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Abstract

Ecosystems and the species and communities within them are highly complex systems that defy predictions with any degree of certainty. Managing and conserving these systems in the face of uncertainty remains a daunting challenge, particularly with respect to developing networks of marine reserves. Here we review several modelling frameworks that explicitly acknowledge and incorporate uncertainty, and then use these methods to evaluate reserve spacing rules given increasing levels of uncertainty about larval dispersal distances. Our approach finds similar spacing rules as have been proposed elsewhere – roughly 20–200 km – but highlights several advantages provided by uncertainty modelling over more traditional approaches to developing these estimates. In particular, we argue that uncertainty modelling can allow for (1) an evaluation of the risk associated with any decision based on the assumed uncertainty; (2) a method for quantifying the costs and benefits of reducing uncertainty; and (3) a useful tool for communicating to stakeholders the challenges in managing highly uncertain systems. We also argue that incorporating rather than avoiding uncertainty will increase the chances of successfully achieving conservation and management goals.

Keywords

Dispersal, marine protected areas, marine reserves, metapopulation model, reserve networks, spacing, uncertainty.

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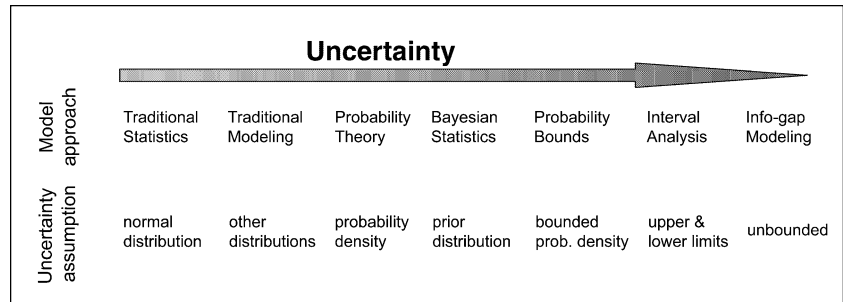
INTRODUCTION

In general, the aim of science is to reduce uncertainty or to make inferences about the world in the face of uncertainty. Experiments are designed and implemented, models are parameterized and run, and survey results are collated and synthesized in an effort to provide predictions about and explanations for the nature of the world in which we live. However, many systems are so complex and variable that they preclude the removal of uncertainty, and so a wide variety of academic and applied fields have developed methods for dealing with and accounting for uncertainty. Decision theory, developed for economics, management, and engineering, and probabilistic risk assessment are two of the more well-known examples of modelling frameworks for complex systems that address and treat uncertainty (Raiffa 1970, Jeffrey 1983, Morgan & Henrion 1990, Thompson & Graham 1996, Warren-Hicks *et al.* 1998). Ecological systems are also highly complex, and the conservation and management of these systems – and the species that comprise them – can be a daunting task. Inappropriate strategies and decisions can lead to population crashes or ecosystem failures, which can have profound

ecological and economic impacts, and in many cases management decisions can directly impact species' chances of extinction.

Uncertainty is often modelled stochastically, even though the uncertainty in the system arises from both error in and variation around parameter estimates (Regan *et al.* 2003). The distinction is important—incremental increases in data collection can often provide better estimates of variation, but the variance itself cannot be removed, and it would require a truly deterministic model of the world (and inconceivable amounts of data) to remove all model uncertainty. Only a few of the variety of ways to model uncertainty in ecological systems (Fig. 1) explicitly account for this distinction; it can be valuable to know which source of uncertainty is driving any error in model predictions. The modelling approaches (Fig. 1) also differ in how they mechanistically treat uncertainty. Traditional statistics and probabilistic modelling approaches assume that the different moments (mean, variance, etc.) or probability distributions (normal, log-normal, etc.) provide adequate descriptions of the variation and uncertainty in parameter values. To more explicitly incorporate uncertainty in these parameter values into modelling approaches, assumptions are made about the

Figure 1 Overview of uncertainty and a subset of modelling approaches for dealing with different levels and types of uncertainty. ‘Uncertainty Assumptions’ describe how uncertainty is incorporated into the modelling framework.



probability density functions (under ‘probability theory’ in Fig. 1), the range of possible probability density functions (probability bounds analysis), or the prior distribution (Bayesian statistics). However, all of these modelling approaches only deal with uncertainty that can be expressed probabilistically, which is only a subset of the full range of uncertainty that likely exists in most ecological systems (Regan *et al.* 2002a; Burgman 2005). Under severe uncertainty, it may not be possible to parameterize probability distributions or even decide on an appropriate form for the distribution. If upper and lower bounds are known on possible parameter values, then interval analysis can be used (Moore 1966) to essentially evaluate the worst- and best-case scenarios. If even these bounds are unknown, information-gap theory (info-gap; Ben-Haim 2001) provides a method for evaluating the robustness of model-based decisions when only best guess for model parameters or probability distributions are available. Info-gap analysis adopts a philosophically different approach to modelling and decision-making. It asks how wrong can one be and still get an acceptable result. The best decision is then chosen as the one that is most robust to uncertainty, i.e. is guaranteed to give acceptable outcomes under the greatest degree of uncertainty.

Only very recently have these ideas and modelling approaches begun to percolate into ecological theory and applications, particularly for models used in conservation and management planning (e.g. fisheries) actions where decisions must be made about human efforts to regulate natural systems (Charles 1998, Ben-Haim 2001, Harwood & Stokes 2003, Doyen & Bene 2003, Lande *et al.* 2003, McCarthy *et al.* 2005, Regan *et al.* 2002b, 2005, Grafton *et al.* 2005). For example, Doyen & Bene (2003) use a fuzzy logic approach to model how uncertain fish harvest rates affect population persistence (i.e. robustness to failure), while Regan *et al.* (2005) use info-gap theory to compare different management actions for the Sumatran rhino given uncertain utility and probability functions. In both of these examples, explicit treatments of uncertainty in model parameters led to different management and conservation decisions than when uncertainty was ignored, illustrating why such considerations are more than just academic. There have

also been some attempts to examine uncertainty in estimates of extinction risk and the decisions that use these estimates (McCarthy *et al.* 1996; Ludwig 1999; Fieberg & Ellner 2000; McCarthy *et al.* 2003). However, a comprehensive treatment that considers all aspects of uncertainty in conservation and resource management is in its formative stages – at best there has been a tendency to acknowledge the full scope of the uncertainties rather than to tackle the uncertainties head on.

Marine conservation and resource management efforts are equally limited in their treatment of uncertainty. Traditionally, fisheries management has dealt with uncertainty by trying to reduce it through gathering as much data as possible. These data are used to provide maximally accurate parameter estimates that guide maximum sustainable yield (MSY) estimates. This is a costly and time-consuming endeavour, particularly when fisheries are managed species by species, and MSY can be difficult to achieve given the uncertainty inherent in the model structure and input parameters (Ludwig *et al.* 1993). More recently, interest in using networks of marine reserves for conservation and fisheries management purposes has created additional confluences of uncertainty and management decisions. To design a reserve network, one must choose the sizes of the reserves and the appropriate spacing between the reserves. In general, size and spacing rules are guided by estimates of how far larvae disperse (connectivity between reserves) and the patterns of adult movement (spillover out of reserves; Gerber *et al.* 2003). In particular, larval dispersal is necessary to ensure sustainability of populations for both conservation (supplying populations inside reserves) and fisheries enhancement (supplying populations outside the reserves).

