

Avoiding tipping points in the management of ecological systems: a non-parametric Bayesian approach

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Abstract

Model uncertainty and limited data coverage are fundamental challenges to robust ecosystem management. These challenges are acutely highlighted by concerns that many ecological systems may contain tipping points. Before a collapse, we do not know where the tipping points lie, if they exist at all. Hence, we know neither a complete model of the system dynamics nor do we have access to data in some large region of state-space where such a tipping point might exist. These two sources of uncertainty frustrate state-of-the-art parametric approaches to decision theory and optimal control. I will illustrate how a non-parametric approach using a Gaussian Process prior provides a more flexible representation of this inherent uncertainty. Consequently, we can adapt the Gaussian Process prior to a stochastic dynamic programming framework in order to make robust management predictions under both model and uncertainty and limited data.

Introduction

Decision making under uncertainty is a ubiquitous challenge of natural resource management and conservation. The sudden collapse of fisheries and other ecosystems is an increasingly widespread phenomenon and a pressing concern for ecological management and conservation. Ecological dynamics are frequently complex and difficult to measure, making uncertainty in our understanding a prediction a persistent challenge to effective management. Decision-theoretic approaches provide a framework to determine the best sequence of actions in face of uncertainty, but only when that uncertainty can be meaningfully quantified (???).

Uncertainty enters the decision-making process at many levels: intrinsic stochasticity in biological processes, measurements, and implementation of policy (*e.g.* Reed 1979; C. W. Clark and Kirkwood 1986; ???; Sethi et

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al. 2005), parameteric uncertainty (*e.g.* Ludwig and Walters 1982; ???; ???; Schapaugh and Tyre 2013), and model or structural uncertainty (*e.g.* B. K. Williams 2001; Cressie et al. 2009; Athanassoglou and Xepapadeas 2012). Of these, structural uncertainty incorporates the least a priori knowledge or assumptions and is generally the hardest to quantify. Typical approaches assume a weak notion of uncertainty where a correct or reasonable approximation of the dynamics must be identified from among a handful of alternative models. Here we consider an approach that addresses uncertainty at each of these levels without assuming the dynamics follow a particular (*i.e.* parametric) structure.

An additional source of uncertainty that has recieved less attention¹ arises when applying a dynamical model outside the range of data on which it has been estimated. This extrapolation uncertainty is felt most keenly in decision-theoretic applications, as (a) exploring the potential action space typically involves considering actions that may move the system outside the range of observed behavior, and (b) decision-theoretic alogrithms rely not only on reasonable estimates of the expected outcomes, but depend on the weights given to all possible outcomes (*e.g.* Weitzman 2013).

Concerns over the potential for tipping points in ecological dynamics (Scheffer et al. 2001) highlight the dangers of uncertainty in ecological management and pose a substantial challenge to existing decision-theoretic approaches (Brozović and Schlenker 2011). Because intervention is often too late after a tipping point has been crossed (but see Hughes et al. (2013)), management is most often concerned with avoiding potentially catastrophic tipping points before any data is available at or following a transition that would more clearly reveal these regime shift dynamics (*e.g.* Bestelmeyer et al. 2012).

Map

Here we illustrate how a stochastic dynamic programming (SDP) algorithm (Mangel and Clark 1988; ???) can be driven by the predictions from a Bayesian non-parametric (BNP) approach (Munch, Kottas, and Mangel 2005).

This provides two distinct advantages compared with contemporary approaches. First, using a BNP sidesteps the need for an accurate model-based description of the system dynamics.

Second, the BNP can better reflect uncertainty that arises when extrapolating a model outside of the data on which it was fit.

¹The concept of adaptive probing is one area that has explicitly addressed this kind of uncertainty, reaching rather opposite conclusions than what we observe here. Adaptive probing strategies follow from “Dual Control” or “Active Adaptive Management” approaches (*e.g.* Ludwig and Walters (1982)) that can trade off short term utility by choosing actions that can reduce uncertainty. Adaptive probing strategies arise when it is valuable to intentionally force a system far from the observed values even when the expected value such actions is low, as it provides much faster learning and consequent reduction of model uncertainty that can allow greater value to be derived later on. For instance, Ludwig and Walters (1982) show that it may be advantageous to fish an unexploited population very heavily at first to obtain a better estimate of the recruitment rate. This intuitive strategy when a population is governed by a Ricker or Beverton-Holt-like dynamic would clearly be disastrous if instead the dynamics contained an unforeseen tipping point. The best way to learn where the edge lies may be to walk up to it, but it is also the most dangerous.

We illustrate that when the correct model is not known, this latter feature is crucial to providing a robust decision-theoretic approach in face of substantial structural uncertainty.

Two central challenges:

- We don't know the model
- We don't have data from where we need it most

Why we don't know the model

- Complex dynamics (Glaser et al. 2013)(<http://doi.org/10.1111/faf.12037> “Complex dynamics may limit prediction in marine fisheries”)
- model choice and model averaging approaches

Why we don't have data where we need it

- Concerns of tipping points
- Danger of learning
- *MAP*

This paper represents the first time the SDP decision-making framework has been used without an a priori model of the underlying dynamics through the use of the BNP approach.

In contrast to parametric models which can only reflect uncertainty in parameter estimates, the BNP approach provides a more state-space dependent representation of uncertainty.

This permits a much greater uncertainty far from the observed data than near the observed data. These features allow the GP-SDP approach to find robust management solutions in face of limited data and without knowledge of the correct model structure.

- *Note on “not magic”*: honest uncertainty + SDP

The idea that any approach can perform well without either having to know the model or have particularly good data should immediately draw suspicion. The reader must bear in mind that the strength of our approach comes not from black-box predictive power from such limited information, but rather, by providing a more honest expression of uncertainty outside the observed data without sacrificing the predictive capacity near the observed data. By coupling this more accurate description of what is known and unknown to the decision-making under uncertainty framework provided by stochastic dynamic programming, we are able to obtain more robust management policies than with common parametric modeling approaches.

- Note on: Why fisheries

The economic value and ecological concern have made marine fisheries the crucible for much of the founding work (Gordon 1954; Reed 1979; May et al. 1979; Ludwig and Walters 1982) in managing ecosystems under uncertainty. Global trends (Worm et al. 2006) and controversy (Hilborn 2007; Worm et al. 2009) have made understanding these challenges all the more pressing.

- *Note on comparing models* (via value function rather than by “fit”).

Do we need this?

The nature of decision-making problems provides a convenient way to compare models. Rather than compare models in terms of best fit to data or fret over the appropriate penalty for model complexity, model performance is defined in the concrete terms of the decision-maker’s objective function, which we will take as given. (Much argument can be made over the ‘correct’ objective function, e.g. how to account for the social value of fish left in the sea vs. the commercial value of fish harvested; see Halpern et al. (2013) for further discussion of this issue. Alternatively, we can always compare model performance across multiple potential objective functions.) The decision-maker does not necessarily need a model that provides the best mechanistic understanding or the best long-term outcome, but rather the one that best estimates the probabilities of being in different states as a result of the possible actions.

Background on the Gaussian Process

- Background on non-parametric modeling.

Addressing the difficulty posed by extrapolation without knowing the true model requires a nonparametric approach to model fitting: one that does not assume a fixed structure but rather depends on the size of the data (e.g. non-parametric regression or a Dirichlet process). This established terminology is nevertheless unfortunate, as (a) this approach still involves the estimation of parameters, and (b), Statisticians use non-parametric to mean both this property (structure is not fixed by the parameters) and an entirely different (and probably more familiar) case in which the model does not assume any distribution (e.g. non-parametric bootstrap, order statistics). Some literature thus uses the term semi-parametric, which merely adds ambiguity to the confusion.

This non-parametric property – having a structure explicitly dependent on the data – is precisely the property that makes this approach attractive in face of the limited data sampling challenges discussed above. Having fit a parametric model to some data, the model is completely described by the values (or posterior distributions) of its parameters. The non-parametric model is not captured by its parameter values or distributions alone. Either the model scales with the complexity of the data on which it is estimated (e.g. nonparametric hierarchical approaches such as the Dirichlet process) or the data points become themselves part of the model specification, as in the nonparametric regression used here. we shall see here.

- Definition
- Previous application

The use of Gaussian process (GP) regression (or “kriging” in the geospatial literature) to formulate a predictive model is relatively new in the context of modeling dynamical systems (Kocijan et al. 2005), and was first introduced in the context ecological modeling and fisheries management in Munch et al. (2005). An accessible and thorough introduction to the formulation and use of GPs can be found in Rasmussen and Williams (2006).

- Why it is particularly suited to these two problems
- (Why this is a novel application thereof)

The essence of the GP approach can be captured in the following thought experiment: An exhaustive parametric approach to the challenge of structural uncertainty might proceed by writing down all possible functional forms for the underlying dynamical system with all possible parameter values for each form, and then consider searching over this huge space to select the most likely model and parameters; or using a Bayesian approach, assign priors to each of these possible models and infer the posterior distribution of possible models. The GP approach can be thought of as a computationally efficient approximation to this approach. GPs represent a large class of models that can be thought of as capturing or reasonably approximating the set of models in this collection. By modeling at the level of the process, rather than the level of parametric equation, we can more concisely capture the possible behavior of these curves. In place of a parametric model of the dynamical system, the GP approach postulates a prior distribution of (n-dimensional) curves that can be thought of as approximations to a range of possible (parametric) models that might describe the data. The GP allows us to consider probabilities on a large set of possible curves simultaneously.

The posterior distribution for the hyper-parameters of the Gaussian process model are estimated by Metropolis-Hastings algorithm, again with details and code provided in the Appendix. Rasmussen and Williams (2006) provides an excellent general introduction to Gaussian Processes and Munch et al. (2005) first discusses their application in the context of population dynamics models such as fisheries stock-recruitment relationships.

Approach and Methods

Summary of approach

Statement of the optimal control problem

- Underlying model
- Available data
- Value function

For simplicity we assume profit is simply linear in the realized harvest (only enforcing the restriction that harvest can not exceed available stock)

Parametric models

- Statement of the models

We consider three candidate parametric models of the stock-recruitment dynamics: The Ricker model, the Allen model [Allen 2005](#), the Myers model. The familiar Ricker model involves two parameters, corresponding to a growth rate and a carrying capacity, and cannot support alternative stable state dynamics (though as growth rate increases it exhibits a periodic attractor that proceeds through period-doubling into chaos. We will generally focus on dynamics below the chaotic threshold for the purposes of this analysis.) The Allen model resembles the Ricker dynamics with an added Allee effect parameter [Courchamp](#), below which the population cannot persist. The Myers model also has three parameters and contains an Allee threshold, but has compensatory rather than over-compensatory density dependence (resembling a Beverton-Holt curve rather than a Ricker curve at high densities.)

