Is it Important to Take Account of Fluctuations in Forage Fish Recruitment in Ecosystem Models?

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Introduction

A conspicuous feature of short-lived forage fish species such as sardine and anchovy is the substantial recruitment fluctuations displayed by time series for their annual recruitment. These can lead to high variability in their biomass over time. It is questionable whether popular approaches to ecosystem modelling capture this process appropriately, or when fit to time series of abundance data are able to adequately reflect the fluctuations in those data which arise from recruitment variation.

However, if system dynamics do not change substantially as the extent of such recruitment variation increases, then satisfying those requirements may be of little consequence. This paper uses a relatively simple predator prey model with variable recruitment for a prey species under harvest to examine this question.

Methodology

Mathematical details of the methodology employed are provided in the Appendix. A discrete model of a predator and a forage species prey includes stochastic recruitment for the prey, predator satiation (which sets an upper bound on the per capita growth rate of the predators), removals of prey at a fixed fishing mortality, and density dependent predator mortality which allows for competition amongst the predators and excludes trivial solutions to the equations. The choice of specific parameter values deliberately has the predator annual natural mortality rate some 20-25% that of the prey, so that the predator has slower dynamics, which precludes it from taking full advantage of brief upward fluctuations in prey abundance.

This model is used to project the dynamics forward in time under different prey fishing mortalities to compute the associated catch of the prey, as well as predator and prey biomasses. Because of the prey and consequently predator fluctuations in abundance, results for relationships such as sustainable catch as a function of biomass are obtained by averaging over a large number of years. This number runs into many thousands to reduce the impact of Monte Carlo error on the results of interest.

Results

Fig. 1 shows typical time trajectories of the prey and the predator with and without prey harvest and in the presence of some prey recruitment fluctuation. The predator has a smoother trajectory as it essentially “integrates” over the more variable prey. As fishing mortality increases, prey and also predator abundance drops, though the latter in particular shows greater variability in abundance.

Fig. 2 (a) shows what is in effect a sustainable yield curve for the prey, and how this changes as recruitment variability σ_R increases. The main features are a decrease in this yield and an increase in the prey MSY biomass compared to its pre-exploitation level. For the predators in Fig. 2 (b), the higher σ_R, the faster predator abundance decreases as prey abundance drops as a result of increased prey fishing mortality.

Fig. 3 shows how various quantities change as σ_R is increased: prey abundance drops, but predator abundance drops faster. Predator abundance, when the prey is fished at a mortality rate that yields MSY, decreases with σ_R. This trend is less marked if instead the predator abundance, when the prey is fished at a rate that keeps it on average at 75% of pristine abundance, is shown as a proportion of its level when prey is unexploited.

Concluding remarks

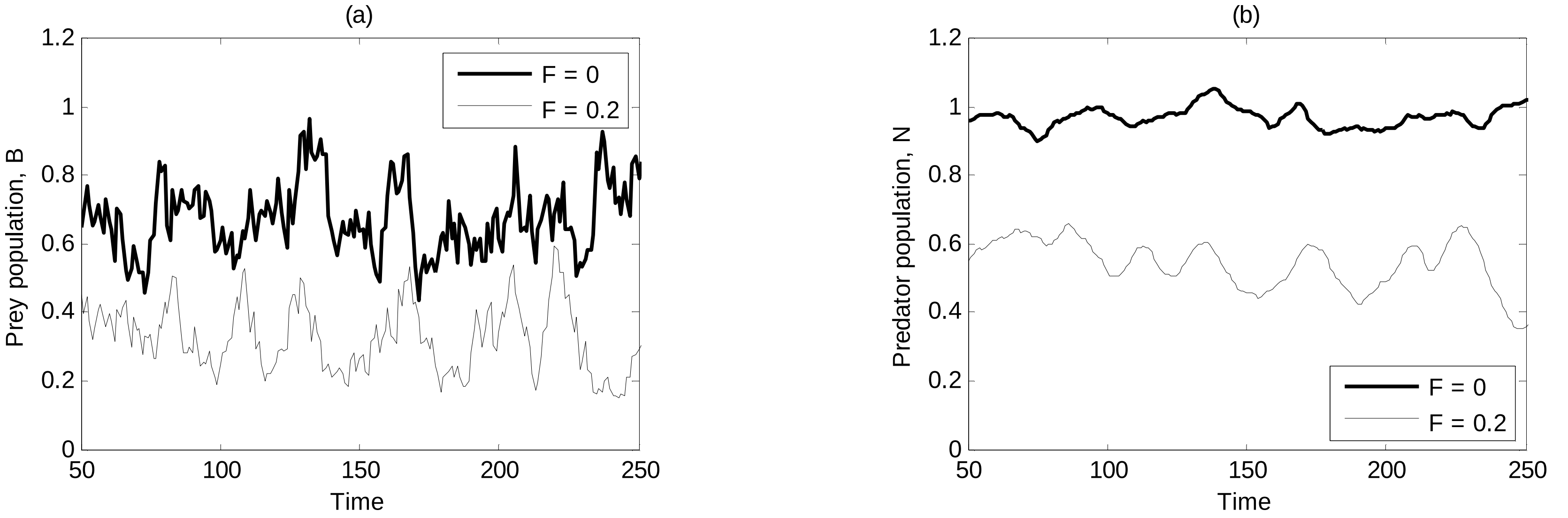
The results obtained certainly show that important features of this predator-prey system, when under harvest, can change appreciably for different levels of the extent of recruitment fluctuation as measured by σ_R. Of itself this suggests that care needs to be taken with more complex ecosystem models to ensure that recruitment fluctuations of forage fish are reflected realistically.

