

Marine Protected Areas: Evaluating MPA effectiveness in an uncertain world

Craig Syms and Mark H. Carr

Department of Ecology and Evolutionary Biology, University of California, Santa Cruz

Email: syms@biology.ucsc.edu

1. Introduction

Marine Protected Areas (MPA's) are receiving increased attention as a tool to manage, conserve, and augment marine resources (Dugan and Davis 1993, Agardy 1994, Creese and Cole 1995, Allison et al. 1998, Lauck et al. 1998, Murray et al. 1999). This increased attention has resulted in greater scrutiny of the status of protection afforded by existing MPA's along the west coast of North America (e.g., McArdle 1997, Freitas et al. 1998, Murray 1998a,b, Tuya et al. 2000, Jamieson and Levings 2001). In the recent climate of accountability and performance-oriented conservation goals, resource management agencies are increasingly compelled to provide clear statements of the outcome they expect to achieve by creating MPA's, and about how they will demonstrate their effectiveness over time. In some recent examples, MPA's have been created with "sunset clauses" that require demonstrable conservation results after a fixed – and often short – time in operation. Clearly, the design of realistic and achievable conservation targets, and the measurement of their effectiveness, will be crucial to the successful establishment of new MPA sites and to their long-term success through adaptive management (Carr and Raimondi 1999).

This challenge is made all the more complex by different types of uncertainty in the ways in which ecosystems function and the manifestations of those processes in the natural resources protected by an MPA. Setting conservation targets is a form of prediction in which a result is hypothesized to occur as a consequence of a management decision. Uncertainty weakens the precision with which predictions of both the magnitude and the time frame of the outcome can be made. Natural sources of uncertainty that routinely affect fundamental aspects of the structure and function of Pacific coast ecosystems (e.g., ENSO events, recruitment variability), may interact with anthropogenically-induced changes such as climate shifts, exotic species invasions, disease outbreaks and catastrophes (Table 1) to make setting and evaluating targets difficult. This

paper is intended to provide a source of discussion for a workshop sponsored by the North American Commission for Environmental Cooperation, to be held on 1-3 May 2001 in Monterey, California. The workshop will focus on setting realistic and achievable conservation targets for Pacific MPA's, and on developing practical and rigorous means of measuring their effectiveness in meeting their objectives.

We will first contrast the effects that MPA's have on the organisms they protect, versus their effectiveness in achieving their stated goals. We then consider the concept of conservation targets and limits, and emphasize the need to explicitly quantify the objectives of a MPA and develop predicted measures of effects that can be used to evaluate effectiveness. We then identify several examples of measures that might be used to evaluate effectiveness of MPA's in fulfilling three classes of objectives: fisheries, biodiversity, and migratory species conservation. Finally, we explore in more detail the role uncertainty plays in developing effectiveness monitoring programs, and how conclusions drawn from effectiveness assessment are subject to uncertainty at many levels.

Table 1. Examples of process uncertainties operating on the Pacific coast

Uncertainty source	Characteristics	Impacts on setting targets
Climate change (e.g., global warming)	Average climate conditions or cycles may change. Variability and intensity of stochastic events such as storms might increase. Community structure might change in response.	Might generate non-independence of MPA and control area. Temporal and spatial projection of monitoring might become restricted.
Species invasions (e.g., <i>Batillaria attramentaria</i> , <i>Carcinus maenas</i> , <i>Hymeniacidon sinapium</i>)	Interaction strengths between organisms may change. Some species might be displaced. Physical habitat structure may be altered.	'Baseline' communities will undergo directional change, making projection of monitoring difficult. Community structure following invasion will be difficult to predict.
Disease outbreaks (e.g., withering foot syndrome in black abalone)	Onset of disease is not predictable, but effects may be.	Alters mortality schedule of target population.
Trophic cascades (e.g., re-introduction of sea otters)	Generates relatively predictable community changes	Might alter baseline community and interaction strengths.
Anthropogenic catastrophes (e.g., oil spills)	Occurrence of particular events are not predictable, but likelihood of catastrophes can be calculated	Resets community structure at different spatial scales

MPA effects vs effectiveness

There is a growing body of research that demonstrates that MPA's have an effect on resident assemblages of organisms (e.g., Edgar and Barrett 1997, 1999, Babcock et al. 1999, Garcia Charton et al. 2000, Planes et al. 2000, Jamieson and Levings 2001). However fewer authors have ventured appraisals of how these effects enable MPA's to achieve their intended objectives (but see Rowley 1994, Freitas et al. 1998). There is increasing pressure for evaluation of MPA's with respect to their intended objectives (Carr and Raimondi 1999, Murray et al. 1999). This has implications for the setting of targets – the emphasis changes from simply detecting effects, to parameterizing the magnitude of effects, evaluating them with respect to stated objectives, and providing a statement of confidence in these results. The first stage in this process is recognizing different MPA objectives, and then identifying targets (and inherent limits) by which a MPA might be deemed 'effective'. This information will ultimately inform management actions taken by MPA agencies through an adaptive management approach.

Effectiveness targets and limits

Effectiveness can only be evaluated with respect to a stated objective and target. The objective of a MPA (e.g., fisheries conservation) is usually set by a combination of governmental agencies, stakeholders, and other interested parties. The target for a given objective should be set on the basis of scientific advice. The challenge, therefore, is to develop a set of realistic targets against which MPA effectiveness can be gauged.

The first requirement is to develop a parameter or set of parameters that represent criteria by which to measure effectiveness (Fig. 1). In practice, *effectiveness parameters* will usually be a comparative variable that compares MPA to control areas (see 'causal uncertainty' below). For example, effectiveness parameters might be species richness or spawning biomass of a target species. The second step is to define a '*target*' level of the effectiveness parameter. The difference between the parameter value of the MPA and the target represents the 'performance' of the MPA. For example, a target level might be a 25% increase in species richness or spawning biomass of a target species within a MPA relative to unprotected areas outside the MPA. This target may be 'vague' or 'fuzzy', because of uncertainty in knowing whether the effectiveness target will be sufficient to achieve the objective. For example, the 25% increase in species richness or spawning biomass may or may not suffice to sustain the structure and function of the protected community or viability of the protected population, respectively. A 'fuzzy' target may

also offset uncertainty in measurement of the effectiveness parameter (see ‘Planning for uncertainty’ below). Thus, in addition to the ‘target’, it is also necessary to define limits within which we consider the target to have been achieved with a stated level of confidence.

The effectiveness target will also have a *temporal* component. Biological processes often occur with temporal lags, and these intervals must be defined. In addition, there is likely to be pressure from MPA opponents to set an upper temporal limit beyond which a MPA should be deemed non-effective and MPA status revoked. There is a need to define both upper and lower limits on time to minimize risk of otherwise effective MPA’s being deemed non-effective because insufficient time has elapsed for the effectiveness parameter to respond, and minimize the cost of recommending maintenance of non-effective MPA’s.

