

MATH3070 Final Assignment

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Question 1

(a) We have the function

$$f(x) = x + (r - 1)x \left(1 - \left(\frac{x}{k}\right)^\phi\right) \quad (1)$$

which is plotted for 3 values in Figure 1.

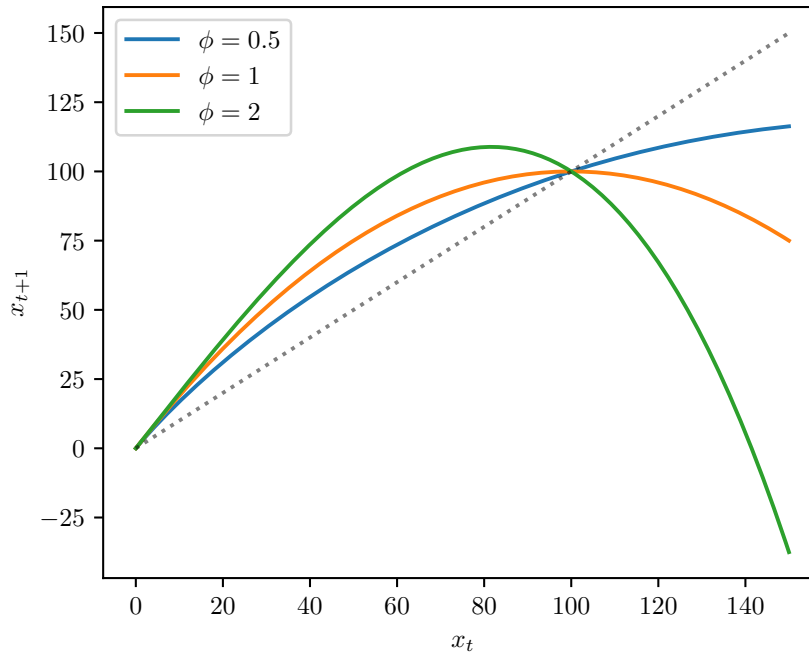


Figure 1. Plots for 3 characteristic values of ϕ in the equation (1) for $r = 2$ and $k = 100$. A dotted 1:1 line is shown to compare population growth vs decay.

If we take the model

$$x_{t+1} = f(x_t) \quad (2)$$

then increasing the value of ϕ corresponds to a larger rate of change (in magnitude) in the population for most values of x_t . That is, the value of ϕ may correspond to the species' utilisation of resources in the ecosystem, where more utilisation (a larger ϕ) means a generally steeper curve; the species better utilise available resources to grow quickly when $x < k$, and the species quickly uses all resources (leaving many to die) when $x > k$.

(b) The proliferation of a model is given by the derivative at $x = 0$. To make the differentiation easier, we rewrite the model as

$$f(x) = x + (r - 1) \left(x - \frac{x^{\phi+1}}{k^\phi}\right) \quad (3)$$

which has the derivative

$$f'(x) = 1 + (r - 1) \left(1 - (\phi + 1) \frac{x^\phi}{k^\phi}\right) \quad (4)$$

at $x = 0$, we see a proliferation of $f'(x = 0) = r$, independent of k or ϕ .

(c) We find the equilibria in the model when $x_t = x_{t+1} = f(x_t)$. That is,

$$\begin{aligned} x &= x + (r-1)x \left(1 - \left(\frac{x}{k}\right)^\phi\right) \\ 0 &= (r-1)x \left(1 - \left(\frac{x}{k}\right)^\phi\right) \end{aligned}$$

Hence we see equilibria when $r = 1$ (which is not biologically interesting and holds for any value of x), when $x = 0$ (corresponding to the extinction of the species), and when $(x/k)^\phi = 1 \Rightarrow x = k$. Since $\phi > 0$ we don't need to worry about the equilibrium when $x \neq k$, and $k > 0$ means that our $x = k$ equilibrium will be biologically meaningful for any value of k .

(d) For a discrete time model such as this, we have that an equilibrium is stable when $|f'(x^*)| < 1$. We already have our derivative in equation (4), and so for our extinction equilibrium,

$$f'(x^* = 0) = (r-1)(1-0) + 1 = r$$

and hence $|f'(x^* = 0)| < 1$ when $-1 < r < 1$, and the extinction equilibrium is unstable otherwise. Since we have that $r > 0$, we can strengthen this constraint to $0 < r < 1$.

