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. Press 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 Environmal 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 porfolio 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

Marc Mangel

Center for Stock Assessment Research (CSTAR) and Department of Applied Mathematics and Statistics, University of California, Santa Cruz, CA 95064, USA E-mail: msmangel@ucsc.edu

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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