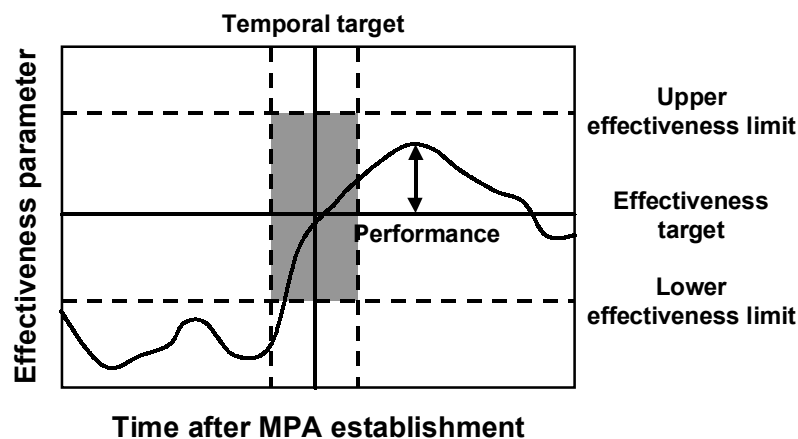


Figure 1. Effectiveness of a MPA is evaluated by the trajectory of the effectiveness parameter (e.g., species richness or spawning biomass) of a MPA over time. Targets and limits occur with respect to the parameter (e.g., 25% increase in richness or biomass), and the time within which the target should be achieved.

2. Conservation targets and effectiveness measures

In this section we consider examples of effectiveness measures that might be used to evaluate MPAs designed for three distinct purposes: conservation of all fisheries conservation; biodiversity; and conservation of migratory or pelagic species. A single MPA or MPA network may be established with the intent of achieving more than one of these objectives, so this classification is not mutually exclusive but simply a device to focus on different sets of effectiveness parameters.

Fisheries objectives

Marine protected areas have been suggested both as alternate and auxiliary means of conserving, maintaining or augmenting fisheries (Beverton and Holt 1957, Roberts and Polunin 1991, 1993, Bohnsack 1993, 1998, 2000, Guénette et al. 1998, Sladek Nowlis and Roberts 1998, Murray et al. 1999). It has been hypothesized that fisheries MPA's fulfill this broad objective in two ways.

1. *Fisheries conservation.*

Spatial refuges from fishing may be intended to conserve or safeguard a fishery against over-exploitation. Essentially, the subset of a fishery stock contained within a MPA acts as an "insurance policy" against overfishing an entire stock (Botsford et al. 1997). Modeling approaches have suggested that MPA's may increase resilience to overfishing (e.g., Quinn et al. 1993, Man et al. 1995, Lauck et al. 1998, Sladek Nowlis and Roberts 1997, 1999). However, in order for a MPA to fulfil this objective, it is necessary that the protected sub-population be capable of restocking a fishery should a catastrophic collapse of the fishery occur (Carr and Reed 1993, Tegner 1993). There are additional benefits. MPA's also reduce the spatial extent of fishing practices that damage critical habitat (e.g., Hall 1998).

2. *Fisheries augmentation and management.*

For many reasons, it can be difficult to convince fishing industries that "insurance policies" are necessary. Consequently, a frequently stated alternative objective of fisheries MPA's is to contribute to and augment the fishery. There are two mechanisms by which this is hypothesized to occur. First, movement of individuals outside MPA's might result in catch by local fishermen, but the evidence for the extent to which spillover contributes to the fishery is equivocal

(Polacheck 1990, Russ and Alcala 1996a,b, Zeller and Russ 1998, Kramer and Chapman 1999, Cole et al. 2000). Second, it has been hypothesized that MPA's can augment fisheries by exporting larvae to the fishery. Although this mechanism is likely to operate, the process has been difficult to demonstrate empirically (Carr and Reed 1993, Quinn et al. 1993, Man et al. 1995, Sladek Nowlis and Roberts 1997, 1999, Mangel 1998, 2000a, Hastings and Botsford 1999).

Uncertainties

Fisheries parameters are difficult to estimate accurately and precisely, yet accuracy is essential for the validity of model development. Environmental variability might decouple key relationships (e.g., stock-recruitment). There is uncertainty in defining the stock, and measuring the degree of linkage between sub-populations at different sites. The required targets for percentage of stock protected are themselves subject to uncertainty. How well, for example, would 35% stock protection safeguard against a fisheries collapse? If MPA's have local effects on species size-structure, will this introduce other processes or non-linearities into the system? For example, the strength of demographic processes may change with local changes in density. Increase in density may result in increased competition, predation rates, and movement rates (e.g., Chapman and Kramer 1999, St. Mary et al. 2000). The population size and sex structure of many fish species might also change. Many marine fishes are hermaphroditic with social inhibition of growth and sex change. These indirect responses of populations to changes in density will alter the effectiveness of a MPA.

Effectiveness parameters and targets

A MPA's ability to fulfill fisheries objectives centers on its ability to replenish both itself and non-protected areas (Table 2). These properties may act in opposition to each other. A MPA that is entirely self-replenishing will not be able to repopulate an exhausted stock, whereas a MPA that exports its entire larval production will not provide a secure insurance because it too will be affected by recruitment overfishing (Lundberg and Jonzén 1999). These factors may be altered if MPA's are organized as a network. The differences between demographic parameters inside and outside MPA's provide the means to gauge fisheries MPA effectiveness.

An important initial step is to measure how much of the stock is contained within and outside the MPA, and assess this relative to a target level. Measurement of a stock is not easy,

and deciding on a target level is not a trivial matter (Carr and Reed 1993, Mangel 1998, 2000a, Hastings and Botsford 1999, Sladek Nowlis and Roberts 1999). In addition, it is necessary to measure demographic rates (mortality schedules in particular), within and outside MPA's and ascertain the target levels of fishing mortality that can be compensated for by protected areas. It is also necessary to have an accurate and precise estimate of fishing mortality, because the benefits of a MPA are conditional on the level of fishing pressure. In general, an accurate estimate of the stock-recruitment relationship is notoriously difficult to estimate precisely. However, for fisheries applications, the projected yield per recruit will suffice, and is generally easier to measure (Beverton and Holt 1957). For this purpose, estimates of larval production contributed from protected and non-protected populations are necessary.

Optimizing export of fish from MPA's both as adults and larvae is one of the most critical targets to address. Excessive adult export will reduce the effect of protection, but might increase local fisheries catch (Alcala and Russ 1990, Russ and Alcala 1996a,b, Kramer and Chapman 1999, Cole et al. 2000). Larval dispersal presents one of the greatest challenges to setting targets. Dispersal ranges and degrees of retention versus advection from the source are not well known, despite modeling efforts. It is clear that effectiveness is conditional on the retention/advection ratio, but measuring the contribution of MPA's to a fishery is not an impossible task (Botsford et al. 1993, Tegner 1993).

Table 2. Effectiveness parameters and sources of uncertainty in fisheries objectives

Effectiveness parameter	Predicted change with protection	Uncertainties
Abundance (targeted and bycatch species)	Increased abundance of MPA population relative to unprotected populations	Recruitment success is variable, density-dependent mortality may regulate abundance changes
Size structure (targeted and bycatch species)	Increase in proportion of larger individuals in MPA population relative to unprotected populations	Social inhibition of growth, time lags in growth, large individuals might be rare and difficult to precisely count
Larval production (targeted and bycatch species)	Increase in larval production in protected areas relative to unprotected populations	Dispersal distance and dynamics unknown, source of recruits to MPA and control areas unknown
MPA population stability (targeted and bycatch species)	Decreased temporal variability of large, mature individuals and larval production relative to unprotected populations	Degree to which sub-population within MPA can be replenished by local production unknown
Stock stability (increased buffering of environmental fluctuations by storage effect)	Decreased temporal variability of recruitment to exploited populations and fishery	Degree to which sub-population within MPA replenishes exploited population unknown
Habitat	Persistence of or recovery to a natural state.	Natural perturbations, temporal lags in recovery
Fishery yield (increased benefit to fishery by increased and less variable larval production, and spillover effects)	Dampen temporal variability of yield, increased yield, increase catch and average size of individuals closer to MPA by spillover	Depends upon stability of MPA population, extent to which MPA population replenishes exploited population, and rate of exploitation (degree of growth and recruitment overfishing). Spillover difficult to measure
Genetic diversity	Maintain or increase genetic diversity of MPA populations and stock	Depends on relative contribution of MPA and exploited populations to recruitment of each

Biodiversity objectives

In contrast with fisheries, biodiversity objectives are more diffusively defined and thus present a greater problem in assigning objectives and targets. Biodiversity objectives can be defined at a range of organizational levels from species (including genetic diversity), through community to landscape levels (Franklin 1993), and hence may be scale-dependent. However, the underlying objective is to conserve the ecological and evolutionary processes that generate and maintain diversity. This broad objective is frequently re-specified as a focused set of specific objectives that are assumed to act as proxies for these processes – focal species objectives, and community/landscape objectives.

