

This is a repository copy of *Application of ecological criteria in selecting marine reserves and developing reserve networks*.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/344/>

Article:

Roberts, C.M. orcid.org/0000-0003-2276-4258, Bustmante, R.H., Dugan, J. et al. (9 more authors) (2003) Application of ecological criteria in selecting marine reserves and developing reserve networks. ECOLOGICAL APPLICATIONS. S215-S228. ISSN 1051-0761

[https://doi.org/10.1890/1051-0761\(2003\)013\[0215:AOECIS\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)013[0215:AOECIS]2.0.CO;2)

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

APPLICATION OF ECOLOGICAL CRITERIA IN SELECTING MARINE RESERVES AND DEVELOPING RESERVE NETWORKS

CALLUM M. ROBERTS,^{1,11} GEORGE BRANCH,² RODRIGO H. BUSTAMANTE,³ JUAN CARLOS CASTILLA,⁴ JENIFER DUGAN,⁵ BENJAMIN S. HALPERN,⁶ KEVIN D. LAFFERTY,⁷ HEATHER LESLIE,⁸ JANE LUBCHENCO,⁸ DEBORAH MCARDLE,⁹ MARY RUCKELSHAUS,¹⁰ AND ROBERT R. WARNER⁶

¹Environment Department, University of York, York, YO10 5DD, UK

²Zoology Department, University of Cape Town, Rondebosch 7701, South Africa

³Charles Darwin Research Station, Santa Cruz, Galapagos Islands, Casilla 17-01-3891, Quito, Ecuador

⁴Departamento de Ecología, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago de Chile, Chile

⁵Marine Science Institute, University of California, Santa Barbara, California 93106 USA

⁶Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106 USA

⁷U.S. Geological Survey, Marine Science Institute, University of California, Santa Barbara, California 93106 USA

⁸Department of Zoology, Oregon State University, Corvallis, Oregon 97331 USA

⁹University of California Sea Grant, 105 East Anapamu #5, Santa Barbara, California 93101 USA

¹⁰National Marine Fisheries Service, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, Washington 98112 USA

Abstract. Marine reserves are being established worldwide in response to a growing recognition of the conservation crisis that is building in the oceans. However, designation of reserves has been largely opportunistic, or protective measures have been implemented (often overlapping and sometimes in conflict) by different entities seeking to achieve different ends. This has created confusion among both users and enforcers, and the proliferation of different measures provides a false sense of protection where little is offered. This paper sets out a procedure grounded in current understanding of ecological processes, that allows the evaluation and selection of reserve sites in order to develop functional, interconnected networks of fully protected reserves that will fulfill multiple objectives. By fully protected we mean permanently closed to fishing and other resource extraction. We provide a framework that unifies the central aims of conservation and fishery management, while also meeting other human needs such as the provision of ecosystem services (e.g., maintenance of coastal water quality, shoreline protection, and recreational opportunities). In our scheme, candidate sites for reserves are evaluated against 12 criteria focused toward sustaining the biological integrity and productivity of marine systems at both local and regional scales. While a limited number of sites will be indispensable in a network, many will be of similar value as reserves, allowing the design of numerous alternative, biologically adequate networks. Devising multiple network designs will help ensure that ecological functionality is preserved throughout the socioeconomic evaluation process. Too often, socioeconomic criteria have dominated the process of reserve selection, potentially undermining their efficacy. We argue that application of biological criteria must precede and inform socioeconomic evaluation, since maintenance of ecosystem functioning is essential for meeting all of the goals for reserves. It is critical that stakeholders are fully involved throughout this process. Application of the proposed criteria will lead to networks whose multifunctionality will help unite the objectives of different management entities, so accelerating progress toward improved stewardship of the oceans.

Key words: biodiversity conservation; ecosystem functioning; ecosystem services; fisheries management; marine reserve selection; reserve evaluation criteria; reserve networks.

INTRODUCTION

There are now well over 1300 marine protected areas in the world, and hundreds, perhaps thousands, more are in the planning stages (Kelleher et al. 1995). Two core objectives have motivated the establishment of most marine reserves: conservation and sustainable

provision for human uses. Conservation goals include, among others, (1) biodiversity conservation, (2) conservation of rare and restricted-range species, (3) maintenance of genetic diversity, (4) maintenance and/or restoration of natural ecosystem functioning at local and regional scales, and (5) conservation of areas vital for vulnerable life stages. Goals for human uses include (1) managing fisheries (using reserves to sustain or enhance yields, restore or rebuild stocks of overexploited species, and provide insurance against management failure), (2) recreation, (3) education, (4) research, and (5) fulfilling aesthetic needs.

Manuscript received 4 February 2000; revised 7 January 2001; accepted 25 January 2001; feature accepted 21 February 2002. For reprints of this Special Issue, see footnote 1, p. S3.

¹¹ E-mail: cr10@york.ac.uk

The above categorization suggests a dichotomy between conservation goals and human needs whereas in fact there is a great deal of overlap. Fisheries will not be sustained unless the vulnerable life stages of exploited species are protected, nor will production be supported if essential natural ecosystem functioning is impaired. Furthermore, fishery managers may wish to protect genetic diversity of exploited populations to maintain resilience in the face of changing conditions. Consequently, since there is an overlap in objectives, it is likely that places that are good for conservation may also be good for fishery management and vice versa. Maintenance of ecosystem services to provide for human needs forms a separate objective for reserves, but will often overlap with conservation and fishery objectives. For example, protection of coastal wetlands to help filter and process nutrients from land runoff may also protect vulnerable life stages of fishery species and conserve biodiversity.

At a broader scale, conservation, sustainable use, and other interests also converge upon an overarching goal that is often overlooked in the pursuit of narrow, sectoral objectives: to maintain the ecological processes that underpin the functioning of marine ecosystems. Those processes are critical to the services that ecosystems supply to humanity, including fishery production. If we are to safeguard the delivery of goods and services to people over long time scales, then we need to look after those processes (Daily 1997).

Despite this great overlap of interests, protection of the sea has been dogged by the problem of fragmentation of responsibility among different management entities. This has led to a proliferation of protected areas, often overlapping and with many different objectives (McArdle 1997). In general, they provide partial and uncoordinated solutions to management problems, and under some circumstances may create problems rather than resolve them. What is needed is a framework that unites the common goals of fishery managers, conservationists, and other stakeholders. In this study, we provide guidance for the evaluation of candidate sites for reserves, based on what we know of how marine ecosystems work. Our aim is to improve the scientific basis for site selection. To do this, we develop a process to apply the ecological criteria for reserve selection set out in the companion paper by Roberts et al. (2003). Our evaluation framework is intended to be easy to apply wherever reserves are being considered. Above all, we aim to promote the design of reserve networks that simultaneously serve multiple goals. This represents a departure from most previous schemes which have had their focus on individual site selection (exceptions being Hockey and Branch 1997, and Day and Roff 2000). While our criteria are directed toward the evaluation of individual sites as reserves, our approach emphasizes their role in relation to other existing or planned reserves. At the broadest scale,

reserve networks must protect ecological processes essential for ecosystem functioning (described in more detail in Roberts et al. 2003), even in the face of changing conditions of both human and natural origin.