We assume multiplicative log-normal noise perturbs the growth predicted by the each of the deterministic model skeletons described above. This introduces one additional parameter σ that must be estimated by each model.

As we simulate training data from the Allen model (ref section), we will refer to this as the structurally correct model. The Ricker model is thus a reasonable approximation of these dynamics far from the Allee threshold (but lacks threshold dynamics), while the Myers model shares the essential feature of a threshold but differs in the structure. Thus we have three potential parametric models of the stock dynamics.

- Bayesian inference of parametric models

We infer posterior distributions for the parameters of each model in a Bayesian context using Gibbs sampling (implemented in R (???) using jags, (???)). We choose uninformative uniform priors for all parameters (See Appendix, Figures S1-S3, and Table S1, and the R code provided). One-step-ahead predictions of these model fits are shown in Figure 1.

- SDP via parametric models

An optimal policy function is then inferred through stochastic dynamic programming for each model given the posterior distributions of the parameter estimates. This policy maximizes the expectation of the value function integrated over the parameter uncertainty. (code implementing this algorithm provided in the Appendix).

The Gaussian Process model

- Statement of model

... more on GP ... [Munch 2005](#)

We also estimate a simple Gaussian Process defined by a radial basis function kernel of two parameters: ℓ , which gives the characteristic length-scale over which correlation between two points (e.g. any two points X_t, X_{t+1} , and $X_{t+\tau}, X_{t+1+\tau}$) in state-space decays, and σ , which gives the scale of the process noise by which observations Y_{t+1} may differ from their predicted values X_{t+1} given an observation of the previous state, X_t .

- Inference of the model

Also unlike parametric models, this posterior distribution is still conditional on the training data. As such, the uncertainty near the observed data.

We use a Metropolis-Hastings Markov Chain Monte Carlo to infer posterior distributions of the two parameters of the GP (Figure S4, code in appendix), under weakly informative Gaussian priors (see parameters in table S5). As the posterior distributions differ substantially from the priors (Figure S4), we can be assured that most of the information in the posterior comes from the data rather than the prior belief.

- SDP via the model

Though we are unaware of prior application of this type, it is reasonably straight-forward to adapt the Gaussian Process for Stochastic Dynamic Programming. Recall that unlike the parametric models the Gaussian process with fixed parameters already predicts a distribution of curves rather than a single curve. We must first integrate over this distribution of curves given a sampling of parameter values drawn from the posterior distribution of the two GP parameters, before integrating over the posterior of those parameters themselves.

Results

```
require(MASS)
step_ahead <- function(x, f, p){
  h = 0
  x_predict <- sapply(x, f, h, p)
  n <- length(x_predict) - 1
  y <- c(x[1], x_predict[1:n])
  y
}
```

```

step_ahead_posteriors <- function(x){
gp_f_at_obs <- gp_predict(gp, x, burnin=1e4, thin=300)
df_post <- melt(lapply(sample(100),
  function(i){
    data.frame(time = 1:length(x), stock = x,
      GP = mvnrm(1, gp_f_at_obs$Ef_posterior[,i], gp_f_at_obs$Cf_posterior[[i]]),
      True = step_ahead(x,f,p),
      MLE = step_ahead(x,f,est$p),
      Allen = step_ahead(x, allen_f, pardist[i,]),
      Ricker = step_ahead(x, ricker_f, ricker_pardist[i,]),
      Myers = step_ahead(x, myers_f, myers_pardist[i,]))
  }), id=c("time", "stock"))
}

df_post <- step_ahead_posteriors(x)

ggplot(df_post) + geom_point(aes(time, stock)) +
  geom_line(aes(time, value, col=variable, group=interaction(L1,variable)), alpha=.1) +
  scale_colour_manual(values=colorkey, guide = guide_legend(override.aes = list(alpha = 1)))

```

Figure 1 shows the mean inferred state space dynamics of each model relative to the true model used to generate the data, predicting the relationship between observed stock size (x-axis) to the stock size after recruitment the following year. All models except the MLE model estimate a distribution around the means shown here, and all models estimate a level of process noise, which is independent of the state value (x). Note that in contrast to the other models shown, the mean Gaussian process corresponds to a distribution of curves - as indicated by the gray band - which itself has a mean shown in black. Note that this mean GP is thus more certain of the dynamics in the region where data is available than where it is not.

While it would be straight forward to condition the GP on passing through the origin (0,0), the estimate shown here is based only on the observed data. The observed data from which each model is estimated is also shown. The observations come from only a limited region of state space corresponding to unharvested or weakly harvested system. No observations occur at the theoretical optimum harvest rate or near the tipping point.

```

policies <- melt(data.frame(stock=x_grid, sapply(OPT, function(x) x_grid[x])), id="stock")
names(policies) <- c("stock", "method", "value")

ggplot(policies, aes(stock, stock - value, color=method)) +

```

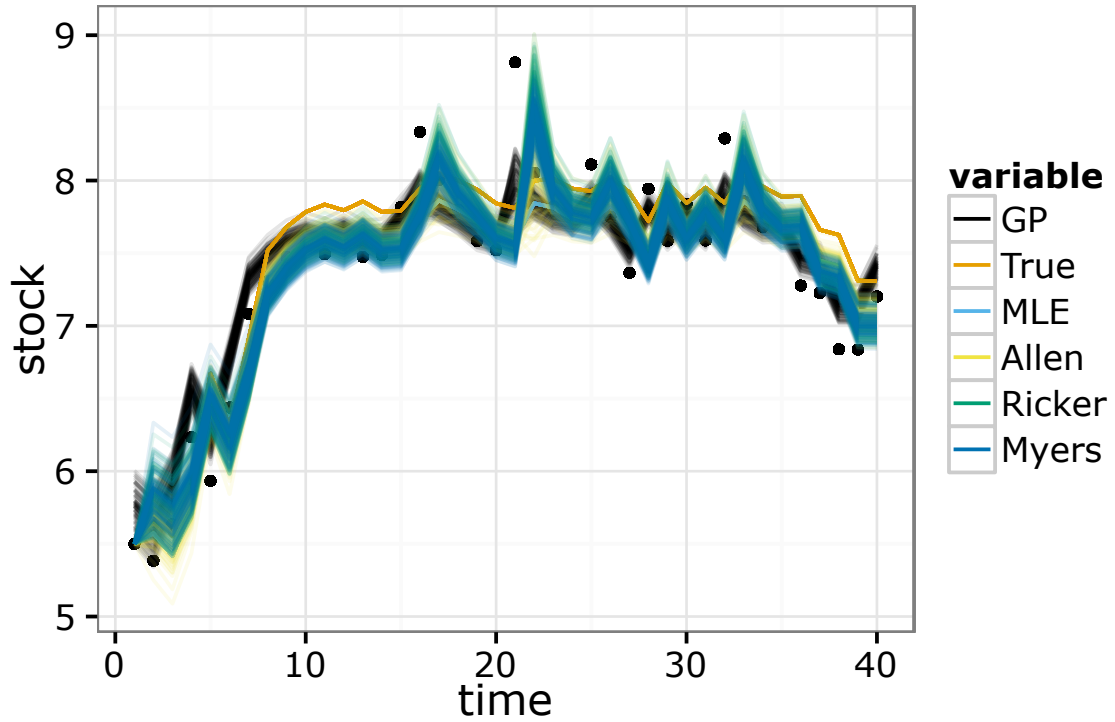



Figure 1: plot of chunk Figureb

```
geom_line(lwd=1.2, alpha=0.8) + xlab("stock size") + ylab("escapement") +
scale_colour_manual(values=colorkey)
```

The resulting optimal management strategy based on each of the inferred models is shown in Figure 2, against the optimal strategy given the true underlying dynamics. Policies are shown in terms of target escapement, S_t . Under models such as this a constant escapement policy is expected to be optimal (Reed 1979), whereby population levels below a certain size S are unharvested, while above that size the harvest strategy aims to return the population to S , resulting in the hockey-stick shaped policies shown.

```
ggplot(sims_data) +
  geom_line(aes(time, fishstock, group=interaction(reps,method), color=method), alpha=.1) +
  scale_colour_manual(values=colorkey, guide = guide_legend(override.aes = list(alpha = 1)))
```

The consequences of managing 100 replicate realizations of the simulated fishery under each of the policies estimated is shown in Figure 3. As expected from the policy curves, the structurally correct model underharvests, leaving the stock to vary around it's un-fished optimum. The structurally incorrect Ricker model over-harvests the population passed the tipping point consistently, resulting in the immediate crash of the stock and thus derives minimal profits.

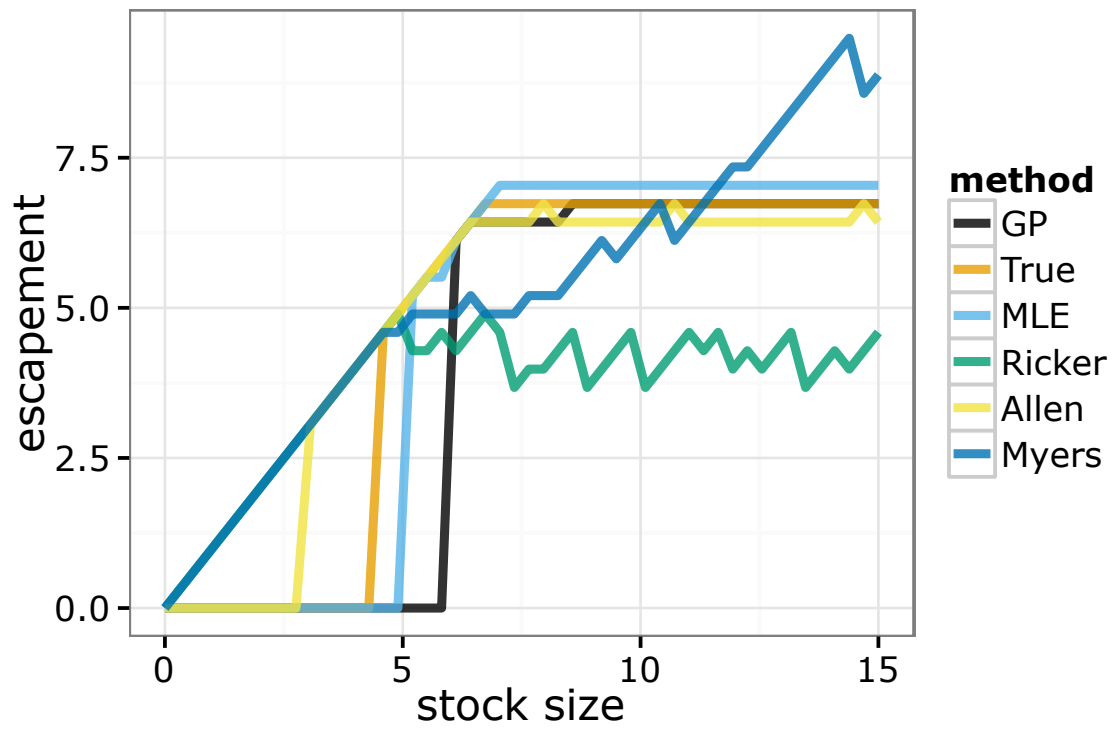


Figure 2: The steady-state optimal policy (infinite boundary) calculated under each model. Policies are shown in terms of target escapement, S_t , as under models such as this a constant escapement policy is expected to be optimal (Reed 1979).