For our carrying-capacity equilibrium, we have

$$f'(x^* = k) = (r-1)(1 - (\phi+1)(1)^\phi) + 1 = -\phi(r-1) + 1$$

and so $|f'(x^* = k)| < 1$ when

$$|\phi(1-r) + 1| < 1$$

Here we need to break this into the case that the value in the absolute value is positive, and when it's negative. For the former, we have

$$\begin{aligned} \phi(1-r) + 1 &< 1 \\ \phi(1-r) &< 0 \end{aligned}$$

and so $r > 1$ is sufficient for stability in this case. In the latter case that the value is negative, we have

$$\begin{aligned} \phi(1-r) + 1 &< -1 \\ (1-r) &< -\frac{2}{\phi} \\ r &> \frac{2}{\phi} + 1 \end{aligned}$$

which is a stronger constraint than $r > 1$ (since $\phi > 0$). Hence, $x^* = k$ is stable for $r > 1 + 2/\phi$ and unstable otherwise. In Figure 1 we see this unstable behaviour in all of the plotted lines (since $r = 2$ which does not meet the stability condition for any of the plotted ϕ values).

(e) We define $S_t = x_t - h_t$, and so if $f(S_t) = x_{t+1}$ is smooth (i.e. infinitely continuously differentiable), and $f(S_t) > S_t$, then $f'(S^*) = 1$ corresponds to the optimal equilibrium escapement S^* .

We note that $f'(S_t)$ is infinitely continuously differentiable (it's a polynomial), and

$$\begin{aligned} f(S_t) &= S_t + (r-1)S_t \left(1 - \left(\frac{S_t}{k}\right)^\phi\right) \\ &= S_t \left(1 + (r-1) \left(1 - \left(\frac{S_t}{k}\right)^\phi\right)\right) \end{aligned}$$

where $f(S_t) > S_t$ under the stability condition of $x^* = k$ above.

So,

$$\begin{aligned} f'(S^*) &= 1 + (r-1) \left(1 - (\phi+1) \left(\frac{S^*}{k}\right)^\phi\right) = 1 \\ 0 &= 1 - (\phi+1) \left(\frac{S^*}{k}\right)^\phi \\ \Rightarrow S^* &= k \left(\frac{1}{\phi+1}\right)^{1/\phi} \end{aligned}$$

is the optimal equilibrium escapement for the model $f(S_t) = x_{t+1}$.

- (f) If we have the data $\{X_0, \dots, X_n\}$ for years $0, \dots, n$, and assuming that $X_i \leq k$ with ϕ and k known, we can evaluate the sum of squared errors as

$$\begin{aligned} SSE(r) &= \sum_{i=0}^{n-1} \left[X_{i+1} - \left(X_i + (r-1)X_i \left(1 - \left(\frac{X_i}{k} \right)^\phi \right) \right) \right]^2 \\ &= \sum_{i=0}^{n-1} \left[X_{i+1} - X_i - X_i r \left(1 - \left(\frac{X_i}{k} \right)^\phi \right) + X_i \left(1 - \left(\frac{X_i}{k} \right)^\phi \right) \right]^2 \end{aligned}$$

To find the least squares estimate for r , \hat{r} , we want to differentiate this with respect to r and set it equal to 0:

$$\begin{aligned} \frac{\partial SSE(r)}{\partial r} &= 0 = 2 \sum_{i=0}^{n-1} \left[X_{i+1} - X_i - X_i \hat{r} \left(1 - \left(\frac{X_i}{k} \right)^\phi \right) + X_i \left(1 - \left(\frac{X_i}{k} \right)^\phi \right) \right] \left[-X_i \left(1 - \left(\frac{X_i}{k} \right)^\phi \right) \right] \\ \sum_{i=0}^{n-1} X_i^2 \hat{r} \left(1 - \left(\frac{X_i}{k} \right)^\phi \right)^2 &= \sum_{i=0}^{n-1} \left(X_{i+1} - X_i + X_i \left(1 - \left(\frac{X_i}{k} \right)^\phi \right) \right) X_i \left(1 - \left(\frac{X_i}{k} \right)^\phi \right) \\ \hat{r} &= \frac{\sum_{i=0}^{n-1} \left(X_{i+1} - X_i \left(\frac{X_i}{k} \right)^\phi \right) X_i \left(1 - \left(\frac{X_i}{k} \right)^\phi \right)}{\sum_{i=0}^{n-1} X_i^2 \left(1 - \left(\frac{X_i}{k} \right)^\phi \right)^2} \end{aligned} \quad (5)$$