To meet both conservation goals and human needs, our best estimate is that networks of fully protected reserves (those closed to all fishing and any other form of consumptive removal of marine life) should cover 20% or more of all biogeographic regions and habitats (Plan Development Team 1990, Roberts and Hawkins 2000, National Research Council [NRC] 2000). A broad array of modeling and empirical studies have examined the question of reserve coverage from the perspectives of ethics, biodiversity representation, maintenance of genetic diversity, and benefits to fisheries management. Most show that benefits from reserves will be maximized when between approximately 20% and 50% of the habitat is protected (NRC 2000, Roberts and Hawkins 2000). Management of such reserves should focus on entire ecosystems (Ballantine 1991, Bohnsack 1992, Roberts 1997) and, in the process, provide protection for all species. Ideally, the planning and development of reserve networks should be embedded within an integrated coastal-zone management strategy (Kelleher and Kenchington 1992, NRC 2000). To provide an overall perspective, Fig. 1 summarizes the criteria, the sequence in which they are employed, and the ways in which they can be measured. Measurement is critical to the effective application of the criteria and in this paper we provide detailed guidance on how to quantify the value of candidate sites according to each criterion.

APPLICATION OF THE CRITERIA

To design functional marine-reserve networks that fulfill multiple goals, we must bring together the objectives of different stakeholder groups (and bring together those groups to discuss them!). In the past, fragmentation of management objectives among different interest groups has led to the establishment of reserves based upon too narrow a set of criteria. This has resulted in wasted effort, higher costs, and a false sense of protection. For example, fishery agencies have often created numerous single-species closures in an attempt to manage species one by one. However, the costs of implementing such closures, in terms of selection, demarcation, and enforcement, may be similar to the costs of establishing fully protected reserves that could achieve a far broader range of objectives, including the protection of commercially important species. In a comparison of 15 objectives for reserves, Hockey and Branch (1997) concluded that single-species reserves could meet only seven of them, whereas fully protected reserves could achieve all of them.

When fishery goals are viewed at a multispecies or ecosystem level, the approach to building reserve networks for fisheries management will be almost identical

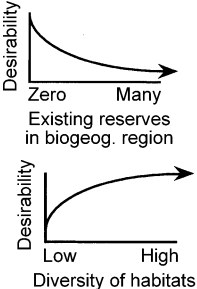
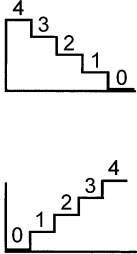
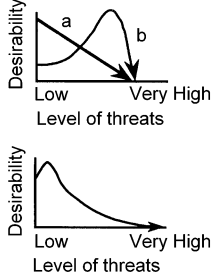
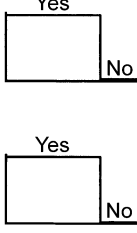
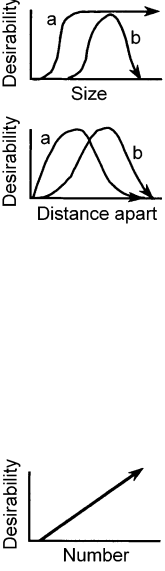

Criteria	Relationship	Possible ranking
<p>Prerequisite criteria</p> <p>1) Biogeography</p> <p>2) Habitats</p> <p>a) Diversity</p> <p>b) Diversity <i>not</i> protected elsewhere</p>		
<p>Excluding criteria</p> <p>3) Human threats</p> <p>a) Non-mitigatable</p> <p>b) Mitigatable</p> <p>4) Natural threats</p>		
<p>Modifying criteria</p> <p>5) Adequacy of size</p> <p>a) for conservation</p> <p>b) for fisheries</p> <p>6) Optimal distance apart</p> <p>a) for conservation</p> <p>b) for fisheries</p> <p>7) Vulnerable habitats</p> <p>8) Vulnerable life stages</p> <p>9) Species of special interest (rare, endemic, etc.)</p> <p>10) Inclusion of exploited species</p> <p>11) Linkages (dependencies) between systems</p> <p>12) Ecosystem services for human needs</p>		

FIG. 1. Summary of criteria used in the evaluation of potential marine reserves. The first two criteria are prerequisites that must be considered first; the second two may exclude an area from further consideration. The remainder modify the evaluation: their sequence does not imply any order of importance.

to that for conservation. While some agencies may not feel it important to consider such criteria as biogeography or habitat if their focus is on the management of particular species, we would argue that those criteria will always be important at larger scales. Almost every biogeographic region and almost every habitat supports some exploited species (M. Ruckelshaus and J. Dugan, *unpublished manuscript*). It is therefore important for fishery production that all habitats are encompassed to maintain that productivity. A focus on larger scale ecological processes should underpin fisheries management at every scale.

Clearly, while individual reserves can provide multiple benefits, not every reserve will serve all objectives equally well. Goals can be viewed at the level of individual reserves or at network level. Networks will include reserves that, through their placement, may perform different primary roles. However, overall goals for the network are achieved through the combined effects of those reserves. The development of multifunctional reserve networks can serve as a means of coordinating the activities of agencies that have different primary goals.

The establishment of marine reserves almost invariably attracts controversy, arising from the proposed restriction of existing activities (Bohnsack 1997). A major impediment to the acceptance of reserve proposals is that often only a single candidate site is under consideration. The process of reserve establishment would be made much easier if there were biologically suitable alternative candidate sites, identified by scientists together with other stakeholders, that could be fed into the socioeconomic stages of selection. Therefore a guiding principle in the development of reserve networks should be to seek multiple alternative network designs that will all perform satisfactorily on biological grounds. Choices can then be made among them according to socioeconomic concerns, without the sacrifice of ecological functionality. Even so, it is important to recognize that some sites may be so important (for instance because of the occurrence of particular rare species or community types) that they will be included in all possible network designs.

Use of the criteria

Fig. 1 lists the criteria developed in the companion paper (Roberts et al. 2003). These criteria are suitable for reserve selection regardless of how many protected areas already exist in a region. At one extreme, the criteria allow the design of networks from scratch. H. Halfpenny and C. M. Roberts (*unpublished manuscript*) describe their use to design a reserve network for north-western Europe, a region currently almost devoid of fully protected reserves. Such circumstances are rare, and the most common case will be where planners seek to add one or more reserves to an area where some are already present. Evaluating sites in these circumstances

requires their characteristics to be examined in relation to existing reserves, and the levels of protection afforded to them. Even if those reserves have been established in a completely ad hoc manner, and their protection status is uncoordinated, applying our criteria compels a shift in perspective to one where existing sites are seen as part of a network. Likewise, the emphasis moves from performance of isolated reserves to collective function.

Reserve establishment can also be approached at many scales including local, regional, and national levels. At the largest scale, planners seek to create networks of reserves that will be sustainable over the longest time scales. However, networks are often built at the national or subnational levels initially, and this scale may be smaller than the scale at which ecological processes operate. It is important for large-scale processes to be considered, whatever the scale of reserve selection. Box 1 summarizes the decision process for developing reserve networks. The criteria can also be applied to local scale problems such as the zoning of multiple-use marine management areas (e.g., Airamé et al. 2003), or defining the boundaries of a single proposed reserve. At these different scales, some criteria assume greater importance than others. For example, in zoning a small reserve, biogeographic representation is probably irrelevant because the entire area lies within a single region. In establishing the boundaries of a single reserve, connectivity with others may also have little influence on design, whereas maximizing the inclusion of viable habitats, and assuring linkages among them, may be of much greater concern.

Criteria and sequence of application

Under most circumstances, there is a logical sequence in which the criteria should be considered, and the first two criteria are of prime importance whether conservation, fisheries management, or other human benefits are the primary goals of the reserve network. They are “biogeographic representation” and “habitat representation and heterogeneity.” These criteria aim to capture the full spectrum of biodiversity in reserve networks. Next, candidate sites are screened according to human threats and the likelihood of natural catastrophes. Sites where risks are too great are rejected. Following this, the relative values of sites as reserves can be gauged with a series of modifying criteria. They can be applied in any sequence, and the order in which they are used depends largely on the objectives envisaged for reserves.