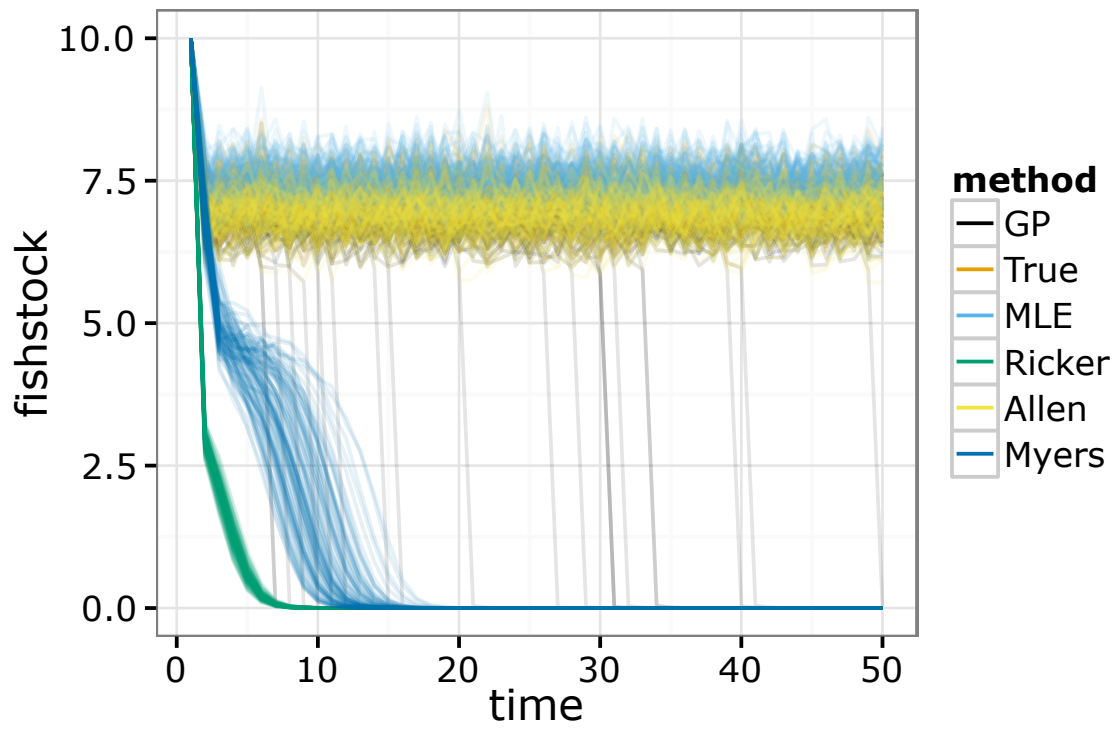


Figure 3: Gaussian process inference outperforms parametric estimates. Shown are 100 replicate simulations of the stock dynamics (eq 1) under the policies derived from each of the estimated models, as well as the policy based on the exact underlying model.

The results shown in Figures 1-3 are not unique to the simulated data or models chosen here, but arises across a range of parameter values and simulations as shown in the supplemental figures. The results across this range can most easily be compared by the relative differences in net present value realized by each of the approaches, as shown in Figure 4. The Gaussian Process most consistently realizes a value close to the optimal solution, and importantly avoids ever driving the system across the tipping point, which results in the near-zero value cases in the parametric models.

```
fig4v1 <- ggplot(actual_over_optimal, aes(value)) + geom_histogram(aes(fill=variable)) +
  facet_wrap(~variable, scales = "free_y") + guides(legend.position = "none") +
  xlab("Total profit by replicate") + scale_fill_manual(values=colorkey) # density plots fail when del

fig4v2 <- ggplot(actual_over_optimal, aes(value)) + geom_histogram(aes(fill=variable), binwidth=0.1) +
  xlab("Total profit by replicate")+ scale_fill_manual(values=colorkey)

fig4v3 <- ggplot(actual_over_optimal, aes(value, fill=variable, color=variable)) + # density plots fail
  stat_density(aes(y=..density..), position="stack", adjust=3, alpha=.9) +
  xlab("Total profit by replicate")+ scale_fill_manual(values=colorkey)+ scale_color_manual(values=col

fig4v2

fig4v3
```

Figure 1: Fitted Models

- All models fit the data quite well
- Information criteria would pick the simple, incorrect model.

Figure 2: Inferred Policies

- Inferred policies differ substantially among models
- The structurally correct model and the GP are close to the true model
- alternatives are not close

Figure 3: Simulated results

-

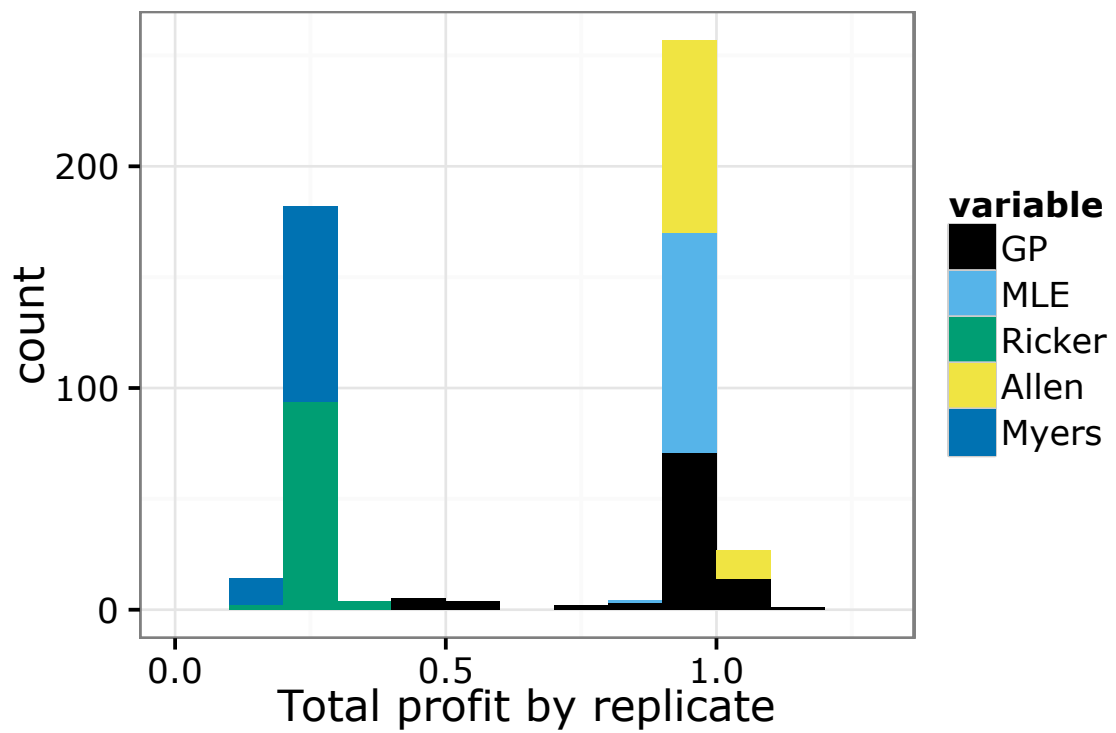


Figure 4: Histograms of the realized net present value of the fishery over a range of simulated data and resulting parameter estimates. For each data set, the three models are estimated as described above. Values plotted are the averages of a given policy over 100 replicate simulations. Details and code provided in the supplement.

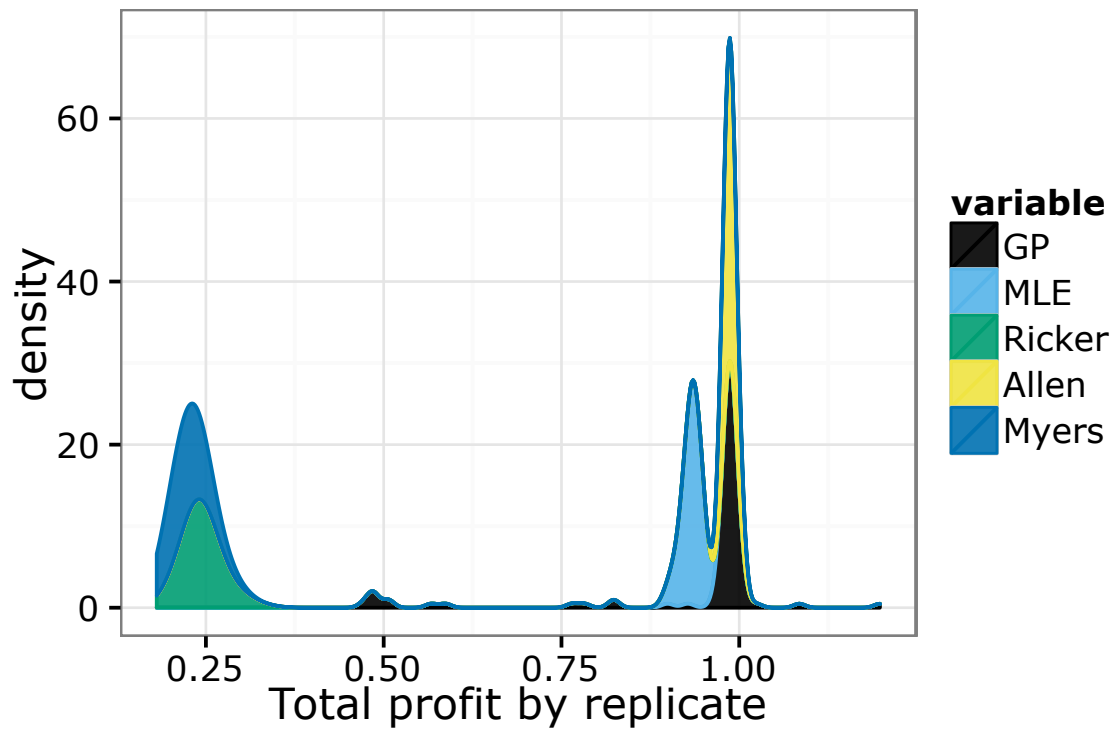


Figure 5: Histograms of the realized net present value of the fishery over a range of simulated data and resulting parameter estimates. For each data set, the three models are estimated as described above. Values plotted are the averages of a given policy over 100 replicate simulations. Details and code provided in the supplement.

