

LETTER

Harvest reserves reduce extinction risk in an experimental microcosm

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Abstract

Overharvesting by humans threatens a substantial fraction of endangered species. Reserves have recently received enormous attention as a means of better conserving harvested resources, despite limited empirical evidence of their efficacy. We used manipulated microcosms to test whether reserves reduce extinction risk in mobile populations of harvested *Tetrahymena thermophila*, a ciliate. Here we show that patterns of population distribution inside and outside reserves can be accurately predicted on the basis of simple models of diffusion coupled with logistic controls on local population growth. No extinctions occurred in eight experimental trials with reserves, whereas extinction occurred in seven of eight trials without reserves, as predicted by population viability models based on stochastic population processes. These results suggest that marine reserves may be an effective means of improving long-term viability in heavily harvested fish species.

Keywords

Ciliate, extinction, fisheries, harvest, logistic, model, population viability, reserve, *Tetrahymena*.

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INTRODUCTION

Overharvesting is one of the most serious global conservation concerns, endangering as much as one-third of threatened species worldwide (Goombridge 1992), particularly in marine fisheries (Pauly *et al.* 1998; Myers & Worm 2003). Despite improvements in analytical methodologies for stock assessment, recruitment forecasting, and stock movement, traditional methods of harvest management are often difficult to successfully implement (Ludwig *et al.* 1993; Hilborn *et al.* 1995; Lande *et al.* 1995). Marine reserves have been enthusiastically endorsed as an alternative method of fishery management (Roberts 1997; Mangel 1998; Hastings & Botsford 1999; Sala *et al.* 2002; Botsford *et al.* 2003; Gerber *et al.* 2003; Lubchenco *et al.* 2003; Rodwell & Roberts 2004).

While recent reviews agree that the theoretical basis for reserves is well-established (Botsford *et al.* 2003; Gerber *et al.* 2003; Lubchenco *et al.* 2003; Neubert 2003; Rodwell & Roberts 2004), empirical evidence for their efficacy lags far behind (Halpern 2003). This is not surprising, given that reserves have only come into widespread use during the past decade. Published reports of improvements in fishery yield, average fish size, and recovering stock levels in previously

overfished stocks are beginning to appear in the literature (Murawski *et al.* 2000; Roberts *et al.* 2001; Halpern 2003), although causal factors are hotly debated (Hilborn 2002; Tupper 2002; Wickstrom 2002). It remains undemonstrated, however, whether reserves can actually reduce extinction risk in biotic systems, using the kind of analytical models often used by resource managers.

To test the effectiveness of harvest reserves in an experimentally tractable system, we used *Tetrahymena thermophila*, a unicellular freshwater organism found in streams, lakes, and ponds (Frankel 2000). Under laboratory conditions, these ciliates can reach densities up to 10^5 mL⁻¹ in a variety of media, with generation times of 2–3 h. *Tetrahymena* is a suitable experimental organism for replicated harvesting experiments, due to the ease with which they can be maintained in the laboratory. *Tetrahymena* has been used as a model organism to study foraging behaviour, interspecific competition, exploitation of patchy environments, and to test complex population growth models (Fredrickson 1991; Diehl & Feissel 2001; Fryxell *et al.* 2005).

We conducted two independent sets of experimental trials with *Tetrahymena* populations maintained in shallow dishes equipped with a small cube of spongy polyurethane foam in the center. The foam unit acted as a spatial refuge,

allowing unrestricted movement in and out, but also making it simple to differentiate between individuals that were in the harvest reserve vs. those that were not. In the first set of trials, we estimated demographic and diffusion parameters by recording changes in *Tetrahymena* density over time inside vs. outside the refuge. This allowed us to develop a predictive diffusion model of *Tetrahymena* population dynamics when exposed to intense constant quota harvesting, in the presence or absence of a harvest reserve. These predictions were then tested using a second set of trials in which we applied harvesting to experimental replicates.