1) *Biogeographic representation*.—The objective in applying this criterion is to ensure representative coverage of all biogeographic regions in protected areas, including transition zones. This is fundamental for the protection of biodiversity. To apply this criterion, it is first necessary to determine what biogeographic regions exist within the overall target area. As a first

Box 1. Process for Developing Reserve Networks

- 1) Define the goals of the network.
- 2) Define area of interest.
- 3) Divide it into possible reserve units. These may be defined in many ways, for example through grids of uniform sized blocks (e.g., 10 km²), stretches of coastline, habitat classification schemes, or other means.
- 4) Select criteria for the evaluation of those units that are appropriate to the goals.
- 5) Decide how to quantify the information needed for determining the level achieved for each criterion.
- 6) Assemble information on those units (e.g., species or habitats present, levels of threat, etc.).
- 7) The evaluation process
 - a) Characterize or “score” sites based on the following characteristics:
 - i) Define biogeographic regions, scoring sites based on what region they occur in. At this stage, sites could be stratified according to region, with site selection decisions made separately for each region. The latter approach would be most useful where a large geographic area is being considered and there are many potential sites from which to choose.
 - ii) Define habitats within each biogeographic region for representation.
 - iii) Exclude sites subject to excessive levels of threat from human or natural sources.
 - iv) Include sites that are already reserves.
 - v) Score potential reserves on the basis of habitat heterogeneity and representation criteria, ensuring that reserve units will be sufficiently large to include viable populations.
 - vi) Rank or score sites within each habitat type according to other modifying criteria.
 - b) Set conservation targets for each of the above criteria (e.g., decide what proportion of the region and of each habitat to protect, what level of replication is required, levels of connectivity desired, etc.).
 - c) Select among sites for inclusion in the network (this can be done with an algorithm, by ranking or scoring, or by delphic methods). Criteria may be given different weightings at this stage in order to meet specific network objectives. Map the various possible biologically adequate reserve networks.
 - d) Ensure that the networks resulting from the above selection process are sufficiently connected.
- 8) Use information on alternative, biologically adequate reserve networks to inform final network selection according to socioeconomic criteria.

step, the distribution patterns of the fauna and flora should be analyzed to determine if there are distinctive biogeographic provinces within the region. Multivariate analyses of assemblage composition, such as the cluster analysis in Fig. 2, can help in evaluating how abrupt the boundaries are between regions or whether clear boundaries exist at all. The results provide a guide to the placement of reserves to achieve the objective of biogeographic representation. For example, Bustamante et al. (1999) defined different biogeographic regions of the Galapagos Islands based on composition of fish, invertebrate, and seaweed assemblages. They used this information to help select sites for fully protected zones within the Galapagos Marine Reserve. Day and Roff (2000) set out a detailed scheme for classifying marine habitats and biogeographic regions in Canada as a basis for designing a representative system of marine protected areas for the country.

Ballantine (1997) also emphasizes the need for replication of reserves within biogeographic regions. Iso-

lated reserves may provide little long-term protection for species or habitats (see *Application of the criteria: Criteria and sequence of application: 6) Connectivity* below for further discussion of this point). Replication also provides a safety factor, lessening the probability that catastrophic events might wipe out entire populations of protected species.

Some schemes for prioritizing conservation of biodiversity specifically seek to include sites with the greatest number of species. However, applied unthinkingly, this would lead to all of the highest value sites being clustered in the biogeographic region of greatest species richness, which would mean southeast Asian seas for most tropical taxa (Roberts et al. 2002). One way of achieving a more balanced biogeographic representation while also placing extra weight on the numbers of species present would be to use complementarity analysis (Williams et al. 1996, Csuti et al. 1997). This gives the greatest conservation weight to the site with the most species. The next highest weight goes to the site that contains the greatest number of species

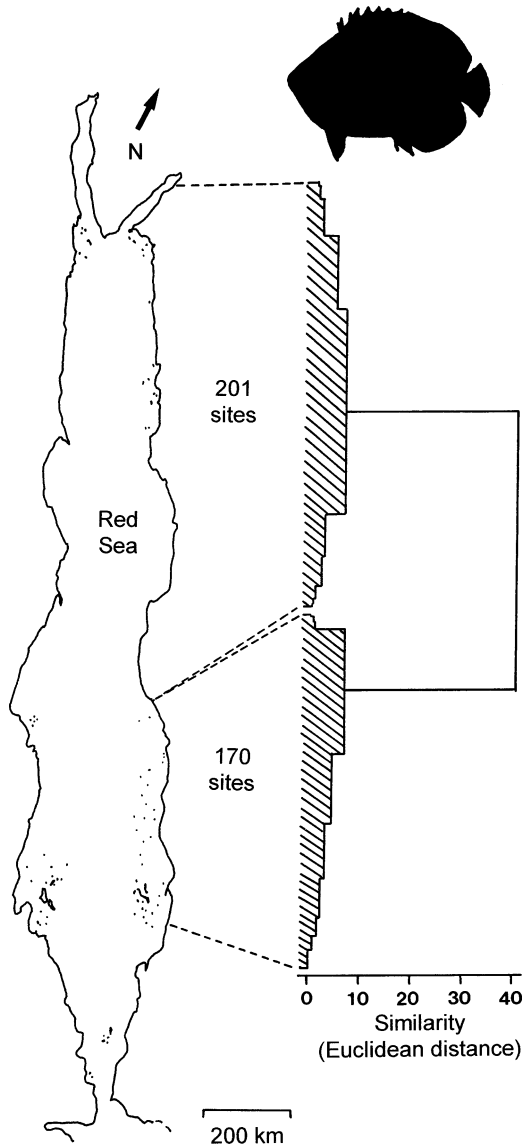


FIG. 2. Abrupt division of Red Sea coral reefs into two biogeographic regions based on a cluster analysis of the presence of butterfly-fish species on transects at 371 sites (Ward's method). The locations of only 9% of sites were misclassified as to their geographic origin by this analysis, indicating that the faunas of the different regions are highly distinctive. Reproduced from Roberts (1991) with permission.

not present in the first. The third site chosen would be the one that had the greatest number of species not represented in the first and second, and so on. In this way, a network of sites can be built that represents all of the species in a region. Csuti et al. (1997) also describe other possible approaches to prioritizing among sites using similar methods.

Conserving the functioning of an ecosystem, i.e., maintaining the ecological processes of that system, requires attention not only to species but also to func-

tional groups of species. In a species-poor ecosystem, each primary process (primary production, decomposition, nitrogen fixation, capture of water, habitat creation, recycling of nutrients, etc.) may be provided by many fewer species than in a species-rich ecosystem. Hence, from a functional standpoint, maintaining species-poor systems may be as important as the more traditional focus on species-rich systems. In a species-rich system, many species are likely to coexist with others that perform similar roles (Mooney et al. 1995, Roberts 1995). Therefore, removal of any particular species may not result in serious disruption of the process because other functionally similar species may be able to compensate for the lost species. However, species loss in a low-diversity system may lead to complete loss of a process. For example, the devastating El Niño of 1982–1983 destroyed >95% of corals throughout large areas of the eastern Pacific, a low diversity area where only 4–8 genera of corals were responsible for reef growth (Glynn 1997). Coral reefs in the eastern Pacific have declined further since this El Niño (Glynn 1990), whereas recovery may have been possible from a similar event in the western Pacific where >50 genera are reef builders (Veron 1993). (This question can now be tested empirically in diverse areas of the Indo-West Pacific where reefs were devastated by extensive El Niño related coral bleaching in 1998 [Goreau et al. 2000].)

