Emprical dynamic programming: A step towards model-free ecosystem based management.

Stephan B. Munch
Fisheries Ecology Division,
Southwest Fisheries Science Center
National Oceanic and Atmospheric Administration
110 Shaffer Rd. Santa Cruz, CA 95060

Marc Mangel
Department of Applied Mathematics and Statistics,
University of California, Santa Cruz, CA 95064
and
Department of Biology,
University of Bergen, 9020 Bergen, Norway

George Sugihara
Scripps Institution of Oceanography, UC San Diego
9500 Gilman Drive # 0202
La Jolla CA, 92093-0202

Alec MacCall
Fisheries Ecology Division,
Southwest Fisheries Science Center
National Oceanic and Atmospheric Administration
110 Shaffer Rd. Santa Cruz, CA 95060

Abstract

Quantitative ecosystem-based management frequently begins by developing ecosystem models. However, it may be possible or even preferable, to develop tools for management that are based on the observed dynamics of the system. Here we hypothesize that near-optimal management policies can be constructed from observed time series by merging methods of time delay embedding and stochastic dynamic programming. We find that this 'empirical dynamic programming' approach performs well in the 2-d cases we have examined and outperforms over-simplified parametric alternatives. We expect this first step toward model-free ecosystem based management to be of use wherever ecosystem-wide data are limited or ecosystem dynamics are uncertain.

Significance Statement

All of the species we harvest from the ocean are part of an ecosystem, but most fisheries management decisions are based on mathematical models that only include the target species. It is certainly possible to build ecosystem models, but the details of these are often highly uncertain and difficult to test directly. Rather than make assumptions about the way marine ecosystems work, we propose to use the observed dynamics of the system to construct management policy. Here we show that our new approach, dubbed 'empirical dynamic programming,' significantly outperforms single-species models.

Introduction

In recent decades there has been a push to engage in Ecosystem Based Management (EBM, Christensen et al 1996, Pikitch et al. 2004, McLeod et al. 2005), which requires us to recognize the interactions between species and make explicit the trade-offs that arise among competing uses (Meffe et al. 2002). Quantitative approaches to EBM typically begin by constructing ecosystem models (Hall and Mainprize 2004, Plaganyi 2007, Traver et al. 2007, Fulton et al. 2011) which are then used to evaluate various management scenarios and quantify trade-offs (Smith et al. 2007, Steffan-Dewinter et al 2007, Essington and Munch 2014). Of necessity, ecosystem models make various simplifying assumptions, beginning with the list of species, the spatial extent, and the environmental drivers included. While it is possible to quantify the relevance of these some of these factors (see e.g. Pinnegar et al. 2007, Hagen et al. 2012), it is beyond the scope of many practical applications.

Still more difficult to evaluate is the importance of model formulation. Super-sensitivity to model structure is likely common (Wood and Thomas 1999, Fussman REF) and there is often little direct empirical justification for a given model formulation. Consider for example the difficulty in quantifying the functional response: Since the pioneering work of Holling (1959), dozens of functional response models have been developed to account for such things as predator interference and spatial refugia of prey (reviewed in Jeschke et al. 2002). Unfortunately, while the choice of functional response has a large effect on predicted dynamics, the available data may be insufficient to distinguish among biologically plausible candidates (Jost and Arditi 2001, Jost and Ellner 2000 Fussman REF).

We are thus lead to ask whether it is possible to develop approaches to quantitative ecosystem based management that are robust to model formulation. One promising avenue stems from the time-delay embedding theorem of Takens (1981), who showed that it is possible to reconstruct the dynamics of an M-dimensional deterministic dynamical system from the lags of a single time series. This idea has since been generalized to stochastic, driven, and nonstationary systems (Starke et al. 2003, Ragwitz and Kantz 2002, REF).

Empirical dynamical modeling via time-delay embedding has been used in ecological and epidemiological forecasting for decades (eg , Sugihara and May 1990, Sugihara 1994, Deyle et al 2013) and analogous methods have been used widely in physics (e.g. Small 2005), finance (e.g. Soofi and Cao 2002), and neurobiology (e.g. Galka 2000). These tools significantly outperform mis-specifiied parametric models for simulated and laboratory data (Perretti et al. 2012a,b) as well as field observations (Ye et al. 2015). Critically, these methods do not require us to specify an ecosystem model in order to predict dynamics. We hypothesize that combining time-delay embedding with dynamic programming will allow us to engage in EBM without the need to explicitly represent all of the relevant species.

We test this idea against a suite of simulation models over a range of dynamical regimes. The simulations represent well documented ecological phenomena such as competition among species, migration in and out of protected areas, maternal effects, and time-varying productivity. Although the present work is clearly motivated by the call to engage in EBM, here we focus on the more modest task

of managing harvest of a single species from each of these two dimensional systems. The dynamics we simulate are admittedly much simpler than we expect to encounter in real applications. However, we regard this as a necessary first step toward the more complicated problems of EBM. Although we focus on harvesting, other scalar objectives, such as minimizing quasi-extinction risk, meeting forage needs of protected species, or maximizing biodiversity could be tackled in this framework with little modification.

We show that it is possible to sustainably manage a target species without an explicit system model by implicitly accounting for interactions with other components of the system through time-delay embedding.