For the model and parameter value choices made, the predator is impacted relatively more heavily by fishing at higher values of prey recruitment variability σ_R. Questions that arise regarding possible further work include:

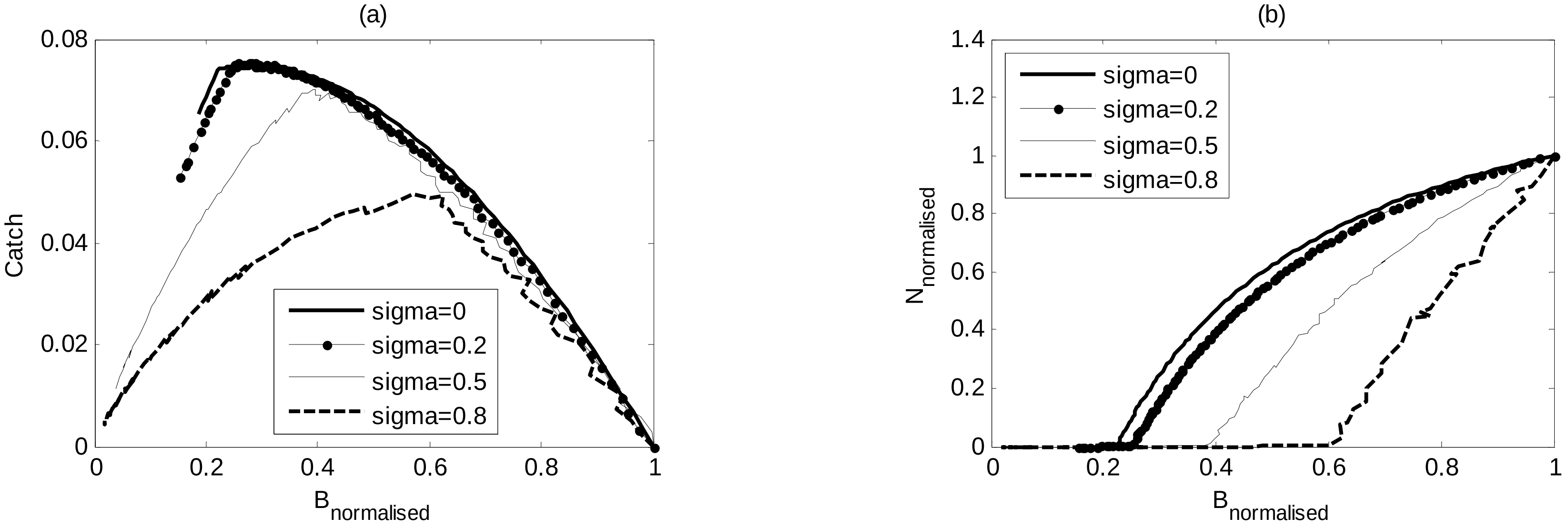
- Does the behaviour of this simple model and variants thereof (e.g. allowing also for another food source for the prey) warrant examination over a wider range of parameter value choices, or do more complex models need to be used instead to ensure greater realism?

- Could alternative harvesting approaches to the constant fishing mortality policy examined here result in less reduction of the predator, while still maintaining the same catch on average over time?