Figure 4: Robustness

- Results hold across range of parameters

(eek, distinguish better between result and discussion?)

Discussion

- All models are “good fits” to the originally observed data.
- (Simple model choice immediately leads us astray)

Though simple mechanistically motivated models offer the greatest potential to increase our basic understanding of ecological processes (Cuddington, Fortin, and Gerber 2013; Geritz and Kisdi 2012), such models can be not only inaccurate but misleading when relied upon in a quantitative decision making framework.

1. We do not know what the correct models are for ecological systems.
2. We have limited data from which to estimate the model – in particular, such models may be misleading in predicting the probability of outcomes outside the training data.

These aspects are common to many conservation decision making problems, which thus merit greater use of non-parametric approaches that can best take advantage of them.

1. Large uncertainty where the data is poor

The parametric models perform worst when they propose a management strategy outside the range of the observed data. The non-parametric Bayesian approach, in contrast, allows a predictive model that expresses a great deal of uncertainty about the probable dynamics outside the observed range, while retaining very good predictive accuracy in the range observed. The management policy dictated by the GP balance this uncertainty against the immediate value of the harvest, and act to stabilize the population dynamics in a region of state space in which the predictions can be reliably reflected by the data.

2. Predictive accuracy where data is good

While expressing larger uncertainty outside the observed data, the GP can also provide a better fit with smaller uncertainty inside the range of the observed data. This arises from the greater flexibility of the Gaussian process, which describes a large family of possible curves. Despite this flexibility, the GP can be described in relatively few parameters and is thus far less likely to overfit.

Future directions

Higher dimensions

In this simulated example, the underlying dynamics are truly governed by a simple parametric model, allowing the parametric approaches to be more accurate. Similarly, because the dynamics are one-dimensional dynamics and lead to stable nodes (rather than other attractors such as limit-cycles resulting in oscillations), the training data provides relatively limited information about the dynamics. For these reasons, we anticipate that in higher-dimensional examples characteristic of ecosystem management problems that the machine learning approach will prove even more valuable.

Online learning

In our treatment here we have ignored the possibility of learning during the management phase, in which the additional observations of the stock size could potentially improve parameter estimates. While we intend to address this possibility in future work in the context of these non-parametric models, we have not addressed it here for pedagogical reasons. In the context presented here, it is clear that the differences in performance arise from differences in the uncertainty inherent in the model formulations, rather than from differing abilities to learn. Because we consider a threshold system, online learning would not change this generic feature of a lack of data in a certain range of the state space which is better captured by the Gaussian process.

Acknowledgments

This work was partially supported by the Center for Stock Assessment Research, a partnership between the University of California Santa Cruz and the Fisheries Ecology Division, Southwest Fisheries Science Center, Santa Cruz, CA and by NSF grant EF-0924195 to MM and NSF grant DBI-1306697 to CB.

Appendix

Model definitions and estimation

Equation S1: Ricker model.

$$X_{t+1} = Z_t X_t e^{r(1 - \frac{S_t}{K})}$$

Figure S1: Ricker model: prior and posterior distributions for parameter estimates.

Table S1: Parameterization of the priors

% latex table generated in R 3.0.1 by xtable 1.7-1 package % Mon Sep 9 14:43:29 2013

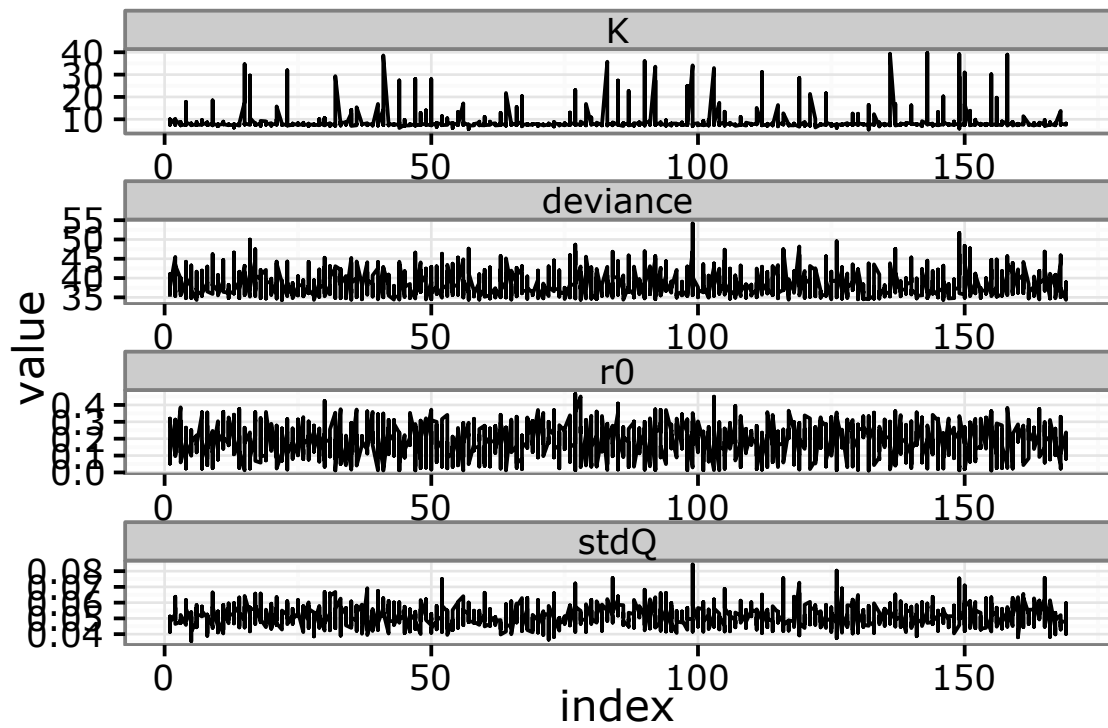


Figure 6: plot of chunk unnamed-chunk-1

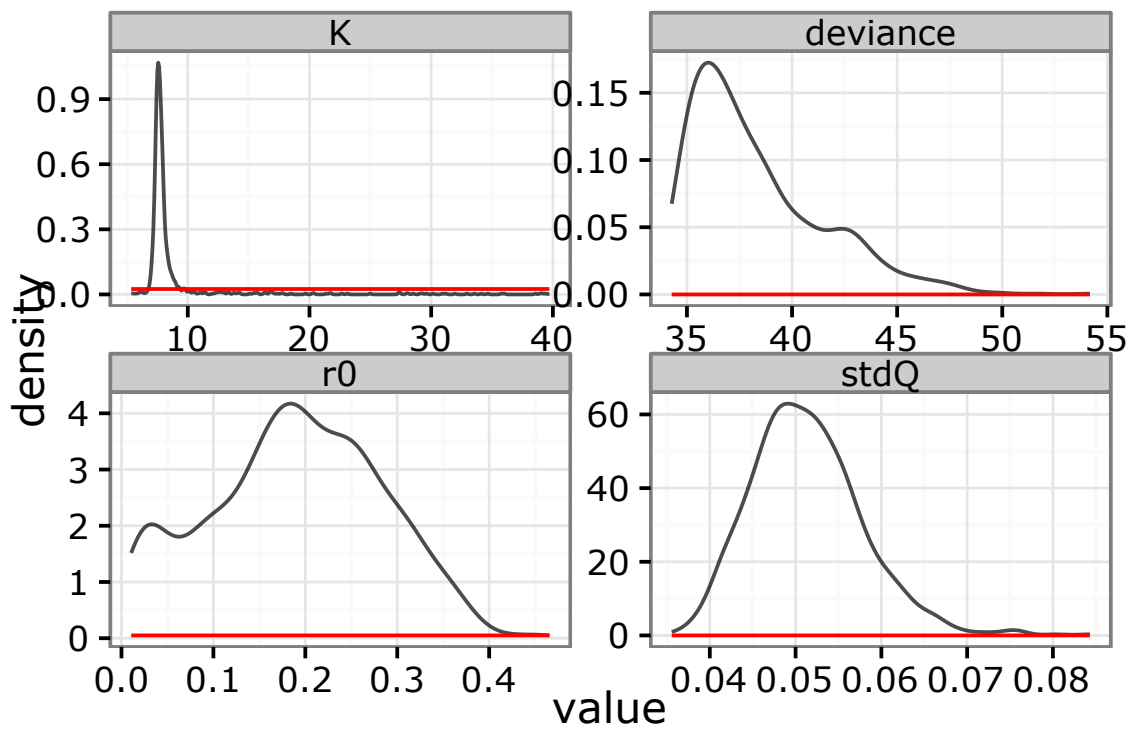


Figure 7: plot of chunk unnamed-chunk-2

	parameter	lower_bound	upper_bound
1	r0	0.00	10.00
2	K	0.00	40.00
3	sigma	0.00	100.00

$$X_{t+1} = Z_t \frac{rS_t^\theta}{1 - \frac{S_t^\theta}{K}}$$

Eq S2: Myers model Figure S2: Myers model: Traces, prior and posterior distributions for parameter estimates.