MATERIALS AND METHODS

The study was conducted during May to August 2002. Populations of *Tetrahymena thermophila* (strain B1975 obtained from Dr J. Frankel, University of Iowa) were maintained via weekly sterile transfer in 1% proteose peptone, 1% yeast extract, and 0.2% dextrose in a controlled, laboratory environment. The microcosms consisted of Pyrex dishes measuring 70 × 50 mm kept out of direct sunlight at room temperature. To prepare the microcosms, sterile containers were provided with 30 mL of a culture medium of dried cereal grass leaves (Cerophyl) and inoculated within 72 h with the bacteria *Enterobacter aerogenes* (obtained from R. Van Twest, Department of Cell and Molecular Biology, University of Guelph). This Cerophyl medium was filtered using Whatman no. 1 paper prior to dilution, autoclaving, and inoculating with bacteria. The microcosms were left for 24 h to allow the bacteria to multiply. A constant volume of 100 µL of a solution of high density ($> 20 \mu\text{L}^{-1}$) *T. thermophila* was then added to each microcosm. The microcosms were gently swirled manually once a day to avoid biomass accumulation at the bottom of the dishes. Microcosms were always mixed manually prior to sampling. While no tests were performed to guarantee that other species of bacteria were not present during the trials, the sterile techniques employed would be expected to considerably reduce this possibility.

The following procedure was used to compare the dynamics of systems with and without harvest refuges. Two sets of eight replicates of dishes were prepared, the first set being the refuge dishes, and the second being the non-refuge dishes. Each of the refuge replicates was prepared with 70 mL of bacterized Cerophyl with a density of $c. 5$ *Tetrahymena* per µL, and a polyurethane foam unit (PFU) was submerged in the Cerophyl. Each PFU could hold $c. 15$ mL of liquid, based on 10 weighed replicates saturated with water. Each of the non-refuge replicates was prepared with 50 mL of bacterized Cerophyl with a density of $c. 5$ *Tetrahymena* per µL.

After an equilibration period of 72 h, the PFU in each of the refuge replicates was removed and the liquid content of

each was emptied into a separate dish. The remaining medium within the initial refuge dishes was swirled to homogenize and sampled, and densities were counted for each dish. The liquid that was removed from the PFU was also sampled and *Tetrahymena* population densities were then counted. Each PFU from the non-refuge dishes was removed and the liquid inside emptied back into the original dish from which it had been taken. This medium was then swirled to homogenize, sampled, and *Tetrahymena* population densities estimated as before.

Harvesting was applied daily in the following manner. A harvest quota $Q = 16.8$ individuals per µL was then removed at 24-h intervals, by removing a variable volume relative to standing *Tetrahymena* population density. This volume of the medium within each dish was then removed, discarded, and replaced with bacterized Cerophyl to bring the volume back to its original level. This procedure ensured that a roughly constant total harvest quota was removed from each population each day. Our earlier work with this experimental system (Fryxell *et al.* 2005) had clearly demonstrated that this level of constant quota harvesting would lead to an appreciable risk of extinction, in the presence of typical levels of stochastic variability due to sample error in population estimates as well as variability in growth rates. Such stochastic variation is unavoidable in real systems and therefore critical to the evaluation of sustainable harvest policies.

RESULTS

Population dynamics without harvesting

In the first experiment, we used a simple diffusion model to predict dynamics over time in a spatially structured population that is not harvested. We used a maximum likelihood approach to estimate the demographic and diffusion parameters for a discretized version of the Fisher diffusion model with logistic growth, assuming no bias in move direction (Fisher 1937; Skellam 1951; Turchin 1998; Neubert 2003):

$$\frac{\partial N(x, t)}{\partial t} = D(x) \frac{\partial^2}{\partial x^2} N(x, t) + g(N(x, t)), \quad (1)$$