However, actual measurements of movement patterns, and more notably larval dispersal distances, for most marine species remain elusive. Although evidence is emerging that can be used to provide best estimates and bounds on possible values (e.g. Kinlan & Gaines 2003, Kinlan *et al.* 2005), movement and dispersal patterns remain largely unknown, and the interactions of these dispersal parameters with population and community dynamics and environmental variables are extremely complex. For example,

uncertainty in larval dispersal estimates arises from imperfect knowledge about reproductive success (how many larvae are actually produced), the behaviour of the pelagic larvae and consequent effects on movement patterns, and the great complexity and uncertainty in the oceanographic processes that affect larvae (e.g. ocean currents, wind and weather, climate change). On top of these biological and physical sources of uncertainty, uncertainty also arises from simple measurement error and variability across time and space. Despite this uncertainty in dispersal patterns, reserve size and spacing rules have been developed based on point estimates of average dispersal distances or models that assume various forms of dispersal distance distributions (reviewed in Gerber *et al.* 2003).

Reducing uncertainty through data collection efforts typically come at very great economic cost and requires huge amounts of effort. For example, effective traditional fisheries management requires annual expenditures of millions of dollars, weeks of boat-time, and months of laboratory and analysis time to parameterize harvest models for each species. Design rules for marine reserve networks rely on the vast resources spent trying to develop estimates of dispersal and movement patterns. Such expenditures may be necessary or highly valuable, depending on the goals of a particular management situation (e.g. strong stakeholder investment in a region may demand precise reserve designs), but if uncertainty analysis can provide reasonable and robust design criteria without these extreme expenditures, then they hold great promise for conservation and management efforts.

$$q = \frac{e^{-\beta \cdot d}(2 \cdot p_e - 1) - (p_e - 1)[2 + (e^{-\alpha \cdot d} - 1) \cdot p_e]}{2} + \frac{\sqrt{4 \cdot (p_e - 1)[(e^{-\beta \cdot d} + p_e - 1)(p_e - 1) - e^{-\alpha \cdot d} \cdot p_e(p_e - e^{-\beta \cdot d} - 1)] + [2 - 3 \cdot p_e - e^{-\alpha \cdot d} \cdot p_e(p_e - 1) + p_e^2 + e^{-\beta \cdot d}(2 \cdot p_e - 1)]^2}}{2} \quad (1)$$

Our aims in this paper are twofold. First, we want to highlight the need for, and value of, a variety of approaches to modelling uncertainty that have been developed in other fields that are currently available for marine as well as terrestrial reserve design. We have introduced some of these approaches above, and will illustrate their use and discuss some important results and caveats below. Second, we want to demonstrate how to use this body of theory to provide concrete guidelines for reserve design, and in particular to evaluate the pros and cons of the different modelling approaches and compare the management recommendations they produce. To that end, we focus on a single question – how far apart should reserves be spaced? – and use a series of approaches to modelling uncertainty to

evaluate rules for optimal reserve spacing given increasing levels of uncertainty about larval dispersal distances.

METHODS

Reserve model

McCarthy *et al.* (2005) developed a multi-patch population model to evaluate the optimal number of reserves within a reserve network necessary to maximize population persistence of a single species, assuming no dispersal among patches. They extended this model to evaluate the effect of colonization (dispersal rates) and correlation between patches of extinction events (e.g. from catastrophic events) on population persistence in a two-patch reserve network. Here we focus on the latter extension of the model. Although this 2-patch colonization-extinction model is a highly simplified version of the dynamics of an actual reserve network, it captures the two primary processes currently used to determine reserve spacing rules – dispersal distances and extinction correlations – while providing a well-developed modelling framework in which to illustrate the implications of uncertainty in reserve design and apply established treatments of uncertainty.

We start from the persistence criterion (q) that McCarthy *et al.* (2005) developed to evaluate if dispersal and extinction correlation affect the optimal number of reserves (q is the second eigenvalue of the reduced matrix \mathbf{R} ; see McCarthy *et al.* 2005, including p. 3 of Appendix S1, for the derivation of this eigenvalue):

where d is the distance between the two reserves, β is a dispersal parameter ($1/\beta =$ mean dispersal distance), p_e is the local probability of extinction within a patch, and α influences the rate at which the correlation in extinction events declines with distance. Both dispersal and patch correlation are assumed to decline exponentially with distance, hence the expressions $e^{-\alpha \cdot d}$ and $e^{-\beta \cdot d}$. Smaller values of β lead to smaller risks of extinction, since smaller values indicate longer mean dispersal distances and higher colonization rates between patches. In contrast, smaller values of α indicate stronger correlations in extinction events and, therefore, higher risks of extinction. The persistence criterion q is approximately equal to the annual probability of persistence of the metapopulation

(particularly for long-time horizons), so maximizing q will approximately maximize the probability of persistence.

Uncertainty models

Here we focus on evaluating the optimal distance between reserves given different assumptions about uncertainty in dispersal distance. In particular, we analyse the persistence criterion (q) in four different ways that evaluate the impact on optimal reserve spacing rules given increasing levels of uncertainty in estimates of a species' mean dispersal distance ($1/\beta$). For simplicity we assume that $p_e = 0.05$ (i.e. an endangered metapopulation, since this is the annual extinction rate) and $\alpha = 0.01$, although we explore the sensitivity of our results to these values by analysing the model with $p_e = 0.01$ or 0.1 and $\alpha = 0.005$ or 0.05 . For estimates of β , we use data from Kinlan & Gaines (2003) for single-generation fish dispersal distances, which show an average $\beta = 0.05$ (which converts to a mean dispersal distance = 20 km) with SD of 0.10 and a range of 0.0019 (527 km) to 0.3704 (2.7 km).

We first solve for q assuming that β is perfectly known, with $\beta = 0.05$. This is the traditional approach to modelling reserve design – establish a reasonable model for describing the population dynamics of a protected species and parameterize it with best estimates for each parameter. However, it is rare that we can be certain of the true value of parameters in ecological models since there is generally a paucity of data, and measurement error and/or variation in the data we do have. The most common method for expressing uncertainty in parameters in ecological models is to assign a probability distribution to the parameter in question with an assumed mean and SD. This strategy is generally meant to represent the temporal and spatial variation in the parameter(s), but is also commonly used to represent uncertainty (Regan *et al.* 2003). Under this strategy, it is assumed that the mean, SD and distribution type (or shape) are all known with certainty. Here, we assign a lognormal distribution to β with a mean of 0.05 and a SD of 0.10 (from Kinlan & Gaines 2003). We chose a lognormal distribution because, of the three types of simple default distributions commonly used to describe variation and uncertainty in parameters (i.e. the normal, lognormal and uniform distributions), it is the one that best fits the inverse dispersal data in Kinlan & Gaines (2003). Latin hypercube sampling (a type of Monte Carlo approach that stratifies the entire parameter space) was then used to propagate the range of values for β throughout the calculation (eqn 1) for a selection of distance (d) values. For each value of d , any value for q on the inverse cumulative distribution function (cdf) is possible.