The traditional emphasis on targeting highly diverse areas for protection is appropriate if the focus is on species. However, low-diversity areas must not be overlooked because they may be in greater need of protection to maintain ecosystem functioning. A focus on species richness alone ignores the vulnerability of low-diversity systems.

2) *Habitat representation and heterogeneity.*—This criterion seeks to achieve protection of the full range of habitats present in a biogeographic region. Habitats should first be defined (e.g., mangrove swamps, sandy beaches, coral reefs) and agreement reached on the overall list of habitats that occur in a region. Candidate sites can then be compared on this basis. Several general rules guide the selection of habitats. (1) All habitats must receive protection. (2) Each habitat should be protected in more than one area, as a guard against local catastrophes, to support exchange of propagules among sites, and to provide replicate sites for monitoring and research. (3) The total area set aside for the protection of each habitat should be approximately related to its relative prevalence in the region. If there is a global target to protect, say, 20% of the marine environment, then 20% of the area of each habitat should fall within reserves. For example, if a habitat covers 50% of a region, then one fifth of that 50% would be incorporated into reserves. (4) Special care should be taken to guarantee inclusion of rare habitats, and if there are any habitats of special concern (as

identified in criteria 5–12, below), they may need additional protection.

Habitat heterogeneity provides an important means of evaluating and comparing rival candidate sites. Ideally, all chosen reserves should contain a mix of habitats. The desirability of an area for conservation will increase in proportion to the diversity of viably sized habitats it encompasses (a viable habitat is one which supports populations capable of long-term persistence). Habitat heterogeneity in a given area can be quantified as the number of habitats present, divided by the possible total number within the biogeographic region. (It is important to compare habitat heterogeneity only for sites within biogeographic regions as there will be intrinsic differences among regions.) A second and complementary measure takes into account whether those habitats are already conserved elsewhere. This can be quantified as the number of habitats in the area that are not protected elsewhere (again expressed as a proportion of the total possible number of habitats). These quantitative measures can be used as such, or they can be converted into a score or rank for the area.

Habitats provide a proxy for species richness which enables decisions to be made regarding the value of sites as reservoirs of biodiversity in the absence of detailed data on the species present in each. However, where sufficient information is available, it may be possible to narrow the definition of habitats to those that demonstrably contain distinctive assemblages of species that will be lost if that habitat is not conserved. Two examples illustrate the point that this decision can be made objectively.

An analysis of open-coast sandy beaches shows that species richness tends to rise with exposure to wave action (McLachlan et al. 1993). It is not simple to measure exposure. Where wave action is strong, the slope of the shore tends to be shallow, dissipating the wave force, depositing fine sediments, and creating a wide surf zone and a broad, flat beach. Such dissipative beaches have a high species richness. Where incoming wave action is low, then steep, coarse-grained beaches are created and (paradoxically) the waves strike the beach face with considerable force. Such reflective beaches are species poor. (Under some conditions, very exposed beaches may be reflective, however, and some sheltered shores dissipative.) Dean's dimensionless parameter integrates these various aspects of the physical environment and provides an overall measure of the effects of wave action (McLachlan et al. 1993). It correlates directly with species richness on sandy beaches in South Africa (Fig. 3). More significantly, beaches at the dissipative end of the wave action spectrum (with high values of Dean's parameter) not only have a high species richness, but subsume the species that occur on more reflective beaches. From a conservation perspective, if

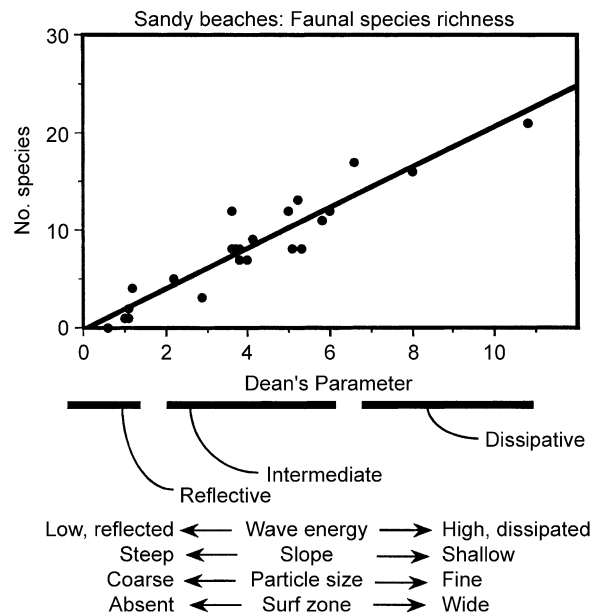


FIG. 3. Species richness on sandy beaches, in relation to exposure to wave action (quantified as Dean's Dimensionless Parameter). The data are from McLachlan et al. (1993).

dissipative beaches in South Africa are protected, they will automatically cover the species found on reflective beaches, although the same may not be true for beaches in other parts of the world (Dugan and Hubbard 1996, Dugan et al. 2000).

Rocky shores are a strong contrast. An analysis of species composition over 1000 km of the west coast of South Africa showed that three types of communities can be recognized, related to different levels of wave action. Communities are more similar if they share similar levels of wave action than if they come from adjacent localities with different wave action (Fig. 4; Emanuel et al. 1992, Dye et al. 1994). Omission of any one of these three communities from a system of reserves would leave unprotected a significantly "different" community.

Thus, there are objective ways of evaluating whether habitats are sufficiently different in their biological composition to justify separate recognition. However, we do not always have the luxury of dealing with detailed data that allow such sophisticated analyses. In such cases, the definition of habitats should not be postponed. Common-sense agreement on the range of available habitats is adequate to proceed with decisions. Refinements can follow as scientific investigations help fill gaps in our knowledge. As Roberts (1998a) has urged, it is a poor strategy to postpone the creation of reserves on the grounds that we are still ignorant of scientific subtleties.

The next two criteria (human threats and natural catastrophes) may eliminate some areas from further consideration. If either human or natural threats will

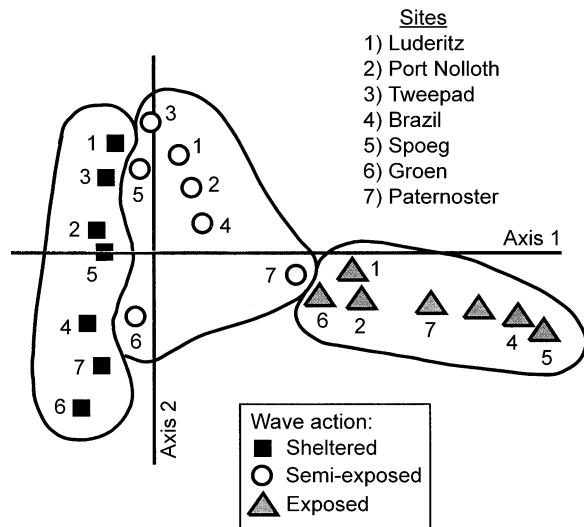


FIG. 4. Multidimensional scaling analysis of the similarities between transects sampled between low and high tide on seven shores between Lüderitz and Paternoster on the West coasts of South Africa and Namibia, covering a distance of 1400 km. The data for each site integrate eight 0.5-m² quadrats successively upshore, for each of three replicate transects. Sites clustered together on the basis of the degree of wave action experienced, rather than on their geographic distance apart, indicating that community composition differs distinctively with different amounts of wave action.

seriously compromise the value of an area as a reserve, that area should be eliminated from the array of candidate sites.