where $g(N)$ represents the logistic growth term and $D(x)$ represents the position-specific diffusion coefficient of the underlying model of simple population spread, assuming Fokker–Planck, rather than Fickian diffusion. We discretized this partial differential equation, assuming a 1-h time step between recursive calculations and a linear array of three cells, connected as a series of stepping stones. In our model, we positioned the reserve in the middle of the array, providing a similar ratio of spatial locations inside vs. outside the reserve as was present in our actual experimental

system. On the basis of formal model evaluation performed in a previous experimental study of the same biological system (Fryxell *et al.* 2005), we used the Ricker logistic model, $g(N) = \exp(r_{\max}[1 - \mu K^{-1}])$, to depict density-dependent limits on the per capita rate of population growth. In this formulation, μ is the mean population density, r_{\max} is the maximum exponential rate of growth (expressed on an hourly basis), and K is the carrying capacity of the system (expressed in individuals per μL).

The best-fit demographic parameters for the system were $r_{\max} = 0.104$ and $K = 35.9$. Analysis of the negative log-likelihood profile in r_{\max} - K parameter space suggested a well-defined minimum for the model (Fig. 1a). Our best estimates suggested that movement rates (expressed on an hourly basis) were three times higher outside the reserve than inside the reserve ($D_{\text{inside}} = 0.010$, $D_{\text{outside}} = 0.032$). Plotting of the negative log-likelihood profile for both diffusion parameters confirmed that there was also a well-defined global minimum for this parameter combination (Fig. 1b). Residual variation in growth rates was distributed in approximately normal fashion (Fig. 2). The model with fitted parameters explained 88% of the observed variation in population densities in the experimental system (Fig. 3).

Analytical solutions of simple diffusion models of this sort predict that at equilibrium, spatial variation in popu-

lation density (i.e. inside vs. outside reserves) should reflect the ratio of respective diffusion rates, the so-called residence index (Turchin 1998, p. 85). Hence, for our system, one would predict at equilibrium three times higher densities of *Tetrahymena* inside the reserve as outside the reserve, with sizeable local variation in densities prior to equilibration. Results of our time series experiments were consistent with the equilibrium predictions of the diffusion model (Fig. 3). Population densities after 90 h of growth inside the reserve

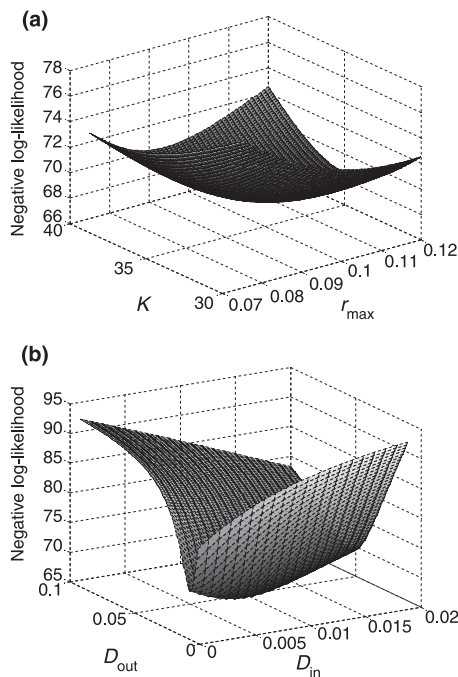


Figure 1 Negative log-likelihood profile in the r_{\max} - K parameter space (a) and $D_{\text{out}}/D_{\text{in}}$ parameter space (b) for assessment of goodness of fit in the demographic and diffusion rate estimation trials.