which is our least squares estimate for \hat{r} in terms of the data, ϕ and k . We'd tested this function with simulated data and can confirm that it does yield the expected result.

Question 2

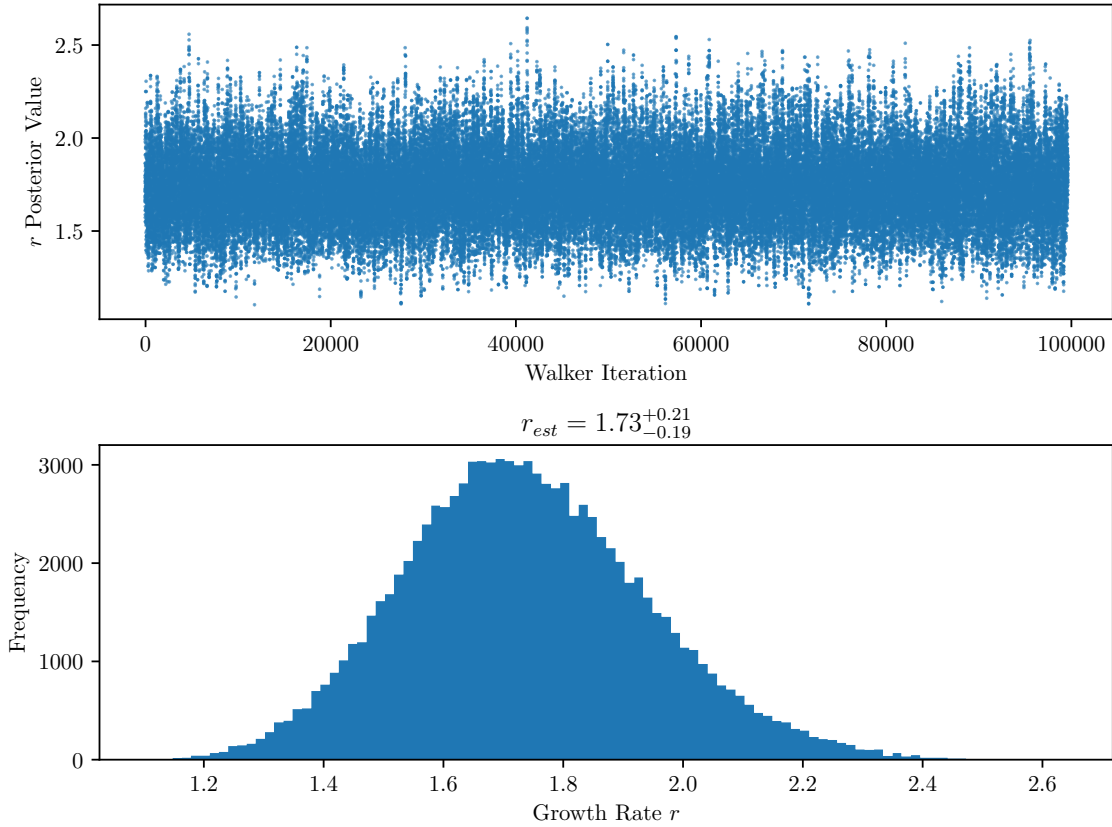


Figure 2. The raw posterior samples at each iteration (*top*), and the posterior distribution for growth rate r (*bottom*) for our Markov Chain Monte Carlo with the government data, assuming a growth model as in equation (1). The quoted value for our growth rate r is the median of the posterior distribution, where the uncertainties were found from the 16th and 84th percentiles in the distribution. The MCMC was performed with uniform priors and the Metropolis algorithm over 10^5 iterations, with a 500 iteration ‘burn-in’.