However, we are seldom certain of the shape of distributions representing uncertainty or variation in model

parameters, and the choice of distribution shape can have a dramatic effect on model output (e.g. Regan *et al.* 2002b). To allow for this uncertainty in the shape of the distribution of β , we used probability bounds analysis (Ferson 2002; Tucker & Ferson 2003). Whereas in the example above a lognormal distribution was assigned to capture the uncertainty in β , in this model formulation we bound all possible distributions within upper and lower cumulative probability bounds, with mean 0.05, a SD 0.10, a minimum of 0, and a maximum of 0.3704 to correspond with moments, the minimum and maximum of the available data (using Risk Calc 4.0, Ferson 2002). Propagation of probability bounds through the equation for q (eqn 1) results in upper and lower bounds on the resultant cumulative probability distributions for the persistence criterion. For each value of d , the resulting bounds contain all possible distributions for q given the available information, without being too wide – every point along the bounds corresponds to a point on some distribution that satisfies the constraints on β . This is similar to a two-dimensional Monte Carlo approach to characterizing uncertainty, although with probability bounds analysis, as applied here, no assumptions are made about the shape of the probability distribution (only its mean, SD and limits) and the bounds are best possible (not based on, for example, fifth and 95th percentiles).

For many if not most marine species, we are uncertain about the value of β to the extent that probability bounds cannot be assigned. Instead, only a best guess (e.g. a mean value based on other species) and bounds within which the true parameter value is sure to lie can be assumed. In this case, an interval analysis can be performed to calculate plausible bounds on the persistence criterion (q) and corresponding bounds on the distances that maximize q . Essentially, the minimum and maximum values believed to be possible for β are used in eqn 1 to define the full range of possible model outputs. Here we take the published range as well as the mean dispersal distances for a variety of fish species (Kinlan & Gaines 2003) and use them as the best guess and plausible range of values. In this case, the best guess for β remains 0.05 but it is now bounded below by 2.7 km and above by 527 km giving a range for β of (0.0019, 0.3704).

Finally, we allow for severe uncertainty and evaluate optimal reserve spacing assuming we only have a best guess for dispersal distance (β) but acknowledge that our best guess is highly uncertain by an unknown amount. Info-gap theory approaches uncertainty analysis from the opposite direction as probabilistic and interval analysis methods. Rather than specifying the extent of uncertainty in parameters at the outset, info-gap theory takes the position that the best strategy is the one that gives us an outcome that is both acceptable and keeps us immune from unacceptable

outcomes given some level of uncertainty (Ben-Haim 2001). That is, we choose a strategy that maximizes the reliability of an adequate outcome (i.e. an acceptable value for the persistence criterion, q). We model uncertainty around β as

$$\frac{|\beta^* - \beta|}{\beta} \leq u \Rightarrow (1 - u)\beta \leq \beta^* \leq (1 + u)\beta \quad (2)$$

where $u \geq 0$ is the unknown and unbounded horizon of uncertainty, β^* is the true but unknown value of the mean inverse dispersal distance and β is our best guess (here $\beta = 0.05$). Alternative info-gap models of uncertainty can be used; we use the simplest form from Ben-Haim (2001) for illustrative purposes. In this info-gap model of uncertainty, β^* varies from its nominal value, β , by no more than a fraction u .

Furthermore, we can define Q as the critical value of the persistence criterion (q) below which the prospects for persistence are regarded as unacceptable. The critical value Q is the minimal requirement that our chosen action (patch spacing d) must adhere to – we would like the value of q to be as large as possible, but it must be no less than Q . The robustness function for a given patch spacing is formulated as follows:

$$\hat{u}(d, Q) = \max \left\{ u : \left[\min_{\beta^* \in [(1-u)\beta, (1+u)\beta]} q(d, \beta^*) \right] \geq Q \right\}. \quad (3)$$

Equation 3 states that the robustness function $\hat{u}(d, Q)$ for distance d and critical threshold Q is equal to the maximum value of u that ensures the minimum persistence probability (q) is greater than or equal to the critical threshold. Since we have specified the critical threshold very generally, the solution to eqn 3 provides reserve spacing rules given different horizons of uncertainty. Analogous to the upper bound in interval analysis and probability bounds analysis, info-gap analysis can also be used to evaluate propitious opportunity (i.e. windfall or gains that exceed our expectations) but we take a precautionary approach here and restrict our analysis to robustness.

RESULTS

Model results

Given the assumption of a known value for β , persistence probability (q) is maximized at 0.964 with optimal reserve spacing of 47.5 km, or *c.* 2.5 times the average dispersal distance (Fig. 2). Treating uncertainty with an assumed probability distribution for β , there is no single distance (d) that consistently maximized q (Fig. 3). The cumulative

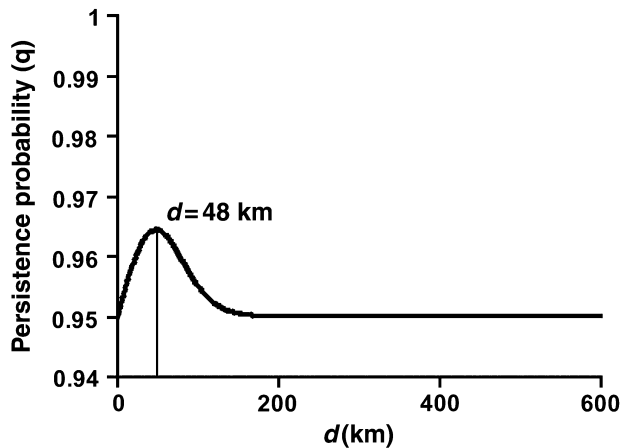


Figure 2 The approximate persistence probability (q) values for different distances between reserves assuming known values of all parameters, including β (dispersal distance). q is maximized ($q = 0.964$) at $d = 48$ km. See Methods for parameter values.