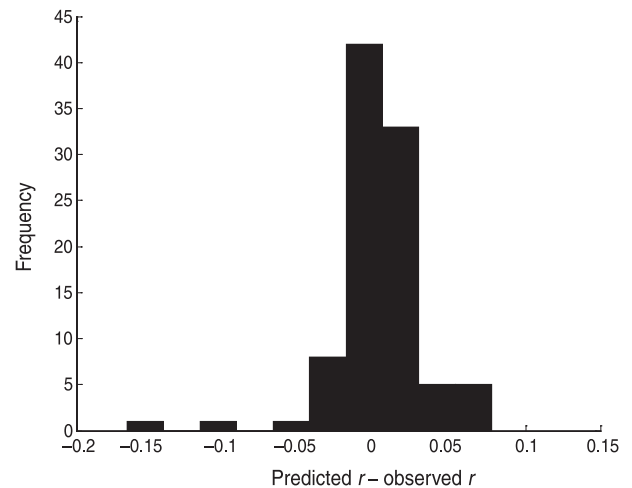


Figure 2 Distribution of residuals of observed - predicted r in the demographic and diffusion rate estimation trials.

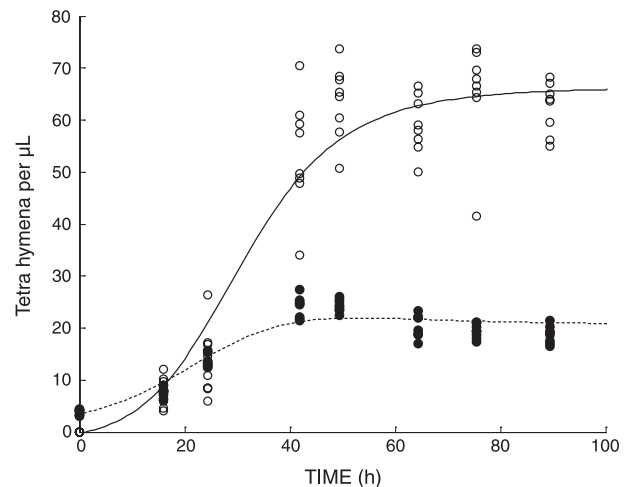


Figure 3 Observed (symbols) vs. predicted changes (lines) over time in the density of *Tetrahymena* ciliates inside (solid line and open symbols) and outside (dotted line and filled symbols) refuges. The deterministic model was based on a Ricker logistic growth process coupled with simple diffusion, with demographic and diffusion rates inside and outside the refuge estimated using maximum-likelihood criteria.

averaged $62.3 \mu\text{L}^{-1}$ (SD = 4.9) vs. $18.7 \mu\text{L}^{-1}$ (SD = 1.7) outside the reserve, a ratio of 3.3–1. Note that differences in diffusion rates alone are sufficient to explain the difference in densities inside vs. outside the reserve – there is no need to invoke differences in carrying capacity or maximum rate of growth.

Population dynamics with harvesting

Using the Fisher diffusion formula derived in the previous experiments as a deterministic skeleton, we then developed predictive models of system dynamics applicable when harvesting was applied at daily intervals, with or without a harvest reserve (Neubert 2003). Harvesting events were applied at a constant daily quota close to the maximum sustainable yield, based on earlier experimental harvesting trials with the same organism (Fryxell *et al.* 2005). This kind of pulsed harvesting might parallel a fishery with short seasonal openings for example. Stochastic growth rates were based on the expectation from the spatial logistic model with an error term that was normally distributed with mean = 0 and SD = 0.030. We generated 1000 independent Monte Carlo replicates for each treatment (harvest reserve or no harvest reserve), recording the frequency of simulated extinction events. We then compared these model predictions to the outcomes of 16 replicated experimental trials: eight conducted with a spatial harvest reserve and eight conducted without a harvest reserve.

The harvesting model predicts that *Tetrabymena* populations in the absence of a harvest reserve should rise and fall in dramatic fashion as a consequence of pulsed harvesting events (Fig. 4a). While model trajectories appear to suggest overcompensatory population dynamics of a periodic nature, the underlying deterministic model is locally stable. It is only harvesting that causes cyclical variation in abundance.