Methods

A harvest policy that maximizes the long-run discounted average yield satisfies an equation of dynamic programming

$$V(\mathbf{x}) = \max_{\mathbf{u}} E\{R(\mathbf{x}', \mathbf{u}) + \gamma V(\mathbf{x}') | \mathbf{x}, \mathbf{u}\}$$
(1)

where $V(\mathbf{x})$ is the long-run average discounted yield given that we start in state \mathbf{x} (Bellman 1958, Mangel and Clarke 1988). $R(\mathbf{x}',u)$ is the expected reward (here, yield) obtained by taking action u (e.g. setting the next harvest rate) while in state \mathbf{x}' and γ is the discount rate. Here, E denotes the expectation over the next state of the system, \mathbf{x}' , given the current state \mathbf{x} and choice of action u. In other applications, alternate 'reward' functions would be relevant (e.g. the quasi-extinction probabilities for species at risk) which can be optimized in this framework with little modification.

To make this concrete, imagine that we would like to manage harvest of species A while accounting for the fact that it interacts with species B and C. To derive an optimal policy using (1), we could begin by letting \mathbf{x} represent the abundances of all relevant species, i.e. $\mathbf{x}_t = \{a_t, b_t, c_t\}$. Doing so would require us to specify transitions (i.e. $P(\mathbf{x}_{t+1}|\mathbf{x}_t)$) for species A,B, and C and this requires either that we have data on all of species or some other way to model their dynamics.

However, note that the dynamic programming equation is the same regardless of how we specify the states or the tool we use to model transitions among them. Using (1) to find an optimal harvest policy only requires some way of taking an expectation over the states of the system one step into the future. This is precisely what we obtain using time-delay embedding for forecasting (Sugihara 1994, Ragwitz and Kantz 2002).

Thus, to manage harvest of species A we may not need an ecosystem model or data on species B and C. Instead, we use the past history of A to reconstruct the dynamics. In delay coordinates, the state at time t would be \mathbf{x}_t ={a_t,...,a_{t-d}} where d is the embedding dimension. Takens (1981) theorem provides a rigorous justification for asserting that \mathbf{x}_{t+1} is some function of the previous state, i.e. $\mathbf{x}_{t+1} = f(\mathbf{x}_t)$. Although, Van Kampen (1992) shows that there are some stochastic systems that can't be embedded in this way (i.e. can't be made Markov precisely), Holstein and Kantz (2009) describe conditions under which we can expect to obtain a reasonable Markov approximation. Here we adopt a Bayesian approach to time-delay embedding in which the unknown function f is treated as random, assigned a

Gaussian process (GP) prior (Rasmussen and Williams 2006), and updated with the observed time series (additional background and algorithmic details provided in Appendix S1).

To make more concrete the connection to fisheries and EBM, assume that we have a time series of catch C and some measure of fishing effort, F, for species A. Because we expect previous removals to effect the dynamics, the past history of effort must also be include in the states. The delay coordinates for the system would therefore be $\mathbf{x_t} = \{C_t, ..., C_{t-d}, F_t, ..., F_{t-d}\}$. The next state of the system, i.e. $\mathbf{x_{t+1}} = \{C_{t+1}, ..., C_{t-d+1}, F_{t+1}, ..., F_{t-d+1}\}$, involves both the next catch and the next effort. We do not attempt to forecast F_{t+1} , but treat this as the action (u) in the dynamic programming model. Forecasts for C_{t+1} are therefore conditional on F_{t+1} as well as $\mathbf{x_t}$. Our empirical dynamic programming (EDP) approach to setting management policy involves iterating (1) to convergence with the expectation taken over the posterior distribution for $\mathbf{x'}$ given a set of training data (see Appendix S2 for algorithmic details). What emerges is a harvest policy for species A that implicitly accounts for species B and C.

Although we have framed our description in terms of managing harvest of a single species from a three-species system, the methods we are proposing are much more generic. Instead of multiple species, we could implicitly account for dynamics occurring over multiple locations or involving several distinct life stages. More generally, these methods could be used to account for unobserved state variables such as early life stages that are impossible to count or other variables affecting a population such as food availability and temperature.

Simulations

To evaluate the performance of management strategies obtained via empirical dynamic programming, we simulated data from four two-dimensional systems representing a range of well-documented ecological scenarios. The first is competition among two species based on the 'generalized Beverton Holt' model of Schoombie and Getz (1998) in which the density of both species reduces the per capita growth rate of each. Only the first species is harvested or observed. The second model involves a single species in space, with local density dependence following a Ricker model and migration in and out of a protected area (Gerber et al. 2002). Here, only individuals from the unprotected area are harvested. The third scenario represents maternal effects and has been modified from the model of Ginzburg and Taneyhill (1994) to allow for a stable fixed point. In this case, the hidden state is not the abundance of individuals from another species or location, but some unobserved measure of maternal quality. The fourth scenario follows a single species in a single location with Ricker density dependence and timevarying productivity. Analogous models are widely used to assess the influence of environmental drivers (e.g. temperature) on population dynamics (e.g. Clark et al. 2003). Here, the unobserved state variable is the environment. These simulations are based on the published models shown in Table 1.

