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Linking models with monitoring data for assessing performance of no-take marine reserves

J Wilson White^{1*}, Louis W Botsford¹, Marissa L Baskett², Lewis AK Barnett^{1,2}, R Jeffrey Barr^{1,3}, and Alan Hastings²

No-take marine reserves are an increasingly popular conservation and management tool. Assessing reserve performance in an adaptive management framework ideally involves predicting the response of populations and communities to reserves (typically in the design process) and testing predicted outcomes against observations. Here we compare existing modeling and empirical studies on no-take marine reserves, and provide a prospectus for their future integration. Numerical models of ecological responses to reserves typically project long-term, steady-state interactions over the relatively broad spatial scales of larval dispersal, reserve configuration, fishing effort, and fish movement. Existing empirical studies focus on short-term outcomes over small scales, typically aggregated over many explanatory factors. Linking models and empirical data together for the adaptive management of marine reserves requires adjusting the spatial and temporal scales of models to match empirically feasible tests, and adjusting the metrics and scale of empirical studies to account for the interacting biological and human factors affecting reserve outcomes.

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The number of marine reserves is growing worldwide (Wood *et al.* 2008), so it is prudent to consider how to assess whether such reserves achieve their goals. The stated goals of marine reserves vary widely, but fundamentally all reserves are designed to achieve some combination of preserving biodiversity and supporting sustainable fisheries (Leslie 2005). Empirical evidence indicates that biomass and biodiversity usually increase inside reserves, but sometimes do not change or even decrease (Lester *et al.* 2009; Figure 1). As governments consider implementing additional reserves, it bears asking: What causes some reserves to perform well while others do not? Also, how can we assess how well

reserves meet specific goals? Note that here we deal primarily with no-take marine reserves, a subset of the broader class of marine protected areas (MPAs; WebPanel 1).

The interplay of models and data is a powerful approach for advancing science (Caswell 1988), a capacity that is embodied in adaptive management (Walters 1986). Adaptive management ideally requires ongoing comparison of empirical data to quantitative expectations derived from models (Grafton and Kompas 2005; see Lindenmayer and McCarthy [2006] for a terrestrial example). However, in the case of marine reserves, model development and monitoring data collection have proceeded independently, with the two only rarely integrated (eg Claudet *et al.* 2010).

Although marine reserve models and empirical studies have been reviewed separately with respect to reserve design and general outcomes (Gerber *et al.* 2003; Lester *et al.* 2009) and the development of indicators from modeling and empirical results (Pelletier *et al.* 2008), here we focus on the integration of models and monitoring data. First, we provide a theoretical perspective on reserve goals and factors affecting their achievement. Then we review recent empirical assessments, placing them in the context of theoretical expectations and assumptions. Finally, we identify directions for integrating models and data in the assessment and adaptive management of marine reserves.

In a nutshell:

- Comparing field-collected data to model predictions is required to assess marine reserve performance
- Currently, empirical analyses focus on short-term responses of aggregated variables in single reserves; however, model projections involve interactions among multiple variables and predict long-term behavior of reserve networks
- Models need to predict short-term, local consequences, whereas empirical analyses need to examine long-term, large-scale interactions of multiple variables
- We suggest strategies for greater integration of modeling and empirical efforts

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■ Factors affecting the achievement of marine reserve conservation goals: model predictions

Modeling approaches to general, strategic questions (models that are a representation of an abstract, idealized

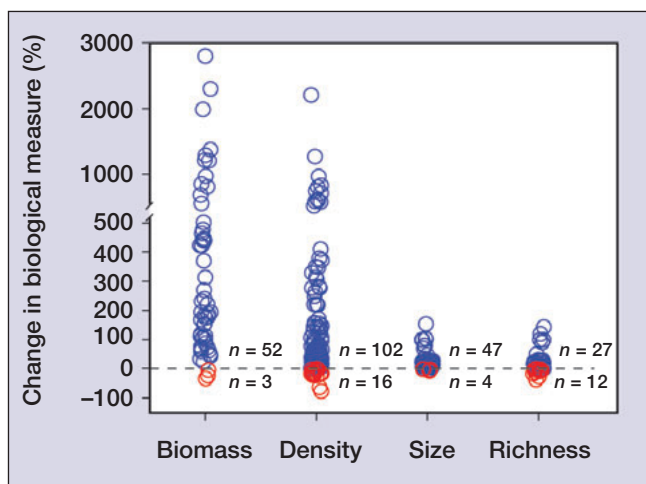


Figure 1. Empirical data on marine reserve effects from a meta-analysis performed by Lester et al. (2009). Data show percent change in four biological variables, measured as the log response ratio of after:before, inside:outside, or (after-inside:before-inside): (after-outside:before-outside), depending on data availability. Each point corresponds to a single study; number of studies with positive (blue symbols) or negative (red symbols) values are indicated by n. Points are jittered horizontally for clarity; note shift in scale on vertical axis. Redrawn from Lester et al. (2009), with permission.

process of interest in that location; they are used to produce results tailored to that system only) for decision making indicate how a variety of factors are expected to affect ecological responses to marine reserves (Table 1 and WebTable 1). Reserve models generally describe both the persistence of fished populations (related to the biodiversity goal) and patterns of fishery yield outside reserve boundaries (related to the sustainable fisheries goal; both goals reviewed by Gerber et al. 2003). Most of these models deal with individual species and incorporate a number of simplifying assumptions (eg deterministic dynamics, no fisherman behavior; see Table 2, as well as Pelletier and Mahevas [2005] for a more comprehensive list), an understanding of which is necessary for comparison to empirical data.

system, used to produce general conclusions of broad applicability) and finer-scale, tactical questions (models that are a representation of a particular real-world system, including all of the interactions thought to affect the

Population persistence in reserves: the replacement concept

Persistence and yield can be understood fundamentally in terms of replacement: a population will persist if an average individual reproduces enough during its lifetime to replace itself. In fishery models, this requirement is expressed in terms of lifetime egg production (LEP) exceeding the “replacement threshold”, at which one egg per individual, on average, survives to recruit back into the population. Fishing decreases LEP, and the fraction of unfished LEP can describe the status of a fished population (Mace and Sissenwine 1993). The value of the replacement threshold (expressed as the fraction of

Table 1. A comparison of how various factors affect marine reserve performance as predicted by models, with examples of empirical studies that have assessed these factors

| Predicted response | Factors affecting response | | | | | Theoretical references | Empirical references |
|--|----------------------------|--------------------------|---------------------------|---------------------------|----------------|---|---|
| | Management factors | | Intrinsic factors | | | | |
| | Marine reserve size | Level of fishing outside | LEP replacement threshold | Larval dispersal distance | Adult movement | | |
| Biomass (population response) | ↑ ↔ | ↓ ↓ | ↓ ? | ↓ ? | ↓ ↓ | Moffitt et al. (2009); White et al. (2010a,b) | Lester et al. (2009); Claudet et al. (2008, 2010); Pelc et al. (2009) |
| Yield (fishery response) | ↑ ↓ ? | ↑ ↓ ? | ↓ ? | ↑ ↑ | ↑ ? | White et al. (2010a,b) | Russ et al. (2004) |
| Average trophic level (community response) | ? ↑ | ? ? | ? ? | ? ? | ? ? | | Micheli et al. (2004) |

Notes: For each response variable, the arrows indicate whether models (blue symbols) and empirical studies (red symbols) have found a positive (up arrow) or negative (down arrow) effect of each factor. Double arrows indicate that the response could be positive or negative, depending on context; a double-headed horizontal arrow indicates no response, and question marks indicate comparisons that have yet to be made. Most of these factors are actually predicted to have complex responses that depend on the other factors in the table. In order to illustrate the range of important factors, we have generalized each response to an up-or-down arrow, but tactical models would be necessary to obtain a quantitative prediction for a specific location. This table deals with only a small subset of important factors and responses; a more complete version is found in the Web-only materials. Some important factors are not amenable to up-or-down predictions; these include local oceanographic factors (including circulation patterns), the distribution of suitable habitat, and socioeconomic factors. LEP = lifetime egg production.