1. Focal species objectives.

It is often prohibitive to measure every single species in a community. Consequently, the objectives of a biodiversity MPA may be defined as its ability to maintain populations of focal species that may either serve as a proxy for measuring whole-community properties, or are themselves the primary targets for protection (for example, threatened or endangered species (e.g., Carlton 1991, Glynn and de Weerd 1991), and keystone species). At least four types of focal species can be recognized (terminology from Zacharias and Roff 2001), but individual taxa may fall into one or many of these types.

a) *Indicator species* are species that act as a proxy for a particular community, habitat, or ecosystem. Two subgroups of this class can be recognized. *Composition indicators* are species that are so closely correlated with the suite of other characteristic species, that the presence of one provides information on the general community composition (e.g., stands of giant kelp). These species are not necessarily ‘important’ to community structure, or necessarily susceptible to anthropogenic effects but they are generally easy to measure. *Condition indicators* are species that are likely to respond quickly and reliably to impacts (e.g., pollution) and hence provide direct measures of change in response to putative impacts (Jones and Kaly 1996). In contrast with composition indicators, the abundance of these species must have at least a hypothesized causal relationship with the source of impact. In MPA evaluation, for example, fish species targeted by fishers would be appropriate condition indicators.

b) *Keystone species* are species that exert a disproportionate effect on a community relative to their abundance or biomass. In general keystones have the ability to strongly modify the

structure or composition of a community. Keystones may occupy a range of trophic levels including predators, mutualists, habitat modifiers, prey, and diseases (Zacharias and Roff 2001). Keystones may be important in MPA monitoring. For example, the introduction of either native or exotic invasive keystones might generate a range of trophic cascades that would necessitate modification of conservation targets. On the Pacific west coast, sea otters occupy a keystone role by preying on grazers.

c) *Umbrella species* are species that the protection of which will result in the protection of a suite of other species (Roff and Taylor 2000). The mechanisms by which these operate may vary. The classic single-species umbrellas are usually large vertebrates that occupy large territories (Noss et al. 1996). For example, sea otters could be considered as umbrella and keystone species.

d) *Flagship (charismatic) species* are species that are the target of conservation in their own right, but the protection of which will not necessarily result in the protection of other species or habitats (e.g., baleen whales). However, many marine flagships (for example, elephant seals) have particular associations with habitats that make them amenable to conservation by MPA's (see migratory species below).

2. *Community-landscape objectives.*

An alternative MPA biodiversity objective may be to conserve community or landscape properties. In contrast with the species-level approach, the interactions between the community or landscape components (i.e. trophic levels, habitat patches) are of central importance. At the community level, this implies that stability of the trophic organization of the system, but not necessarily the component species populations (Pimm 1984), is the objective to be attained. However, it has also been suggested that local stability may be regulated by the diversity of a community (e.g., King and Pimm 1983, Pimm 1984, Tilman and Downing 1994, Tilman et al. 1997, Hixon and Carr 1997). At a landscape level, the key objective is to preserve stability of the landscape, but not necessarily the individual habitats (Forman 1995). As with community objectives, the focal objective is maintaining connectivity between habitat patches and their constituent populations (Hanski 1999), and indeed both community and landscape approaches share many common objectives (Polis et al. 1997).

Uncertainties

There are several key assumptions required in setting biodiversity targets. The scale at which biodiversity is defined and measured must form a key component of any target. There is an implicit assumption about the directionality and benefits of changes in biodiversity parameters. Increased diversity in species composition is implicitly assumed to be a positive benefit. Indicators are assumed to be truly reflective of the biodiversity property that the MPA is intended to preserve. The central uncertainty in developing conservation targets for biodiversity MPA's are that the habitats and biota within these habitats and incorporated within MPA's are, in fact, representative (Flather et al. 1997, Ward et al. 1999). Defining targets may be difficult. Ecosystem-level alterations might generate non-linearities due to changes in trophic structure (e.g., Menge et al. 1994, Dayton et al. 1995, Moreno 2001).

Effectiveness parameters and targets

Population viability will be an important parameter if the objective of the MPA is for conservation of a focal species. A viable population may in itself be the target if the focal species is threatened or endangered. However, if the focal species acts as a biodiversity indicator, the target outcome of MPA protection and the uncertainties the target is subject to might vary (Table 3).

Table 3. Effectiveness parameters and sources of uncertainty in species-based biodiversity objectives

Effectiveness parameter	Predicted change with protection	Uncertainties
Local population viability of endangered or threatened species	Increased stability and abundance of MPA populations relative to unprotected populations	Population viability analysis subject to analytical uncertainty, degree of self-replenishment unknown
Intra-population genetic diversity of endangered or threatened species	Increased diversity in MPA's relative to unprotected populations	Spatio-temporal gene flow difficult to quantify, Directional gene flow may generate problems, Genetic disequilibrium due to changing selective factors
Abundance of indicator species	Increased stability and abundance of MPA populations relative to unprotected populations	Assumption that indicator species adequately reflect community
Abundance of keystone species	Dependent on existing role of target keystone relative to others. In general, abundance and interaction strength of keystone should increase. Increased stability and abundance of MPA populations relative to unprotected populations	Time lags in population recovery, keystones may not function as keystones under all spatial, temporal, and environmental conditions, keystones may generate non-linear trophic cascades
Abundance of umbrella species	Increased stability and abundance of MPA populations relative to unprotected populations	Assumption that protection of umbrella species will result in desired change in biodiversity, dynamics of umbrella species and rest of community may not be tightly coupled
Abundance of flagship species	Increased stability and abundance of MPA populations relative to unprotected populations	Assumption that conservation of flagship species will result in desired biodiversity change

At the community-landscape level, effectiveness parameters must be chosen to reflect processes that operate above the level of individual species (Table 4). Species richness and diversity are intuitive measures of community 'health'. However, these parameters are usually measured for only a subset of the community. For example, microbial diversity is rarely incorporated into measures of community richness. In addition, taxonomic differences might result in different researchers reporting different richness values (Conroy and Noon 1996). Diversity indicators have received much attention both in the resolution of biodiversity issues, and environmental impact assessment (but see Hurlbert 1971). An implicit assumption in the use

of particular species or groups of species is that their abundance is sufficiently correlated with the underlying community 'function' property so as to be useful (Zacharias and Roff 2001). It is probably more instructive to measure species richness with respect to ecological role or trophic organization. For example, a trophic level containing many species may be more robust to loss to individual species because of the interchangeability or redundancy of the species in fulfilling their ecological roles. However, there is a large degree of uncertainty in predicting these effects. Modeling approaches indicate the predicted outcomes might be difficult to measure (Walters et al. 1999), and protection may generate non-linearities or punctuated jumps in community structure and function (e.g., Castilla 1989, Duran and Castilla 1989, Barkai and Branch 1988).