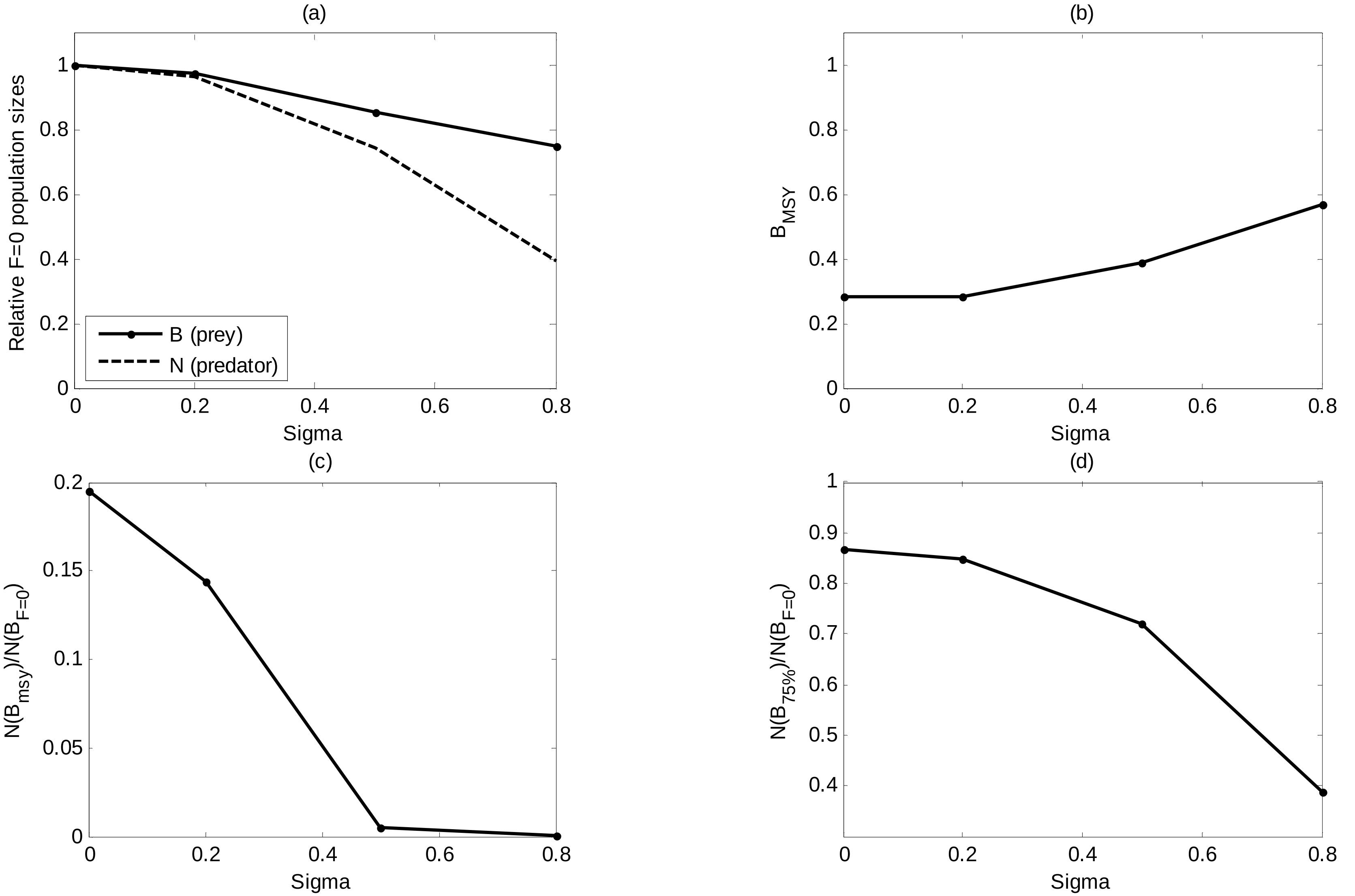
- What are the most pertinent statistics to examine in such models to address the question posed, e.g. rather consider a lower percentile than the mean of biomass distributions?



Figures 1 (a) and (b): Prey (a) and predator (b) population sizes for F = 0 and F = 0.2, shown for a 200 year simulation run, for σ_R=0.15. Note that the first 50 years have been discarded to allow the trajectories to settle.



Figures 2 (a) and (b): Figure (a) shows the mean catch as a function of $B_{normalised}$, where $B_{normalised}$ is B(F)/B(F=0). Figure (b) shows $N_{normalised}$ plotted against $B_{normalised}$, where $N_{normalised}$ is similarly defined as N(F)/N(F=0);



Figures 3 (a)-(d): These figures show a series of quantities plotted against σ_R. Figure (a) shows B(F=0) for each σ_R, relative to B(F=0) for σ_R=0, as well as the similar quantities for N. Figure (b) shows B_{MSY} (normalised relative to $B_{F=0}$). Figure (c) shows N at B_{MSY} relative to N at $B_{F=0}$. Figure (d) shows N at $0.75B_{F=0}$ relative to N at $B_{F=0}$.

Appendix

This Appendix gives the details of the models used for investigating the effect of prey recruitment fluctuations on a fast growing prey population and a slow-growing predator population, where the prey population is under harvest.