Table 2. Assumptions made by typical strategic marine reserve models

| Assumption | Representative examples | Exceptions |
|---|-------------------------------|--|
| <i>Single species models</i> | | |
| Non-spatial (reserves occupy a fraction of space rather than a location on a map) | Mangel (1998) | Botsford <i>et al.</i> (2001); Gaines <i>et al.</i> (2003); Neubert (2003) |
| No size or age structure in population | Mangel (1998); Neubert (2003) | Botsford <i>et al.</i> (2001) |
| Homogenous linear habitat | Botsford <i>et al.</i> (2001) | White <i>et al.</i> (2010b); Costello <i>et al.</i> (2010) |
| Spatially homogenous larval dispersal kernel | Botsford <i>et al.</i> (2001) | White <i>et al.</i> (2010a); Costello <i>et al.</i> (2010) |
| Spatially homogenous fishing effort, or no fisherman behavior | Botsford <i>et al.</i> (2001) | Sanchirico and Wilen (2001); Kellner <i>et al.</i> (2007); Costello <i>et al.</i> (2010) |
| Scorched-earth harvesting (fish are harvested prior to reproduction) | Neubert (2003) | Botsford <i>et al.</i> (2001); Kaplan <i>et al.</i> (2009) |
| No temporal variability in environmental processes (eg stochastic larval survival or rare catastrophes) | Botsford <i>et al.</i> (2001) | White and Rogers-Bennett (2010) |
| Results are for long-term steady-state (>10 years), not short term (< 5 years) | Botsford <i>et al.</i> (2001) | White and Rogers-Bennett (2010) |
| Adults are sessile | Botsford <i>et al.</i> (2001) | Moffitt <i>et al.</i> (2009) |
| Density-dependent competition within a cohort only (juveniles compete with other juveniles, not with adults) | Botsford <i>et al.</i> (2001) | White and Kendall (2007) |
| Animals do not make ontogenetic habitat changes | Botsford <i>et al.</i> (2001) | Mangel and Levin (2005) |
| Animals do not evolve in response to reserves | Botsford <i>et al.</i> (2001) | Baskett <i>et al.</i> (2005) |
| <i>Multi-species models</i> | | |
| Tightly coupled predator–prey dynamics (rather than a complex multi-species food web) | Baskett <i>et al.</i> (2007) | Salomon <i>et al.</i> (2002) |
| Linear interaction strengths (rather than nonlinear functional responses) | Salomon <i>et al.</i> (2002) | Baskett <i>et al.</i> (2007) |
| Bioenergetics not included | Baskett <i>et al.</i> (2007) | Claessen <i>et al.</i> (2009) |
| <p>Notes: Applications of models to monitoring data should account for deviations from these assumptions before testing a model prediction. Examples are given of 1–2 well-known studies employing each assumption (these are merely representative of many other publications making the same assumption) as well as subsequent studies that relax the assumption (see Pelletier and Mahevas [2005] for a more detailed explanation of many such models and assumptions). Any model, by definition, will make simplifying assumptions; appropriate assumptions always depend on the question being asked.</p> | | |

unfished LEP) for each population is a dominant uncertainty in fishery assessment.

Determining when populations will persist in marine reserves requires considering both the spatial distribution of egg production and the dispersal of eggs (larvae) among subpopulations within a metapopulation. Larvae can return to their natal subpopulation, or supply another subpopulation. Larvae that disperse from the natal subpopulation may eventually produce their own larvae, which could make the return trip to replenish the “grandparent” subpopulation. Thus, replacement in a metapopulation includes travel through multiple paths that may involve several locations over several generations (Hastings and Botsford 2006).

A subpopulation within a single marine reserve can be self-persistent if the fraction of larvae retained within that reserve exceeds the replacement threshold (Botsford *et al.* 2001; Hastings and Botsford 2006). This typically requires that the reserve be larger than the average larval dispersal distance (White *et al.* 2010a). Even without any

self-persistent reserves in a reserve network, network persistence can arise when replacement occurs over multiple paths (Hastings and Botsford 2006) if the shortfall in self-replenishment is made up by larval exchange among all reserves. Network persistence requires that the fraction of the population in reserves exceeds a particular threshold. This threshold increases with harvest outside the reserve (to a maximum value equal to the fraction of unfished LEP required for replacement; Botsford *et al.* 2001; White *et al.* 2010a) and with fish mobility, which increases exchange between protected and fished areas (Moffitt *et al.* 2009). Regardless, the threshold amount of reserve area necessary for persistence depends on the difficult-to-measure LEP replacement threshold (White *et al.* 2010a).

Effects of reserves on fishery yield

Models also predict complex effects of marine reserves on fishery yield. Reserves can increase yields in the long run