Landscape properties are particularly important for evaluating MPA networks and the effectiveness of large MPA's that encompass many habitat types. Habitat patch (or MPA) size, number, shape, and arrangement are important descriptors (e.g., Cain et al. 1997) that, in combination with measurements of movement and connectivity between patches, characterize the properties of the landscape (Forman 1995). The types of patch or MPA that form the landscape are also important parameters that can be used to describe the effectiveness of a network. A stable landscape requires a balance of redundancy (i.e., the loss of one habitat type will not lead to loss of landscape integrity) and complementarity (i.e., many different habitat types must be incorporated into the landscape to ensure representativeness and diversity (Pressey et al. 1993, 1999, Riitters et al. 1995)).

Table 4. Effectiveness parameters and sources of uncertainty in community/landscape-based biodiversity objectives

Effectiveness parameter	Predicted change with protection	Uncertainties
Species richness and diversity	Increase relative to unprotected communities	Measurement uncertainty, richness and diversity may not reflect desired biodiversity change
Trophic diversity	Increase in diversity relative to unprotected communities	Trophic diversity may be difficult to measure in systems with external materials input
Landscape integrity (i.e. habitat diversity and composition)	Habitat diversity and composition should be maintained in MPA relative to unprotected areas	Landscape dynamics occur at a range of scales are not well understood and susceptible to anthropogenic perturbation
Habitat representativeness	Amount of habitat contained in MPA's should remain proportional to amount and importance of the habitat in the landscape	Requires knowledge of habitat area and designation of importance or conservation value
Habitat connectivity between MPA's	Habitat connectivity should be maintained at an intermediate level	Trade-off between benefits of high connectivity to maintain landscape integrity, and disadvantages due to synchrony of dynamics and susceptibility to large-scale impacts.
Redundancy	Loss of a single habitat patch or MPA should not unduly affect landscape	Must be evaluated with respect to conflicting property of complementarity
Complementarity	Habitat types within landscape should be diverse	Must be evaluated with respect to conflicting property of redundancy

Migratory species conservation objectives

Many species undertake movements beyond the scale that MPA's typically encompass. If a species is unlikely to spend its entire life protected within the spatial bounds of a MPA, we may refer to this as a migratory species (e.g., tuna, turtles, salmon). Many marine species protected under the Endangered Species Act (ESA) and the Marine Mammal Protection Act (MMPA) fall under this category. Organisms with dispersal phases resulting in movement beyond MPA boundaries do not fall in this category, the benthic or adult phases are the stages that are exploited and larvae are not exploited beyond the bounds of a MPA. The use of MPA's to protect migratory species has received far less attention than the previous objectives. Indeed MPA's are

thought in general to diminish in efficiency as the migratory potential of organisms increases (Polacheck 1990, DeMartini 1993, Carr and Reed 1993). However MPA's and – importantly – carefully designed networks of ecologically linked MPA's - can operate in several ways to contribute to the protection of migratory and pelagic species.

Marine protected areas may be intended to reduce exploitation effort as a function of area (Beverton and Holt 1957, Mangel 2000b). MPA's might also be designed to reduce the vulnerability of a species at critical migratory 'bottlenecks' (e.g., salmonids at river mouths). Catch per unit effort (CPUE) is often considerably higher at these bottlenecks, thus exerting a disproportionate effect on the population. Protection at (and of) breeding grounds may be another objective. Many species migrate to or aggregate at breeding localities (Johannes 1978), and these aggregations might lead to two synergistic effects. First, CPUE may increase as a function of the increased intensity of the organisms at breeding sites. Second, the critical life history stage at which these organisms are targeted can lead to severe recruitment overfishing. For example, this factor (in combination with age underestimates) probably contributed to the collapse of the orange roughy (*Hoplostethus atlanticus*) fishery in the southern hemisphere (Smith et al. 1991). MPA's may be used to protect these critical areas (e.g., Koenig et al. 2000, Mangel 2000b). Protection of nursery areas might also comprise another objective. Many species recruit into different areas from those occupied by adults. The juveniles then undergo ontogenetic migration to the adult areas. Although the juveniles may not be directly targeted, they may derive benefit by being protected from other activities (e.g., mortality as bycatch from other activities, such as juvenile fishes caught by the shrimp fishery).

Uncertainties

An important uncertainty is the effect of the management action on the dynamics of the target population. For example, establishment of an MPA will reduce the amount of area that is available for exploitation, but this may result in increased levels of exploitation in non-protected areas that might increase the impact of exploitation by focusing it in a smaller area. Setting targets for migratory species objectives will be subject to uncertainty associated with factors operating beyond the bounds of the MPA. In addition, many migratory species seem to have inherently complex population dynamics, subject to major oscillations in apparent distribution and abundance, perhaps partly a manifestation of their behavioral complexity and ability to move freely among habitats over great distances.

Effectiveness parameters and targets

When the MPA is designed to reduce mortality (either by exploitation or bycatch), the effectiveness is evaluated by measuring catch effort, and instantaneous mortality rates at these critical stages (i.e., bottlenecks and aggregations). If the MPA is designed to protect breeding grounds, it is necessary to measure birth rates (Table 5). For mammals and birds, this objective can usually be well measured. However, birth rates of fish and invertebrate populations are not so well estimated due to uncertainty in the stock-recruitment relationship (see ‘Fisheries objectives’).

Table 5. Effectiveness parameters and sources of uncertainty in migratory species objectives

Effectiveness parameter	Predicted change with protection	Uncertainties
Mortality rates of exploited stages at bottlenecks	Decreased mortality rate in MPA compared to unprotected areas	Measurement uncertainty of catch effort in unprotected areas
Mortality rate of unexploited stages at nursery grounds (e.g., bycatch of juveniles in nursery grounds)	Decreased mortality rate in MPA compared to unprotected areas	Spatial and temporal variability in use of nursery grounds Difficulty in estimating bycatch rates
Birth rates at breeding ground bottlenecks	Increased birth rate or larval production in MPA compared to unprotected areas	Natural sources of variability in birth rates

3. Planning for uncertainty

Uncertainty is an inherent characteristic of biological systems. Nevertheless, the design and creation of MPAs occurs within a legal and political framework that requires agencies to provide some level of predictions or assurances that specific benefits will accrue from their establishment in specific places. Reconciling these two conflicting pressures – management certainty versus ecological uncertainty – is the main challenge facing MPAs today and is the focus of the May workshop. Predictive or explanatory statements in biology are usually probabilistic in nature, with some estimate of the reliability or conditionality of the prediction. As a consequence, it is difficult to make statements of effect without reference to the set of conditions under which their inference holds (e.g., an oceanographic regime, see ‘Causal uncertainty’ below). Planning for uncertainty has a tradition in management risk analysis, but has only recently been explicitly incorporated into conservation and resource management science (e.g., Nichols et al. 1995, Pascual and Hilborn 1995, Flather et al. 1997, Charles 1998, Taylor et al. 2000). Uncertainties must be considered when selecting effectiveness measures, and incorporated into the setting of conservation targets and limits. Uncertainty operates at many levels, but the terminology for each level differs between authors. For the purposes of this paper, we recognize four classes of uncertainty – process, measurement, model, and causal (Fig. 2).