The model of the system without harvest reserves predicts a probability of extinction is 0.68 over 6 days. Three of our experimental populations went extinct on day 4, four more on day 5, and by the end of 6 days, seven of eight replicates without a harvest reserve had gone extinct (Fig. 4a). Monte Carlo simulations (1000 repetitions of eight trials) indicated that these outcomes were well within the bootstrapped 95% confidence limits at each stage of the trials, suggesting that the logistic model with simple diffusive movement was capable of accurately predicting the impact of harvesting on population viability.

The simulation model predicts that extinction should occur rarely (3% of replicates) in the system with a harvest reserve, at least not at the quotas used in our experiments (Fig. 4b). This was once again closely mirrored by our experimental results: no replicates went extinct over the course of 8 repeated harvesting events and time series

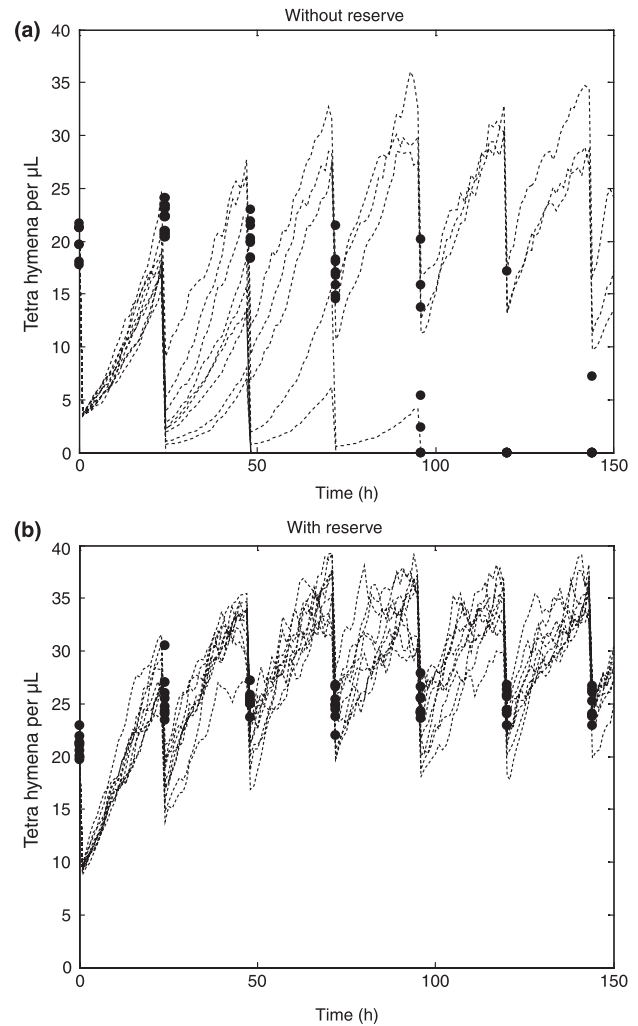


Figure 4 Observed (symbols) vs. predicted (lines) changes in eight replicates over time in the density of ciliates with (a) and without (b) a harvesting refuge, using the best-fit parameters for a logistic growth process coupled with simple diffusion. Harvest was applied at daily intervals, as shown by the sharp drops in population density. Ten independent simulations are displayed to show the expected range of variability in outcomes.

observations of *Tetrabymena* density fell well within the range predicted by our Monte Carlo simulations (Fig. 4b).

Our experimental ciliate populations exhibited different rates of diffusion inside vs. outside the reserve. To test whether our results with respect to long-term viability might be an artefact of spatial heterogeneity in mobility, we repeated the Monte Carlo simulations over a wide range of diffusion rates inside (0.01–0.03) and outside (0.01–0.03) the reserve, in a factorial design with 100 replicates at each set of diffusion parameters. Results of this sensitivity analysis were similar to those recorded for the specific diffusion parameters for our system, suggesting that the extinction patterns observed in our trials were typical.