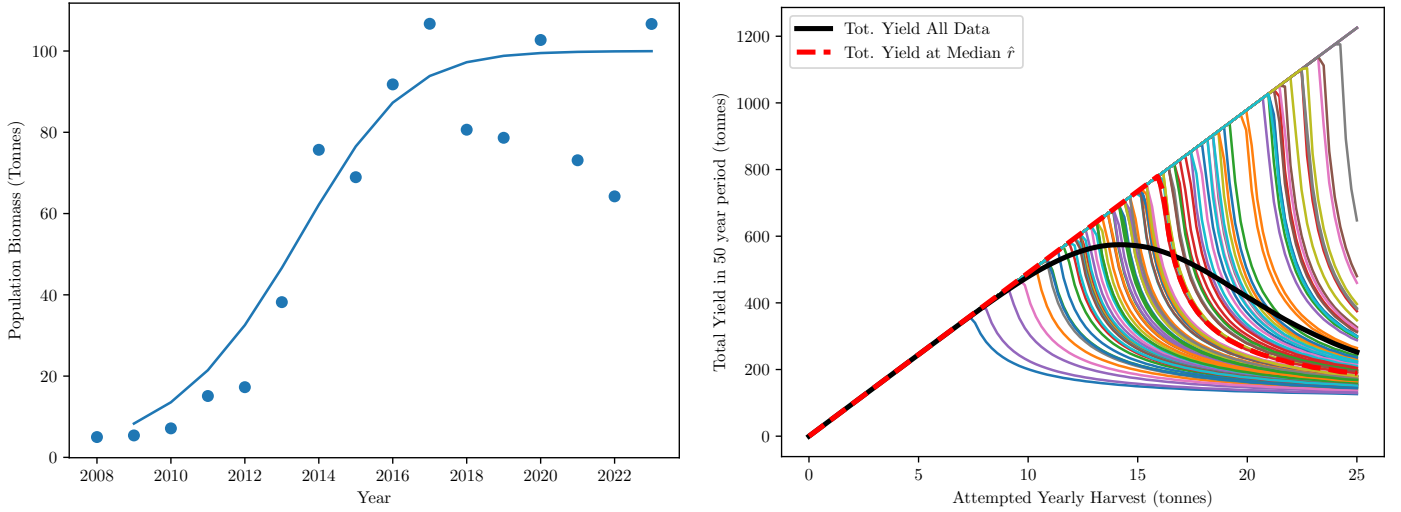


Figure 3. *Left:* The median value of the posterior distribution in Figure 2 yields a good fit to the government data as expected with our population dynamic model. *Right:* We present the total fishing yield in the first 100 posterior samples for a range of yearly fishing quotas. The dashed red line represents the behaviour given the median posterior growth value and the black represents the mean across the entire dataset (not just the first 100 samples).

With the government and university data provided to us for the biomass data of fish species X and Y respectively, we believe that the fish population has recovered to a state that it's reasonable to reopen the fishery.

A nearby university gave us data pertaining to the growth of a sample of fish species Y (which is believed to be similar in growth to our species X) in 10 independent tanks. With each of these populations beginning from 2 individuals, we used the least-squares formula [equation (5)] to estimate the growth rate in the population dynamic model given by equation (1) after one year. We averaged these least squares estimates across the tanks to yield a mean growth value of $\hat{r} \simeq 1.73$ for species Y. However, without uncertainty in this value, we're unable to fairly conclude whether or not the fishery may reopen. With this in mind, we implemented a Markov Chain Monte Carlo (MCMC) algorithm to assess the observed growth rate of species X in their habitat with the government data. Using the least squares estimate as an initial position for our MCMC walker with uniform priors bounded below at 0, we obtained the posterior distribution shown in Figure 2. We see agreement between the least squares and MCMC growth (median) value, the latter being $\hat{r} = 1.73^{+0.21}_{-0.19}$ and almost normal in its distribution. With a mean value in the posterior distribution of $\bar{r} = 1.75$, the species X and Y are truly alike in their growth (at least within uncertainty)!