Several factors influence our ability to forecast – and hence manage - using time-delay embedding. Since empirical dynamic modeling depends on reconstructing the attractor for the system, the most obvious factor is the amount of data available to reconstruct the dynamics. In addition, we expect that the degrees of stochasticity and nonlinearity will interact to affect forecasts. For each of the four scenarios, we simulated data with 3 different parameter sets corresponding to 1) stable fixed points, 2)

stable 4-cycles and 3) either quasi-periodicity or chaos. In the case of time-varying productivity (scenario 4) the dynamics do not settle down to a fixed point. In place of a 'stable' parameter set, the third parameter set in this scenario generates an 8-cycle. Multiplicative lognormal process noise was superimposed on these deterministic skeletons and data were generated using three levels of stochasticity (CV = 0.0, 0.1, and 0.2). Finally, each simulation began with a 'training' interval of T years (T = 30, 50, and 100) during which the population was harvested, with the removal rate starting near zero and increasing according to a logistic AR(1) (cf. Thorson et al. 2013) (Results for alternative exploitation histories are qualitatively the same, see Appendix 3). Although each scenario involves a 2-d state-space, only the catch and effort data for the harvested class were used in forecasting and policy determination. Performance of this empirical dynamic programming (EDP) policy was evaluated by tracking the average yield over the next 100 years.

We considered two benchmarks for evaluating the performance of the EDP policy. The first is the maximum long-run average yield obtainable under a constant harvest rate policy with perfect information. We regard this benchmark as representing a highly idealized 'best-case scenario' in which the true dynamics are known exactly. For our second benchmark, we fit a parametric population model to the same time series used to determine the EDP policy. We then used the posterior in an identical DP algorithm to generate a policy. To ensure adequate flexibility in our benchmark model, we initially chose a 3-parameter generalization of the Ricker model, $n_{t+1} = rn_t^c \exp\left[-bn_t\right]$ (Iles 1994). However, in the absence of additional constraints, we found this model to be unstable and produce extinction-prone harvest policies. We subsequently restricted our attention to c=1 (i.e. a Ricker model).

Obviously, for the 2-d dynamics we are simulating, this single species model is incorrect. However, it is important to note that this and similar scalar models are actually used to set harvest rates in cases where the only available data for the target species are yields and exploitation rates (see e.g. Haddon 2010, Dick and MacCall 2011). The rationale for using the Ricker over other commonly used models (e.g. Pella-Tomlinson) is that two of our scenarios have Ricker as a special case (scenario 2: $m_1=m_2=0$, scenario 4: g=0) and the remaining models have –like the Ricker - a unimodal shape and an asymptotic approach to zero at large population sizes (scenario 1: $m_1=0$, b>1, scenario 3: c>1,).

Each combination of scenario, parameters, noise levels, and training interval was replicated 100 times for a total of 10,800 simulations (4 models x 3 parameter sets x 3 noise levels x 3 training intervals x 100 replicates). Starting values for each simulation were randomly perturbed by \pm -5% from the starting values listed in Table 1.

Imprecise selectivity

In the preceding simulations, it was assumed that only the focal class was harvested. In reality this is unlikely to ever be the case. Non-target sizes, ages, and species are always captured and the boundaries of marine protected areas are often somewhat permeable. Scenarios 1 and 2 include two classes of potentially harvestable individuals and we use these to explore the effects of imprecise targeting or 'bycatch.' We allowed removals of the non-target class at a fraction, q, of the nominal removal rate (see table 1) and aggregated removals across classes. In this analysis, we assume that only the aggregated

removals and only the nominal harvest rate are known (i.e. the catch could not be apportioned among classes). Management then attempted to maximize the aggregated catch.

Results

For the perfect information, constant harvest rate benchmark, the long run average yields were fairly similar for scenarios 1 to 3, with means (SD) of 3.32 (0.611), 3.63 (1.24), 4.27 (0.049), while scenario 4 was substantially lower at 0.634 (0.168). To facilitate comparison across these scenarios we report the results in terms of yield relative to this benchmark (Figures 1 and 2).

Overall the EDP model produced long run average yields that were reasonably close to the constant harvest rate benchmark. The average ratio was 0.84 (0.22). On the other hand, the mean ratio relative to the Ricker benchmark was 14.66 (36.48) and it is tempting to conclude that we could obtain an order of magnitude better yield using EDP. However, the mean ratio is unduly influenced by cases where yield is very low (Figure 1). To avoid such numerical oddities, the remaining results are reported in terms of the median which is more robust. The median (25th, 75th percentiles) yield ratio relative to the constant harvest benchmark was 0.93 (0.78, 0.98) and relative to the Ricker benchmark it was 1.32 (1.00, 1.83). Thus the nonparametric policy produces yields that are typically close to what could be obtained under a constant harvest rate policy with perfect knowledge, and 32% better than what would be obtained using a parametric policy fit to the same data.

The success of the EDP relative to the Ricker policy is driven, in part, by differences in the long run exploitation rate. Relative to the constant harvest rate policy, the median effort ratio under the EDP policy was 0.98 (0.90, 1.01) while for the Ricker it was 1.02 (0.94, 1.10). Although both approaches occasionally overexploit the target, the EDP policy is much less likely to do so; on average the EDP exceeded the optimal constant harvest rate 38% of the time while the Ricker policy did so 66% of the time.