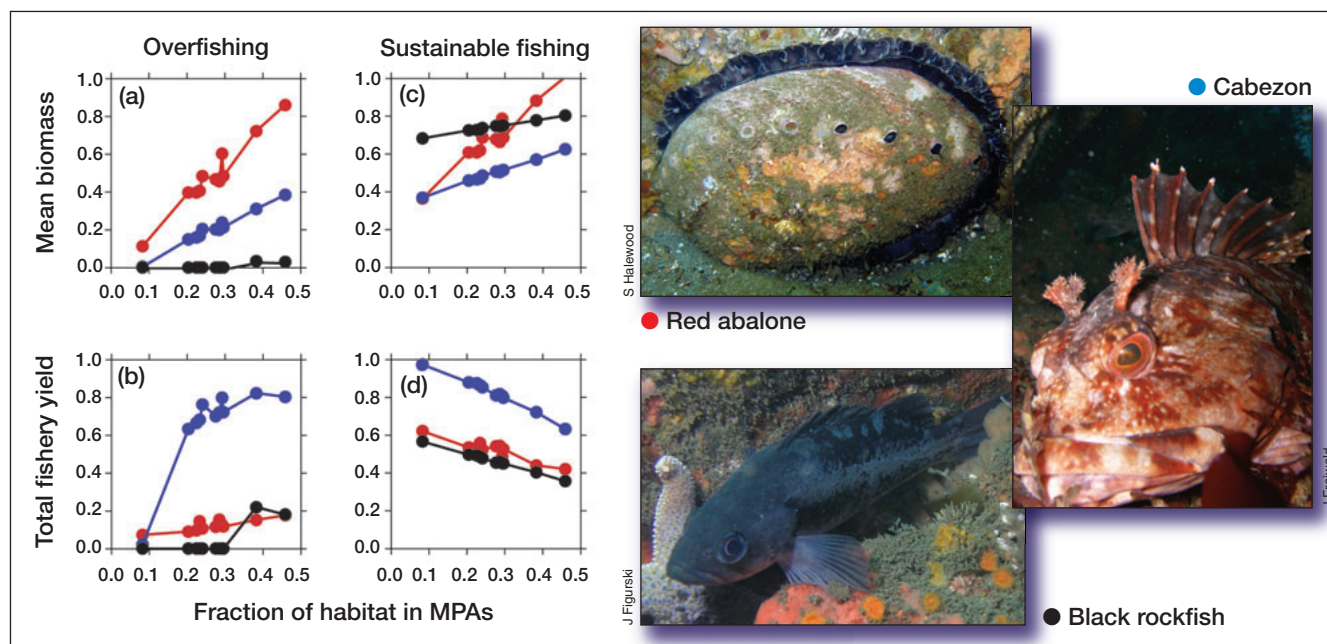


Figure 2. Effect of 11 alternative marine protected area (MPA) networks (including both no-take reserves and MPAs that allow take for some species) on equilibrium population biomass, and fishery yield in the cases where the populations are overfished and sustainably fished, as predicted by a model used for tactical decision making in the North Central Coast region of California. [(a) and (c)] Mean biomass (relative to the unfished maximum), and [(b) and (d)] fishery yield (relative to the maximum sustainable yield without MPAs) for three species. Each point is the region-wide average value for one MPA network for one species. Red abalone (*Haliotis rufescens*; red) have short larval dispersal distance and small adult home range; cabezon (*Scorpaenichthys marmoratus*; blue) have long larval dispersal distance and small adult home range; black rockfish (*Sebastes melanops*; black) have long larval dispersal distance and large adult home range. Results differ among species and depend on the level of fishing outside of MPAs: under overfishing (a, b), populations would not persist without MPAs; under sustainable fishing (c, d), MPAs are not necessary for persistence. Note that the dispersal and movement rates shape the biological effect of protecting a particular fraction of the coastline in MPAs. For example, cabezon (small home range) biomass and yield increase steadily with MPA area in the overfishing scenario, whereas black rockfish (large home range) is not persistent unless > 30% of the coastline is contained in MPAs. Adapted from White *et al.* (2010b).

(see WebPanel 2 for a discussion of time scales) if a population would have otherwise collapsed because of overfishing and the reserve network area is large enough for persistence. However, closing more area than is necessary for persistence given a specific harvest rate can lead to a decrease in yields (Mangel 1998; Hastings and Botsford 1999; White *et al.* 2010b). Under basic model assumptions, adding reserve area to a coastline is essentially approximate to removing fishing effort (Hastings and Botsford 1999). Higher yields with a marine reserve network can occur when accounting for factors such as source–sink dynamics (Costello *et al.* 2010) or new recruits competing with resident adults (White and Kendall 2007); however, whether yields increase or decrease also depends on how fishermen redirect their effort after reserve implementation (Sanchirico and Wilen 2001; Kellner *et al.* 2007).

To illustrate the potential for reserve effects to depend on an interaction between network size, harvest outside, and fish movement, we show how three different species are expected to respond to the same proposed reserve networks (Figure 2). This type of tactical model can incorporate most of the factors likely to affect reserve success, but interactions among those factors occur at spatial and tem-

poral scales much greater than those accounted for in typical empirical studies.

■ Comparing measured marine reserve effects to model predictions

Most field studies test hypotheses that are ultimately derived from model predictions (eg larger reserves should exhibit a higher biomass). Such tests must account for confounding factors predicted by models and ensure that key model assumptions do not oversimplify the study system.

Before–after, inside–outside comparisons: assumptions and limitations

While models predict that the biological response to marine reserves will depend on the interaction between network configuration, fisheries outside reserves, and fish life history, empirical evaluations of reserve performance often test only general, univariate, or even binary responses with just a single explanatory factor (eg reserve size). A common approach is the comparison of a metric (eg biomass, population density) inside versus outside a reserve, or before versus after reserve implementation

through a before–after control–impact (BACI) design. Usually the expectation is that effective reserves will produce values that are higher inside versus outside or after versus before. In addition to evaluations of single reserves, meta-analyses combine after:before and/or inside:outside response ratios to estimate the overall performance of regional or global collections of marine reserves.

Even studies using a BACI approach are vulnerable to several pitfalls in interpretation. First, binary hypothesis tests (eg is there a statistically significant increase in biomass or not?) tend to aggregate over many complex, interacting variables. For example, aggregating responses over species with different movement characteristics confounds tests of reserve size effects, because the effect of reserve size depends on the spatial scale of species movement (Moffitt *et al.* 2009). Second, this approach implicitly assumes that if a reserve “works”, the metric (eg biomass) will be substantially greater inside reserves after implementation (Harborne *et al.* [2008] provided a reasoned explanation of these assumptions). However, models reveal that this expectation may be inappropriate: in some cases (eg with long-distance dispersal), reserves may increase biomass and population density over large spatial scales, so that there is no detectable inside:outside difference (White and Rogers-Bennett 2010; Figure 3d). Additionally, demographic time lags may cause biomass to appear to be unchanged or even decrease initially, even in a reserve that will eventually succeed (WebPanel 2). In general, one does expect to find more and larger fish inside a reserve; the problem is that, depending on the details of the species and the system, a particular monitoring design may not detect a statistically significant inside:outside or after:before difference.

Extrapolating from meta-analyses also requires caution. The aggregated mean response ratio in a meta-analysis – for example, the mean biomass increase of 446% reported by Lester *et al.* (2009; Figure 1) – should not be interpreted to imply that any given reserve is expected to produce a 446% increase in biomass. Rather, the response for any particular reserve will depend on the various factors specific to that location (eg those shown in Table 1).

The problem of spatial scale

Another general limitation of existing empirical assessments is the scale of the study. Nearly all empirical marine reserve assessments focus on the spatial scale of an individual reserve (Lester *et al.* 2009). However, a few studies have evaluated small networks of reserves (eg Cudney-Bueno *et al.* 2009; Hamilton *et al.* 2010), and McCook *et al.* (2010) summarized a well-designed moni-