3) *Human threats*.—Ideally, marine reserves should not be placed where they will be subjected to damaging human impacts, for example in areas close to known sources of contaminants such as outfalls, dumps, or their plumes. A measure that incorporates distance from a source of impact and prevailing currents may help to estimate relative threats from point-source pollution. Nonpoint-source pollution is less easily quantified, but proximity to centers of urban, industrial, or agricultural development may serve as a starting point. However, this is not to say that reserves should never be placed in areas of high risk. Their presence might help mitigate threats, and such areas may be in greatest need of some of the ecological services they could perform, such as water filtration (Daily 1997).

Catastrophic human impacts are often accidents, such as shipwrecks and chemical and oil spills (e.g., Suchanek 1993). These occur on a variety of scales depending on the magnitude and duration of the event. Increased risks are associated with proximity to major ports, shipping lanes, oil pipelines, oil-production platforms and refineries, power-generating plants, and chemical production facilities. These are often non-mitigatable threats. An understanding of the spatial dynamics of such catastrophes will allow reserves to

be placed in relatively low risk areas. Replication of reserves should insure that some reserves in a network always remain unaffected (Allison et al. 2003).

In addition, establishing a marine reserve may increase recreational and educational use to the point of generating negative impacts on the protected resources. For example, reserves may incur trampling of vegetation and sessile animals, damage to the benthos from anchoring (Creed and Filho 1999), increased turbidity from swimmers and boats, and increased contact with and breakage of sensitive species, such as branching corals, by snorkellers and divers (Riegl and Riegl 1996, Hawkins et al. 1999). Reserves may also attract commercial and recreational fishers to their boundaries which may reduce populations of mobile species in small reserves. Poaching may also become a problem as stocks build up. Human threats that follow reserve designation should never be used as an excuse for not proclaiming protected areas. As most are relatively predictable, planners should address them in management plans and consider them in replication schemes.

Reserve sites must be evaluated as to the relative level of threats, both current and anticipated, and the potential for mitigation and/or recovery. In practice, this may often involve a qualitative rating as many areas will have multiple and often overlapping levels of human threats. Sites where the overall level of human threat is too great or for which there is almost no potential for recovery should generally be excluded from consideration. Where human threat levels are moderate, the relative recovery potential of sites and need for replication of site types should be considered. Sites for which overall human threat is low should be rated highly on that basis, especially if protection will reduce anticipated future threats. Protected areas whose presence will mitigate existing threats are of especially high value.

4) *Natural catastrophes*.—Areas that are focal points for episodic catastrophes, if they can be identified, should be avoided as sites for reserves since species will have to recolonize from elsewhere following disturbances. The more frequent and widespread the catastrophe, the less desirable a site will be (Allison et al. 2003). If natural catastrophes are present region-wide, there will be a need for a greater proportion of the area to be protected, and more replication of reserves. One important caveat in applying this criterion is that natural ecosystems may be resilient to catastrophes, such as hurricanes, and damage may be relatively minor. Catastrophes that cause mass mortalities of organisms over large areas, such as severe anoxic events, place the greatest restrictions on candidate reserve sites.

Next are a series of criteria that will modify the value of sites as reserves. Their sequence does not imply any order of priority, and their relative importance will de-

pend on the goals that have been defined for the reserve or network. They are:

5) *Size*.—Reserves must be large enough to be viable and fulfill the desired goals. There are no upper limits on size that are relevant to conservation goals, but to achieve an export of fishable stocks they should not be too large (National Research Council 2000). It is difficult to be precise about what constitutes “too large” because it depends on the species involved and local oceanographic conditions. In general, upper limits are more likely to be set by practical considerations, cost, or user conflict than by biological considerations. Most studies suggest that spillover of juvenile and adult fish from reserves will be localized (Russ and Alcala 1996, Roberts 1998b, Murawski et al. 2000). The probability of fish leaving a given reserve will decrease as the area of the reserve grows (Kramer and Chapman 1999, Chapman and Kramer 2000). Smaller reserves spread over a management area will thus be better than fewer, larger reserves, but only up to the point when reserves become too small to provide effective protection to species. The safest option will be to have a range of reserve sizes in the network, and it is rare that this is not a natural outcome of selecting and combining areas to cover all habitats representatively.

6) *Connectivity*.—Connectivity, defined here as the transfer of offspring between places, is critical to the function of reserves. Reserves in a network must be close enough to allow organisms to transfer among them. Our understanding of connectivity is rapidly growing but we are far from the stage where a simple and robust decision-making process can be defined for networking reserves. However, some rules of thumb might be applied to achieve sufficient connectivity among sites. Recent empirical (Shanks and Grantham 2003) and modeling work (Attwood and Bennett 1995; A. Hastings and L. Botsford, *unpublished manuscript*) suggests that reserve-design optima will differ for short-distance compared to long-distance dispersers. Larger reserves will maximize the probability of self-recruitment within reserves for short-distance dispersers while for long-distance dispersers, smaller reserves spaced at broader intervals may have greater connectivity. Attwood and Bennett (1995) demonstrated how reserve networks can be designed to benefit suites of species with different dispersal characteristics.

The likelihood of populations in different reserves interacting will grow as the distance between reserves falls. Thus, in spacing reserves, locations that lie midway between existing reserves might be favored because they reduce inter-reserve distance and provide a stepping stone for recruitment. Ballantine (1997) has shown how the mean distance between reserves rapidly falls as more reserves are added to a network. Dividing up the total area to be protected into smaller units rather than placing it all in one big unit will bring connectivity benefits (Roberts and Hawkins 2000). However, since

the probability of a reserve providing effective protection to an exploited species is likely to fall with the size of the reserve (Kramer and Chapman 1999, Walters 2000), it is important to be cautious in attempting to maximize connectivity by the establishment of many small reserves. The process of selecting reserve locations according to some of the other criteria outlined here, such as biogeographic and habitat representation, may in itself lead automatically to the development of a network of highly connected reserves (e.g., see Leslie et al. 2003).

The application of the connectivity criterion for fishery management might also be guided by rules of thumb. For example, in places where currents are strongly directional, reserves sited in upstream locations will be more likely to supply recruits to the rest of a management area than those in downstream locations (Roberts 1997). Where currents are complex or reversing, a more even spread of reserve locations would be better.

A final rule of thumb that can be applied is that connectivity is likely to be low across biogeographic boundaries. Locations within the same biogeographic region will be much more likely to interact than locations in adjacent regions. Thus sites within regions should be favored if the objective is to increase connectivity among reserves.

In sum, connectivity represents one of the great challenges to reserve science. Qualitatively, scientists know it is important but are not yet able to quantify it sufficiently to make precise recommendations about spacing and distances between reserves. “Safe” distances, those that provide sufficient connectivity to support populations in reserves, increase with reserve size and the size of reproductive stocks between reserves. Thus there is no absolute figure as to how close reserves should be. If fishing depletes populations between the reserves, or if the habitat there is unsuitable for some of the species, then the distance between reserves must be smaller. For this reason, any habitat that is widely separated from other areas with comparable habitat is unlikely to contain the full potential complement of species (M. N. Dethier and R. R. Strathmann, *unpublished manuscript*), and may be a poor candidate as a reserve. Areas extremely isolated from other parental stocks are also more dangerously prone to recruitment failure. Conversely, reserves should not be positioned too close to one another. This will reduce the chance that a local catastrophe will strike more than one of them. There are too many variables for precise limits to be set for what constitutes “too far” or “too close” and it will be safest to have a range of distances among reserves.

