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

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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

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 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.

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

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.

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

<i>Assumption</i>	<i>Representative examples</i>	<i>Exceptions</i>
<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 non-linear 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> (2008)
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.		

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

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).

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 explication 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 monitoring

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 Symms 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- to 10-year window for several species under different levels of fishing (White and Rogers-Bennett 2010; Figure 3). When monitoring data are evalu-

ated 5 years after implementation (for details, see www.pis-coweb.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 biomasses 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).

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.

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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