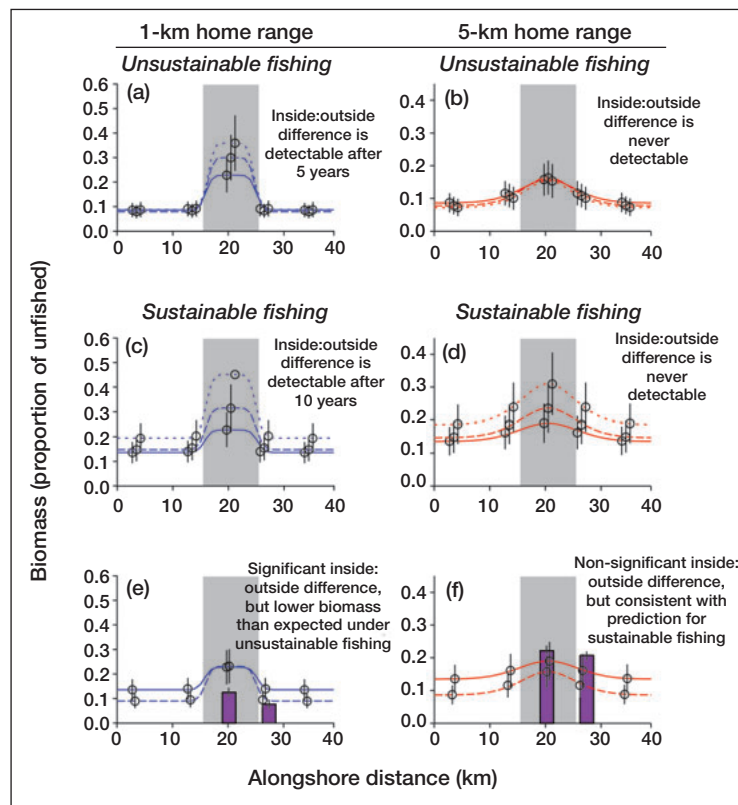


Figure 3. Effects of short-term variability on marine reserve monitoring results. Panels (a–d) show the predicted spatial distribution of biomass 5 years (solid lines), 10 years (dashed lines), and 20 years (dotted lines) after reserve implementation for species with 40-km larval dispersal distance and a home range radius of (a, c) 1 km or (b, d) 5 km. Fishing outside reserves is (a, b) unsustainable (lifetime egg production, LEP = 20% of unfished levels, 25% is needed for persistence) or (c, d) sustainable (LEP = 30% of unfished levels). Open symbols indicate mean and 95% confidence interval (CI) of predicted biomass at several locations to represent inside:outside comparisons. CIs incorporate process error due to variable larval survival (estimated by running multiple simulations with random variation) and observation error (assumed to be 10% of the mean). Monitoring at different locations relative to the reserve boundary will have different statistical power (indicated by overlap of 95% CIs) to detect a “reserve effect” depending on the species and level of fishing. Panels (e) and (f) show how 5-year model projections for sustainable (solid line) or unsustainable (dashed line) fishing could be compared with hypothetical monitoring results (purple bars with 95% CIs) inside and outside reserves. Additional model details are described in White and Rogers-Bennett (2010).

toring program in the network of MPAs on Australia’s Great Barrier Reef. Such efforts are crucial, because modeling results suggest that many reserves – especially non-self-persistent reserves – depend on effects at relatively large scales. Expanding the scale beyond the immediate area of the reserve must be done carefully, because even BACI designs can be confounded by temporal and spatial variability. For example, the density of fish immediately outside reserve boundaries depends on the movement of adult fish (Moffitt *et al.* 2009) and the distribution of fishing effort after reserve implementation, including harvesters who choose to “fish the line” (ie focus effort just

outside of the reserve boundary; Kellner *et al.* 2007). These factors produce spatial variability in biomass that is difficult to control for without careful selection of “inside” and “outside” study sites (Kellner *et al.* 2007; Figure 3) or sampling along a large-scale transect spanning the reserve boundary (eg Pelc *et al.* 2009; Hamilton *et al.* 2010) where these factors are uncertain. The importance of network-scale effects also precludes traditional, replicated, hypothesis-testing analyses of reserve effects, because it is essentially impossible to replicate at the scale of entire networks.

The differences between Figures 1 and 2 illustrate the mismatch between our understanding of reserve effects from models and the current state of empirical research. Figure 1 summarizes empirical tests of reserve effects, focusing on comparisons at the scale of single reserves, averaged over multiple species. In contrast, the model results in Figure 2 present effects of multiple reserves on each single species on coast-wide scales. The model showed wide variation in performance of different species within the same reserve networks, so multi-species averages could be misleading. Further, the model results indicate that the biomass within a particular reserve depends on factors such as larval dispersal, adult fish movement, fishing outside the reserve, and the placement of other reserves along the coast (White *et al.* 2010a,b; Table 1; Figure 2), complicating the interpretation of results measured at the scale of a single reserve.

Empirical tests of model predictions: reserve size, reserve age, and larval spillover

Several individual empirical studies and meta-analyses go beyond the simple, aggregated, binary hypothesis tests to examine factors driving variation in responses. We now review some of these tests, many of which attempted the difficult task of expanding sampling beyond the local scale.

Common sense suggests that marine reserve size will positively affect abundance and biomass. Indeed, models predict that for lone, self-persistent reserves and a given level of fishing, larger reserves will lead to higher biomass of protected species (White *et al.* 2010a). However, in the network-persistent case, the fraction of total habitat inside reserves will have a much greater effect than individual reserve size (White *et al.* 2010a). Few, if any, empirical studies examine this level of complexity in network dynamics. The empirical evidence for the effects of reserve size is mixed: most meta-analyses do not find an effect (Micheli *et al.* 2004; Lester *et al.* 2009), but Claudet *et al.* (2008, 2010) found a positive effect of reserve size on the density of highly mobile exploited species, consistent with model predictions (Moffitt *et al.* 2009). The lack of an effect in some meta-analyses may be due to the aggregation of data over multiple species (Lester *et al.* 2009), whereas Claudet *et al.* (2008) tested a single group of species.

There is also conflicting evidence regarding whether reserve age has an effect on biomass (Halpern and Warner 2002; Claudet *et al.* 2008). This discrepancy could be a result of temporal or spatial environmental heterogeneity, such as annual-to-decadal variability in recruitment (Carr and Syms 2006; White and Rogers-Bennett 2010), as well as taxonomic aggregation (Micheli *et al.* 2004). The discrepancy could also depend on the variety of time scales over which different processes operate (WebPanel 2). To date, most models make predictions about long-term equilibria, and the subsequent limited understanding of changes over short time scales represents a major shortcoming in applying existing models to empirical monitoring studies.

The potential effect of marine reserves on larval supply to outside fisheries is often discussed in terms of “spillover”, expected to be a gradient in supply extending from the reserve edge. Models suggest that this effect will be more detectable in more heavily exploited species with shorter larval dispersal distances in self-persistent reserves (White *et al.* 2010a), and several studies have detected such patterns (eg Cudney-Bueno *et al.* 2009; Figure 4a). When dispersal distances are greater or larval production is high outside of reserves (White *et al.* 2010b), models predict that larval supply should increase on coast-wide scales, an effect that is logistically difficult to detect (Botsford *et al.* 2009). Increases in larval supply should also depend on the placement of reserves relative to directional larval dispersal patterns (Gaines *et al.* 2003; Costello *et al.* 2010; White *et al.* 2010a), but to date only one empirical study has explicitly linked patterns of larval production and recruitment to ocean currents (Cudney-Bueno *et al.* 2009). Even in that study it was unclear whether the upstream “source” reserve is self-persistent or if the entire metapopulation (and thus the larval supply effect) depends on network persistence.

Beyond a single species

As mentioned above, most marine reserve models focus on single species, and thus there are few broad model predictions for community-level reserve responses. One could interpret the single-species results to suggest that reserves should enhance persistence of many species and therefore increase species richness; many – but not all – reserves show this response (Lester *et al.* 2009; Figure 1). However, no model makes explicit predictions about species richness. Rather, models that include multiple species typically focus on a collection of interacting species to investigate changes in ecosystem structure (reviewed by Baskett *et al.* 2007). The focus on species interactions admits the possibility of some species declining within reserves in response to increases in fished competitors or predators (eg trophic cascades), depending on the relative harvest rates of the interacting species (Baskett *et al.* 2007; WebPanel 3). Thus some of the species declines in Figure 1 may represent reserve success

in restoring ecosystem structure. Overall, investigating patterns arising from particular species interactions can provide a greater understanding of reserve effects than looking for changes in diversity.

■ Integrating models and data in the adaptive management of marine reserves

Adaptive management will require mechanistic, tactical models that can make short-term, context-specific predictions. In adaptive management, model predictions are compared directly with observations to determine whether predicted results have been obtained (Walters 1986). If they have not, analysts and managers refine model assumptions and revise management. The process of testing observed responses against predicted outcomes, and then making adaptive changes, is a continuing, iterative process. In addition, this approach can test theoretical hypotheses regarding the factors influencing reserve performance and therefore enable an understanding of the drivers of monitoring results. Below, we describe some approaches necessary to integrate models and data for adaptive management. Not every model or monitoring design need include every complexity we describe, but models should include the details appropriate for the study system and management questions at hand.