7) *Vulnerable habitats*.—The presence of intact habitats that can easily be damaged or changed by human activities increases priority of an area as a reserve. Vulnerable habitats often contain structures that are

biologically generated rather than the result of physical processes. Vulnerable marine habitats include, for example, coral reefs, deep-sea coral communities, oyster reefs, salt marshes, mangroves, and sea-grass beds. Typically, such habitats are easily disturbed or transformed by human action, but recovery is slow, if it occurs at all. Because of slow recovery there is a great premium to be placed upon protection before human disturbance or damage modifies vulnerable systems. For example, once the rich invertebrate communities have been scraped from the tops of deep-sea mounts by trawling, there is little hope of recovering them by subsequent protection, at least not on human timescales (Watling and Norse 1998). Pre-emptive protection is essential.

8) *Vulnerable life stages*.—The inclusion of localities where a species becomes especially vulnerable, or which are vital for completion of their life cycles, also adds value to a candidate site. A typical example might be the spawning ground of a commercially important species, or an area where it aggregates to breed and thus becomes vulnerable. If a site is clearly identified with the completion of a critical life stage, it must rank highly as a candidate for a reserve. However, we must be cautious in applying this criterion without a careful analysis of what stages are critical. This criterion is most easily applied at the level of individual species. However, if a habitat or site is critical for several key species, it will attract higher priority for a reserve. For example, H. Halfpenny and C. M. Roberts (*unpublished manuscript*) produced a contour map showing the number of commercially important species that use different regions of the seas of northwestern Europe as spawning or nursery grounds. This enabled prioritization of candidate reserve sites based on their multispecies value as critical habitats for vulnerable life stages.

9) *Species and populations of special interest*.—The presence of rare, endangered, relict, or restricted-range species, or populations with unique genetic composition, may heighten the need to protect an area. The relative value of different sites as reserves could be measured as the total number of species of special concern present. Alternatively, depending on the stated objectives for the reserve(s), presence of some species might be weighted more heavily than others.

10) *Exploitable species*.—Protection of populations of exploitable species is a prerequisite for reserves to provide any fishery benefit. The degree to which protection of an area will enhance stocks and aid with their management are measures of value particularly relevant to fishery management. The relative value of sites can be gauged in several ways: as the total number of exploited species present, their aggregate abundance or biomass, or by some weighting approach according to economic value of the species present (e.g., see H. Halfpenny and C. M. Roberts, *unpublished manu-*

script). All of these approaches measure the relative importance of candidate sites in restoring or sustaining stocks or aiding with their management. Often, the objective of a reserve is to help recover populations of severely overexploited species and so it is necessary to estimate the potential of each candidate site to support population recovery. This could be gauged by the past importance of a site as fishing grounds, based on historical records or interviews with people who have been fishing in the local area for a long time (e.g., Murray 1998).

11) *Ecosystem linkages*.—Maintenance of ecosystem functioning is a vital goal influencing the placement of reserves. Areas that support other habitats have a high value for meeting both conservation and fisheries objectives. Conversely, those dependent on other habitats are vulnerable unless adjacent support habitats are also protected (Polis et al. 1997, Anderson and Polis 1998). Important links among habitats must not be overlooked in assessment of candidate reserve sites. Here we define such linkages as the flow, or prevention of flow, of materials from one habitat to another that allows, modifies, or modulates the functioning of a given marine and coastal area. For example, protecting bird colonies without protecting their feeding grounds may be a waste of effort. Protecting rocky shores without protecting the adjacent kelp forests (that dampen wave action and contribute most of the carbon and nitrogen for benthic suspension feeders) may also fail to conserve the rocky-shore communities. To evaluate sites under this criterion we ask (1) is the area dependent on linkages from elsewhere and are those linkages secure, (2) to what extent does the area serve as a link to other areas, and (3) does the overall network of conserved areas incorporate links necessary for the survival of the ecosystems represented?

12) *Ecological services for humans*.—Services such as coastal protection or water purification, arising from the natural properties of ecosystems, add conservation value to areas (Daily 1997). Evaluation of reserve sites according to the ecosystem services they provide should be guided by the extent to which such services will depend on protection. If the service will be provided irrespective of protection then it should not influence site selection. Where protection will help guarantee a service or services, then the demand for them (both local and remote from the site if there are linkages) should be used to help prioritize sites. Ecological-economic valuation may be a useful tool in assigning relative values to different sites although the methods are still under development (Neher 1990).

Evaluating a candidate site for inclusion in a reserve network

There are four approaches to selecting and prioritizing candidate sites for inclusion in reserve networks: (1) ad hoc or opportunistic choice, (2) relative scoring

or ranking by expert or informed opinion, (3) mathematical site-selection algorithms, and (4) some combination of the above (H. Leslie, *unpublished manuscript*).

Ad hoc approaches refer to reserve selection driven by opportunity, rather than strategic goals and objectives. We believe that systematic selection of reserves increases the chances of creating effective networks, because these approaches are repeatable, transparent, and defensible. While chances to develop reserves will also arise opportunistically in a haphazard way, they can best be capitalized upon within a systematic, strategic approach to reserve selection, such as the two we sketch below. However, we should note that in the early stages of network building it may be best to take advantage of all opportunities for reserve establishment. Delaying implementation in order to undertake detailed evaluation risks missing the chance of setting up a reserve.

Scoring and ranking systems allocate a relative score or rank to each site in terms of predetermined criteria, and these values can be summed to compare sites for inclusion within the network (Fig. 1). Some criteria can be given greater weight if they can justifiably be considered more central to the fulfillment of articulated reserve network goals. Scoring approaches are straightforward, easily explained, and require little technical expertise to implement. But in past cases they have often mixed social and biological criteria, a tendency which could place undue weight on one or other aspect of reserve selection. For example, legislation in Britain will not permit the establishment of marine reserves if *any* parties object to them (Gibson and Warren 1995). Hence Britain's only two marine protected areas are remote islands and both allow fishing. Care should be taken to document the process by which criteria were evaluated and sites ranked, so that the relative weightings given to different criteria are apparent.

Siting algorithms provide a mathematical means of finding network solutions that achieve specified conservation objectives, e.g., protection of 20% of all habitat types within a region (Csuti et al. 1997). They can also provide some guidance to the importance of a particular site to the reserve network (its "irreplaceability"). The implicit goal of all algorithms is to minimize cost, often expressed as the area occupied by reserves or the cost of reserve implementation, while meeting the constraints imposed by the objectives. They require explicit, specific goals as a starting point and generate multiple biologically suitable networks of reserves. However, algorithms require a significant amount of technical expertise, as well as specific, quite extensive data sets. They are most effective when used in an indicative fashion, identifying possible sites which can then be further prioritized through expert workshops or by overlaying other relevant biological and social factors (e.g., Airamé et al. 2003). Reserve-

siting algorithms are currently being used to develop a more representative network of fully protected zones in the Great Barrier Reef Marine Park in Australia (Great Barrier Reef Marine Park Authority 1999).

