980) Subdivision of nature reserves and the maintenance of species diversity. *Nature*, 285, 567–568.

Hastings, A. & Botsford, L.W. (1998) Equivalence in yield from marine reserves and traditional fisheries management. *Science*, 284, 1537–1538.

Higgs, A.J. & Usher, M.B. (1980) Should nature reserves be large or small? *Nature*, 285, 568–569.

Holland, D.S. & Brazee, R.J. (1996) Marine reserves for fishery management. *Mar. Res. Econ.*, 11, 157–171.

Lauck, T., Clark, C.W., Mangel, M. & Munro, G.R. (1998) Implementing the precautionary principles in fisheries management through marine reserves. *Ecol. App.*, 8, S72–S78.

Ludwig, D., Hilborn, R. & Walters, C. (1993) Uncertainty, resource exploitation and conservation: lessons from history. *Science*, 260, 17 and 36.

Mace, P.M. (1994) Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. *Can. J. Fish. Aquat. Sci.*, 51, 110–122.

Mace, P.M. & Sissenwine, M.P. (1993) *How Much Spawning Per Recruit is Enough? Risk Evaluation and Biological Reference Points for Fisheries Management* (eds, Smith, S.J., Hunt, J.J. & Rivard, D.). Canadian Special Publication of Fisheries and Aquatic Sciences, NRC Press, Ottawa, 120, 101–118.

Mangel, M. (1998) No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. *Ecol. Lett.*, 1, 87–90.

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

Mangel, M. (2000b) Irreducible uncertainties, sustainable fisheries and marine reserves. *Evol. Eco. Res.*, 2, 547–557.

McClanahan, T.R. (2000) Recovery of a coral reef keystone predator, *Balistapus undulatus*, in East African marine parks. *Biol. Conservation*, 94, 191–198.

Murray, S.N., Ambrose, R.F., Bohnsack, J.A., *et al.* (1999) No-take reserve networks: sustaining fishery populations and marine ecosystems. *Fisheries*, 24, 11–25.

Myers, R.A., Bridson, J. & Barrowman, N.J. (1995) *Summary of Worldwide Spawner and Recruitment Data.* Canadian Technical Report of Fisheries and Aquatic Science, 2024, 274 pp.

Olafsson, E.B., Peterson, C.H. & Ambrose, W.G. Jr (1994) Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanogr. Mar. Biol. Ann. Rev.*, 32, 65–110.

Pressey, R.L., Humphries, C.J., Margules, C.R., Vane-Wright, R.I. & Williams, P.H. (1993) Beyond opportunism: key principles for systematic reserve selection. *TREE*, 8, 124–128.

Quinn, J.F., Wing, S.R. & Botsford, L.W. (1994) Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *Am. Zool.*, 33, 537–550.

Roberts, C.M. (1997) Connectivity and management of Caribbean coral reefs. *Science*, 278, 1454–1457.

Roughgarden, J., Gaines, S. & Possingham, H.P. (1988) Recruitment dynamics in complex life cycles. *Science*, 241, 1460–1466.

Schmidt, K.F. (1997) 'No-take' zones spark fisheries debate. *Science*, 277, 489–491.

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.

Sladek Nowlis, J. & Roberts, C.M. (1999) Fisheries benefits and optimal design of marine reserves. *Fish. Bull., U.S.*, 97, 604–616.

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.

Travis, J.M.J. & French, D.R. (2000) Dispersal functions and spatial models: expanding our dispersal toolbox. *Ecol. Lett.*, 3, 163–165.

Van Kirk, R.W. & Lewis, M.A. (1997) Integrodifference models for persistence in fragmented habitats. *Bull. Math. Biol.*, 59, 107–137.

Wahle, R.A. & Steneck, R.S. (1991) Recruitment habitats and nursery grounds of the American lobster (*Homarus americanus*): a demographic bottleneck? *Mar. Ecol. Prog. Ser.*, 69, 231–243.

BIOSKETCH

L.W. Botsford works on the dynamics of marine populations with age, size and spatial structure. He is interested in the effects of environmental forcing and climate change, as well as marine conservation and fishery management. He is currently involved in several efforts implementing marine reserves.

Editor, U. Sommer
Manuscript received 18 September 2000
First decision made 30 October 2000
Manuscript accepted 6 December 2000