Accounting for process and observation error

When managing adaptively, managers are drawing inferences from variable populations observed with error, and the associated uncertainty must be accounted for. One approach is to use stochastic models. Monitoring data will include both process error and observation error. As with any ecological experiment, the signal (biological effect of the reserve) must be detectable in spite of the noise (process and observation error) to conclude that the observed pattern is not due to chance alone. If estimates of the magnitude of variability in key processes are available, models can incorporate that variability and project the distribution of possible outcomes for monitoring metrics such as density, biomass, and size. This need not involve a complicated model-fitting exercise to partition different sources of error. Rather, one could add variability in certain processes to a deterministic skeleton model (eg Higgins *et al.* 1997) or, even better, include stochasticity directly in the demographic equations (eg Melbourne and Hastings 2008). For example, in the case of a recently implemented MPA network in California, major sources of short-term uncertainty are interannual variation in larval supply and the intensity of fishing outside MPAs. We are currently adapting the equilibrium-based deterministic model used in the design of these MPAs (White *et al.* 2010b) to incorporate observation error, as well as variability in larval survival and adult growth, to predict the range of likely outcomes over a 5–10 year window for several species under different lev-

els of fishing (White and Rogers-Bennett 2010; Figure 3). When monitoring data are evaluated 5 years after implementation (for details, see www.piscoweb.org/mlpa-marine-protected-area-monitoring), comparison to model projections could reveal – for example – whether a finding of no inside:outside difference is within the range of expected results (eg Figure 3f) or whether inside:outside differences in biomass are less than those predicted for the expected level of fishing (eg Figure 3e), suggesting a possible failure of reserve enforcement.

This type of model can also be used to predict signal strength so that observations can be designed accordingly, both in terms of the number of replicates (to obtain the desired statistical power) and their location (see Pelletier *et al.* [2008] for further discussion of this topic). Importantly, data from a time before (or soon after) reserve implementation are required to set the initial conditions for this type of modeling (Figure 4b).

Finding the appropriate spatial scale

In addition to temporal scale, adaptive management will require a closer match between the spatial scale of models and monitoring data. Model projections typically have moderate spatial resolution (eg kilometers) and a coast-wide spatial extent (eg hundreds of kilometers), whereas monitoring data have either fine resolution (hundreds of meters) and limited extent (monitoring within a single reserve) or coarse resolution and broad extent (conventional fisheries monitoring data aggregated over the coastline). A better match of scales requires both downscaling model predictions (eg biomass in a 1-km² model cell) to empirical measurement scales (eg biomass on a 100-m² transect inside a kelp forest) and scaling up reserve monitoring to incorporate the larger network context (eg McCook *et al.* 2010). It may also be possible to include information on long-term, population-wide trends from conventional large-scale fisheries monitoring (compare with White and Rogers-Bennett 2010). In addition, integrating these approaches will require estimating larval production and dispersal from multiple sources over large spatial scales (Botsford *et al.* 2009; Watson *et al.* 2010) to bridge the modeling focus on mean larval dispersal distances and the empirical focus on self-recruitment in a location-specific context (Botsford *et al.* 2009). Information on juvenile and adult movement, including ontogenetic shifts in habitat use, is equally crucial to accounting for spatial dynamics (Moffitt *et al.* 2009).

Selecting useful monitoring metrics

Reserve monitoring efforts tend to focus on a limited set of metrics (eg density, size, biomass, diversity), but some better alternatives may be available. Meta-analyses typically examine biomass and density (eg Lester *et al.* 2009), but these metrics are limited because different combinations of mortality and recruitment can produce equivalent bio-

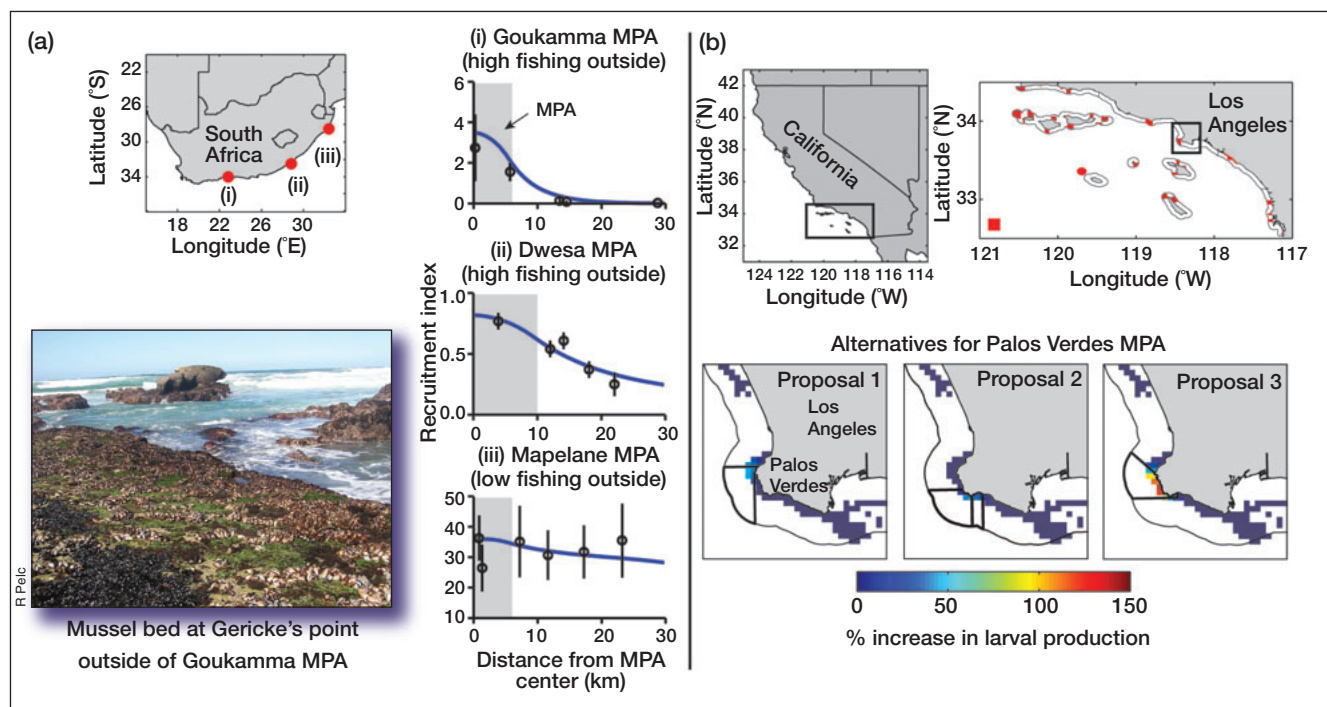


Figure 4. Examples of the potential interaction between data and models for marine reserve assessment. (a) In South Africa, spillover of mussel larvae into unprotected areas was evident for two reserves (i and ii) but not a third (iii). Black symbols indicate mean \pm standard error of recruitment index. This result, considered in isolation, could suggest that the third reserve was not effective. However, stricter management occurred outside reserves in the third location (iii) as compared with that of the first two (i and ii), and fitting a model that included harvest levels outside reserves, spatial variation in larval production, and larval dispersal (blue lines) confirmed that the lower harvest level explained the lack of response and provided an estimate of spillover for the first two reserves (Pelc *et al.* 2009; note that the estimates of larval dispersal distance used in the model were drawn from these same data). (b) In southern California, a tactical model of the kelp rockfish (*Sebastes atrovirens*) population was used to decide among alternative marine protected area (MPA) proposals for the region. The population model included benthic habitat data and dispersal information from an ocean circulation model. The population model was used to predict changes in successful larval production (the number of larvae produced in a location that actually settled in suitable habitat), indicated by color for 1-km² model cells containing rocky reef habitat. Some MPA configurations proposed for the contentious Palos Verdes region near Los Angeles were predicted to produce large increases in larval production (Proposal 3), but others would not (Proposals 1 and 2) (White and Rassweiler unpublished data). The model was only able to make predictions for a long-term equilibrium. Only when combined with monitoring data to establish initial conditions would shorter-term predictions necessary for adaptive management be possible.

masses or densities. An alternative (or complement) could be age structure, which reveals past mortality and recruitment rates and information on population persistence (such as LEP). Collecting age data is labor intensive, so size structure or mean size is often used as a proxy; unfortunately, conversion from size to age distributions with age–size relationships is difficult because of the saturating growth curve of most fish species. Additionally, large recruitment pulses will skew estimates of mean size. However, estimates of vital rates from size distributions are possible (eg Smith *et al.* 1998), and either age or size distributions could reveal whether short-term changes in density are due to increased survival of older fish or increased larval recruitment (see WebPanel 2).