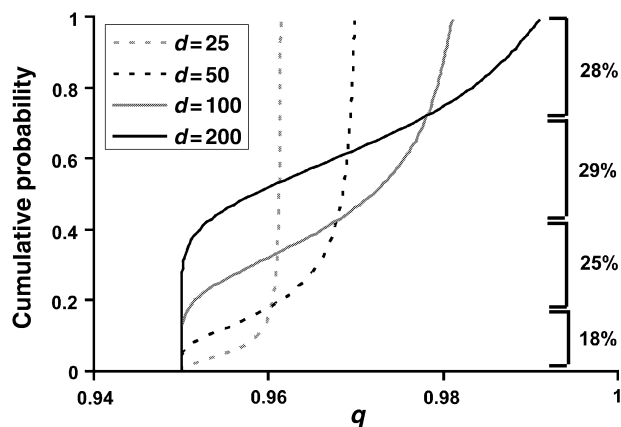


Figure 3 Cumulative distribution functions of the persistence criterion (q) at four possible reserve spacing values (d) using precise probability distributions for β . Percentages on the right-hand side of the figure indicate the amount of cumulative probability over which each distance maximizes q . See Methods for parameter values.

probability tells us the chance that the persistence criterion (q) will have a value up to that specified on the horizontal axis, and we are guaranteed a q -value of at least 0.95 for all distances. Consequently, conservative attitudes to risk (i.e. risk-averse) operate at the lower end of the cumulative probability distribution, while optimistic (i.e. risk taking) choices operate at the upper end. As we read along the horizontal axis in Fig. 3 from left to right (conservative to optimistic risk attitudes), we see that for the first 18% of cumulative probability $d = 25$ km consistently results in the highest q -values ($0.950 \leq q < 0.961$). Then there is a 25%

chance that $d = 50$ km results in the highest q -values ($0.961 \leq q < 0.968$), followed by a 29% chance that $d = 100$ km results in the highest q -values ($0.968 \leq q < 0.978$), and finally under optimistic attitudes there is a 28% chance that the greatest values of q occur with $d = 200$ km ($0.978 \leq q < 0.99$). Distances greater than 200 km had only marginal potential for providing higher persistence probabilities, and distances greater than 420 km were never optimal (results not shown). Since the probability is cumulative, the decision to attempt to maximize persistence probabilities by selecting a reserve spacing of $d = 200$ km runs a substantial risk of achieving persistence probabilities less than all the other lower distances considered. For instance, there is a 72% chance that a reserve spacing of $d = 200$ will result in persistence probabilities less than those for $d = 100$, a 61% chance that it will achieve q -values less than those for $d = 50$ and a 53% chance that it will result in the lowest persistence probabilities of all reserve spacing distances considered. Thus, choosing the optimal reserve spacing under probabilistic uncertainty in β essentially becomes an exercise in risk management. How much is one willing to trade-off a more definite result for the chance of a bigger pay-off? Although there is a 61% chance that $d = 50$ does better than $d = 200$, $d = 50$ can never give $q > 0.97$ while $d = 200$ can result in q -values up to 0.99 (Fig. 3).

Using probability-bounds analysis, we get a slightly different outcome for optimal reserve spacing compared with the treatment with precise probability distributions above. Focusing on the lower bounds (i.e. the conservative or worst-case scenario), a distance of $d = 200$ km never results in the highest persistence probabilities (Fig. 4). Once again, following the lower bound cdfs from left to right, q is maximized over 35% of the cdf for $d = 25$ km, 35% of the cdf for $d = 50$ km and 30% of the cdf for $d = 100$ km.

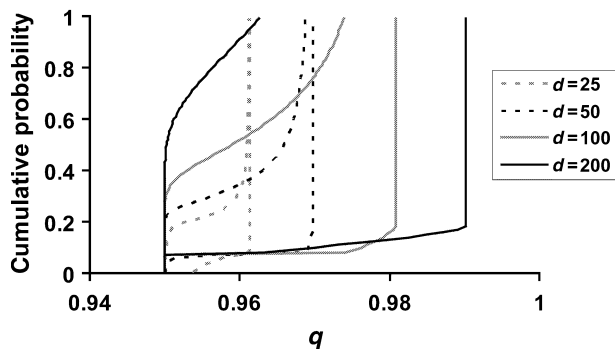


Figure 4 Upper and lower cumulative probability bounds for the persistence criterion (q) at four possible reserve values (d) assuming a bounded distributions for β . Minimum and maximum possible values for β were derived from Kinlan & Gaines (2003). See Methods for parameter values.

Focusing on the upper bounds (i.e. the risk taking or best-case scenario), we see that $d = 200$ km nearly always maximizes the persistence probability, although persistence probability begins to decrease when $d > 340$ km (result not shown). It is clear that the sensitivity of q to the probability bounds depends on the distance between reserves (the area between the lower and upper bounds increases as d increases). Hence, uncertainty about the values and the shape of the distribution for β is such that in order to make a decision about patch spacing, one needs to decide on an appropriate level of risk aversion. Extremely risk-averse decision makers would opt for the lower end of the lower probability bounds ($d = 25$ km) while extreme risk takers would base their decision on the upper end of the upper bounds ($d = 200$ km). Again, extremely conservative choices miss out on potentially large pay-offs, whereas extremely optimistic choices run the risk of minimizing the chance of persistence. Decision makers with intermediate levels of risk aversion may base their decision somewhere in between. For instance, one can evaluate the amount of cumulative probability for which the worst-case scenario (lower bounds) for one distance does better than the best-case scenario (upper bounds) for another distance. Here we see that there is a 23% chance that the lower bound for $d = 100$ km results in higher persistence probabilities than the best-case scenario for $d = 50$ km, and there is a 46% chance that it does better than $d = 25$ km (Fig. 4).

Interval analysis shows that plausible maximum persistence probability (q) bounds of 0.9529 and 0.9929 give reserve spacing values of $d \approx 10$ –350 km (Fig. 5). Hence, under uncertainty in the mean dispersal distance, the maximum chance of persistence (q) could be as low as 0.953 and as high as 0.993, or anywhere in between. Likewise, the distance that maximizes q could be as low as 10 km or as high as 344 km, or anywhere in between. If we were more certain about the plausible values for average dispersal distance for the particular species of interest and could tighten the bounds on β , then we would achieve tighter bounds on the maximum q and optimal d .

With info-gap analysis, there are two ways to evaluate results to make reserve spacing decisions. First, one can assign critical values of Q below which the persistence probability is regarded as unacceptably low and then choose the distance that maximizes the robustness to uncertainty in β . For instance, with a critical threshold of $Q = 0.963$ we see that only a spacing of $d = 50$ km is acceptable (Fig. 6). However, since the corresponding uncertainty in β is low ($\hat{u} < 0.13$), this choice is not very robust to uncertainty – we would need to be fairly confident in our nominal value in order to satisfy our performance criterion. If the critical threshold is lower, say $Q = 0.960$, then we see that $d = 50$ and 25 km give results that are tolerable, but of these $d = 25$ km satisfies this condition up to the greatest level of