Basic population dynamics

The prey equation (A1) and predator equation (A2) are given by

$$B_{y+1} = \left(B_y + \frac{\alpha B_y}{\beta + B_y} e^{\varepsilon_y - \sigma_R^2/2} \right) e^{-M} - \lambda \frac{B_y N_y}{1+\mu B_y} - F B_y \tag{A1}$$

$$N_{y+1} = \left(N_y + \lambda^* \frac{B_y N_y}{1+\mu B_y} \right) e^{-M^*\left(1+\omega N_y\right)} \tag{A2}$$

where

B_y	is the prey biomass in year *y*,
N_y	is the predator population size in numbers in year *y*,
α and β	are the Beverton-Holt stock recruitment relationship parameters,
M and M^*	are the natural mortality rates for the prey population *B*, and the predator population, *N*, respectively,
λ and μ	are parameters determining the mortality of the prey owing to predator consumption,
λ^*	is a parameter determining the growth of the predator population that results from consumption of prey,
F	is the prey fishing mortality,
ω	is a parameter that limits the predator population growth by increasing natural mortality when the population is large (i.e. density dependent mortality), and
$\varepsilon_y \sim N\left(0,\, \sigma_R^2\right)$	reflects log-normally distributed fluctuations in the recruitment.

The value of σ_R is varied to investigate the effect of increasing recruitment fluctuations on the population dynamics.

Equilibrium relationships

For $\sigma_R = 0$ and under equilibrium, Equation (A1) and (A2) become:

$$1 = \left(1 + \frac{\alpha}{\beta + B} e^{\varepsilon_y - \sigma_R^2/2} \right) e^{-M} - \lambda \frac{N}{1+\mu B} - F \tag{A3}$$

$$1 = \left(1 + \lambda^* \frac{B}{1+\mu B} \right) e^{-M^*\left(1+\omega N\right)} \tag{A4}$$

where *B* and *N* are the respective prey and predator equilibrium population sizes, and the rest of the symbols are as defined above.

Model parameters

The following assumptions are made to provide specific values for the model parameters:

1) When $F = 0$ and $N = 0$, let $B = K_B = 1$.
   Substituting this information into Equation (A4) gives:

$$\alpha = (\beta + 1)(e^M - 1) \tag{A6}$$

2) When $F = 0$ and $N = 0$, let the recruitment at $B = 0.2K_B = 0.2$ be given by the parameter *h* (measure of the steepness of the stock recruitment curve). Substituting this information into Equation (A3) yields:

$$\alpha = \frac{0.8(e^M - 1)}{h - 0.2(e^M - 1)} \tag{A7}$$

By setting $h = 0.75$, the values of α and β follow.

3) Assume that $M = 1$ and $M^* = 0.2$.
These values are chosen to ensure that the prey population is fast-growing relative to a slow-growing predator population.

4) Choose λ, μ and λ^* such that
    i. when $F = 0$ predators keep the prey population at $B = 0.7K_B = 0.7$, and
    ii. when $F = 0$ and $B = 0.10$ the single predator consumption rate, given by $\frac{\lambda B}{1 + \mu B}$, is reduced to half its maximum value when $B = 0.7$.

By further by setting $N = 1$ when $F = 0$ (i.e. define *N* relative to its equilibrium population size when there is no fishing), λ, μ and λ^* can be calculated.

5) Lastly, the value for ω was chosen so that (with zero recruitment fluctuations) the predator population *N* does not go into extinction for $F < 0.5$. $\omega = 0.5$ is used here.

Simulation process

The simulation process involves starting both the predator and prey populations at 1, and computing the population sizes for a long time series while letting the recruitment fluctuate each year. This fluctuation is achieved by drawing a different ε value from $N(0, \sigma_R^2)$ each year. In order to attain some degree of smoothness, this simulation was run for 30 000 years, and the mean population size values were taken over the last 29 000 years of the series.

Catches exceeding prey population size

To avoid irregularities arising when catches taken from the prey population exceed the actual population size, the following adjustments are made:

Let $B_{y+1}^* = \left(B_y + \frac{\alpha B_y}{\beta + B_y} e^{\varepsilon_y - \sigma_R^2/2} \right) e^{-M} - \lambda \frac{B_y N_y}{1 + \mu B_y}$ (i.e. recruitment less loss to predators).

If $B_{y+1}^* > FB_{y+1} + 0.001$, then $C_y = FB_y$ and $B_{y+1} = B_{y+1}^* - FB_{y+1}$ as usual.

If $B_{y+1}^* < FB_{y+1} + 0.001$, then $C_y = B_{y+1}^* - 0.001$ and $B_{y+1} = 0.001$.

In this manner, the size of *B* is restricted to remain above 0.001, with catches being reduced in the years concerned to ensure this.