Both scoring and algorithmic approaches have great advantages over ad hoc methods as they compel a systematic consideration of goals and criteria. Taken in combination, in what may be termed an integrative approach (H. Leslie, *unpublished manuscript*), they are even more powerful. However, no single approach will work all the time or in every place. Consequently, choice of approach will be dictated by information and resources available and the sociopolitical context, as well as temporal and spatial scales of the reserve-selection effort. What is clear, however, is that the development and careful application of biologically based criteria hold enormous promise. The approach we have outlined above demands that reserve planners rationally set out the reasons why decisions are made and why particular areas and networks are favored over others. It lays a firm foundation upon which other considerations can be built.

Applying the foregoing criteria will maximize the opportunities for creating effective reserve networks which can fulfill multiple goals. However, there may be circumstances under which organizations would wish to create reserves to achieve more narrow objectives. For example, fishery agencies could establish additional protected areas that would be targeted toward particular species or groups of species, in which case they might apply a more limited set of criteria (e.g., presence of the species, presence of vulnerable life stages for that species). Some fishery agencies may feel that certain criteria, for example biogeographic representation, are irrelevant to them. But fishing is widespread and everywhere depends on intact, functional ecosystems being maintained. Nevertheless, a core reserve network may not provide sufficient protection for highly migratory species and additional closures may need to be added for them. Similarly, sites close to cities might not rank highly enough to feature in a network due to the proximity of threats. However, they might be added according to more specific criteria such as providing valuable services to people (e.g., coastal protection or educational opportunities).

We have said little in this paper about the role of stakeholders in selecting reserves. By placing the emphasis on biology first, socioeconomics later, our scheme might appear to exclude stakeholders, or at least defer their involvement until later in the process. However, taking this approach would be disastrous. Numerous studies have convincingly demonstrated that efforts to create reserves without close stakeholder involvement will fail (Kelleher and Recchia 1998, National Research Council 2000). It is critical that stakeholders are involved from the very beginning, including during the evaluation of sites according to ecolog-

ical attributes. In fact, stakeholder participation in ecological evaluations should give them a much greater appreciation of the biological constraints underlying reserve performance. Armed with such knowledge and a set of agreed objectives, it should be easier to reach agreement on siting reserves.

CONCLUSIONS

In this paper we have described a process that aims to develop reserve networks that conserve biodiversity, support fishery production and management, and provide other ecological services of value to people. Our criteria are fully grounded in what we currently know about marine ecological processes and our approach is explicitly directed toward development of reserve networks that will simultaneously fulfill multiple goals. For example, this strategy allows the marrying of conservation and fishery objectives. By following clearly defined criteria, biologically defensible networks of reserves can be delineated. Nonetheless, for those wishing simply to compare alternative candidate reserves, or define the boundaries of a single reserve, the criteria remain equally valid.

A central objective for reserve networks is the maintenance of intact functional ecosystems at regional scales. There is still considerable uncertainty about how to safeguard critical ecological processes, and even what some of those processes are. However, we believe that piecemeal efforts to manage marine resources based on a profusion of reserves with narrow objectives and varying levels of protection will fail to account for essential processes. By contrast, representative, replicated, and fully protected reserves within well-connected networks are much more likely to lead to persistence and resilience of these processes in a changing world. Even so, it will be critical to monitor and assess the performance of reserve networks over time to verify the continued viability of key ecosystem processes.

Fully protected marine reserves have tremendous advantages over other tools for solving management problems in the marine environment. They can achieve so much more than many other piecemeal measures that proliferate, confuse users, and sometimes conflict. However, it must be remembered that reserves form one of a series of tools available to managers and will be most successful when embedded within integrated management structures, and employed in a complementary manner with the full gamut of tools available to fisheries and coastal-zone managers.

ACKNOWLEDGMENTS

This is contribution number 33 from the Working Group on the Science of Marine Reserves of the National Center for Ecological Analysis and Synthesis, a center funded by NSF (Grant No. DEB-94-21535), the University of California–Santa Barbara, the California Resources Agency, and the California Environmental Protection Agency. We are very grate-

ful to Julie Hawkins for her help with preparing the manuscript.

LITERATURE CITED

- Airamé, S., J. E. Dugan, K. D. Lafferty, H. M. Leslie, D. A. McArdle, and R. R. Warner. 2003. Applying ecological criteria to marine reserve design: a case study from the California Channel Islands. *Ecological Applications* **13**: S170–S184.
- Allison, G. W., S. D. Gaines, J. Lubchenco, and H. P. Possingham. 2003. Ensuring persistence of marine reserves: Catastrophes require adopting an insurance factor. *Ecological Applications* **13**:S8–S24.
- Anderson, W. B., and G. A. Polis. 1998. Marine subsidies of island communities in the Gulf of California: evidence from stable carbon and nitrogen isotopes. *Oikos* **81**:75–80.
- Attwood, C. G., and B. A. Bennett. 1995. Modeling the effect of marine reserves on the recreational shore-fishery of the south-western cape, South Africa. *South African Journal of Marine Science* **16**:227–240.
- Ballantine, W. J. 1991. Marine reserves for New Zealand. *Leigh Laboratory Bulletin* 25. University of Auckland, Auckland, New Zealand.
- Ballantine, W. J. 1997. Design principles for systems of 'no-take' marine reserves. Page 4 in T. J. Pitcher, editor. *The design and monitoring of marine reserves*. Volume 9, Number 1. Fisheries Centre, University of British Columbia, Vancouver, British Columbia, Canada.
- Bohnsack, J. A. 1992. Reef resource habitat protection: the forgotten factor. *Marine Recreational Fisheries* **14**:117–129.
- Bohnsack, J. A. 1997. Consensus development and the use of marine reserves in the Florida Keys, U.S.A. Pages 1927–1930 in H. Lessios and I. G. Macintyre, editors. *Proceedings of the Eighth International Coral Reef Symposium*. Volume 2. Smithsonian Tropical Research Institute, Balboa, Republic of Panama.
- Bustamante, R. H., P. Martinez, F. Rivera, R. Bensted-Smith, and L. Vinuesa. 1999. A proposal for the initial zoning scheme of the Galapagos Marine Reserve. Charles Darwin Research Station Technical Report. Charles Darwin Research Station, Galapagos, Ecuador.
- Chapman, M. R., and D. L. Kramer. 2000. Movements of fishes within and among fringing coral reefs in Barbados. *Environmental Biology of Fishes* **57**:11–24.
- Creed, J. C., and G. M. A. Filho. 1999. Disturbance and recovery of the macroflora of a seagrass (*Halodule wrightii* Ascherson) meadow in the Abrolhos Marine National Park, Brazil: an experimental evaluation of anchor damage. *Journal of Experimental Marine Biology and Ecology* **235**:285–306.
- Csuti, B., S. Polasky, P. H. Williams, R. L. Pressey, J. D. Camm, M. Kershaw, A. R. Keister, B. Downs, R. Hamilton, M. Huso, and K. Sahr. 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biological Conservation* **80**:83–97.
- Daily, G. C. 1997. *Nature's services, societal dependence on natural ecosystems*. Island, Washington, D.C., USA.
- Day, J. C., and J. C. Roff. 2000. Planning for representative marine protected areas: a framework for Canada's oceans. World Wildlife Fund, Toronto, Ontario, Canada.
- Dugan, J. E., and D. M. Hubbard. 1996. Local variation in populations of the sand crab, *Emerita analoga*, on sandy beaches in southern California. *Revista Chilena de Historia Natural* **69**:579–588.
- Dugan, J. E., D. M. Hubbard, J. M. Engle, D. L. Martin, D. M. Richards, G. E. Davis, K. D. Lafferty, and R. F. Ambrose. 2000. Macrofauna communities of exposed sandy beaches on the southern California mainland and Channel