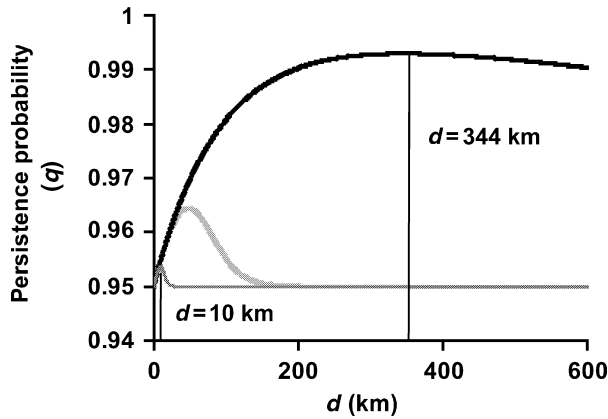


Figure 5 Maximum and minimum possible values for the persistence criterion (q) and reserve spacing (d) given minimum and maximum possible values of β , using interval analysis. With minimum dispersal ($\beta = 0.3704$), optimal reserve spacing is 10 km ($q = 0.953$); with maximum dispersal ($\beta = 0.0019$), optimal reserve spacing is 344 km ($q = 0.993$). See Methods for parameter values.

uncertainty (up to $\hat{u} = 0.87\%$). So we see that based on critical thresholds in persistence probability, our reserve spacing decision would change according to different tolerances to uncertainty among the alternatives. Second, if we do not assign a critical threshold to persistence probability, then we must decide on our attitude towards uncertainty in order to make a decision. If we are truly ignorant in the level of uncertainty in β then we would choose $d = 25$ km because the greatest persistence probability is achieved across most levels of uncertainty (Fig. 6), i.e. $d = 25$ km is the reserve spacing most robust to uncertainty in β . Only when we believe uncertainty in β is fairly small ($\hat{u} < 0.37$, which is equivalent to our best guess for dispersal distance being fractionally within 37% of the truth) does reserve spacing $d = 50$ km achieve the greatest persistence probability. Essentially, persistence probability decreases as uncertainty increases. Likewise, optimal reserve spacing decreases as uncertainty increases. This trade-off is the price of uncertainty.

Sensitivity of results to other parameters

Changing the local extinction probability (p_e) to 0.01 or 0.1 had only marginal effects on the results from the different modelling approaches, besides simply squeezing or expanding the probability distribution functions into a smaller or larger range of q -values (i.e. 0.99–0.999 or 0.9–0.98 instead of 0.95–0.99, respectively). In contrast, changing α , which reflects the rate at which correlation in extinction events declines with distance, had significant and important effects on model results for all types of uncertainty modelling (see

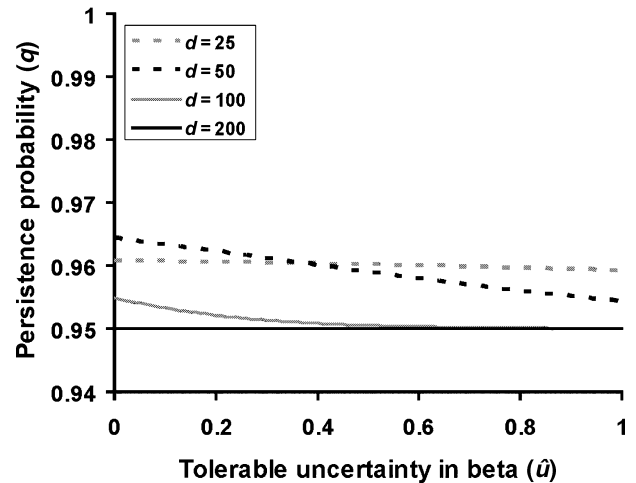


Figure 6 Values for the persistence criterion (q) for four different distances between reserves (d) given increasing uncertainty in β , using information-gap analysis. See Methods for parameter values.

Appendix S1 for all figures for these results). For precise probability distribution analysis, $\alpha = 0.05$ (less correlation for a given distance) led to higher absolute possible q values, smaller distances (d) necessary to achieve those q values, and a much larger average q achievable by any given d , while $\alpha = 0.005$ led to the opposite results. Changes in α had similar results for probability bound analysis; higher α led to larger possible q values and a greater probability that the lower bounds of smaller distances achieved desired persistence probabilities. For interval analysis, higher α led to higher q values for minimum, average, and maximum scenarios with optimal distances converging on the distance for the minimum scenario (lower α led to opposite patterns). Finally, higher α in info-gap analysis led to larger possible q values and $d = 25$ km being the only optimal distance across all possible values of uncertainty around β , while lower α values had little effect on model results except to slightly lower the maximum possible q .

DISCUSSION

We have presented and demonstrated the use of several of the more common methods for dealing with uncertainty in model parameters when designing reserve networks. These efforts have provided four key results. First, all of the approaches explicitly allow one to quantify the effects of uncertainty on model results and the consequences for subsequent decisions made in the face of uncertainty. The ability to quantify the impact of uncertainty creates flexibility in the management decision process and provides a mechanism for describing realistic outcomes. In some cases,

stakeholders may be willing to take greater risks if such risk creates the potential for a larger pay-off; in other cases, stakeholders will demand that any action provide the greatest amount of certainty in results. However, under the precautionary principle these decisions should be based on worst-case scenarios. Increases in persistence probability pay the price of requiring greater certainty in key model parameters, and this tension is quantified in these uncertainty models.

Second, we have shown that greater levels of uncertainty in dispersal distance lead to a decrease in the optimal distance between reserves. This is not necessarily a surprising result – if one is uncertain about a species' dispersal distance, it makes sense to put reserves closer together to ensure connectivity exists – but it illustrates how assumptions about parameter distributions can affect important reserve design decisions. As we note above, assumptions about the distribution of parameter values can have significant consequences for model results (Regan *et al.* 2002b). Allowing for uncertainty in these distribution estimates increases the likelihood of meeting appropriate management or conservation goals. Furthermore, as the importance of certainty about an outcome increases (not just the expected value of the outcome), there will be a tendency to choose smaller distances between reserves.

Third, although the results from the models presented here do not provide exact guidelines for optimal reserve spacing, they do give useful minimum and maximum values for distances between reserves that should be used to ensure population persistence. Given a best guess estimate of dispersal distance for fishes ($\beta = 0.05$, mean dispersal distance = 20 km) but high levels of uncertainty about this value, interval analysis shows us that reserves need not be closer than 10 km and should not be greater than 344 km apart (precise probability distribution analysis gives 420 km as an upper limit). If greater certainty exists about possible values for dispersal distance, then this range of potential reserve spacing values could be reduced.

Finally, info-gap analysis provides a truly precautionary approach to management and conservation. If the goal is to design a reserve network with a success rate that is robust to uncertainty, info-gap analysis tells us that unless we are fairly certain about our estimate of dispersal distance ($u < 37\%$), reserves should be spaced *c.* 25 km from each other. This is roughly equal to the estimated average dispersal distance for the species modelled here, providing a potential rule of thumb when faced with extreme uncertainty in dispersal distance estimates. Botsford *et al.* (2001) developed a similar rule of thumb using a different approach to modeling dispersal distance.

The trade-off between certainty in parameter values and the size of the range of possible spacing distances demonstrated in our results illustrates how these models

can also be used to evaluate the potential costs and benefits of reducing uncertainty in parameters. Data gathering to refine parameter estimates can be hugely expensive and time-consuming, and in some cases may not be possible. When there are differences in model results arising from different levels of certainty, such as with our results, then the trade-off between data gathering and social tolerance for precautionary approaches will need to be explicitly weighed. Management can more confidently proceed in the face of severe uncertainty when the different uncertainty models provide similar reserve spacing rules. Of course, one must still accept that the underlying model accurately represents population and community dynamics, but this is always the case.