DISCUSSION

Our results suggest that simple models of diffusion, linked with density-dependent growth rate parameters, may be useful in predicting changes in the spatial abundance of harvested populations (Neubert 2003). This encourages us in the belief that simple mathematical tools can be usefully applied in such a management context. The demographic submodel, parameters, and indeed the methods used to estimate those parameters, are similar to those often used to manage harvested fish populations. While the movement submodel is not a common feature of most fishery applications, simple diffusion models have been successfully applied to some mobile fish species (Skalski & Gilliam 2000; Acosta 2002).

Previous theoretical work suggests that the efficacy of reserves depends on reserve size, vital rates, environmental and demographic stochasticity, harvest levels, and patterns and levels of fish mobility (Roberts 1997; Mangel 1998; Hastings & Botsford 1999; Acosta 2002; Lockwood *et al.* 2002; Sala *et al.* 2002; Botsford *et al.* 2003; Gerber *et al.* 2003; Lubchenco *et al.* 2003; Neubert 2003; Rodwell & Roberts 2004). Recent work suggests that other biological details also greatly influence the outcome of harvest perturbations, such as which life stage is harvested (Benton *et al.* 2004; Cameron & Benton 2004) and whether there are compensatory trade-offs in somatic growth associated with enhanced survival (Gårdmark *et al.* 2006).

Given that details of biology have enormous influence on the outcome of models of fisheries with harvest reserves, results of any general model, including ours, should be viewed cautiously. Of particular importance, the diffusion model used here presumes no population stage structure and no density-, resource-, or time-dependent effects on dispersal rates. In real fisheries, dispersal would often (but not always) be restricted to larval stages. Although more complex models of movement might be more appropriate for many aquatic species (Jonson *et al.* 2003; Newlands *et al.* 2004), it is not unusual to find that relatively simple movement models often provide useful first order explanations for spatial patterns (Turchin 1998).

We also assume a relatively constant pattern of environmental stochasticity. At the landscape scale of real systems, environmental stochasticity might well vary in magnitude and degree of synchrony among reserve and harvest zones, but these complications would not be difficult in principle to introduce into our spatially explicit modelling framework. In real systems, demographic stochasticity would also be expected to come into play at low population densities, further accentuating the risk of overharvesting. Accommodating this effect would require additional information on expected variability in vital rates in small vs. large populations.

Dispersal rates and the spatial pattern of distribution of dispersal are particularly troublesome to measure, yet have profound influence on the dynamics of spatially structured marine populations (Lundberg & Jonzén 1999a,b; Tuck & Possingham 2000; Acosta 2002; Lockwood *et al.* 2002; Siegal *et al.* 2003; Guichard *et al.* 2004; Guichard 2005). Given the potential for diffusion-based models to illuminate the possible dynamics of spatially structured fisheries, the enormous cost and effort required to estimate dispersal distributions is clearly justifiable.

Our experimental system had the interesting feature of exhibiting slower diffusion rates within the reserve than outside. This resulted in elevated population abundance inside the reserve, even in the absence of harvesting (Fig. 3). It is difficult to know whether similar processes might occur in real systems. It is conceivable, however, that this would be the case if organisms have a sense of the 'spatial risk' associated with different parts of the landscape. This is often thought to be the case in terrestrial nature reserves, but we would not care to speculate about marine systems. If true, it further argues for the importance of measuring spatial heterogeneity in diffusion coefficients.

Given that harvest reserves necessarily imply some loss of income potential, at least in the short-term, it is attractive for practical reasons to limit reserves to the smallest size needed to stabilize long-term persistence. Our experimental trials demonstrated that a 25% reserve system was sufficient to strongly stabilize a harvested population that otherwise went extinct in > 80% of trials under a constant harvest yield policy. We plan to repeat our trials over a wide range of reserve dimensions, to see how important this feature may prove in practice. Similar experimental systems could also be used to test whether spatial reserves actually optimize long-term yields (Neubert 2003).