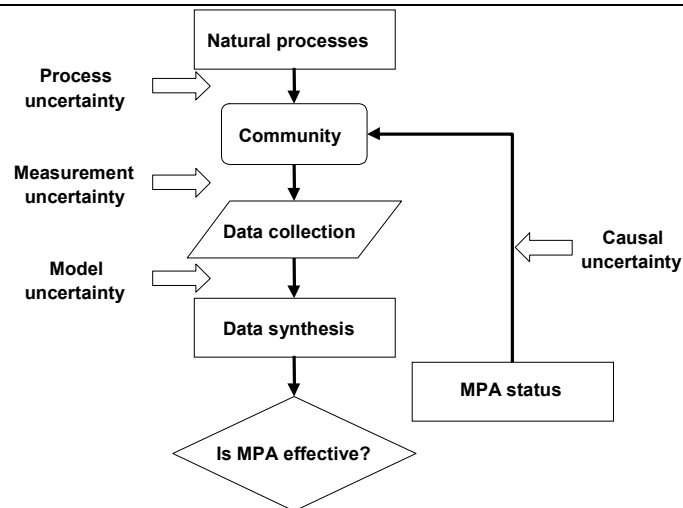


Figure 2. Sources of uncertainty that operate when evaluating MPA effectiveness

Process uncertainty

The biological processes that generate pattern, even in the absence of anthropogenic influences, are subject to uncertainty, much of which may be scale dependent. Some biological processes are inherently unpredictable at some level of resolution. Random, rare, events such as extinction-causing meteorites cannot be predicted at present. However, many events have some degree of predictability. These uncertainties may be conveniently designated as 1st, 2nd, and higher order uncertainties. First order uncertainties are those in which the average value (in statistical terms, the 1st order moment) changes over time and/or space. For example, trends due to climate change, or the spread of invasive species might generate 1st order uncertainty. The implication for MPA assessment would be that predictions or observations made on MPA effectiveness might not be able to be generalized to other times or places, because other important conditions are changing along those dimensions. However, there is potential for these uncertainties to be incorporated into effectiveness measures as covariables. First order changes need not be confined to linear trends. Cyclical changes (e.g., climate cycles) may also exert effects that result in a change of the mean value over time, and can also be modeled using a covariate approach.

Second order uncertainties are those in which the distribution of occurrences has an identifiable statistical distribution (e.g., Poisson), but the occurrence of a single event cannot be predicted as a function of time. In other words, the event occurs randomly, but we know its variance (2nd order moment) properties. In this case, the researcher must accept that point-occurrence hypotheses might not be attainable, but targets might be set as confidence intervals within which the process might be expected to operate. Higher order uncertainties, such as chaotic dynamics, undoubtedly exist in nature (e.g., Schaffer and Kot 1986, Lloyd 1994, Stone and Ezrati 1996), but are generally not reliably parameterized within the lifetime of single researchers.

Potential solutions

The key to dealing with process uncertainty is simply to learn more about the system (Charles 1998). It is important to recognize that, although many ecological phenomena appear ‘unpredictable’, there are different levels of unpredictability. Part of the resolution of these

problems lies in identifying the temporal and spatial scaling domains (Wiens 1989) of ecological processes, and using these properties to establish inferential domains.

Measurement uncertainty

Having selected a parameter to sample, the next stage is to estimate that parameter. The use of sampling schemes to estimate some population parameter generates inherent uncertainty in our level of knowledge of the world. The form of this uncertainty depends on both the sampling theory invoked (e.g., design vs model-based, De Gruijter and Ter Braak 1990), and the interpretation of degree of belief in the parameter estimates (e.g., classical vs Bayesian).

Consider the central notion of classical sampling theory, the population. The population may be defined as the set of all units of interest. For example, if we wished to estimate the density of organisms at a site the population would be defined as all of the possible transects we could sample at that site. In order to sample this population, we would select a subset of these transects. Our estimate of the density would consist of an estimated mean density, plus some measure of sample variability or statistical error. There is uncertainty in our estimate, the magnitude of which is defined by our degree of sampling error.

This form of uncertainty is important because it is still not clear where the true value of the population parameter lies. The classic confidence interval is defined as the region of values within which a percentage of sample parameter estimates would lie (commonly 95% in keeping with an α level of 0.05). It does not explicitly provide the likelihood that the true value is contained within the interval. In contrast, Bayesian confidence intervals explicitly describe ‘belief’ about where the true value lies, but this requires acceptance of other conditions particular to the Bayesian framework.

The researcher can control the magnitude of measurement variability. Increasing replication will generally decrease the statistical error, thereby providing more powerful tests. Measurement uncertainty may also affect estimation of parameters other than means. For example, estimates of variances are required in random factor and nested models, and are central to developing power analyses. Inadequate sampling may also fail to detect the underlying spatial distribution of samples (Legendre et al. 1989), or the presence of rare species (McArdle 1990, Green and Young 1993).

Potential solutions

The general solution to measurement uncertainty is to collect more data to reduce sampling error, and in most cases reduce bias as much as possible. Increased precision and accuracy of parameter estimates must of course be balanced against sampling resources available. Sampling programs should be designed to increase accuracy and precision of key parameter estimates. In many cases this can be an informal procedure guided by analysis of fabricated data sets. Formal cost-benefit analyses can be instructive, but should not determine the development of a sampling program (McArdle and Pawley 1994). Power analyses can also be instructive, but do not provide a panacea. Power calculations are dependent on the estimate of the variance, and hence must be presented with their own confidence intervals (Koele 1982, Thomas 1997). These confidence intervals are usually large. If key parameters cannot be measured directly with great precision, including concomitant variables in the analysis might increase reliability of parameter estimates (Nickerson and Brunell 1997). Finally, the construction of the confidence intervals with respect to the location of the ‘true’ population mean should be considered (ie. classical vs Bayesian approaches).

Model uncertainty

Model uncertainty (also called ‘structural uncertainty’ (Charles 1998)) describes the uncertainty that the observer’s view of the system is correct. This is a fundamental, yet largely unrecognized source of uncertainty that is apparent at all levels of a scientific investigation. It involves core decisions of what to measure, what form the parameters take, and what to assume about their relationships (Fig. 3).

Model uncertainty is best indicated by example. A scientist may elect to study temporal change of abundance in a species following establishment of a MPA. The first step of such an investigation would be to list the factors that could influence the target population (e.g., competition, predation). This list would undoubtedly be prohibitively large, so the scientist must then select a subset of these factors based on experience, tractability or some other set of criteria. The form of the parameters must then be guessed at. For example, are the responses assumed linear or non-linear? Are effects in the model assumed to be additive or multiplicative? These (albeit educated) ‘guesses’ are important because we impose an implicit structure on the world, and this is likely to be an approximation at best. Decision rules based on model frameworks such

as the Neyman-Pearson formulation of the General Linear Model with normal errors (e.g., Mapstone 1995), are only valid if the underlying model is correct in the first place. Strict adherence to decision rules should be tempered by the uncertainty that the model might not be appropriate.