We now break these results down by the main effects (Table 2). The EDP policy was relatively insensitive to the training interval and noise level (Fig. 1A,C), somewhat more sensitive to the dynamical regime (Fig 1 B), and most sensitive to the ecological scenario (Fig. 1D). The median yield ratio increased with increasing stability from 0.85 in the chaotic regime to 0.98 in the stable regime. The ecological scenario had the biggest effect on performance; The median yield ratio was lowest in the maternal effects scenario (0.76), better in the two-location scenario (0.85) and quite good in the time-varying productivity and competition scenarios (0.94 and 0.95 respectively).

In contrast to the constant harvest benchmark, all of the main effects seem to influence the yield ratio relative to the Ricker benchmark. Median yields relative to the Ricker benchmark were least sensitive to the training interval, ranging from 1.42 for the 30 year training interval to 1.24 for the 100 year training interval. Hence, the approximation provided by the Ricker model improves with more data.

Yield relative to the Ricker benchmark was somewhat more sensitive to the dynamical regime and noise level. The relative yield was highest in the chaotic regime (1.30) and decreased in the stable regime (1.03) suggesting – not surprisingly - that the Ricker approximation is best when the dynamics are stable. It is worth noting, however, that the interquartile range was greatest for stable dynamics with yield ratios ranging from 1.00 to 32.7; when the Ricker policy fails in the stable regime, it really fails. The results were analogous for the effects of noise. The low noise level produced the highest median relative yield (1.50) which declined to 1.13 in the high noise case. Since performance of the EDP policy against the constant harvest benchmark was insensitive to noise, this result suggests that the Ricker policy improves with the addition of noise. Apparently the decreased predictability masks the effect of flattening the 2-d dynamics down to 1.

In keeping with results for the constant harvest benchmark, the median yield ratio against the Ricker is most sensitive to the ecological scenario. The smallest relative yields were obtained in the maternal effects and time-varying r scenarios (0.97 and 1.01 respectively). The two location scenario produced a median yield ratio of 1.45. Performance of the Ricker-based policy was poor under the competition scenario and the median yield ratio was 40.10. Thus, the EDP produced policies that were no worse than Ricker and sometimes markedly better.

Imprecise selectivity

It is often the case that a single gear captures more than one species or that MPA boundaries are somewhat permeable. The average (SD) yield under the perfect information constant harvest policy increased linearly with q from 0.63 (0.17) to 1.05 (0.27) in the competition scenario and from 4.27 (0.05) to 6.31 (0.15) in the two location scenario.

For both ecological scenarios, relative yields under the EDP policy appear robust to imprecise selectivity while the Ricker policy is considerably more sensitive (Figure 2). In the two location scenario, the median yield ratio under the EDP policy was slightly dome shaped with respect to q. In contrast, the median yield ratio for the Ricker policy increased linearly from 0.58 to 0.87. Under the competition scenario, the median yield ratio for the EDP policy was much less sensitive, decreasing with q from 0.95 to 0.92. The Ricker policy performs poorly for this scenario with a median yield ratio of 0.02 at q=0. Interestingly, the Ricker policy improves considerably with increasing q to a maximum of 0.51.

Discussion

Several of our results are counterintuitive and merit further consideration. First, it appears that EDP improves with increasing stability. Relative to the Ricker, however, performance degrades with both stability and stochasticity. Both process noise and chaos result in increased exploration of the state space which improves our ability to recover the dynamics. However, stable dynamics with noise can be described by a stiff GP model while chaotic dynamics require more flexible GP models. This increased flexibility is of little consequence in regions where data are dense, but limit our ability to extrapolate

effectively. Since the EDP algorithm requires a forecast on a grid over the full state space, noisy stable dynamics are easier to manage than chaotic systems.

This reflects a common feature of nonparametric approaches: forecasts deteriorate outside the observed state space. But, the severity of this problem depends strongly on the smoothness of the underlying attractor. Smooth systems, without sharp changes in curvature, are generally much easier to fill in and in these cases nonparametric methods are likely to perform nearly as well as correctly specified parametric models.

Our approach assumes that the system is stationary, i.e. that the rules that govern changes in state are fixed through time. However, natural systems exhibit various signatures of nonstationarity (Hare and Mantua 2000, Sheffer and Carpenter 2003, Henden et al. 2009) and technological innovations change the efficiency of harvest (e.g. Wilberg et al 2009, Thorson and Berkson 2010) leading us to question whether EDP can be applied in these cases. Much depends on the rate at which the system is changing. When the rate of change is slow relative to the sampling interval, it may still be possible to reconstruct dynamics using one of several 'overembedding' approaches (Hegger et al. 2000, Verdes et al. 2006) or time-varying parameters as in dynamic linear models (West and Harrison 1999, Carpenter and Brock 2006). If the system is changing rapidly, however, it may be difficult to forecast adequately using any approach.