Both the models and our experimental results strongly confirm the prediction that harvest reserves can be an effective means of conserving marine resources, even in the face of intense exploitation. We acknowledge that there is always legitimate concern that the simplicity of microcosm studies may mask uncertainties that would plague real fishery management in complex natural settings. Nonetheless, preliminary testing using tractable experimental systems is a vital first step in the long-term assessment of costly and logistically challenging conservation and management measures (Belovsky *et al.* 1999; Ellner *et al.* 2001; Benton *et al.* 2004; Cameron & Benton 2004).

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REFERENCES

- Acosta, C.A. (2002). Spatially explicit dispersal dynamics and equilibrium population sizes in marine harvest refuges. *ICES J. Mar. Sci.*, 59, 458–468.
- Belovsky, G.E., Mellison, C., Larson, C. & Van Zandt, P.A. (1999). Experimental studies of extinction dynamics. *Science*, 286, 1175–1177.
- Benton, T.G., Cameron, T.C. & Grant, A. (2004). Population responses to perturbations: predictions and responses from laboratory mite populations. *J. Anim. Ecol.*, 73, 983–995.
- Botsford, L.W., Fiorenza, M. & Hastings, A. (2003). Principles for the design of marine reserves. *Ecol. Appl.*, 13, S25–S31.
- Cameron, T.C. & Benton, T.G. (2004). Stage-structured harvesting and its effects: an empirical investigation using soil mites. *J. Anim. Ecol.*, 73, 996–1006.
- Diehl, S. & Feissel, M. (2001). Intraguild prey suffer from enrichment of their resources: a microcosm experiment with ciliates. *Ecology*, 82, 2977–2983.
- Ellner, S.P., McCauley, E., Kendall, B.E., Briggs, C.J., Hosseini, P.R., Woods, S.N. *et al.* (2001). Habitat structure and persistence in an experimental community. *Nature*, 412, 538–543.
- Fisher, R.A. (1937) The wave of advance of advantageous genes. *Ann. Eugen.*, 7, 355–369.
- Frankel, J. (2000). Cell biology of *Tetrahymena thermophila*. In: *Methods in Cell Biology Vol. 62: Tetrahymena thermophila* (eds Asai, D.J. & Forney, J.D.). Academic Press, London, pp. 27–125.
- Fredrickson, A.G. (1991). Segregated, structured, distributed models and their role in microbial ecology: a case study based on work done on the filter-feeding ciliate *Tetrahymena thermophila*. *Microb. Ecol.*, 22, 139–159.
- Fryxell, J.M., Smith, I. & Lynn, D.H. (2005). Evaluation of alternate harvesting strategies using experimental microcosms. *Oikos*, 111, 143–149.
- Gårdmark, A., Jonzén, N. & Mangel, M. (2006). Density-dependent body growth reduces the potential of marine reserves to enhance yields. *J. Appl. Ecol.*, 43, 61–69.
- 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.
- Goombidge, B. (1992). *Global Biodiversity: Status of the Earth's Living Resources*. Chapman and Hall, New York, NY.
- Guichard, F. (2005). Interaction strength and extinction risk in a metacommunity. *Proc. Royal Soc. Lond. (B)*, 272, 1571–1576.
- Guichard, F., Levin, S.A., Hastings, A. & Siegal, D. (2004). Toward a dynamic metacommunity approach to marine reserve theory. *Bioscience*, 54, 1003–1011.
- Halpern, B. (2003). The impact of marine reserves: do reserves work and does reserve size matter? *Ecol. Appl.*, 13, S117–S137.
- Hastings, A. & Botsford, L.W. (1999). Equivalence of yield from marine fisheries and traditional fisheries management. *Science*, 284, 1537–1538.
- Hilborn, R. (2002). Marine reserves and fisheries management. Marine reserves and fisheries management. *Science*, 295, 1233–1234.