At the community level, empirical studies often focus on diversity, whereas models focus on ecosystem structure, as mentioned above. Development of empirically measurable metrics of ecosystem structure and related properties, as well as a deeper theoretical understanding

of how reserves affect such metrics, will advance an understanding of the potential for reserves to achieve conservation goals. A key question is whether MPAs can enhance the resistance and resilience of socioeconomically desirable ecological states to disturbance, and metrics that tie the theory of these properties to empirically measurable values (eg Carpenter *et al.* 2001) will advance our understanding of how reserves affect these drivers of ecosystem structure. For example, Mumby *et al.* (2006) used a model to suggest that intense grazing by herbivorous fishes (such as those that might occur in a reserve) could enhance the resilience of reef-building coral populations. This prediction was supported by evidence of faster recovery rates from a coral bleaching event in a Bahamian reserve (Mumby and Harborne 2010). However, enhanced coral resilience is not always found in reserves elsewhere in the world (McClanahan *et al.* 2001), so predictive models for reef communities

should include other local factors, such as nutrient loading, that may overwhelm reserve effects.

With respect to measuring the achievement of fisheries goals, fishery yield and catch per unit effort have proven to be useful metrics (eg Russ *et al.* 2004) and can be compared directly with model predictions if collected at an appropriate spatial resolution. Both models and monitoring studies should account for the way fishermen adjust spatial patterns of effort in response to reserves (eg Sanchirico and Wilen 2001; Kellner *et al.* 2007).

■ Conclusions

Now that marine reserve networks have been implemented worldwide, the time is ripe for the implementation of adaptive management. This requires defining goals clearly and determining appropriate monitoring programs to test those goals. To date, empirical evaluations of reserves have largely focused on assessing the performance of individual reserves with respect to single reserve design factors, by asking questions such as, “What is the effect of reserve size on biomass?” In contrast, modeling results indicate that a complex interdependence of factors (reserve size, fishing intensity, larval dispersal patterns) shapes the biological response to reserves over large spatial and temporal scales. Tactical models can integrate these factors to provide a more nuanced set of predictions on the appropriate scales to be tested by field data, allowing the question asked by field assessments to evolve from “Do marine reserves work?” to “When and why do marine reserves work, how long does it take, and what should we be measuring?” If reserve managers are able to utilize model predictions in an adaptive management framework, they can determine whether reserves are working as intended, and make adjustments as needed. This effort will require increasingly close collaboration among modelers, empiricists, and managers.

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WebPanel 1. Terms used in this paper

Adaptive management: an iterative research and decision-making process in the face of uncertainty. In this paper, we specifically mean a process in which (1) models predict the outcomes of alternative policies; (2) after a policy is chosen, the model prediction is tested with monitoring data; (3) the model–data comparison refines and improves the model; and (4) a new round of predictions are generated to inform the next management decision (Walters 1986). This process is often labeled “passive” adaptive management, in contrast to “active” adaptive management in which different management “treatments” are applied within a large-scale experimental framework in order to determine the best strategy. We know of no examples of active adaptive management in marine reserves.

Before–after control–impact (BACI): statistical approach to detecting effects of management action. For marine reserves, the quantity of interest (eg biomass) is compared inside (“impact”) and outside (“control”) the reserve, both before and after the reserve is implemented.

Catch per unit effort: an index of fish abundance that can also be viewed as a measure of cost efficiency in a fishery. In the models described here, the biomass of fishery yield divided by the effort (including all gear types) spent obtaining it (eg boat-days, hook-hours).

Deterministic versus stochastic model: for a given set of initial conditions, stochastic models simulate process error and lead to a random distribution of numerous possible outcomes, whereas deterministic models do not include process error and yield a unique outcome.

Ecological state: a configuration of an ecological community with a distinct composition. For example, a rocky temperate reef could be a kelp forest or an urchin barren.

Fishery yield: in the models described here, this refers to the biomass of fish landed, regardless of market value.

Lifetime egg production (LEP): reproductive output of an average individual over its lifespan, given specific levels of growth, mortality, and harvest.

Marine protected area (MPA): a clearly defined intertidal or subtidal area – including the overlying water – that is recognized, dedicated, and managed, through legal or other means, to achieve some combination of (potentially conflicting) goals of long-term conservation of nature with associated ecosystem services and cultural values within the MPA and increased fishery yields outside the MPA (compare with Dudley 2008).

Marine reserve: a marine protected area where fishing is banned, also referred to as a “no-take” marine protected area.

Metapopulation/subpopulation: metapopulations are collections of

individual subpopulations (local populations in discrete, isolated patches of habitat) that are linked by dispersal.

Observation error/process error: observation error in a quantity is noise introduced by the measurement procedure itself (eg a mistake when counting the individuals in a school of fish). Process error is noise introduced by natural variations of the system being observed (eg fluctuations in recruitment due to environmental conditions).

Overfishing: in the models described here, fishing at levels high enough to lead to eventual population collapse. Note that this usage is distinct from the legal definitions of this term used by the US and other governments.

Population persistence: a population persists through time if it has a long-term steady state abundance that is greater than zero (deterministic models) or if it remains above zero for some specified amount of time (stochastic models). Both definitions require that individuals replace themselves with at least one offspring within their lifetime.

Resistance: how much a system deviates from its steady state when a disturbance occurs.

Resilience: the likelihood of a switch between ecological states following a disturbance (Carpenter et al. 2001).

Self persistence/network persistence: in a self-persistent subpopulation, individuals within the subpopulation replace themselves within a single generation, regardless of immigrants from elsewhere in the metapopulation. A network-persistent metapopulation is one in which a group of connected populations that are not individually self-persistent can persist because of connectivity among them. In this case, self-replacement occurs over multiple generations, when offspring that disperse away from a subpopulation produce their own offspring which return to the “grandparent” subpopulation (Hastings and Botsford 2006).

Species richness: the total number of species present in an ecological community, or within a sampled area.

Strategic versus tactical models: strategic models are a representation of an abstract, idealized system, used to produce general conclusions of broad applicability (eg early models comparing marine reserves to conventional fishery management; Hastings and Botsford 1999). Tactical models are a representation of a particular real-world system, including all of the interactions thought to affect the process of interest in that location. They are used to produce results tailored to that system only (eg models used in decision analysis to implement reserves; White et al. 2010).

Trophic cascade: the propagation of changes in abundances down a food chain. When a top predator increases (decreases) in abundance, its prey decreases (increases); in turn, the resource consumed by the prey will increase (decrease).