- Islands. Pages 339–346 in D. Browne, editor. Proceedings of the Fifth California Islands Symposium. U.S. Department of the Interior, Minerals Management Service, Camarillo, California, USA.
- Dye, A. H., G. M. Branch, J. C. Castilla, and B. A. Bennett. 1994. Biological options for the management of the exploitation of intertidal and subtidal resources. Pages 131–154 in R. W. Siegfried, editor. Rocky shores. exploitation in Chile and South Africa. Springer-Verlag, London, UK.
- Emanuel, B. P., R. H. Bustamante, G. M. Branch, S. Eekhout, and F. J. Odendaal. 1992. A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. *South African Journal of Marine Science* **12**:341–354.
- Gibson, J., and L. Warren. 1995. Legislative requirements. Pages 32–60 in S. Gubbay, editor. *Marine protected areas: principles and techniques for management*. Chapman and Hall, London, UK.
- Glynn, P. W. 1997. Eastern Pacific reef coral biogeography and faunal flux: Durham's dilemma revisited. Pages 371–378 in H. Lessios and I. G. Macintyre, editors. Proceedings of the Eighth International Coral Reef Symposium. Volume 1. Smithsonian Tropical Research Institute, Balboa, Republic of Panama.
- Glynn, P. W. 1990. Coral mortality and disturbance to coral reefs in the tropical eastern Pacific. Pages 55–126 in P. W. Glynn, editor. *Global ecological consequences of the 1982–1983 El Niño–Southern Oscillation*. Elsevier, Amsterdam, The Netherlands.
- Goreau, T., T. McClanahan, R. Hayes, and A. Strong. 2000. Conservation of coral reefs after the 1998 global bleaching event. *Conservation Biology* **14**:5–15.
- Great Barrier Reef Marine Park Authority (GBRMPA). 1999. An overview of the Great Barrier Reef Marine Park Authority Representative Areas Program. Great Barrier Reef Marine Park Authority, Townsville, Queensland, Australia.
- Hawkins, J. P., C. M. Roberts, T. van't Hof, K. de Meyer, J. Tratalos, and C. Adams. 1999. Effects of recreational scuba diving on Caribbean coral and fish communities. *Conservation Biology* **13**:888–897.
- Hockey, P. A. R., and G. M. Branch. 1997. Criteria, objectives and methodology for evaluating marine protected areas in South Africa. *South African Journal of Marine Science* **18**: 369–383.
- Kelleher, G., C. Bleakley, and S. Wells, editors. 1995. A global representative system of marine protected areas. Volume 1. Great Barrier Reef Marine Authority, World Bank, and World Conservation Union (IUCN). Environment Department, World Bank, Washington, D.C., USA.
- Kelleher, G., and R. Kenchington. 1992. Guidelines for establishing marine protected areas: a marine conservation and development report. World Conservation Union (IUCN), Gland, Switzerland.
- Kelleher, G., and C. Recchia. 1998. Editorial—lessons from marine protected areas around the world. *Parks* **8**(2):1–4.
- Kramer, D. L., and M. R. Chapman. 1999. Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes* **55**:65–79.
- Leslie, H., M. Ruckelshaus, I. R. Ball, S. Andelman, and H. P. Possingham. 2003. Using siting algorithms in the design of marine-reserve networks. *Ecological Applications* **13**: S185–S198.
- McArdle, D. A., editor. 1997. *California marine protected areas*. University of California–San Diego, La Jolla, California, USA.
- McLachlan, A., E. Jaramillo, T. E. Donn, and F. Wessels. 1993. Sandy beach macrofauna communities and their control by the physical environment: a geographic comparison. *Journal of Coastal Research* **15**:27–38.
- Mooney, H. A., J. Lubchenco, R. Dirzo, and O. E. Sala. 1995. Biodiversity and ecosystem functioning: ecosystem analyses. Pages 327–452 in V. H. Heywood, editor. *Global biodiversity assessment*. Cambridge University Press, Cambridge, UK.
- Murawski, S. A., R. Brown, H.-L. Lai, P. J. Rago, and L. Hendrickson. 2000. Large-scale closed areas as a fishery management tool in temperate marine ecosystems: the Georges Bank experience. *Bulletin of Marine Science* **66**: 775–798.
- Murray, M. R. 1998. The status of marine protected areas in Puget Sound. Puget Sound/Georgia Basin Environmental Report Series **8**:103–104.
- National Research Council (NRC). 2000. *Marine protected areas: tools for sustaining ocean ecosystems*. National Academy Press, Washington, D.C., USA.
- Neher, P. A. 1990. *Natural resource economics—conservation and exploitation*. Cambridge University Press, Cambridge, UK.
- Plan Development Team (PDT). 1990. The potential of marine fishery reserves for reef management in the U.S. South Atlantic. National Oceanic and Atmospheric Administration Technical Memorandum NMFS-261. Contribution CRD/89-90/04.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* **28**:289–316.
- Riegl, B., and A. Riegl. 1996. Studies on coral community structure and damage as a basis for zoning marine reserves. *Biological Conservation* **77**:269–277.
- Roberts, C. M. 1991. Larval mortality and the composition of coral reef fish communities. *Trends in Ecology and Evolution* **6**:83–87.
- Roberts, C. M. 1995. Effects of fishing on the ecosystem structure of coral reefs. *Conservation Biology* **9**:988–995.
- Roberts, C. M. 1997. Connectivity and management of Caribbean coral reefs. *Science* **278**:1454–1457.
- Roberts, C. M. 1998a. Sources, sinks, and the design of marine reserve networks. *Fisheries* **23**:16–19.
- Roberts, C. M. 1998b. No-take marine reserves: unlocking the potential for fisheries. Pages 127–132 in R. C. Earll, editor. *Marine environmental management: review of events in 1997 and future trends*. Candle Cottage, Kempsey, Gloucester, UK.
- Roberts, C. M., et al. 2003. Ecological criteria for evaluating candidate sites for marine reserves. *Ecological Applications* **13**:S199–S214.
- Roberts, C. M., and J. P. Hawkins. 2000. Fully-protected marine reserves: a guide. World Wildlife Fund–US, Washington, D.C., and University of York, York, UK.
- Roberts, C. M., D. J. McClean, J. E. N. Veron, J. P. Hawkins, G. R. Allen, D. E. McAllister, C. G. Mittermeier, F. W. Schueler, M. Spalding, F. Wells, C. Vynne, and T. B. Warner. 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* **295**:1280–1284.
- Russ, G. R., and A. C. Alcala. 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series* **132**:1–9.
- Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagate dispersal distance and the size and spacing of marine reserves. *Ecological Applications* **13**:S159–S169.
- Suchanek, T. H. 1993. Oil impacts on marine invertebrate populations and communities. *American Zoologist* **33**:510–523.
- Veron, J. E. N. 1993. *A biogeographic database of hermatypic corals of the Indo-Pacific*. Australian Institute of Marine Science, Townsville, Queensland, Australia.
- Walters, C. 2000. Impacts of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine

- protected areas: how large should protected areas be? *Bulletin of Marine Science* **66**:745–758.
- Watling, L., and E. A. Norse. 1998. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearing. *Conservation Biology* **12**:1180–1197.
- Williams, P., D. Gibbons, C. Margules, A. Rebelo, C. Humphries, and R. Pressey. 1996. A comparison of richness hotspots, rarity hotspots and complementary areas for conserving diversity using British birds. *Conservation Biology* **10**:155–174.