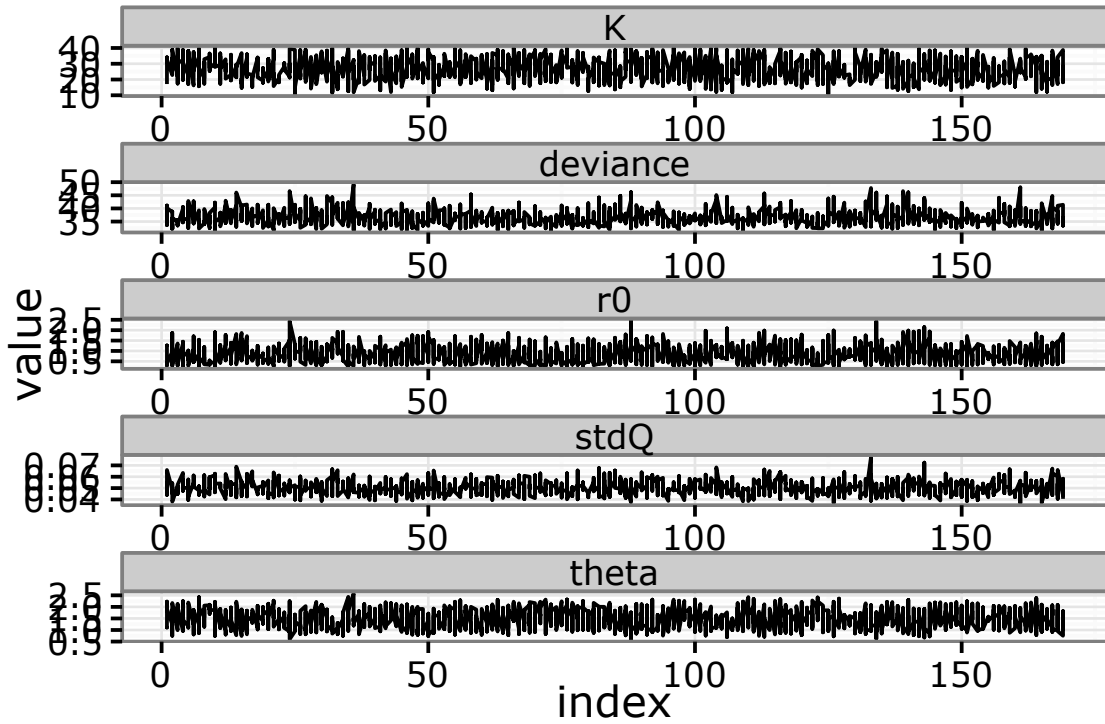


Figure 8: plot of chunk unnamed-chunk-4

Table S2: Parameterization of the priors % latex table generated in R 3.0.1 by xtable 1.7-1 package % Mon Sep 9 14:43:37 2013

Eq S3: Allen model

$$f(S_t) = S_t e^{r(1 - \frac{S_t}{K})(S_t - C)}$$

Figure S3: Allen model: prior and posterior distributions for parameter estimates.

Table S3: Parameterization of the priors

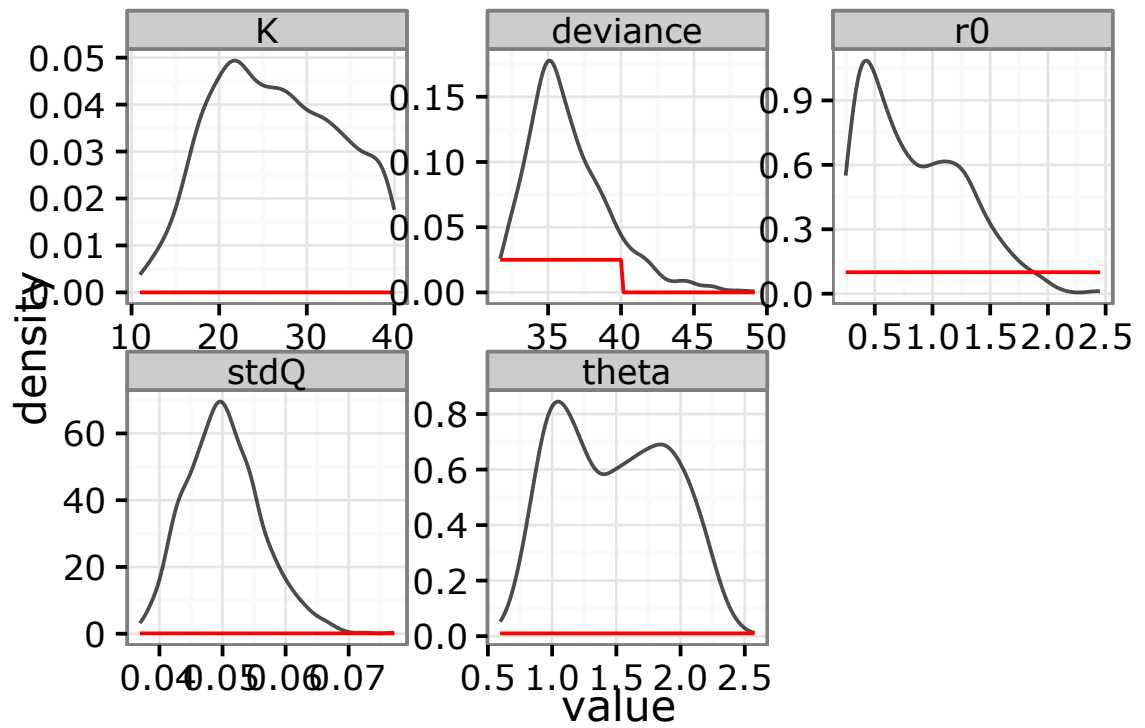


Figure 9: plot of chunk unnamed-chunk-5

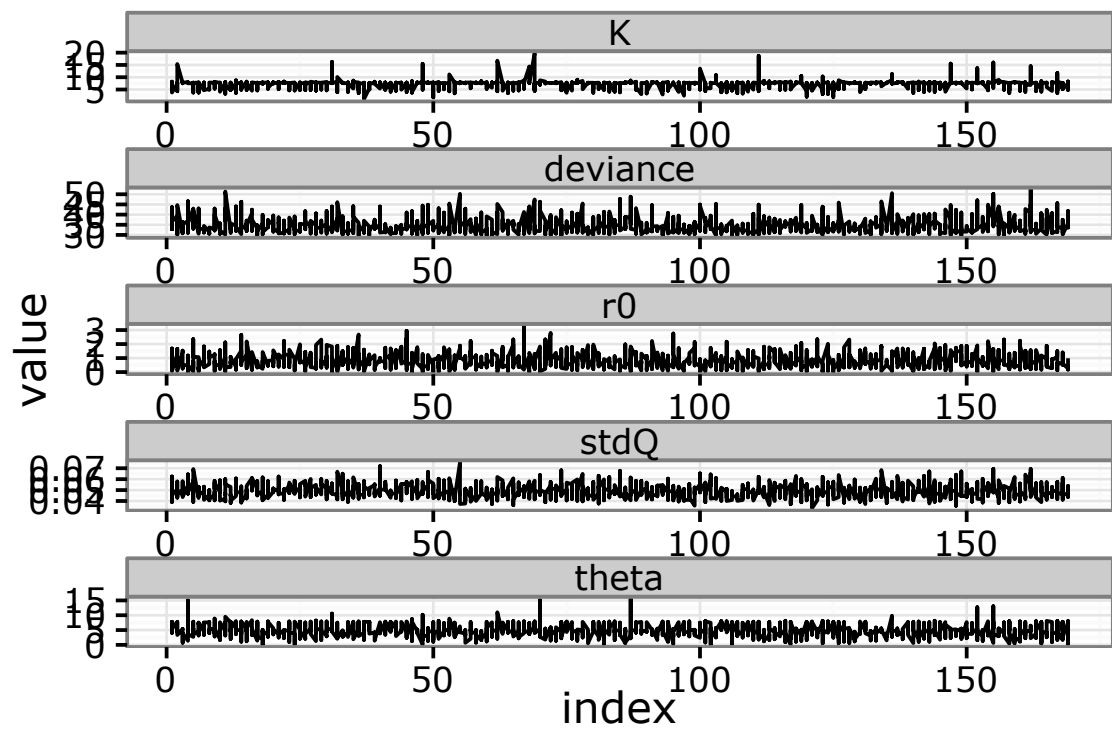


Figure 10: plot of chunk unnamed-chunk-7

	parameter	lower_bound	upper_bound
1	r0	0.00	10.00
2	K	0.00	40.00
3	theta	0.00	10.00
4	sigma	0.00	100.00

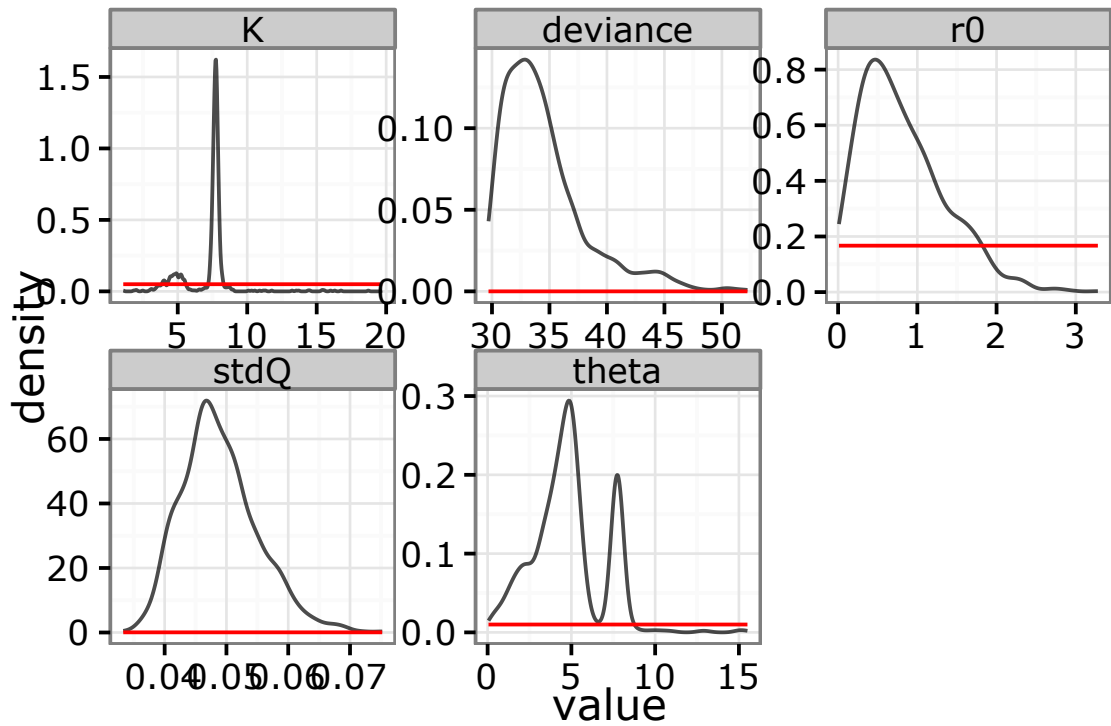


Figure 11: plot of chunk unnamed-chunk-8

% latex table generated in R 3.0.1 by xtable 1.7-1 package % Mon Sep 9 14:43:45 2013

Eq S4: GP model Figure S4: GP model: prior and posterior distributions for parameter estimates.