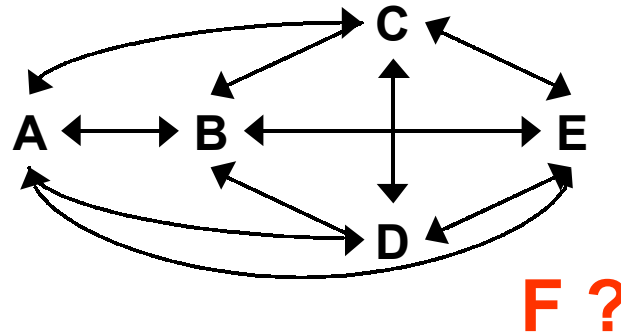


Figure 3. Model uncertainty. The causal factor (A) operates on a set of interacting factors. Interaction direction and form must be ‘guessed’. Uncertainty lies in identifying the correct underlying model, prior to testing. There is an inherent danger that an important factor (F) is not included in the model, yet is in ‘reality’ important, and hence the parameters of the model will be invalid.

Potential solutions

The only counter to model uncertainty is experience, circumspection, and flexibility in application of analysis. Alternative models and hypotheses must be considered, unless confidence in the degree of belief in the underlying model, and the analytical framework used to parameterize it, are high.

Causal uncertainty

Scientists working on MPA effectiveness are likely to find themselves in the position of making statements about the degree to which they believe protection ‘caused’ a change in population or community structure. It is often unrecognized that scientific and laypersons views on what constitutes a ‘cause’ may differ. A laypersons view of causality is generally experiential and intuitive. For example, if placement of a MPA preceded an increase in abundance of fish in that MPA, then it might be perceived that protection ‘caused’ that change. Conversely, if fish abundance actually declined, this might be interpreted as a failure of the MPA to provide any

meaningful protection. This is not how scientific causality operates. It is important for scientists to understand these differences when communicating results to managers and the public. The potential cost for adopting a scientific view of causality is a lack of faith from the layperson's point of view (for the perceived inability to see the 'obvious'); conversely the adoption of the laypersons point of view will reduce standing and reputation amongst other scientists.

The scientific view of causality is framed in the context of experimental setting, and probabilities of events. For example, before we can make a statement about whether MPA's cause increase in fish abundance, we must consider what happens to fish abundance outside MPA's. This is the basis of modern experimental design (Mills 1843), and the philosophical reason for employing controls. In addition, strictly deterministic relationships between cause and effect are rare in biology. If we predict that MPA's should, *on average*, have a measurable effect, there will be some cases where we might not measure an effect. Marine Protected Area effects must be expressed as *probabilities*. Probabilities are distributions of events; hence we need more than one event (in this case, "MPA's") to make a probability statement. In other words, establishing causality requires *replication*. In addition, we need randomization of assignment to experimental 'treatment' (Rubin 1978). The reason for this is that we can't re-run time to look at what would happen at a given site with and without protection. Finally, it needs to be made sure that the outcome of an experiment must not be due to an unmeasured 3rd or *confounding* variable (Suppes 1970).

The requirements of a scientific statement of causality appear glaringly different from those of non-scientists, and the 'real world' might not allow strict statements of causality. The challenge to scientists lies in evaluating degree of belief in a hypothesis and qualifying statements of 'causality' in a way that preserves professional integrity, yet maintains the confidence of managers and laypersons.

Potential solutions

The keys to testing 'causality' are comparison with controls, and removal of confounding. The most robust way of assigning causality to MPA's is by experimentation. In an ideal world, this would require sampling replicate areas before and after protection, with areas assigned to 'protected' and 'control' treatments randomly. This rarely occurs. Causality can be determined in less-than-ideal conditions if enough is known about the system. This approach uses the condition of covariate sufficiency (Stone 1993), in which knowledge about key parameters in the system

can be modeled to remove confounding associated with non-random assignment of sites to the treatment. A similar approach is implicit in the notion of a ‘controlled’ (cf. randomized) experiment, and may be analyzed using path models (Shipley 1999).

4. Summary

Marine Protected Areas have progressed beyond the perception as ‘marine parks’ to becoming an important management and conservation tool (Dayton et al. 2000). There are, in addition to benefits, many social and economic costs of establishing MPA’s. These costs, in combination with conflicting interests of many stakeholders, have led to an increased need for accountability and the explicit statement of performance-oriented conservation goals. Consequently, there is an immediate need to set realistic MPA objectives, expressed as well-defined, tractable, and measurable targets. In addition, MPA evaluation assumes greater importance by providing managers with information on which to make decisions on the fate of existing MPA’s, and generate policy on the development of new ones (Murray et al. 1999, Carr and Raimondi 1999).

The challenge is to develop targets and evaluation protocols that are robust to the many sources of uncertainty inherent in managing natural systems. Effectiveness targets must be established with the understanding that the natural world is variable, and there is a degree of uncertainty at every level of inquiry and management action. However, variability is not a ‘black box’ of the unknowable. A structured approach can incorporate variability into setting targets and evaluating performance, which can in turn be explicitly incorporated into management plans (e.g., Sainsbury et al. 2000).

Finally, effectiveness targets and evaluations must be presented in a form that is compatible with management plans. For example, it is likely that a strict decision-based framework employed from a scientist’s perspective (i.e., minimizing Type I error) will be too conservative to be acceptable to managers, unless they are charged with precautionary management. The degree of uncertainty in assigning targets and measuring the position of the ‘real world’ is likely to be large and undermine confidence in the science behind any recommendations. Frequently, management is concerned with trading off different sources of risk. Perhaps this is the framework that must be employed when communicating science to managers (Harwood 2000). The careful, science-based design of realistic objectives and targets,

combined with a rigorous approach to tracking the status of protected resources, will enable MPAs to be established more readily and will allow their continuous adaptive management as environmental conditions, external threats and conservation needs change over time.

Literature cited

- Agardy, M. T. 1994. Advances in marine conservation: the role of marine protected areas. *Trends in Ecology and Evolution* **9**:267-270.
- Alcala, A. C., and G. R. Russ. 1990. A direct test of the effects of protective management on abundance and yield of tropical marine resources. *Journal du Conseil International pour l'Exploration de la Mer* **46**:40-47.
- Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* **8**:S79-S92.
- Babcock, R. C., S. Kelly, N. T. Shears, J. W. Walker, and T. J. Willis. 1999. Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series* **189**:125-134.
- Barkai, A., and G. M. Branch. 1988. The influence of predation and substratal complexity on recruitment to settlement plates: a test of the theory of alternate states. *Journal of Experimental Marine Biology and Ecology* **124**:215-237.
- Beverton, R. J. H., and S. J. Holt. 1957. *On the dynamics of exploited fish populations*. Chapman and Hall, London.
- Bohnsack, J. A. 1993. Marine reserves: they enhance fisheries, reduce conflicts, and protect resources. *Oceanus* **36**:63-71.
- Bohnsack, J. A. 1998. Application of marine reserves to reef fisheries management. *Australian Journal of Ecology* **23**:298-304.
- Bohnsack, J. A. 2000. A comparison of the short-term impacts of no-take marine reserves and minimum size limits. *Bulletin of Marine Science* **66**:635-650.
- Botsford, L. W., J. F. Quinn, S. R. Wing, and J. G. Brittnacher. 1993. Rotating spatial harvest of a benthic invertebrate, the red sea urchin, *Strongylocentrotus franciscanus*. *International Symposium on Management Strategies for Exploited Fish Populations*, Alaska Sea Grant College Program, pp 409-428.
- Cain, D. H., K. Riitters, and K. Orvis. 1997. A multi-scale analysis of landscape statistics. *Landscape Ecology* **12**:199-212.
- Carlton, J. T., G. J. Vermeij, D. R. Lindberg, D. A. Carlton, and E. C. Dudley. 1991. The first historical extinction of a marine invertebrate in an ocean basin: The demise of the Eelgrass Limpet *Lottia alveus*. *Biological Bulletin* **180**:72-80.
- Carr, M. H., and P. T. Raimondi. 1999. Marine protected areas as a precautionary approach to management. *CalCOFI Report* **40**:71-76.
- Carr, M. H., and D. C. Reed. 1993. Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:2019-2028.
- Castilla, J. C. 1989. Human exclusion from rocky intertidal of Las Cruces, central Chile: effects on *Durvillea antarctica* (Phaeophyta, Durvilleales). *Marine Ecology Progress Series* **50**:203-214.