The scenarios analyzed here differ from real systems in several other ways. First, they all involve species with rapid turnover, while most fisheries typically focus on species with generation times of several years or more. Current assessment methods use single species models with age structure to filter data from these fisheries. This approximation is likely to be accurate for long-lived species where mortality rates are low and in systems with many generalist predators where fluctuations in abundance are damped by prey switching. Thus although we have shown that the EDP algorithm clearly outperforms policies generated with a single-species model, we suspect that the margin will decrease as both the complexity of the system and the lifespan of the species involved increase. Consequently nonlinear forecasting approaches may be most valuable for relatively short lived species such as, e.g. anchovy (Deyle et al. 2013) and salmonids (Ye et al 2015). Second, heavily managed species typically have time series of multiple data types (landings, survey indices, length compositions, growth trajectories, etc) that reflect harvesting by multiple gears over large spatial areas. This information is currently synthesized through state-of-the-art statistical models (Methot and Wetzel 2013). Extending the EDP approach to incorporate all of this additional information is an important area for future work.

Obviously there is more work to be done before the EDP approach can be applied to any particular management problem. The most pressing is the need to manage larger systems for multiple objectives such as simultaneously harvesting predators and forage species or balancing yield and conservation goals. But, many other questions remain including how to deal with significant observation errors and how to integrate information on multiple species. Nevertheless we believe that there is a clear case to be made for generic approaches to management. Current approaches are often strongly sensitive to assumptions on 'steepness' or on the shape of the stock-recruitment curve (Mangel et al 2013). As we

move toward EBM and multi-species management, the sensitive dependence on parametric assumptions is only likely to increase.

We have shown that EDP can be used to sustainably manage a variety of ecological scenarios, with dynamics ranging from stable to chaos and deterministic to stochastic. This was achieved without modifying the EDP algorithm to accommodate each scenario; the policy is based solely on the observed dynamics of the system. In light of this, EDP and similar algorithms may provide the foundation for robust approaches to EBM that work whether or not we know the true dynamics of the system.

Citations

Bellman, R. (1958). Dynamic programming and stochastic control processes. *Information and control*, 1(3), 228-239.

Bertsekas, D. P. (1995). Dynamic programming and optimal control. Belmont, MA: Athena Scientific.

Jost, C. & S. Ellner. 2000. Testing for predator dependence in predator-prey dynamics: a nonparametric approach. Proc. Roy. Soc. Lond. B 267: 1611-1620

Jost, C. and R. Arditi. 2001. From pattern to process: Identifying predator-prey models from time-series data. Population Ecology, 43:229–243.

Holling, CS. 1959. Some characteristics of simple types of predation and parasitism. The Canadian Entomologist, 91:385–398

Carpenter, S. R., & Brock, W. A. (2006). Rising variance: a leading indicator of ecological transition. Ecology letters, 9(3), 311-318.

Christensen NL, Bartuska AM, Brown JH, et al. 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. Ecol. Appl. 6: 665–91

Clark, R. A., Fox, C. J., Viner, D., & Livermore, M. (2003). North Sea cod and climate change—modelling the effects of temperature on population dynamics. Global Change Biology, 9(11), 1669-1680.

Cressie, N., C. A. Calder, J. S. Clark, J. M. Ver Hoef, and C. K. Wikle. 2009. Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. Ecological Applications 19:553–570.

Deisenroth, M. P., Rasmussen, C. E., & Peters, J. (2009). Gaussian process dynamic programming. *Neurocomputing*, 72(7), 1508-1524.

Deyle, E. R., Fogarty, M., Hsieh, C. H., Kaufman, L., MacCall, A. D., Munch, S. B., ... & Sugihara, G. (2013). Predicting climate effects on Pacific sardine. *Proceedings of the National Academy of Sciences*, 110(16), 6430-6435.

Engel, Y., Mannor, S., & Meir, R. (2003). Bayes meets Bellman: The Gaussian process approach to temporal difference learning. ICML (Vol. 20, No. 1, p. 154).

Fulton E. A., Link J. S., Kaplan I. C., Savina-Rolland M., Johnson P., Ainsworth C., Horne P., et al. 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries 12:171-188.

Galka, A. (2000). *Topics in nonlinear time series analysis: with implications for EEG analysis* (Vol. 14). World Scientific.

Gerber, L. R., Kareiva, P. M., & Bascompte, J. (2002). The influence of life history attributes and fishing pressure on the efficacy of marine reserves. Biological Conservation, 106(1), 11-18.

Ginzburg, L. R., & Taneyhill, D. E. (1994). Population cycles of forest Lepidoptera: a maternal effect hypothesis. Journal of Animal Ecology, 79-92.

Haddon, M. (2010). Modelling and quantitative methods in fisheries. CRC press.

Hagen, M, Kissling, WD, Rasmussen, C, Carstensen, DW, Dupont, YL, KaiserBunbury, CN, O'Gorman, EJ, Olesen, JM, De Aguiar, MAM, Brown, LE, AlvesDos-Santos, I, Guimarães, PR, Maia, KP, Marquitti, FMD, Vidal, MM, Edwards, FK, Genini, J, Jenkins, GB, Trøjelsgaard, K, Woodward, G, Jordano, P, Ledger, ME, Mclaughlin, T, Morellato, LPC and Tylianakis, JM (2012) Biodiversity, Species Interactions and Ecological Networks in a Fragmented World. Advances in Ecological Research, 46. 89 - 120.

Hall, S. J. and Mainprize, B. (2004), Towards ecosystem-based fisheries management. Fish and Fisheries, 5: 1–20

Hare, S. R., & Mantua, N. J. (2000). Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in oceanography, 47(2), 103-145.

Harrison, J., & West, M. (1999). Bayesian Forecasting & Dynamic Models. Springer.