With some uncertainty in the growth of the species population, we're able to more accurately predict the optimal harvest. We chose to investigate the population dynamics with harvest over a 50 year period; this is low enough to be computationally cheap, but high enough to largely avoid an unsustainable overfishing bias that we may get in a short time-simulation. If we assume the median growth rate of $\hat{r} = 1.73$, the yearly harvest quota which maximises the yield of species X is approximately 15.91 tonnes per year. We can, however, utilise all of the samples in the posterior distribution (Figure 2) to obtain a more conservative estimate of the maximum sustainable yield – one that is robust to our uncertainties in the species' intrinsic growth rate. To do this, we initialised a suite of population growth simulations beginning at the 2023 biomass in the government data (growing according to equation (1)). We simulated a harvest of a consistent amount from the existing population at each time step across a simulation for each growth posterior sample (testing multiple harvest quotas for each growth sample), allowing the population to grow at each time before harvesting. For each harvest quota, computing the mean yield across the simulations for each growth sample gave us an overall optimal quota of 14.14 tonnes per year (given by the peak in the black line on the right Figure 3). This result is our conservative recommendation for a limit on the yearly quota in the fishery, and accounts for our uncertainty in the species X growth rate.

Question 3

- (a) One of the fundamental differences that modelling ecology differs from physics is that (at least most of) physics can be derived from first principles, whereas biology (at least mostly) cannot. That is, using fundamental theories like general relativity, someone motivated enough may be able to describe the way light behaves around a black hole; at the same time, using population growth models we may never predict the exact moment that a tiger may prey on another species in the wilderness.

Similarly, modelling the complexity of thousands-to-millions of species in an ecological system is difficult, and rela-

tionships between individuals and species aren't deterministic. While we can model chaotic behaviour in physical systems, even the most stochastic physics problems seldom compare to the most basic ecological system. At best, we can make inferences on the short/long term behaviour of an ecological *system* rather than the behaviour of individuals in that system.

- (b) One reason for why modellers tend to avoid using individual species when modelling ecosystems is that there are just so many of them. There are usually so many species in any one system that most species would need to be ignored for any semblance of computational/mathematical efficiency in a model; if not, then we also risk making unfounded decisions about the system where we may not have the accuracy in our model/parameters to do so. Further, when using species as a parameter, the modeller *must* make some assumptions on the system (e.g. that a specific species has a larger impact/prevalence than others) that they may not need to make when modelling by size. Another key reason to use size rather than individual species is that *most* species within an ecological niche would be subject to the same underlying physical processes anyway. That is, all similarly sized predators within one system probably prey on individuals that are of the same size (with orders of magnitude), and probably have the same metabolism, etc properties too. That is, there is not really a need to model individual species as long as the general behaviour of collections of species are modelled accurately enough.
- (c) Allometry involves studying the effect of an individual's size on its other biological parameters. For example, the metabolic rate of an animal is dependent on its size, as is the size of an animal's ideal food and its rate of body growth (among many other parameters). Since the size (or mass) of an individual is a cheap and precise observable quantity, we're able to infer many deeper quantities of an animal by looking at its size. A key example of this is to do with metabolic rates. A rabbit has a very high metabolic rate to maintain a high enough body temperature given their small size, while an elephant has a much lower metabolic rate (proportionally) to avoid overheating as larger volumes radiate heat less efficiently. Both of these animals typically eat plant matter and even though the rabbit has a higher metabolic rate, the elephant eats more (by mass) in a day on account of its size.
- (d) Allometry allows us to infer the relationships and dynamics in ecosystems while keeping our mathematical framework relatively simple (at least in comparison to a species-based approach). As described before, there may be thousands of species relevant to a single ecological system, which would require (at least) thousands of variables to represent the interrelationships of the species; using an allometric approach, we can reduce the model size to look at species size and not species number. Hence allometric models make the modelling easier and more resistant to small perturbations in the initial conditions of the model (for example, if we modelled all species we may see unrealistic behaviour with species stochastically going extinct or overpopulating when we wouldn't see this in real life). Finally, using allometric models can still be accurate since the fundamental biological processes are still described with a size-based approach, and so we get this mathematical efficiency effectively for free.