\$traces_plot

\$posteriors_plot

Table S4: Parameterization of the priors

Optimal Control Problem

We seek the harvest policy $h(x)$ that maximizes:

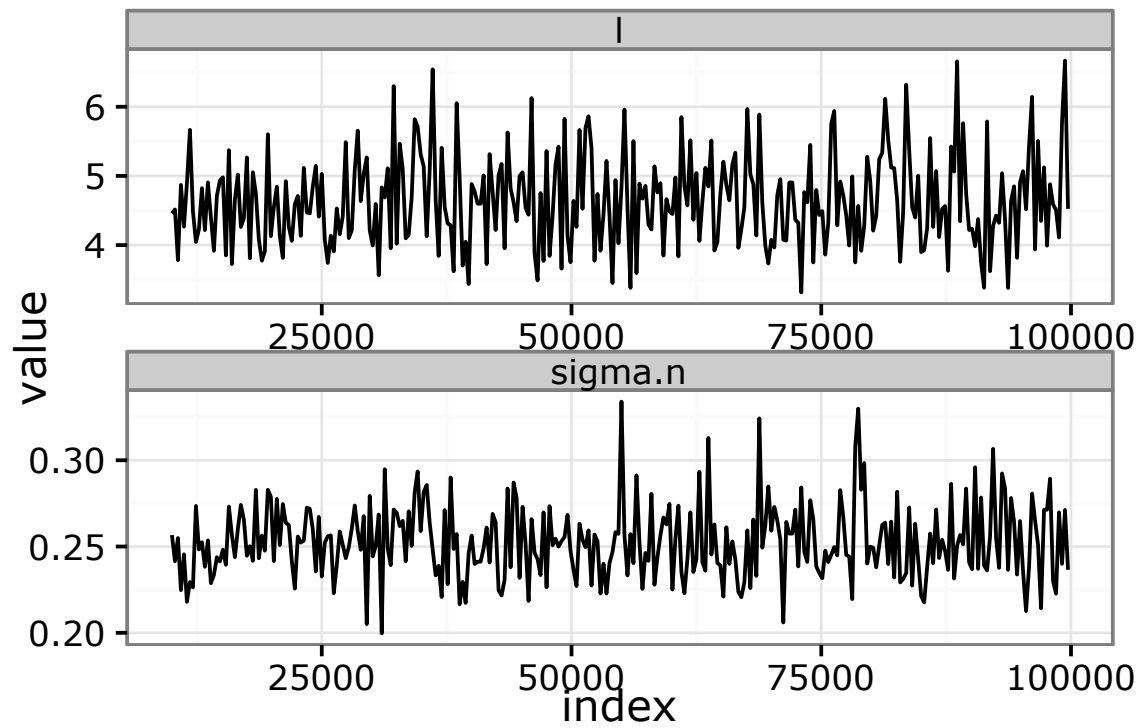


Figure 12: plot of chunk unnamed-chunk-10

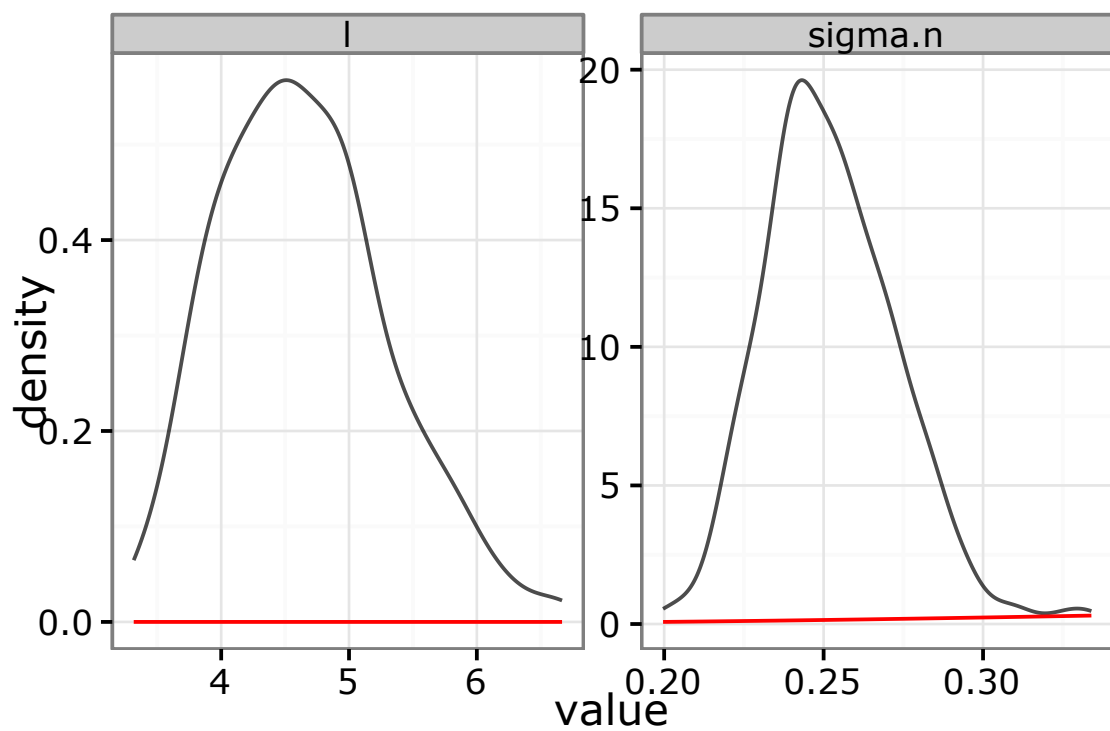


Figure 13: plot of chunk unnamed-chunk-10

	parameter	lower_bound	upper_bound
1	r0	0.00	10.00
2	K	0.00	40.00
3	theta	0.00	10.00
4	sigma	0.00	100.00

$$\max_{h_t} \sum_{t=0}^{\infty} \Pi_t(X_t, h_t) \delta^t$$

subject to the profit function $\Pi(X_t, h)$, discount rate δ , and the state equation

$$X_{t+1} = Z_t f(S_t)$$

$$S_t = X_t - h_t$$

Where Z_t is multiplicative noise function with mean 1, representing stochastic growth. We will consider log-normal noise with shape parameter σ_g .

Form this we can write down the Bellman recursion as:

$$V_t(x_t) = \max_h \mathbf{E} (\Pi(h_t, x_t) + \delta V_{t+1}(Z_{t+1} f(x_t - h_t)))$$

For simplicity we assume profit is simply linear in the realized harvest (only enforcing the restriction that harvest can not exceed available stock), $\Pi(h, x) = \min(h, x)$.

Pseudocode for the Bellman iteration

```
V1 <- sapply(1:length(h_grid), function(h){
  delta * F[[h]] %*% V + profit(x_grid, h_grid[h])
})
# find havest, h that gives the maximum value
out <- sapply(1:gridsize, function(j){
  value <- max(V1[j,], na.rm = T) # each col is a diff h, max over these
  index <- which.max(V1[j,]) # store index so we can recover h's
  c(value, index) # returns both profit value & index of optimal h.
})
# Sets V[t+1] = max_h V[t] at each possible state value, x
V <- out[1,] # The new value-to-go
D[,OptTime-time+1] <- out[2,] # The index positions
```

Training data

Each of our models $f(S_t)$ must be estimated from training data, which we simulate from the Allen model with parameters $r = \mathbf{r_p}[1]$, $K = \mathbf{r_p}[2]$, $C = \mathbf{r_p}[3]$, and $\sigma_g = \mathbf{r_sigma_g}$ for $T = 40$ timesteps, starting at initial condition $X_0 = 5.5$. The training data can be seen in Figure 1.

Abstract

Decision-theoretic methods often rely on simple parametric models of ecological dynamics to compare the value of a potential sequence of actions. Unfortunately, such simple models rarely capture the complexity or uncertainty found in most real ecosystems.

Further, the data on which a model has been parameterized frequently fails to cover the possible state-space over which management decisions must operate. Consequently a model does well in the region of state-space in which it was estimated, but gives erroneous confidence to predictions outside of that region.

This problem is keenly felt in any system where a potential threshold or tipping point is a concern. Such a tipping point, if it exists at all, will lay outside the observed range of the observed data.

We demonstrate how nonparametric Bayesian models can provide robust solutions to decision making under uncertainty without knowing the structural form of the true model.

While methods that account for *parametric* uncertainty can be very successful with the right model, structural uncertainty of not knowing what model best approximates the dynamics poses considerably greater difficulty.

Introduction

Opening.

Models for decision-making under uncertainty. Decision-theoretic or optimal control tools require a model that can assign probabilities of future states (e.g. stock size of a fishery) given the current state and a proposed action (e.g. fishing harvest or effort).

Management frequently faces a sequential decision-making problem – after selecting an action, the decision-maker may receive new information about the current state and must again choose an appropriate action – such as setting the harvest limits each year based on stock assessments the year prior.

The decision maker typically seeks to determine the course of actions (also referred to as the policy) that maximizes the expected value of some objective function such as net present value derived from the resource

over time.

Though much can be said on how to choose this value function appropriately (e.g. see (Halpern et al. 2013)(<http://doi.org/10.1073/pnas.1217689110> “Achieving the triple bottom line in the face of inherent trade-offs among social equity, economic return, and conservation.”)) we will assume this is given. (Nor is this approach necessarily constrained to maximizing the expected value of such a function - the decision-theoretic framework can be adapted to alternatives such as minimizing the maximum cost or damage that might be incurred; see Polasky et al. (2011)).

In representing future states with probabilities and maximizing expectations, this approach provides a natural framework for handling uncertainty.

The value function typically depends on the action or policy taken, as well as the state of the system, in each interval of time. The state of the system, in turn, is usually described by a dynamical model.

(B. K. Williams 2001; Athanassoglou and Xepapadeas 2012).

While simple mechanistic models can nevertheless provide important insights into long-term outcomes, such approaches are not well-suited for use in forecasting outcomes of potential management options. Non-parametric approaches offer a more flexible alternative that can both more accurately reflect the data available while also representing greater uncertainty in areas (of state-space) where data is lacking.