- Hilborn, R., Walters, C.J. & Ludwig, D. (1995). Sustainable exploitation of renewable resources. *Annu. Rev. Ecol. Syst.*, 26, 45–67.
- Jonson, I.D., Myers, R.A. & Flemming, J.M. (2003). Meta-analysis of animal movement using state-space models. *Ecology*, 84, 3055–3063.
- Lande, R., Engen, S. & Saether, B.-E. (1995). Optimal harvesting of fluctuating populations with a risk of extinction. *Am. Nat.*, 145, 728–745.
- Lockwood, D.R., Hastings, A. & Botsford, L.W. (2002). The effects of dispersal patterns on marine reserves: does the tail wag the dog? *Theor. Popul. Biol.*, 61, 297–309.
- Lubchenco, J., Palumbi, S.R., Gaines, S.D. & Andelman, S. (2003). Plugging a hole in ocean: the emerging science of marine reserves. *Ecol. Appl.*, 13, S3–S7.
- Ludwig, D., Hilborn, R. & Walters, C. (1993). Uncertainty, resource exploitation, and conservation: lessons from history. *Science*, 260, 36–38.
- Lundberg, P. & Jonzén, N. (1999a). Spatial population dynamics and the design of marine reserves. *Ecol. Lett.*, 2, 129–134.
- Lundberg, P. & Jonzén, N. (1999b). Optimal population harvesting in a source-sink environment. *Evol. Ecol. Res.*, 1, 719–729.
- Mangel, M. (1998). No-take reserves for sustainability of harvested species and a conservation invariant for marine reserves. *Ecol. Lett.*, 1, 87–90.
- Murawski, S.A., Brown, R., Lai, H.L., Rago, P.J. & Hendrickson, L. (2000). Large-scale closed areas as a fishery-management tool in temperate marine systems: the Georges Bank experience. *Bull. Mar. Sci.*, 66, 775–798.
- Myers, R.A. & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, 423, 280–283.
- Neubert, M.G. (2003). Marine reserves and optimal harvesting. *Ecol. Lett.*, 6, 843–849.
- Newlands, N.K., Lutcavage, M.E. & Pitcher, T.J. (2004). Analysis of foraging movements of Atlantic bluefin tuna (*Thunnus thynnus*): individuals switch between two modes of search behaviour. *Popul. Ecol.*, 46, 39–53.
- Pauly, D.V., Christensen, J., Dalsgaard, R., Froese, R. & Torres, F. Jr (1998). Fishing down marine food webs. *Science*, 279, 860–863.
- Roberts, C.M. (1997). Ecological advice for the global fisheries crisis. *Trends Ecol. Evol.*, 12, 35–38.
- Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P. & Goodridge, R. (2001). Effects of marine reserves on adjacent fisheries. *Science*, 294, 1920–1923.
- Rodwell, L.D. & Roberts, C.M. (2004). Fishing and the impact of marine reserves in a variable environment. *Can. J. Fish. Aquat. Sci.*, 61, 2053–2068.
- Sala, E., Aburto-Oropeza, O., Paredes, G., Barrera, J.C. & Dayton, P.K. (2002). A general model for designing networks of marine reserves. *Science*, 298, 1991–1993.
- Siegal, D.A., Kinlan, B.P., Gaylord, B. & Gaines, S.D. (2003). Lagrangian descriptions of marine larval dispersal. *Mar. Ecol. Prog. Ser.*, 260, 83–96.
- Skalski, G.T. & Gilliam, J.F. (2000). Modeling diffusive spread in a heterogeneous population: a movement study with stream fish. *Ecology*, 81, 1685–1700.

- Skellam, J.G. (1951). Random dispersal in theoretical populations. *Biometrika*, 38, 196–218.
- Tuck, G.N. & Possingham, H.P. (2000). Marine protected areas for spatially structured exploited stocks. *Mar. Ecol. Prog. Ser.*, 192, 89–101.
- Tupper, M.H. (2002). Marine reserves and fisheries management. *Science*, 295, 1233.
- Turchin, P. (1998). *Quantitative Analysis of Movement*. Sinauer Associates Inc., Sutherland, MA.
- Wickstrom, K. (2002). Marine reserves and fisheries management. *Science*, 295, 1233.

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