Here we modelled reserve spacing rules for a single species. Ultimately, reserves are expected and need to protect multiple species to be effective. There are at least two possible ways to extend our modelling efforts here to evaluate potential reserve spacing rules for networks designed to protect entire communities. First, one could model optimal reserve spacing for many individual species and compare results. There may be a narrow range of optimal reserve designs that captures most or all of the target species. Alternatively, one could treat β as a measure of estimated average dispersal distance for multiple species and then model the consequences for reserve spacing rules of uncertainty in this estimate. In this case, one would bound β by estimates of minimum and maximum average dispersal distances for different species within the community, but the approaches to modelling uncertainty would be identical to those presented here.

For the purposes of illustration, we have focused on uncertainty in a single parameter value and assumed that all other parameters were known. This approach assists the comparison of the different methods. However, all of these modelling approaches can be adapted to model uncertainty in multiple parameters simultaneously. Given that our results were sensitive to the value of α we chose, it would seem prudent to model uncertainty in both α and β before prescribing optimal reserve spacing rules. It may be particularly important to include uncertainty in α in the model as this parameter is likely to be susceptible to regional-scale oceanographic processes such as ENSO events, which have unpredictable frequency and intensity over the long-term. We would expect that because of compounding uncertainty in multiple parameters, the bounds on results would be wider. Furthermore, we have based our models on one approach to modelling connectivity between reserve patches (McCarthy *et al.* 2005). Although this model captures important variables that likely influence connectivity (dispersal distance and extinction correlation), it does not include other variables that may also be important, such as local habitat quality (e.g. Tupper &

Boutillier 1997), spiky or long-tailed dispersal kernels (Siegel *et al.* 2003, Kinlan *et al.* 2005), and oceanographic current patterns (i.e. asymmetrical dispersal; Largier 2003, Gaines *et al.* 2003). Uncertainty modelling can be applied to any initial model formulation, and so we emphasize again that our results here are illustrative rather than prescriptive. In fact, models aimed at addressing questions other than reserve spacing, such as how large should individual reserves be, would also benefit from uncertainty modelling approaches such as those presented here.

Current guidelines for reserve spacing rules, based on estimates of average dispersal distances for marine organisms, range from 10 to 20 km (Shanks *et al.* 2003) to 10–100 km for invertebrates and 50–200 km for fish (Palumbi 2004). It is encouraging that our results generate fairly similar guidelines, but our approach to generating these results offers two critical improvements over these past approaches. By acknowledging and modelling uncertainty in parameter estimates, we have provided an explicit tool for describing and explaining to stakeholder groups the realities of the state of scientific understanding and the consequences of the uncertainty inherent in that understanding. More importantly, the uncertainty modelling approaches presented here provide a mechanism for stakeholder groups to quantitatively evaluate acceptable levels of risk and then make informed decisions about reserve network designs based on those evaluations. By acknowledging and quantifying the consequences of inherent uncertainty in our estimates of biological processes, rather than avoiding treatments of uncertainty, we should be able to more effectively manage and conserve into the future the marine resources we want to use and protect.

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REFERENCES

- Ben-Haim, Y. (2001). *Information-Gap Decision Theory: Decisions Under Severe Uncertainty*. Academic Press, San Diego.
- Botsford, L.W., Hastings, A. & Gaines, S.D. (2001). Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol. Lett.*, 4, 144–150.
- Burgman, M.A. (2005). *Risks and Decisions for Conservation and Environmental Management*. Cambridge University Press, Cambridge.
- Charles, A.T. (1998). Living with uncertainty in fisheries: analytical methods, management priorities and the Canadian groundfishery experience. *Fish. Res.*, 37, 37–50.
- Doyen, L. & Bene, C. (2003). Sustainability of fisheries through marine reserves: a robust modeling analysis. *J. Envir. Manag.*, 69, 1–13.
- Ferson, S. (2002). *RAMAS Risk Calc 4.0 Software: Risk Assessment with Uncertain Numbers*. Lewis Publishers, Boca Raton, FL.
- Fieberg, J. & Ellner, S.P. (2000). When is it meaningful to estimate an extinction probability? *Ecology*, 81, 2040–2047.
- Gaines, S.D., Gaylord, B. & Largier, J.L. (2003). Avoiding current oversights in marine reserve design. *Ecol. Appl.*, 13, S32–S46.
- Gerber, L.R., Botsford, L.W., Hastings, A., Possingham, H.P., Gaines, S.D., Palumbi, S.R. *et al.* (2003). Population models for marine reserve design: a retrospective and prospective synthesis. *Ecol. Appl.*, 13, S47–S64.
- Grafton, R.Q., Kompas, T. & Lindenmayer, D. (2005). Marine reserves with ecological uncertainty. *Bull. Math. Biol.*, 67, 957–971.
- Harwood, J. & Stokes, K. (2003). Coping with uncertainty in ecological advice: lessons from fisheries. *Trends Ecol. Evol.*, 18, 617–622.
- Jeffrey, R.C. (1983). *The Logic of Decision*, 2nd edn. University of Chicago Press, Chicago, IL.
- Kinlan, B.P. & Gaines, S.D. (2003). Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology*, 84, 2007–2020.
- Kinlan, B.P., Gaines, S.D. & Lester, S.E. (2005). Propagule dispersal and the scales of marine community process. *Div. Dist.*, 11, 139–148.
- Lande, R., Engen, S. & Bernt-Erik, S. (2003). *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford.
- Largier, J.L. (2003). Considerations in estimating larval dispersal distances from oceanographic data. *Ecol. Appl.*, 13, S71–S89.
- Ludwig, D., Hilborn, R. & Walters, C. (1993). Uncertainty, resource exploitation, and conservation: lessons from history. *Science*, 260, 17–18.
- Ludwig, D. (1999). Is it meaningful to estimate a probability of extinction? *Ecology*, 80, 298–310.
- McCarthy, M.A., Andelman, S.J. & Possingham, H.P. (2003). Reliability of relative predictions in population viability analysis. *Conserv. Biol.*, 17, 982–989.
- McCarthy, M.A., Burgman, M.A. & Ferson, S. (1996). Logistic sensitivity and bounds on extinction risks. *Ecological Modelling*, 86, 297–303.
- McCarthy, M.A., Thompson, C.J. & Possingham, H.P. (2005). Theory for designing nature reserves for single species. *Am. Nat.*, 165, 250–257.
- Moore, R.E. (1966). *Interval Analysis*. Prentice-Hall, Englewood Cliffs, NJ.
- Morgan, M.G. & Henrion, M. (1990). *Uncertainty: A Guide to Dealing with Uncertainty in Quantitative Risk and Policy Analysis*. Cambridge University Press, Cambridge.
- Palumbi, S.R. (2004). Marine reserves and ocean neighborhoods: The spatial scale of marine populations and their management. *Ann. Rev. Envir. Res.*, 29, 31–68.
- Raiffa, H. (1970). *Decision Analysis*. Addison-Wesley, Reading, MA.