- Chapman, M. R., and D. L. Kramer. 1999. Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. *Marine Ecology Progress Series* **181**:81-96.
- Charles, A. T. 1998. Living with uncertainty in fisheries: analytical methods, management priorities and the Canadian groundfishery experience. *Fisheries Research* **37**:37-50.
- Cole, R. G., E. Villouta, and R. J. Davidson. 2000. Direct evidence of limited dispersal of the reef fish *Parapercis colias* (Pinguipedidae) within a marine reserve and adjacent fished areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* **10**:421-436.
- Conroy, M. J., and B. R. Noon. 1996. Mapping of species richness for conservation of biological diversity: conceptual and methodological issues. *Ecological Applications* **6**:763-773.
- Creese, R. G., and R. G. Cole. 1995. Marine conservation in New Zealand. *Pacific Conservation Biology* **2**:55-63.
- Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems* **5**:205-232.
- Dayton, P. K., E. Sala, M. J. Tegner, and S. Thrush. 2000. Marine reserves: parks, baselines, and fishery enhancement. *Bulletin of Marine Science* **66**:617-634.
- De Gruijter, J. J., and C. J. F. Ter Braak. 1990. Model-free estimation from spatial samples: a reappraisal of classical sampling theory. *Mathematical Geology* **22**:407-415.
- DeMartini, E. E. 1993. Modeling the potential of fisheries reserves for managing Pacific coral reef fishes. *Fishery Bulletin* **91**:414-427.
- Dugan, J.E., and G.E. Davis. 1993. Applications of marine refugia to coastal fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:2029-2042.
- Duran, L. R., and J. C. Castilla. 1989. Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. *Marine Biology* **103**:555-562.
- Edgar, G. J., and N. S. Barrett. 1997. Short term monitoring of biotic changes in Tasmanian marine reserves. *Journal of Experimental Marine Biology and Ecology* **213**:261-279.
- Edgar, G. J., and N. S. Barrett. 1999. Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *Journal of Experimental Marine Biology and Ecology* **242**:107-144.
- Flather, C. H., W. K.R., D. J. Dea, and W. C. McComb. 1997. Identifying gaps in conservation networks: of indicators and uncertainty in geographic-based analyses. *Ecological Applications* **7**:531-542.
- Forman, R. T. T. 1995. Some general principles of landscape and regional ecology. *Landscape Ecology* **10**:133-142.
- Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? *Ecological Applications* **3**:202-205.
- Freitas, J., R. M. Fujita, and V. Willingham. 1998. A review of the performance of some U.S. west coast marine reserves. Environmental Defense Fund, Oakland, CA.
- Garcia Charton, J. A., I. D. Williams, A. P. Ruzafa, M. Milazzo, R. Chemello, C. Marcos, M. S. Kitsos, A. Koukouras, and S. Riggio. 2000. Evaluating the ecological effects of Mediterranean marine protected areas: habitat, scale and the natural variability of ecosystems. *Environmental Conservation* **27**:159-178.
- Glynn, P. W., and W. H. de Weerd. 1991. Elimination of two reef-building hydrocorals following the 1982-1983 El Niño warming event. *Science* **253**:69-71.

- Green, R. H., and R. C. Young. 1993. Sampling to detect rare species. *Ecological Applications* **3**:351-356.
- Guénette, S., T. Lauck, and C. Clark. 1998. Marine reserves: from Beverton and Holt to the present. *Reviews in Fish Biology and Fisheries* **8**:251-272.
- Hall, S. J. 1998. Closed areas for fisheries management - the case consolidates. *Trends in Ecology and Evolution* **13**:297-298.
- Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos* **87**:209-219.
- Harwood, J. 2000. Risk assessment and decision analysis in conservation. *Biological Conservation* **95**:219-226.
- Hastings, A., and L. W. Botsford. 1999. Equivalence in yield from marine reserves and traditional fisheries management. *Science* **284**:1537-1538.
- Hixon, M. A. and M. H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science* **277**:946-949.
- Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**:577-586.
- Jamieson, G. S., and C. O. Levings. 2001. Marine protected areas in Canada - implications for both conservation and fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:138-156.
- Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes* **3**:65-84.
- Jones, G. P., and U. L. Kaly. 1996. Criteria for selecting marine organisms in biomonitoring studies. Pages 39-56 *in* R. J. Schmitt and C. W. Osenberg, editors. *The design of ecological impact studies: conceptual issues and application in coastal marine habitats*. University of California Press, California.
- King, W. A., and S. L. Pimm. 1983. Complexity, diversity, and stability: a reconciliation of theoretical and empirical results. *American Naturalist* **122**:229-239.
- Koele, P. 1982. Calculating power in analysis of variance. *Psychological Bulletin* **92**:513-516.
- Koenig, C. C., F. C. Coleman, C. B. Grimes, G. R. Fitzhugh, K. M. Scanlon, C. T. Gledhill, and M. Grace. 2000. Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. *Bulletin of Marine Science* **66**:593-616.
- 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.
- Lauck, T., C. W. Clark, M. Mangel, and G. R. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications* **8**:S72-S78.
- Legendre, P., M. Trouselier, V. Jarry, and M.-J. Fortin. 1989. Design for simultaneous sampling of ecological variables: from concepts to numerical solutions. *Oikos* **55**:30-42.
- Lister, N.-M. E. 1998. A systems approach to biodiversity conservation planning. *Environmental Monitoring and Assessment* **49**:123-155.
- Lloyd, A. L. 1994. Chaos and forecasting. *Trends in Ecology and Evolution*. **9**:244-245.
- Lundberg, P., and N. Jonzén. 1999. Spatial population dynamics and the design of marine reserves. *Ecology Letters* **2**:129-134.
- Man, A., R. Law, and N. V. C. Polunin. 1995. Role of marine reserves in recruitment to reef fisheries: a metapopulation model. *Biological Conservation* **71**:197-204.