We demonstrate how a Gaussian Process model of stock recruitment can lead to nearly optimal management through stochastic dynamic programming, comparable to knowing the correct structural equation for the underlying simulation. Meanwhile, parametric models that do not match the underlying dynamics can perform very poorly, even though they fit the data as well as the true model.

Ecological research and management strategy should pay closer attention to the opportunities and challenges nonparametric modeling can offer.

Approach and Methods

The optimal control problem in fisheries management

We focus on the problem in which a manager must set the harvest level for a marine fishery each year to maximize the net present value of the resource, given an estimated stock size from the year before.

To permit comparisons against a theoretical optimum we will consider data on the stock dynamics simulated from a simple parametric model in which recruitment of the fish stock X_{t+1} in the following year is a stochastic process governed by a function f of the current stock X_t , selected harvest policy h_t , and noise process Z ,

$$X_{t+1} = Z_t f(X_t, h_t)$$

Given parameters for the function f and probability distribution Z , along with a given economic model determining the price/profit $\Pi(X_t, h_t)$ realized in a given year given a choice of harvest h_t and observed stock X_t . This problem can be solved exactly for discretized values of stock X and policy h using stochastic dynamic programming (SDP) (Mangel and Clark 1988). Problems of this sort underpin much marine fisheries management today.

A crux of this approach is correctly specifying the functional form of f , along with its parameters. The standard approach uses one of a handful of common parametric models representing the stock-recruitment relationship, usually after estimating the model parameters from any available existing data. Uncertainty in the parameter estimates can be estimated and integrated over to determine the optimal policy under uncertainty (Mangel and Clark 1988; Schapaugh and Tyre 2013). Uncertainty in the model structure itself can only be addressed in this approach by hypothesizing alternative model structures, and then performing some model choice or model averaging (B. K. Williams 2001; Athanassoglou and Xepapadeas 2012).

Underlying Model

To illustrate the value of the non-parametric Bayesian approach to management, we focus on example of a system containing such a tipping point whose dynamics can still be described by a simple, one-dimensional parametric model.

We will focus on a simple parametric model for a single species (derived from first principles by Allen et al. 2005) as our underlying “reality”.

$$\begin{aligned} X_{t+1} &= Z_t f(S_t) \\ S_t &= X_t - h_t \\ f(S_t) &= S_t e^{r(1-\frac{S_t}{K})(S_t-C)} \end{aligned}$$

Where Z_t is multiplicative noise function with mean 1, representing stochastic growth. We will consider log-normal noise with shape parameter σ_g . We start with an example in which the parameters are $r = 2$, $K = 8$, $C = 5$ and $\sigma_g = 0.1$.

As a low-dimensional system completely described by three parameters, this scenario should if anything be favorable to a parametric-based approach. This model contains an Allee effect, or tipping point, below which the population is not self-sustaining and shrinks to zero (Courchamp, Berec, and Gascoigne 2008).

Simulated training data. We generate initial observational data under the model described in Eq 1 for $T_{\text{obs}} = 40$ time steps, under a given arbitrary sequence of harvest intensities, h_t . We consider the case in which most of the data comes from a limited region of state space (e.g. near a stable equilibrium), leaving us without observations of the population dynamics at very low levels which would be useful in discriminating between recruitment curves

[@] or demonstrating the existence of a tipping point (Scheffer et al. 2001).

Using data simulated from a specified model rather than empirical data permits the comparison against the true underlying dynamics, setting a bar for the optimal performance possible.

Parametric Models

We consider three candidate parametric models for the stock-recruitment function, which we refer to by the first authors of the publications in which they were first proposed.

We generate the data with a four-parameter model that contains a tipping point, as discussed above (equation 1), (an Allee effect, see (???) below which the stock decreases to zero,

$$X_{t+1} = Z_t S_t e^{r(1-\frac{S_t}{K})(\frac{S_t-\theta}{K})}$$

$$S_t = X_t - h_t$$

The parameter C reflects the location of the tipping point, K the carrying capacity of the stock, and r the base recruitment rate. S_t represents the stock size after a harvest h_t has been implemented. Z_t represents a log-normal random variable of log-mean zero and log-standard deviation parameter σ .

We consider two alternative candidate models: the Ricker (???) stock-recruitment curve,

$$X_{t+1} = Z_t X_t e^{r(1-\frac{S_t}{K})}$$

and an alternative four-parameter model adapted from (???)

$$X_{t+1} = Z_t \frac{r S_t^\theta}{1 - \frac{S_t^\theta}{K}}$$

which contains a tipping point for $\theta > 2$ and becomes a Beverton-Holt model at $\theta = 1$.

Bayesian Inference of Parametric models

Given the sample data, we infer posterior distributions for each of the three models listed above using a Markov Chain Monte Carlo Gibbs Sampler (jags, see appendix for implementation details and code) given uniform priors. We run six chains for 10^6 steps each and then assess convergence by Gelman-Rubin criterion and inspection of the traces, see appendix.

SDP via GP

Once the posterior Gaussian process (GP) has been estimated (e.g. see Munch et al. 2005), it is necessary to adapt it in place of the parametric equation for the stochastic dynamic programming (SDP) solution (see Mangel and Clark 1988 for a detailed description of parametric SDP methods) to the optimal policy. The essence of the idea is straight forward – we will use the estimated GP in place of the parametric growth function to determine the stochastic transition matrix on which the SDP calculations are based. The SDP is solved in a discretized state space – both the continuously valued population densities X and harvest quotas h are first mapped to a bounded, discrete grid. (For simplicity we will consider a uniform grid, though for either parametric or GP-based SDP it is often advantageous to use a non-uniform discretization such as a basis function representation, e.g. see (Deisenroth, Rasmussen, and Peters 2009)).

The SDP approach then computes a transition matrix, \mathbf{F} . We demonstrate that calculation is just as straight forward based on the GP as it is in the classical context using the parametric model. The i, j of the transition matrix F entry gives the probability of transitioning into state x_i given that the system is in state x_j in the previous time-step. To generate the transition matrix based on the posterior GP, we need only the expected values at each grid point and the corresponding variances (the diagonal of the covariance matrix), as shown in Figure 1. Given the mean of the GP posterior at each grid-point as the vector E and variance at that point as vector V , the probability of transitioning from state x_i to state x_j is

$$\mathcal{N}(x_j | \mu = E_i, \sigma = \sqrt{V_i})$$

where \mathcal{N} is the Normal density at x_j with mean μ and variance σ^2 . Strictly speaking, the transition probability should be calculated by integrating the normal density over the bin of width Δ centered at x_j . For a sufficiently fine grid that $f(x_j) \approx f(x_j + \Delta)$, it is sufficient to calculate the density at x_j and then row-normalize the transition matrix. The process can then be repeated for each possible discrete value of our control variable, (harvest h).

Pseudocode for the determining the transition matrix from the GP

```
for(h in h_grid)
  F_h = for(x_j in grid)
    for(i in 1:N)
      dnorm(x_j, mu[i]-h, V[i])
```

Using the discrete transition matrix we may write down the Bellman recursion defining the stochastic dynamic programming iteration:

$$V_t(x_t) = \max_h \mathbf{E}(h_t + \delta V_{t+1}(Z_{t+1}f(x_t - h_t))) \quad (1)$$

where $V(x_t)$ is the value of being at state x at time t , h is control (harvest level) chosen. Numerically, the maximization is accomplished as follows. Consider the set of possible control values to be the discrete values corresponding the grid of stock sizes. Then for each h_t there is a corresponding transition matrix \mathbf{F}_h determined as described above but with mean $\mu = x_j - h_t$. Let \vec{V}_t be the vector whose i th element corresponds to the value of having stock x_i at time t . Then let Π_h be the vector whose i th element indicates the profit from harvesting at intensity h_t given a population x_i (e.g. $\max(x_i, h_t)$ since one cannot harvest more fish then the current population size). Then the Bellman recursion can be given in matrix form as

$$V_t = \max_h (\Pi_{h_t} + \delta \mathbf{F}_h V_{t+1})$$

where the sum is element by element and the expectation is computed by the matrix multiplication $\mathbf{F}V_{t+1}$.

Pseudocode for the Bellman iteration

```
V1 <- sapply(1:length(h_grid), function(h){
  delta * F[[h]] %*% V + profit(x_grid, h_grid[h])
})
# find havest, h that gives the maximum value
out <- sapply(1:gridsize, function(j){
  value <- max(V1[j,], na.rm = T) # each col is a diff h, max over these
  index <- which.max(V1[j,]) # store index so we can recover h's
  c(value, index) # returns both profit value & index of optimal h.
})
# Sets V[t+1] = max_h V[t] at each possible state value, x
V <- out[1,] # The new value-to-go
D[,OptTime-time+1] <- out[2,] # The index positions
```

This completes the algorithm adapting the GP to the sequential decision-making problem through SDP, which has not been previously demonstrated.

We further provide an R package implementation as described in the supplemental materials.

Estimating parametric models

We estimate posterior distributions for two parametric models: one using the structurally correct model as given in Eq (1), which we refer to as the “Parametric Bayes” model, and another using the familiar Ricker model,

using a Gibbs sampler as described (with source code) in the appendix). In addition we estimate the parameters of the structurally correct model by maximum likelihood.

Results

Discussion

Big picture: Linking GP to SDP. rambling

Non-parametric Bayesian methods have received far too little attention in ecological modeling efforts that are aimed at improved conservation planning and decision making support. Such approaches may be particularly useful when the available data is restricted to a limited area of state-space, which can lead parametric models to underestimate the uncertainty in dynamics at population levels (states) which have not been observed. One reason for the relative absence of nonparametric approaches in the natural resource management context may be the lack of existing approaches for adapting the non-parametric Bayesian models previously proposed (Munch et al. 2005) to a decision-theoretic framework. Adapting a non-parametric approach requires modification of existing methods for decision theory. We have illustrated how this might be done for a classic stochastic dynamic programming problem, opening the door for substantial further research into how these applications might be improved.

Code to replicate the analysis, along with complete log of this research can be found at: <https://github.com/cboettig/nonparametric-bayes>

Markov Chain Monte Carlo Analysis

Allen, Linda J. S., Jesse F. Fagan, Göran Högnäs, and Henrik Fagerholm. 2005. "Population Extinction in Discrete-time Stochastic Population Models with an Allee Effect." *Journal of Difference Equations and Applications* 11 (4-5) (apr): 273–293. doi:10.1080/10236190412331335373. <http://www.tandfonline.com/doi/abs/10.1080/10236190412331335373>.