WebPanel 2. The time scale of biological responses to marine reserve implementation

The biological effects of marine reserves will accrue over a range of time scales, with some changes appearing over short time scales (months to years), while others will not manifest for many years or decades. This variation in time scale arises because different ecological processes operate at different rates for different species. However, the distinctions between these rates are often not apparent in modeling results, which focus on long-term equilibrium outcomes (eg White *et al.* 2010).

The most immediate effect of reserve implementation will be a decrease in the mortality rate of fished species. This will produce an increase in overall density and a shift in the age and size distributions of the species toward older, larger individuals over a relatively short time scale. The rate of change will likely depend on the magnitude of change in the mortality rates (both natural and fishing-associated) and the growth rates of the species under consideration (Jennings 2001).

Over somewhat longer time scales, the increased density of older, larger individuals may lead to higher recruitment rates, which would further increase overall density. The time scale of this response could be longer and less predictable, given that recruitment success is often affected by variable ocean conditions, and recruitment increases will depend on spatial patterns of larval connectivity, the spatial scale over which larval production has increased, and the reproductive rate of the species (Carr and Syms 2006; Costello *et al.* 2010; see Cudney-Bueno *et al.* [2009] for an example of a rapid increase in recruitment). The rate at which these changes in recruitment occur will determine the time scale over which the population approaches equilibrium density and age structure. Furthermore, the time lag between recruitment and reproductive maturity could lead to cyclic

dynamics, in which population densities and biomass may vary widely in the first several years after reserve implementation, with the period of oscillations proportional to the age of maturity (compare with Cohen [1979]; this is sometimes called the “cohort resonance effect”). This could lead to misleading “drops” in biomass after reserve implementation, despite an overall upward trajectory.

Changes in interspecific effects within and between trophic levels will also play out over longer time scales. Reductions in fishing are usually expected to increase predator densities, but organisms belonging to lower trophic levels may also be released from fishing pressure, and the initial “transient” response to changes in densities of interacting species is likely to be complex and difficult to predict (eg Babcock *et al.* [2010] found that direct effects of reserves on target species occurred much more rapidly than indirect effects of those target species on lower trophic levels; also see WebPanel 3). The initial trajectories of change may be substantially different from the long-term equilibrium (Hastings 2004), which will only be reached over years to decades (if ever) as mortality and recruitment rates of each species stabilize, especially in highly variable environments.

Even longer time scales will be needed to observe certain changes, such as physical changes to biogenic habitat within the reserve. This can include recovery from human disturbances (eg bottom trawling) or changes that are mediated by fished species (eg herbivores promoting coral reef accretion by reducing algal overgrowth). Evolutionary effects, such as increases in the age of maturity, may also appear over longer time scales, although these effects may occur over shorter time scales than one typically associates with evolutionary change (Baskett *et al.* 2005).

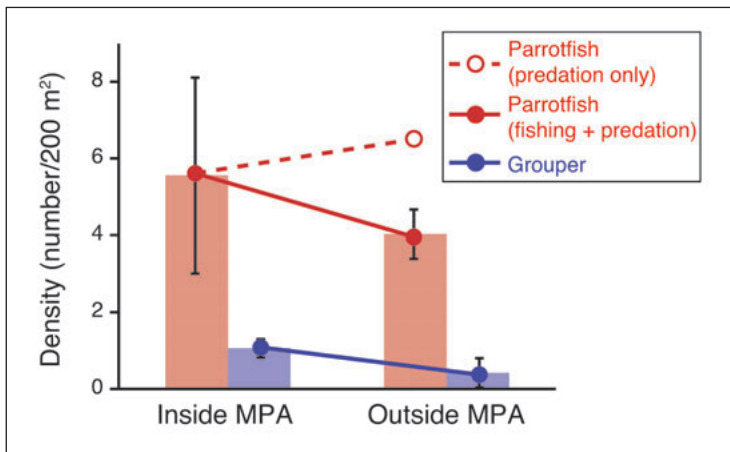
WebPanel 3. Trophic cascades inside marine reserves

Given the tendency for fisheries to target top predators, one expectation for community-level responses to marine reserves is trophic cascades: inside reserves, top predators (eg piscivores) increase in abundance, their prey (eg herbivores) decrease, and producers (eg macroalgae) increase. Whether this outcome is considered positive by managers can depend on the context: in kelp forests, an increased prevalence of kelp-dominated states as compared with the less-diverse urchin barrens is generally seen as desirable, whereas in coral reefs a decreased abundance of herbivores and an increase in macroalgae could present a problem for the reef-building corals that form the foundation of the ecosystem.

However, trophic cascades after reserve establishment are not a ubiquitous outcome. Meta-analyses do not indicate an overall pattern of trophic cascades occurring after reserve establishment, but the magnitude of response to reserves does depend on trophic group (Micheli *et al.* 2004). An array of ecological processes can reduce the potential for cascades by increasing complexity in trophic interactions beyond a simple linear food chain (eg cannibalism, complex food webs, spatial refuges from predation). For example, Shears *et al.* (2008) found that the potential for predator–urchin–kelp cascades in New Zealand

reserves depended on the context, with cascades less likely to occur in sites where environmental conditions impeded urchin survival or grazing. Furthermore, harvest on multiple trophic levels increases the potential for both prey and predators to benefit from reserves (Kellner *et al.* 2010). In Bahamian marine reserves, trophic cascades were not observed in a (piscivorous) grouper/(herbivorous) parrotfish system (Mumby *et al.* 2006). Models indicate Mumby *et al.*'s (2006) hypothesis that harvest of both groupers and parrotfish before reserve establishment, potentially in combination with a prey size refuge (groupers cannot eat large parrotfish), could possibly explain the lack of cascades in that system (Kellner *et al.* 2010). Accounting for harvest on multiple trophic levels in such models leads to accurate predictions of the species' responses to reserve establishment (Kellner *et al.* 2010). This use of models to predict species responses, along with an example of the more typical trophic cascade expectation, is shown in WebFigure 1.

These examples illustrate how an understanding of abiotic factors, key species interactions, and the distribution of harvest across interacting species is necessary to formulate appropriate expectations for community-wide responses, such as trophic cascades, after reserve establishment.



WebFigure 1. Trophic cascades (or the lack thereof) in a Bahamian marine reserve. Kellner et al. (2010) modeled the interaction between groupers (predators; blue) and parrotfish (prey; red). They predicted that if both the groupers and parrotfish are heavily fished outside of the reserve (fishing effort on parrotfish was assumed to be 30% of that on grouper), both species would have higher densities inside the reserve (solid lines and symbols). This prediction matched the density of those species observed from surveys inside and outside the reserve (bars indicate mean density, error bars are 1 standard deviation). If parrotfish were not fished, one would expect a more typical trophic cascade inside the reserve: parrotfish would have higher densities outside the reserve, where predation is lower, and lower densities inside the reserve, where predators are more abundant. We approximated this scenario (dashed line and open symbol) using Kellner et al.'s (2010) prediction for parrotfish density with no fishing and no predation by groupers (essentially assuming that grouper density would be very low outside of the reserve). Adapted from Kellner et al. (2010).

WebTable 1.