- Mangel, M. 1998. No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. *Ecology Letters* **1**:87-90.
- Mangel, M. 2000a. On the fraction of habitat allocated to marine reserves. *Ecology Letters* **3**:15-22.
- Mangel, M. 2000b. Trade-offs between fish habitat and fishing mortality and the role of reserves. *Bulletin of Marine Science* **66**:663-674.
- Mapstone, B. D. 1995. Scalable decision rules for environmental impact studies: effect size, type I, and type II errors. *Ecological Applications* **5**:401-410.
- McArdle, B. H. 1990. When are rare species not there? *Oikos* **57**:276-277.
- McArdle, B. H., and M. D. M. Pawley. 1994. Cost benefit analysis in the design of biological monitoring programs: is it worth the effort? Pages 239-253 in D. J. Fletcher and B. F. J. Manly, eds. *Statistics in Ecology and Environmental Monitoring*. University of Otago Press, Dunedin.
- McArdle, D. A. 1997. California marine protected areas. Publication Number T-039. California Sea Grant College System, University of California, La Jolla, California.
- Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* **64**:249-286.
- Mill, J. S. 1843. *A System of Logic*, Longmans, London.
- Murray, M. R. 1998a. The status of marine protected areas in Puget Sound. Volume 1. Puget Sound Water Quality Action Team, Olympia, Washington. Puget Sound/Georgia Basin Environmental Report Series 8.
- Murray, M. R. 1998b. The status of marine protected areas in Puget Sound. Volume 2. Puget Sound Water Quality Action Team, Olympia, Washington. Puget Sound/Georgia Basin Environmental Report Series 8.
- Murray, S. N., R. F. Ambrose, J. A. Bohnsack, L. W. Botsford, M. H. Carr, G. E. Davis, P. K. Dayton, D. Gotshall, D. R. Gunderson, M. A. Hixon, J. Lubchenco, M. Mangel, A. MacCall, D. A. McArdle, J. C. Ogden, J. Roughgarden, R. M. Starr, M. J. Tegner, and M. M. Yoklavich. 1999. No-take reserve networks: sustaining fishery populations and marine ecosystems. *Fisheries* **24**:11-25.
- Nichols, J. D., F. A. Johnson, and B. K. Williams. 1995. Managing North American waterfowl in the face of uncertainty. *Annual Review of Ecology and Systematics* **26**:177-199.
- Nickerson, D. M., and A. Brunell. 1997. Power analysis for detecting trends in the presence of concomitant variables. *Ecology* **79**:1442-1447.
- Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Pacquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology* **10**:949-963.
- Pascual, M. A., and R. Hilborn. 1995. Conservation of harvested populations in fluctuating environments: the case of the Serengeti wildebeest. *Journal of Applied Ecology* **32**:468-480.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* **307**:321-326.
- Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. *Nature* **350**:669-674.
- Planes, S., R. Galzin, A. Garcia Rubies, R. Goñi, J. G. Harmelin, L. Le Diréach, P. Lenfant, and A. Quetglas. 2000. Effects of marine protected areas on recruitment processes with special reference to Mediterranean littoral ecosystems. *Environmental Conservation* **27**:126-143.

- Polacheck, T. 1990. Year around closed areas as a management tool. *Natural Resource Modeling* **4**:327-354.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology. *Annual Review of Ecology and Systematics* **28**:289-316.
- Pressey, R. L., C. J. Humphries, C. R. Margules, R. I. Vane-Wright, and P. H. Williams. 1993. Beyond opportunism: key principles for systematic reserve selection. *Trends in Ecology and Evolution* **8**:124-128.
- Pressey, R. L., H. P. Possingham, V. S. Logan, J. R. Day, and P. H. Williams. 1999. Effects of data characteristics on the results of reserve selection algorithms. *Journal of Biogeography* **26**:179-191.
- Quinn, J. F., S. R. Wing, and L. W. Botsford. 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *American Zoologist* **33**:537-550.
- Riitters, K. H., R. V. O'Neill, C. T. Hunsaker, J. D. Wickham, D. H. Yankee, S. P. Timmins, K. B. Jones, and B. L. Jackson. 1995. A factor analysis of landscape pattern and structure matrices. *Landscape Ecology* **10**:23-39.
- Roberts, C. M., and N. V. C. Polunin. 1991. Are marine reserves effective in management of reef fisheries? *Reviews in Fish Biology and Fisheries* **1**:65-91.
- Roberts, C.M. and N.V.C. Polunin. 1993. Marine reserves: simple solutions to managing complex fisheries? *Ambio* **22**:363-368.
- Roff, D. A., and M. E. Taylor. 2000. National frameworks for marine conservation - a hierarchical geophysical approach. *Aquatic Conservation: Marine and Freshwater Ecosystems* **10**:209-223.
- Rowley, R. J. 1994. Marine reserves in fisheries management. *Aquatic Conservation: Marine and Freshwater Ecosystems* **4**:233-254.
- Rubin, D. B. 1978. Bayesian inference for causal effects: the role of randomization. *Annals of Statistics* **6**:34-58.
- Russ, G. R., and A. C. Alcala. 1996a. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series* **132**:1-9.
- Russ, G. R., and A. C. Alcala. 1996b. Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecological Applications* **6**:947-961.
- Sainsbury, K. J., P. Raven, A. E. Punt, and A. D. M. Smith. 2000. Design of operational management strategies for achieving fishery ecosystem objectives. *ICES Journal of Marine Science* **57**:731-741.
- Schaffer, W. M., and M. Kot. 1986. Chaos in ecological systems: the coals that Newcastle forgot. *Trends in Ecology and Evolution* **1**:58-63.
- Shipley, B. 1999. Testing causal explanations in organismal biology: causation, correlation and structural equation modelling. *Oikos* **86**:374-382.
- Sladek Nowlis, J., and C. M. Roberts. 1997. You can have your fish and eat it, too: theoretical approaches to marine reserve design. *Proceedings of the Eighth International Coral Reef Symposium* **2**:1907-1910.
- Sladek Nowlis, J., and C. M. Roberts. 1999. Fisheries benefits and optimal design of marine reserves. *Fishery Bulletin* **97**:604-616.
- Smith, P. J., R. I. C. C. Francis, and M. McVeigh. 1991. Loss of genetic diversity due to fishing pressure. *Fisheries Research* **10**:309-316.

- St. Mary, C. M., C. W. Osenberg, T. K. Frazer, and W. J. Lindberg. 2000. Stage structure, density dependence and the efficacy of marine reserves. *Bulletin of Marine Science* **66**:675-690.
- Stone, L., and S. Ezzati. 1996. Chaos, cycles and spatiotemporal dynamics in plant ecology. *Journal of Ecology* **84**:279-291.
- Stone, R. 1993. The assumptions on which causal inferences rest. *Journal of the Royal Statistical Society* **55**:455-466.
- Suppes, P. C. 1970. *A Probabilistic Theory of Causality*, North-Holland Publishers, Amsterdam.
- Taylor, B. L., P. R. Wade, D. P. De Master, and J. Barlow. 2000. Incorporating uncertainty into management models for marine mammals. *Conservation Biology* **14**:1243-1252.
- Tegner, M. J. 1993. Southern California abalones: can stocks be rebuilt using marine harvest refugia? *Canadian Journal of Fisheries and Aquatic Sciences* **50**:2010-2018.
- Thomas, L. 1997. Retrospective power analysis. *Conservation Biology* **11**:276-280.
- Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. *Nature* **367**:363-365.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* **277**:1300-1302.
- Tuya, F., M. Soboil, and J. Kido. 2000. An assessment of the effectiveness of marine protected areas in the San Juan Islands, Washington, USA. *ICES Journal of Marine Science* **57**:1218-1226.
- Walters, C., D. Pauly, and V. Christensen. 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* **2**:539-554.
- Ward, T. J., M. A. Vanderklift, A. O. Nicholls, and R. A. Kenchington. 1999. Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. *Ecological Applications* **9**:691-698.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**:385-397.
- Zacharias, M. A., and J. C. Roff. 2001. Use of focal species in marine conservation and management: a review and critique. *Aquatic Conservation: Marine and Freshwater Ecosystems* **11**:59-76.
- Zeller, D. C., and G. R. Russ. 1998. Marine reserves: patterns of adult movement of the coral trout (*Plectropomus leopardus* (Serranidae)). *Canadian Journal of Fisheries and Aquatic Science* **55**:917-924.