Hegger, R., Kantz, H., Matassini, L., & Schreiber, T. (2000). Coping with nonstationarity by overembedding. Physical Review Letters, 84(18), 4092.

Henden, J. A., Ims, R. A., & Yoccoz, N. G. (2009). Nonstationary spatio-temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. Journal of animal ecology, 78(3), 636-645.

Hsieh, C. H., Anderson, C., & Sugihara, G. (2008). Extending nonlinear analysis to short ecological time series. *The American Naturalist*, 171(1), 71-80.

Iles, T.C. 1994. A review of stock–recruitment relationships with reference to flatfish populations. Neth. J. Sea Res. 32: 399–420

Jeschke, J. M., M. Kopp, and R. Trollrian. 2002. Predator functional responses: Discriminating between handling and digesting prey. Ecological Monographs, 72:95–112.

Jiao, Y., Smith, E. P., O'Reilly, R., & Orth, D. J. (2012). Modelling non-stationary natural mortality in catch-at-age models. ICES Journal of Marine Science: Journal du Conseil, 69(1), 105-118.

Judd, K. (2003). Chaotic-time-series reconstruction by the Bayesian paradigm: Right results by wrong methods. Physical Review E, 67(2), 026212.

Judd, K., & Nakamura, T. (2006). Degeneracy of time series models: The best model is not always the correct model. Chaos: An Interdisciplinary Journal of Nonlinear Science, 16(3), 033105.

Larkin PA. 1996. Concepts and issues in marine ecosystem management. Rev Fish Biol Fisher 6: 139–64.

Luo, Y., Weng, E., Wu, X., Gao, C., Zhou, X., & Zhang, L. (2009). Parameter identifiability, constraint, and equifinality in data assimilation with ecosystem models. *Ecological Applications*, 19(3), 571-574.

Mangel, M., & Clark, C. W. (1988). Dynamic modeling in behavioral ecology. Princeton University Press.

Mangel, M., MacCall, A.D., Brodziak, J., Dick, E.J., Forrest, R.E., Pourzand, R., and S. Ralston. 2013A perspective on steepness, reference points, and stock assessment. Canadian Journal of Fisheries and Aquatic Sciences 70:930-940

McLeod KL, Lubchenco SR, Palumbi SR, and Rosenberg AA. 2005. Scientific consensus statement on marine ecosystem-based management. Communication Partnership for Science and the Sea (COMPASS).

Meffe, G., L. Nielsen, R.L. Knight, and D. Schenborn 2002. Ecosystem Management: Adaptive, Community-based Conservation. Island Press. Washington.

Methot, R. D., & Wetzel, C. R. (2013). Stock synthesis: A biological and statistical framework for fish stock assessment and fishery management. Fisheries Research, 142, 86-99.

Pikitch, E. K., C. Santora, E. A. Babcock, A. Bakun, R. Bonfil, D. O. Conover, P. Dayton, P. Doukakis, D. Fluharty, B. Heneman, E. D. Houde, J. Link, P.A. Livingston, M. Mangel, M. K. McAllister, J. Pope, K. J. Sainsbury. 2004. Ecosystem-based fishery management. Science 305:346-347

Pinnegar, J. K., Blanchard, J. L., Mackinson, S., Scott, R. D., & Duplisea, D. E. (2005). Aggregation and removal of weak-links in food-web models: system stability and recovery from disturbance. *Ecological Modelling*, 184(2), 229-248.

Pinnegar, J.K., Blanchard, J.L., Mackinson, S., Scott, R.D. and Duplisea, D.E. 2005. Aggregation and removal of weak-links in food-web models: system stability and recovery from disturbance. Ecol. Model., 184: 229-248.

Plagányi, É.E. 2007. Models for an ecosystem approach to fisheries. FAO Fisheries Technical Paper. No. 477. Rome, FAO. 108p.

Quince, C., Higgs, P.G. and McKane, A.J. 2005. Topological structure and interaction strengths in model food webs. Ecol. Model., 187: 389-412.

Ragwitz, M., & Kantz, H. (2002). Markov models from data by simple nonlinear time series predictors in delay embedding spaces. Physical Review E, 65(5), 056201.

Rasmussen, CE and CKI Williams 2006. Gaussian Processes for Machine Learning. MIT Press, Cambridge, MA.

Sainsbury, KJ, Punt AE, Smith ADM (2000) Design of operational management strategies for achieving fishery ecosystem objectives. ICES J Mar Sci 57: 731-741.

Scheffer, M., & Carpenter, S. R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in ecology & evolution, 18(12), 648-656.

Schoombie, S. W., & Getz, W. M. (1998). Evolutionary stable strategies and trade-offs in generalized Beverton and Holt growth models. Theoretical population biology, 53(3), 216-235.

Small, M. (2005). *Applied nonlinear time series analysis: applications in physics, physiology and finance* (Vol. 52). Singapore: World Scientific.

Smith ADM, Fulton EJ, Hobday AJ, Smith DC, Shoulder P (2007) Scientific tools to support the practical implementation of ecosystem-based fisheries management. ICES J Mar Sci 64: 633-639.

Soofi, A. S., & Cao, L. (Eds.). (2012). *Modelling and forecasting financial data: techniques of nonlinear dynamics* (Vol. 2). Springer Science & Business Media.