Theoretical predictions and empirical tests of relationships between several management and intrinsic biological factors and various ecological responses to MPA implementation. For each factor, the theoretical (blue) or empirical (red) relationship reported by a paper is indicated by a symbol: positive (+), negative (−), no effect (0), intermediate optimum (^), or some effect that may vary in direction (×). Relationships that have not been examined (to our knowledge) are indicated by a question mark (?). Empirical references that are meta-analyses are indicated by italics. In general, most of these predictions are highly context-dependent, and the magnitude of the change depends on the other factors in the table; thus the entries in this table represent generalizations. The time scale over which a response is expected to manifest is given as intra-, inter-, or multi-generational, by which we mean time scales on the order of 0.1, 1, and 10 generations, respectively. “MPA fragmentation” refers to the degree to which an MPA network is composed of many small rather than few large MPAs (analogous to the Single Large Or Several Small [SLOSS] dichotomy in terrestrial conservation biology). The effects of harvest (or other negative impacts) can depend on whether it occurred in the same location as the MPA but before MPA implementation, or outside of the MPA after the MPA is in place. “Population growth rate” may refer to the parameter r in a logistic population model (eg Mangel 2000a), or to the slope at the origin of the stock-recruit curve in an age-structured model with density-dependent recruitment (eg White *et al.* 2010). Greater “population stability” and “catch stability” correspond to lower temporal variation in population density and catch, respectively. “Resistance” and “resilience” are defined in WebPanel 1. Some factors are known to have an effect but those effects are not necessarily directional and do not readily fit into this framework. These include the placement of MPAs relative to productive, high-quality habitats (Crowder *et al.* 2000; Rodwell *et al.* 2003), larval retention zones (White *et al.* 2010) or directional oceanographic currents (Crowder *et al.* 2000; Gaines *et al.* 2003; Costello *et al.* 2010), and the manner in which fishermen choose to distribute their effort in response to MPA implementation (eg “fishing the line”, Kellner *et al.* 2007; or the use of mandatory buffer zones, Salomon *et al.* 2002). We also did not include some response variables for which it is difficult to assign a directional prediction, such as changes in community structure (eg Baskett *et al.* 2006, 2007; Salomon *et al.* 2002; Ault *et al.* 2005) or economic metrics such as long-term value. Finally, because we are focused on no-take marine reserves, we do not include the level of protection inside a partial-take MPA as a management factor.

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WebTable 1a. Management factors affecting the biological response to MPAs.

| | Predicted response | Time scale | Management factors | | | | | | | | | | |
|---|------------------------|------------|---|--|--|---|-----------------------|--|---|------------------------|--|--|--|
| | | | MPA size | | MPA fragmentation (SLOSS) | | Harvest/impact before | | Harvest/impact outside | | MPA age | | |
| Proxies for population persistence (inside the MPA) | Biomass | Intra | + | 0 | - | ? | ? | + | - | ? | + | 0 | |
| | | | (Guenette and Pitcher 1999, Kaplan et al. 2009, White et al. 2010a) | (Lester et al. 2009) × | (Botsford et al. 2001, Kaplan et al. 2009) | | | (Guidetti and Sala 2007) | (Guenette and Pitcher 1999, Kaplan et al. 2009, White et al. 2010b) | | (Mangel and Levin 2005) | (Halpern and Warner 2002, McClanahan et al. 2009) + | |
| | | | | (McClanahan et al. 2009) | | | | | | | | (Stobart et al. 2009) | |
| | Age and size structure | Intra | ? | 0 | ? | ? | ? | ? | ? | ? | ? | 0 | |
| | | | | | (Halpern 2003) + | | | | | | | (Halpern and Warner 2002) + | (Guidetti 2006, Stobart et al. 2009, Goñi et al. 2010) |
| | | | | | (Edgar and Barrett 1999) | | | | | | | | |
| Larval supply | Inter | + | ? | - | ? | ? | ? | - | ? | ? | ? | ? | |
| | | | (Die and Watson 1992, Botsford et al. 2001) | | (Botsford et al. 2001, Kaplan et al. 2009.) | | | | (Botsford et al. 2001, Kaplan et al. 2009, White et al. 2010b) | | | | |
| Density | Inter | + | 0 | - | ? | ? | + | - | + | + | 0 | | |
| | | | (Hannesson 1998, Kellner et al. 2008, Kaplan et al. 2009, White et al. 2010a) | (Claudet et al. 2008) + | (Quinn et al. 1993, Kritzer 2004, Kaplan et al. 2009.) | | | (Micheli et al. 2004b, Ashworth and Ormond 2005, Molloy et al. 2009) | (Quinn et al. 1993, Kritzer 2004, Kaplan et al. 2009, White et al. 2010b) | (Mosquera et al. 2000) | (Acosta 2002, Gaines et al. 2003, Kellner et al. 2008) | (Micheli et al. 2004b) + | |
| | | | | (Edgar and Barrett 1999, Halpern 2003) | | | | | | | | (Molloy et al. 2009) - | |
| | | | | (Halpern 2003) | | | | | | | | (Goñi et al. 2010) | |
| Population stability | Inter | ? | ? | - | ? | ? | ? | - | ? | ? | ? | ? | |
| | | | | | (Kritzer 2004) | | | | (Kritzer 2004) | | | | |
| Life history evolution | Multi | + | ? | - | ? | ? | ? | - | ? | ? | ? | ? | |
| | | | (Baskett et al. 2005) | | (Baskett et al. 2005) | | | | (Baskett et al. 2005) | | | | |
| Community-level response (inside the MPA) | Alpha diversity | Inter | ? | 0 | ? | ? | ? | ? | ? | ? | ? | 0 | |
| | | | | (Halpern 2003) + | | | | | | | | (Halpern and Warner 2002, Stobart et al. 2009) + | |
| | | | | (Edgar and Barrett 1999, McClanahan et al. 2009) | | | | | | | | (Russ and Alcalá 2010) × | |
| | | | | | | | | | | | | (McClanahan et al. 2009) | |

| | | | | | | | | | | | | | |
|--|---------------------------|-------|--|---|---|---|---|---|---|--|---|--|-------------------------|
| | Beta diversity (evenness) | Inter | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 (Stobart et al. 2009) × (Micheli et al. 2004b) | |
| | Average trophic level | Inter | + (Micheli et al. 2004a) | ? | ? | ? | ? | ? | ? | ? | ? | + (Stobart et al. 2009) | |
| | Resistance | Inter | ? | ? | ? | ? | ? | ? | ? | ? | ? | + (Selig and Bruno 2010) | |
| | Resilience | Inter | + (Baskett et al. 2006) | ? | ? | ? | ? | ? | ? | ? | ? | ? | |
| Response of fisheries (outside the MPA) | CPUE | Intra | ? | ? | ? | ? | ? | ? | ? | ? | ? | + (Russ et al. 2004; Stobart et al. 2009) | |
| | Total yield | Inter | ^ Guenette and Pitcher 1999 - (Mangel 2000a) + (Stefansson and Rosenberg 2005) × (Holland and Brazee 1996, Hastings and Botsford 2003, Botsford et al. 2004, Kaplan et al. 2006, Kellner et al. 2008) | ? | ^ (Quinn et al. 1993) + (Kritzer 2004) | ? | ? | ? | ? | ^ (Quinn et al. 1993, Guenette and Pitcher 1999, Lundberg and Jonzen 1999, Kritzer 2004, Stefansson and Rosenberg 2005) × (Holland and Brazee 1996, Hastings and Botsford 1999, White et al. 2010b) | ? | Depends on harvest outside (Hilborn et al. 2006) + (Kellner et al. 2008) | + (Russ et al. 2004) |
| | Catch stability | Multi | + (Sladek Nowlis and Roberts 1999, Mangel 2000b) | ? | + (Kritzer 2004) | ? | ? | ? | ? | - (Kritzer 2004) | ? | ? | ? |
| | Catch sustainability | Multi | + (Stefansson and Rosenberg 2005) | ? | ? | ? | ? | ? | ? | - (Stefansson and Rosenberg 2005) | ? | ? | ? |

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