Athanassoglou, Stergios, and Anastasios Xepapadeas. 2012. "Pollution Control with Uncertain Stock Dynamics: When, and How, to Be Precautious." *Journal of Environmental Economics and Management* 63 (3) (may): 304–320. doi:10.1016/j.jeem.2011.11.001. <http://linkinghub.elsevier.com/retrieve/pii/S0095069611001409>.

Bestelmeyer, Brandon T., Michael C. Duniway, Darren K. James, Laura M. Burkett, and Kris M. Havstad. 2012. "A Test of Critical Thresholds and Their Indicators in a Desertification-prone Ecosystem: More Resilience Than We Thought." Edited by Katharine Suding. *Ecology Letters* (dec). doi:10.1111/ele.12045. <http://doi.wiley.com/10.1111/ele.12045>.

- Brozović, Nicholas, and Wolfram Schlenker. 2011. “Optimal Management of an Ecosystem with an Unknown Threshold.” *Ecological Economics* (jan): 1–14. doi:10.1016/j.ecolecon.2010.10.001. <http://linkinghub.elsevier.com/retrieve/pii/S0921800910004167>.
- Clark, Colin W., and Geoffrey P. Kirkwood. 1986. “On Uncertain Renewable Resource Stocks: Optimal Harvest Policies and the Value of Stock Surveys.” *Journal of Environmental Economics and Management* 13 (3) (sep): 235–244. doi:10.1016/0095-0696(86)90024-0. <http://linkinghub.elsevier.com/retrieve/pii/0095069686900240>.
- Courchamp, Franck, Ludek Berec, and Joanna Gascoigne. 2008. *Allee Effects in Ecology and Conservation*. Oxford University Press, USA. <http://www.amazon.com/Effects-Ecology-Conservation-Franck-Courchamp/dp/0198570309>.
- Cressie, Noel, Catherine a Calder, James S. Clark, Jay M. Ver Hoef, and Christopher K. Wikle. 2009. “Accounting for Uncertainty in Ecological Analysis: the Strengths and Limitations of Hierarchical Statistical Modeling.” *Ecological Applications* 19 (3) (apr): 553–70. doi:10.1890/07-0744.1. <http://www.ncbi.nlm.nih.gov/pubmed/19425416>.
- Cuddington, Kim M., M. J. Fortin, and L. R. Gerber. 2013. “Process-based Models Are Required to Manage Ecological Systems in a Changing World.” *Ecosphere* 4 (February): 1–12. doi:10.1890/ES12-00178.1. <http://www.esajournals.org/doi/abs/10.1890/ES12-00178.1>.
- Deisenroth, Marc Peter, Carl Edward Rasmussen, and Jan Peters. 2009. “Gaussian Process Dynamic Programming.” *Neurocomputing* 72 (7-9) (mar): 1508–1524. doi:10.1016/j.neucom.2008.12.019. <http://linkinghub.elsevier.com/retrieve/pii/S0925231209000162>.
- Geritz, Stefan A. H., and Eva Kisdi. 2012. “Mathematical Ecology: Why Mechanistic Models?” *Journal of Mathematical Biology* 65 (6-7) (dec): 1411–5. doi:10.1007/s00285-011-0496-3. <http://www.ncbi.nlm.nih.gov/pubmed/22159789>.
- Glaser, Sarah M., Michael J. Fogarty, Hui Liu, Irit Altman, Chih-Hao Hsieh, Les Kaufman, Alec D. MacCall, Andrew a Rosenberg, Hao Ye, and George Sugihara. 2013. “Complex Dynamics May Limit Prediction in Marine Fisheries.” *Fish and Fisheries* (apr). doi:10.1111/faf.12037. <http://doi.wiley.com/10.1111/faf.12037>.
- Gordon, H. S. 1954. “The Economic Theory of a Common-property Resource: the Fishery.” *The Journal of Political Economy* 62 (2): 124–142. <http://www.jstor.org/stable/10.2307/1825571>.
- Halpern, Benjamin S., Carissa J. Klein, Christopher J. Brown, Maria Beger, Hedley S. Grantham, Sangeeta Mangubhai, Mary Ruckelshaus, et al. 2013. “Achieving the Triple Bottom Line in the Face of Inherent Trade-offs Among Social Equity, Economic Return, and Conservation.” *Proceedings of the National Academy of Sciences of the United States of America* 110 (15) (apr): 6229–34. doi:10.1073/pnas.1217689110. <http://www.ncbi.nlm.nih.gov/pubmed/23530207> <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3625307> \&to
- Hilborn, Ray. 2007. “Reinterpreting the State of Fisheries and Their Management.” *Ecosystems* 10 (8) (oct):

- 1362–1369. doi:10.1007/s10021-007-9100-5. <http://www.springerlink.com/index/10.1007/s10021-007-9100-5>.
- Hughes, Terry P., Cristina Linares, Vasilis Dakos, Ingrid a van de Leemput, and Egbert H. van Nes. 2013. “Living Dangerously on Borrowed Time During Slow, Unrecognized Regime Shifts.” *Trends in Ecology & Evolution* 28 (3) (mar): 149–55. doi:10.1016/j.tree.2012.08.022. <http://www.ncbi.nlm.nih.gov/pubmed/22995893>.
- Kocijan, Juš, Agathe Girard, Bla\ vz Banko, and Roderick Murray-Smith. 2005. “Dynamic Systems Identification with Gaussian Processes.” *Mathematical and Computer Modelling of Dynamical Systems* 11 (4) (dec): 411–424. doi:10.1080/13873950500068567. <http://www.tandfonline.com/doi/abs/10.1080/13873950500068567>.
- Ludwig, Donald, and Carl J. Walters. 1982. “Optimal Harvesting with Imprecise Parameter Estimates.” *Ecological Modelling* 14 (3-4) (jan): 273–292. doi:10.1016/0304-3800(82)90023-0. <http://linkinghub.elsevier.com/retrieve/pii/0304380082900230>.
- Mangel, Marc, and Colin W. Clark. 1988. *Dynamic Modeling in Behavioral Ecology*. Edited by John Krebs and Tim Clutton-Brock. Princeton: Princeton University Press.
- May, Robert M., John R. Beddington, Colin W. Clark, Sidney J. Holt, and R. M. Laws. 1979. “Management of Multispecies Fisheries.” *Science (New York, N.Y.)* 205 (4403) (jul): 267–77. doi:10.1126/science.205.4403.267. <http://www.ncbi.nlm.nih.gov/pubmed/17747032>.
- Munch, Stephan B., Athanasios Kottas, and Marc Mangel. 2005. “Bayesian Nonparametric Analysis of Stock recruitment Relationships.” *Canadian Journal of Fisheries and Aquatic Sciences* 62 (8) (aug): 1808–1821. doi:10.1139/f05-073. <http://www.nrcresearchpress.com/doi/abs/10.1139/f05-073>.
- Munch, Stephan B., Melissa L. Snover, George M. Watters, and Marc Mangel. 2005. “A Unified Treatment of Top-down and Bottom-up Control of Reproduction in Populations.” *Ecology Letters* 8 (7) (may): 691–695. doi:10.1111/j.1461-0248.2005.00766.x. <http://doi.wiley.com/10.1111/j.1461-0248.2005.00766.x>.
- Polasky, Stephen, Stephen R. Carpenter, Carl Folke, and Bonnie Keeler. 2011. “Decision-making Under Great Uncertainty: Environmental Management in an Era of Global Change.” *Trends in Ecology & Evolution* (may): 1–7. doi:10.1016/j.tree.2011.04.007. <http://www.ncbi.nlm.nih.gov/pubmed/21616553>.
- Rasmussen, Carl Edward, and C. K. I. Williams. 2006. *Gaussian Processes for Machine Learning*. Edited by Thomas Dietterich. Boston: MIT Press,. www.GaussianProcess.org/gpml.
- Reed, William J. 1979. “Optimal Escapement Levels in Stochastic and Deterministic Harvesting Models.” *Journal of Environmental Economics and Management* 6 (4) (dec): 350–363. doi:10.1016/0095-0696(79)90014-7. <http://www.sciencedirect.com/science/article/pii/0095069679900147> <http://linkinghub.elsevier.com/retrieve/pii/0095069679900147>
- Schapaugh, Adam W., and Andrew J. Tyre. 2013. “Accounting for Parametric Uncertainty in Markov Decision Processes.” *Ecological Modelling* 254 (apr): 15–21. doi:10.1016/j.ecolmodel.2013.01.003. <http://linkinghub.elsevier.com/retrieve/pii/S0304380013000306>.

- Scheffer, Marten, Stephen R. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. "Catastrophic Shifts in Ecosystems." *Nature* 413 (6856) (oct): 591–6. doi:10.1038/35098000. <http://www.ncbi.nlm.nih.gov/pubmed/11595939>.
- Sethi, Gautam, Christopher Costello, Anthony Fisher, Michael Hanemann, and Larry Karp. 2005. "Fishery Management Under Multiple Uncertainty." *Journal of Environmental Economics and Management* 50 (2) (sep): 300–318. doi:10.1016/j.jeem.2004.11.005. <http://linkinghub.elsevier.com/retrieve/pii/S0095069605000057>.
- Weitzman, Martin L. 2013. "A Precautionary Tale of Uncertain Tail Fattening." *Environmental and Resource Economics* 55 (2) (mar): 159–173. doi:10.1007/s10640-013-9646-y. <http://link.springer.com/10.1007/s10640-013-9646-y>.
- Williams, Byron K. 2001. "Uncertainty , Learning , and the Optimal Management of Wildlife." *Environmental and Ecological Statistics* 8: 269–288. doi:10.1023/A:1011395725123.
- Worm, Boris, Edward B. Barbier, Nicola Beaumont, J. Emmett Duffy, Carl Folke, Benjamin S. Halpern, Jeremy B. C. Jackson, et al. 2006. "Impacts of Biodiversity Loss on Ocean Ecosystem Services." *Science (New York, N.Y.)* 314 (5800) (nov): 787–90. doi:10.1126/science.1132294. <http://www.ncbi.nlm.nih.gov/pubmed/17082450>.
- Worm, Boris, Ray Hilborn, Julia K. Baum, Trevor A. Branch, Jeremy S. Collie, Christopher Costello, Michael J. Fogarty, et al. 2009. "Rebuilding Global Fisheries." *Science (New York, N.Y.)* 325 (5940) (jul): 578–85. doi:10.1126/science.1173146. <http://www.ncbi.nlm.nih.gov/pubmed/19644114>.