Stark, J., D. S. Broomhead, M. E. Davies, and J. Huke (2003) Delay embeddings for forced systems. II.Stochastic forcing. J. Nonlinear Sci. Vol. 13: pp. 519–577.

Steffan-Dewenter, I., Kessler M, Barkmann J, Bos MM, Buchori D, Erasmi S, Faust H, Gerold G, Glenk G, Gradstein SR, Guhardja E, Harteveld M, Hertel D, Höhn P, Kappas M, Köhler S, Leuschner C, Maertens M, Marggraf R, Migge-Kleian S, Mogea J, Pitopang R, Schaefer M, Schwarze S, Sporn SG, Steingrebe A, Tjitrosoedirdjo SS, Tjitrosoemito S, Twele A, Weber R, Woltmann L, Zeller M, and Tscharntke T (2007) Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. PNAS 104: 4973.

Thorson, J. T., & Berkson, J. (2010). Evaluating single-and multi-species procedures to estimate time-varying catchability functional parameters. Fisheries Research, 101(1), 38-49.

Thorson, J. T., Minto, C., Minte-Vera, C. V., Kleisner, K. M., & Longo, C. (2013). A new role for effort dynamics in the theory of harvested populations and data-poor stock assessment. Canadian Journal of Fisheries and Aquatic Sciences, 70(12), 1829-1844.

Travers M., Shin Y., Jennings S., Cury P. 2007. Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. Progress in Oceanography 75:751-770.

van Kampen, N. 1992 Stochastic Processes in Physics and Chemistry. Elsevier Science, Amsterdam.

Verdes, P. F., Granitto, P. M., & Ceccatto, H. A. (2006). Overembedding method for modeling nonstationary systems. Physical review letters, 96(11), 118701.

Wilberg, M. J., Thorson, J. T., Linton, B. C., & Berkson, J. (2009). Incorporating time-varying catchability into population dynamic stock assessment models. Reviews in Fisheries Science, 18(1), 7-24.

Wood, S. N. (2010). Statistical inference for noisy nonlinear ecological dynamic systems. Nature, 466(7310), 1102-1104.

Ye, H., Beamish, R. J., Glaser, S. M., Grant, S. C., Hsieh, C. H., Richards, L. J., Schnute, J.T. & Sugihara, G. (2015). Equation-free mechanistic ecosystem forecasting using empirical dynamic modeling. Proceedings of the National Academy of Sciences, 112(13), E1569-E1576.

Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology, 69: 508-515.

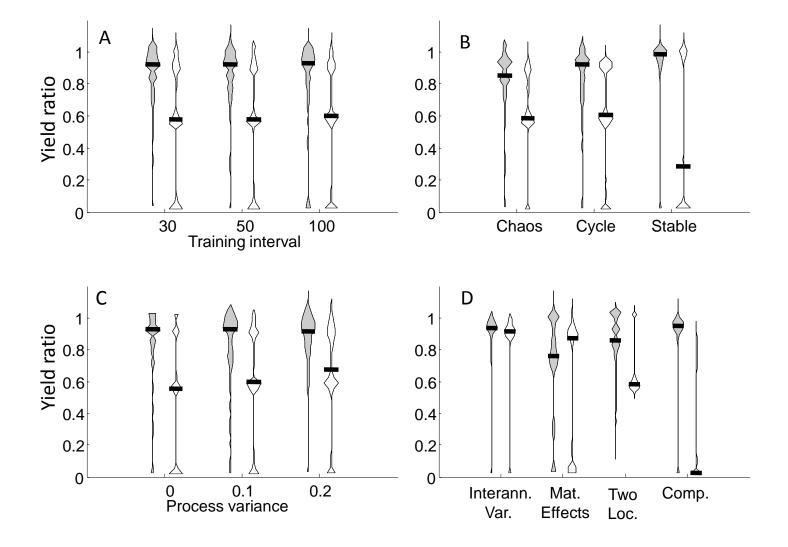
Yodzis, P. 1998. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. J. Anim. Ecol., 67: 635-658.

Yodzis, P. 2000. Diffuse effects in food webs. Ecology, 81: 261-266.

Figure Captions

Figure 1 A-D. Yield ratios for the EDP policy (grey) and Ricker-based (white) policies relative to the perfect information constant harvest strategy. The width of each blob indicates the relative frequency with which a given yield ratio appeared, scaled such that the maximum width is fixed across all plots. The bold horizontal black line indicates the mean yield ratio for each policy and main effect. A. results aggregated by training interval, B. by dynamical regime, C. by process variance, and D. by ecological scenario.

Figure 2. Effects of imprecise selectivity on the yield ratios, relative to the constant harvest policy. The dashed and solid lines indicate the median yield ratios for the EDP and Ricker policies, respectively, while the light grey and dark grey patches indicate the upper and lower quartiles. Left: Yield ratios under the two-location scenario. Right: Yield ratios under the competition scenario.