- Regan, H.M., Ben-Haim, Y., Langford, B., Wilson, W.G., Lundberg, P., Andelman, S.J. *et al.* (2005). Robust decision making under severe uncertainty for conservation management. *Ecol. Appl.*, 15, 1471–1477.
- Regan, H.M., Akçakaya, H.R., Ferson, S., Root, K.V., Carroll, S. & Ginzburg, L.R. (2003). Treatments of uncertainty and variability in ecological risk assessment of single-species populations. *Human Ecol. Risk Assess.*, 9, 889–906.
- Regan, H.M., Colyvan, M. & Burgman, M.A. (2002a). A taxonomy and treatment of uncertainty for ecology and conservation biology. *Ecol. Appl.*, 12, 618–628.
- Regan, H.M., Hope, B.K. & Ferson, S. (2002b). Analysis and portrayal of uncertainty in a food-web exposure model. *Human Ecol. Risk Assess.*, 9, 1757–1777.
- Shanks, A.L., Grantham, B.A. & Carr, M.H. (2003). Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. Appl.*, 13, S159–S169.
- Siegel, D.A., Kinlan, B.P., Gaylord, B. & Gaines, S.D. (2003). Lagrangian descriptions of marine larval dispersion. *Mar. Ecol. Prog. Ser.*, 260, 83–96.
- Thompson, K.M. & Graham, J.D. (1996). Going beyond the single number: using probabilistic risk assessment to improve risk management. *Human Ecol. Risk Assess.*, 2, 1008–1034.
- Tucker, W.T. & Ferson, S. (2003). *Probability Bounds Analysis in Environmental Risk Assessments*. Applied Biomathematics, Setauket, NY. Available at: <http://www.ramas.com/pbawhite.pdf>, accessed on 3 June 2005.
- Tupper, M. & Boutilier, R.G. (1997). Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. *Mar. Ecol. Prog. Ser.*, 151, 225–236.
- Warren-Hicks, W., Moore, D.R.J. & SETAC and SETAC Foundation for Environmental Education (1998). Uncertainty analysis in ecological risk assessment. *Proceedings of the Society of Environmental Toxicology and Chemistry (SETAC); Pellston Workshop*. SETAC Press, Pensacola, FL.

SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article from <http://www.Blackwell-Synergy.com>:

Appendix S1 Results for four modelling approaches with alternate alpha values.

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COMMENTARY: ACCOUNTING FOR UNCERTAINTY IN MARINE RESERVE DESIGN

I thank the editors for inviting me to contribute this commentary and the authors for having written such an interesting paper. In this note, I will discuss the classification of uncertainty, describe what Halpern *et al.* (2006) did, discuss a few nitpicks and conclude with the broad implications of their work.

Uncertainty in natural systems can broadly be classified into two types (Ferson & Ginzburg 1996). Epistemic uncertainty is due to limited information; it is observation error (Hilborn & Mangel 1997). Epistemic uncertainty is reducible by further observation and is a property of the analyst. Aleatory uncertainty is due to randomness in the system; it is process stochasticity or natural variability. Aleatory uncertainty is irreducible and is an inherent property of the system. Although they are often treated identically, these two kinds of uncertainty are not interchangeable as they represent the difference between the real biology of the system and our measurement of the biology. The work of Halpern *et al.* suggests that we might add biological ignorance – situations in which a parameter is fixed but unknown and likely never to be so, and in which its distribution may not even be known – to observation error and process stochasticity.

Halpern *et al.* focus on such biological ignorance about dispersal, in the context marine reserves. They borrow a result from McCarthy *et al.* (2005) and compute the annual probability of persistence for long time horizons of a two-patch metapopulation. This probability depends upon biological and environmental variables such as the rate at which correlation in extinction events declines with distance, the mean dispersal distance and the probability of extinction within one of the two identical patches; it also depends upon the distance between the patches, which is the operational variable for decision making.

In such a situation, we may ask ‘How should distance between patches be picked to maximize the persistence of the metapopulation?’. Halpern *et al.* show that there are many answers to this question, depending upon how one deals with the biological ignorance about dispersal distance.

For example, if the dispersal distance were known perfectly, one can plot persistence probability vs. distance between reserves and find that there is an optimal distance that maximizes persistence. To deal with biological ignorance, Halpern *et al.* assign a log-normal distribution to the reciprocal of the dispersal distance and show a very clever way to use this distribution. They fix the operational parameter, vary the persistence probability and ask for the probability that dispersal is the right size to achieve the given value of persistence. This approach shows the most

important take-home message of this paper: that there is no single 'best' value of spacing between reserves and that one must approach the problem as one of risk analysis (Anand 2002). Recognizing that the log-normal distribution is only one of many, Halpern *et al.* next use a risk calculation tool that works to produce a similar result but using only the mean, standard deviation, maximum and minimum of the dispersal distance. An interval analysis uses only the bounds on dispersal distance and produces bounds on the probability of persistence and thus suggests bounds for the operational parameter. Finally, Halpern *et al.* approach the problem using information gap theory (Ben-Haim 2001). Info-gap approaches make no assumptions about distributions, but only about the level of our biological ignorance and our sense of what an acceptable level of uncertainty is. The result is that the probability of persistence is a function of the acceptable level of uncertainty in dispersal. Info-gap theory, although a hard subject to master, has much to offer to conservation biology and evolutionary ecology. For example, the portfolio approach of info-gap theory could be used for dealing with multispecies considerations briefly mentioned by Halpern *et al.* I encourage readers to investigate info-gap. The bottom line is that there is no single or simple answer to the question about the spacing of reserves – we need to think carefully about the question and embrace uncertainty.

Now a few nitpicks. To make the paper applicable and accessible, the authors oversimplified some complicated matters. For example, we do not regulate ecological systems, we regulate human intervention in them (e.g. Mangel *et al.* 1996, Pikitch *et al.* 2004). Even if one does everything right, there may be population crashes or ecosystem failures because of uncertainty and/or stochasticity; one of the challenges for theory is to understand the likelihood of this occurring. Few fisheries are managed to achieve Maximum Sustainable Yield (MSY), which can take uncertainty into account when computed properly (Mangel *et al.* 2002).

Halpern *et al.* are a bit cavalier about expectations of nonlinear functions, in this case the expectation of the reciprocal of the dispersal distance. As in general the expectation of a nonlinear function of a random variable is not the function of the expectation, if the mean of the reciprocal dispersal distance is 0.05 km^{-1} the mean dispersal distance cannot be 20 km but for a minor miracle. I estimated mean dispersal distance using the data given by Halpern *et al.* and conclude that it is *c.* 22 km, rather than 20 km. This may sound pedantic, but in a paper focused on uncertainty, one expects greater care taken regarding the mean of a nonlinear function of the unknown variable.