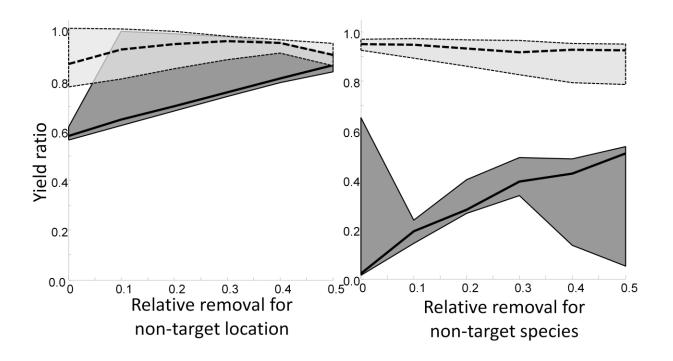


Table 1. Model specification.

Model	Function	Parameters	Source
1. Competition	$n_{1,t+1} = r_1 S_{1,t} e^{\varepsilon_t} [1 + (S_{1,t} + m_1 S_{2,t})^b]^{-1}$ $n_{2,t+1} = r_2 S_{2,t} e^{\varepsilon_t} [1 + (S_{2,t} + m_2 S_{1,t})^b]^{-1}$	$r_1 \in \{2.4, 3.6, 4.5\}$ $r_2 = 2/3r_1$ $m_1 = 2, m_2 = 1$ b = 4	Schoombie and Getz (1998)
2. Migration and protected areas	$ \begin{bmatrix} n_{1,t+1} \\ n_{2,t+1} \end{bmatrix} = \begin{bmatrix} 1 - m_1 & m_2 \\ m_1 & 1 - m_2 \end{bmatrix} \begin{bmatrix} S_{1,t} e^{r_1 - S_{1,t} + \varepsilon_t} \\ S_{2,t} e^{r_2 - S_{2,t}} \end{bmatrix} $	$r_1 \in \{7, 13, 15\}$ $r_2 = 18$ $m_1 = 0.65$ $m_2 = 0.75$	Gerber et al. (2002)
3. Maternal effects	$n_{t+1} = e^r S_t \frac{q_t^c}{1 + q_t^c} e^{\varepsilon_t}$ $q_{t+1} = \frac{g}{1 + n_{t+1}}$	$r \in \{1.75, 4, 3.5\}$ g = 10 c = 5	Ginzburg and Taneyhill (1994)**
4. Time varying productivity	$n_{t+1} = S_t e^{r[1+gT_t] - S_t + \varepsilon_t}$ $T_{t+1} = \cos(\varphi) T_t + \sin(\varphi) \sqrt{1 - T_t^2}$	r = 1.95 g = 0.4 $P_0 = 0$ $\varphi \in \{8,3,4\}$	Clark et al. (2003)
Exploitation history	$logit(F_{t+1}) = \alpha logit(F_t) + (1 - \alpha)\sigma_F z_t$	$\alpha = 0.98$ $\sigma_F = 5$ $F_0 = 0.001$	

In each model the top line represents the target for harvesting. S_t represents the density of individuals remaining in the population following removals, i.e. $S_{1,t}=(1-F_t)n_t$. To allow for imprecise selectivity, non-focal classes are removed at a fraction q of the nominal effort such that survival is $S_{2,t}=(1-qF_t)n_t$. The noise terms, $\varepsilon_t \sim N(-\frac{\sigma_\varepsilon^2}{2},\sigma_\varepsilon^2)$, caricature random variation in productivity. The logistic AR(1) model used to construct the exploitation history is given on the final line, where $z_t \sim N(0,1)$. Under this model, F eventually converges to a mean of roughly 0.5, but does so on a time scale longer than the maximum training interval. *The first set of parameters for this model generates an 8-cycle rather than a fixed point, which is impossible here. **The maternal effects model (2) presented by Ginzburg and Taneyhill (1994) has c=1 and $q_{t+1}=gq_t[1+n_{t+1}]^{-1}$ which produces cycles and chaos but no fixed points. It has been modified to allow for a stable equilibrium.

Table 2. Yield ratios by main effect.

Effect		EDP:Constant	GP:Ricker
Dynamic	Chaos	0.85 (0.77, 0.94)	1.36 (1.04, 1.61)
regime	Limit cycle	0.92 (0.75, 0.96)	1.26 (0.96, 1.70)
	Stable	0.98 (0.92, 1.00)	1.12 (1.00, 32.70)
Noise	0.0	0.93 (0.78, 0.96)	1.50 (1.00, 23.39)
level	0.1	0.93 (0.77, 0.98)	1.27 (1.00, 1.78)
	0.2	0.92 (0.80, 0.98)	1.13 (0.98, 1.6)
Training	30	0.92 (0.79, 0.97)	1.42 (1.00, 7.58)
interval	50	0.92 (0.79, 0.97)	1.38 (1.00, 1.87)
	100	0.93 (0.75, 0.98)	1.24 (1.00, 1.67)
Scenario	Time varying r	0.94 (0.92, 0.98)	1.01 (0.99, 1.04)
	Mat. effect	0.76 (0.68, 0.96)	0.97 (0.80, 18.6)
	Two locations	0.85 (0.78, 1.01)	1.45 (1.09, 1.62)
	Competition	0.95 (0.92, 0.97)	40.10 (1.32, 73.40)

Yield ratios are given for the EDP policy relative to the perfect information constant harvest policy (EDP:constant) and relative to the Ricker-based policy (EDP:Ricker). The first number is the median and the numbers in parentheses are the lower and upper quartiles.