Finally, Halpern *et al.* actually use a very unconservative criterion, the probability that the stock is not extinct, presumably because that is the tool they have available. However, most of us would likely prefer healthier stocks.

We then must define persistence as the probability that the stock stays above a specified critical level for the duration of the planning horizon. An example of such a calculation, with process stochasticity but no biological ignorance, is found in Mangel (2000). An important message of that paper, which resonates with the message of Halpern *et al.*, is that there are crucial social and policy questions that need to be addressed (e.g. what is the appropriate critical population size, what is an acceptable level of persistence and what is a tolerable level of uncertainty). I concluded there "The answer to the question: 'How much habitat needs to be allocated to reserves' is not a single number. Rather, it is a procedure that can be employed once biological, operational" and social information are provided'. The work of Halpern *et al.* reinforces this conclusion and is welcome. These are complicated problems and must be treated as such.

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REFERENCES

- Anand, P. (2002). Decision-making when the science is ambiguous. *Science*, 295, 1839.
- Ben-Haim, Y. (2001). *Information-gap Decision Theory. Decisions Under Severe Uncertainty*. Academic Press, San Diego, CA.
- Ferson, S. & Ginzburg, L.R. (1996). Different methods are needed to propagate ignorance and variability. *Reliab. Eng. Sys. Safe*, 54, 133–144.
- Halpern, B.S., Regan, H.M., Possingham, H.P. & McCarthy, M.A. (2006). Accounting for uncertainty in marine reserve design. *Ecol. Lett.*, 9, 2–11.
- Hilborn, R. & Mangel, M. (1997). *The Ecological Detective. Confronting models with data*. Princeton University Press, Princeton, NJ.
- Mangel, M. (2000). On the fraction of habitat allocated to marine reserves. *Ecol. Lett.*, 3, 15–22.
- Mangel, M., Talbor, L.M., Meffe, G.K., Agardy, T., Alverson, D.L. & Barlow, J. (1996). Principles for the conservation of wild living resources. *Ecol. Appl.*, 6, 338–362.
- Mangel, M., Marinovic, B., Pomeroy, C. & Croll, D. (2002). Requiem for Ricker: unpacking MSY. *Bull. Mar. Sci.*, 70, 763–781.
- McCarthy, M.A., Thompson, C.J. & Possingham, H.P. (2005). Theory for designing nature reserves for single species. *Am. Nat.*, 165, 250–257.
- Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O. *et al.* (2004). Ecosystem-based fishery management. *Science*, 305, 346–347.

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REJOINDER: UNCERTAINTY AND DECISION MAKING

As we (Halpern *et al.* 2006) and Mangel (2006) point out, there are essentially two types of numerical uncertainty – one type can be removed with more data (epistemic uncertainty) and the other type cannot (natural variation or aleatory uncertainty). Biological ignorance, *sensu* Mangel, is simply a combination of these two types. In the context of choosing between management options, the techniques we described in our paper can deal with both types of uncertainty. Probability bounds address both types of uncertainty explicitly in a probabilistic framework. Other bounding techniques, such as interval and info-gap analyses, subsume both types of uncertainty within bounds. While we recognize that the mathematical notation for techniques such as info-gap can be an initial challenge, info-gap is conceptually straightforward. The analysis of robustness using info-gap simply asks: which is the best management option if the model's parameters are x per cent worse than expected? By plotting the management outcome, e.g. extinction probability vs. x for each management option, one can find the option that provides an acceptable outcome and is at the same time most robust to uncertainty. Ignoring uncertainty can have profound implications. As pointed out in our paper, management decisions can be suboptimal if uncertainty is ignored.

Although we agree with Mangel that our criterion of metapopulation persistence (i.e. the species does not go extinct) is not particularly conservative for achieving fisheries management goals, it is a reasonable minimum criterion for conservation, and the approaches to evaluating uncertainty that we describe can easily be applied to fisheries population models if one wants to minimize the chance a stock falls below a certain level (or quasi-extinction).

What Mangel clearly exposes with his comment is that decision making under uncertainty is not always an objective problem that can be solved exclusively with scientific information. Management and conservation are necessarily value-driven activities where people decide how much of something they want or are willing to risk losing. Is our objective to minimize the risk of a catastrophic outcome such as extinction or the risk of an unfavourable yield such as a poor harvest, or a combination of the two? These are decisions that need to be hammered out during a problem definition phase, which is often the hardest part of any environmental decision making. While different groups will define the problem in different ways, dealing with this higher level of uncertainty, i.e. problem definition uncertainty, is beyond the scope of our work.

The info-gap model presented in our paper assumes a risk-averse decision maker at the outset. Other methods of

uncertainty analysis, such as precise probability distributions and probability bounds, require positions on acceptable levels of risk and attitudes to risk in order to make a final decision. But even when a decision is based upon a model, no particular outcome can be guaranteed. Very low probability but high consequence events, such as catastrophes are difficult to fully anticipate and account for in models. Mangel points this out when he states that even well-managed systems can still 'crash'. His point strengthens the case for using uncertainty modelling methods such as those presented in our paper. One can decide how resistant to uncertainty a management plan needs to be and then model appropriate management solutions. Tools for making decisions under uncertainty will perform better than methods that ignore the probability of such crashes.

Finally, we wish to clarify a point in Mangel's response. In eqn 1, the parameter $1/\beta$ is the mean dispersal distance (and not simply 'dispersal distance' as stated by Mangel). A log-normal probability distribution is constructed for β using the average and standard deviation of all the reciprocal mean dispersal distances for fishes in Kinlan & Gaines (2003). Mangel is correct that, in general, the average of the reciprocal of a distribution is not the reciprocal of the average of the distribution. However, we did not present the 'average' of the mean dispersal distance (which from Kinlan & Gaines 2003, is 112 km and not 22 km as Mangel calculates). Rather, we simply presented the mean dispersal distance that corresponds to the value $\beta = 0.05$ or $1/\beta$, because that is how beta is defined.

Although the treatment of uncertainty can seem daunting to incorporate into conservation planning, people have long accepted it in many aspects of their daily lives. We fly in aeroplanes, we drive across bridges, and we manufacture and use chemicals. Engineers and risk assessors have figured out how to make these activities relatively safe for us despite the uncertainty inherent in such complex systems. We argue here that conservationists and resource managers can learn a lot from the techniques developed in these fields of research. The methods we present in our paper are not exhaustive. There is no single best tool for dealing with uncertainty – the best choice will depend on the management context and the quality and quantity of data available. Most importantly, such tools need to be integrated into management and conservation planning if we are to have any hope of making effective decisions.

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REFERENCES

Halpern, B.S., Regan, H.M., Possingham, H.P. & McCarthy, M.A. (2006). Accounting for uncertainty in marine reserve design. *Ecol. Lett.*, 9, 2–11.

Kinlan, B.P. & Gaines, S.D. (2003). Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology*, 84, 2007–2020.

Mangel, M. (2006). Commentary: accounting for uncertainty in marine reserve design. *Ecol. Lett.*, 9, 11–12.

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