QERM Qualifying Exam 2017
DUE: 5:00 pm, Monday June 19th.

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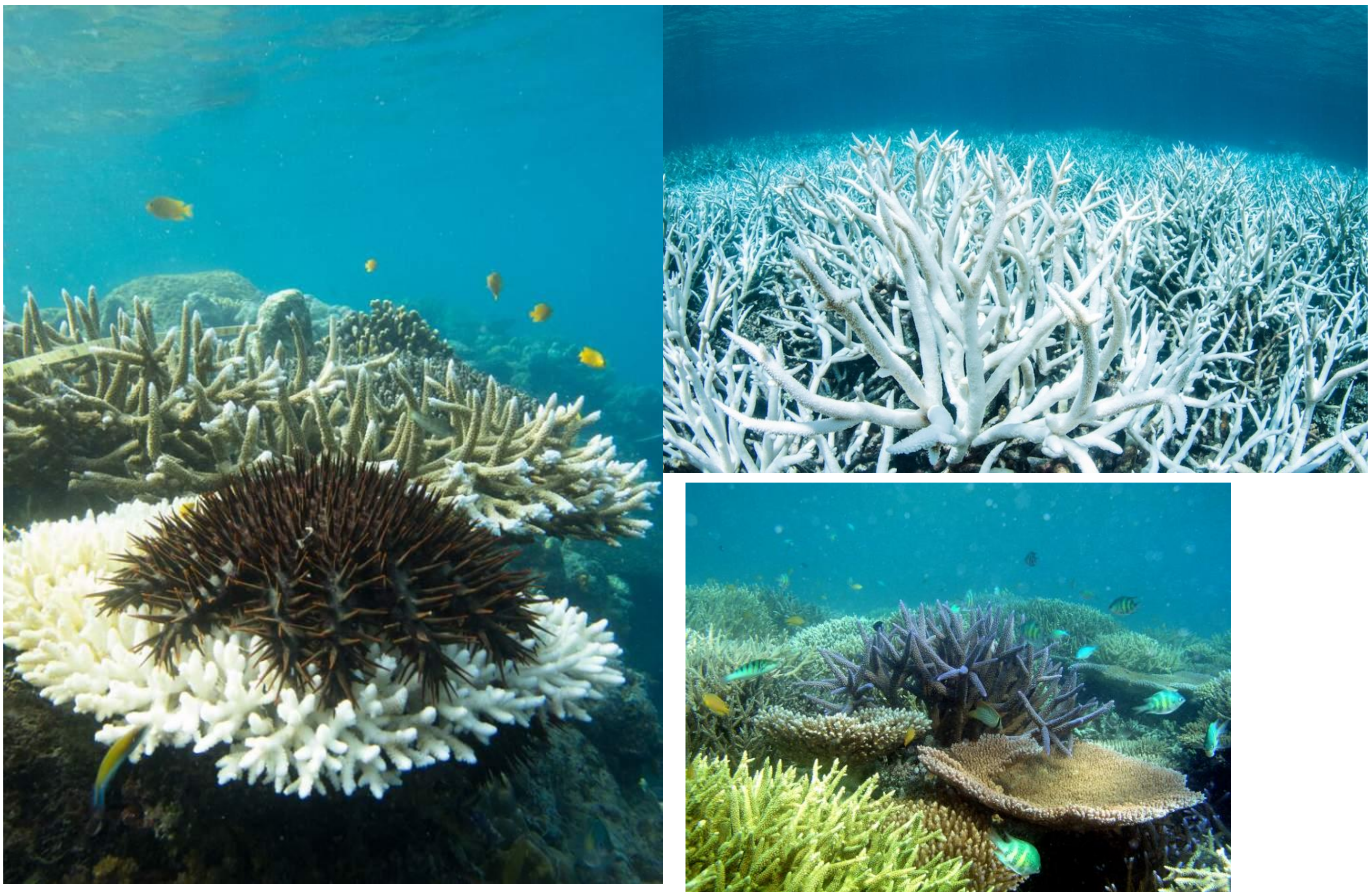
Coral reefs face a number of threats in the Anthropocene. Overfishing of herbivorous fishes allows macroalgae to flourish and convert coral reefs into algal turfs. Invasive species such as crown-of-thorn starfish pose a direct threat by consuming vulnerable species. Ocean acidification is changing the saturation point for aragonite and carbonate, potentially shifting the balance from coral accretion to dissolution. Finally, higher temperatures pose risk due to coral bleaching.

This exam will examine several threats that corals face.



Clockwise from left. A crown of horns starfish on a Acropora coral. Credit: James Cook University. Bleached coral in the Great Barrier Reef, Feb 20 2017. Credit: Brett Monroe Garner. Healthy coral reef in the Caribbean Ocean. Credit: NOAA

Question 1: Mathematical Ecology

Background

Coral reefs are some of the most diverse — and threatened — ecosystems on the planet. In the Indian and Pacific Oceans, outbreaks of the crown-of-thorns starfish (*Acanthaster planci*) have had an especially devastating effect on coral reefs. Outbreaks of this coral-eating predator can be intense disturbances that decimate entire reefs (Kayal et al. 2012). De'ath et al. (2012) estimated that 42% of recent coral losses on the Great Barrier Reef are due to this starfish.

Numerous hypotheses have been proposed to account for starfish outbreaks. One of the most important is the *predator removal hypothesis*, which argues that outbreaks occur because humans have overfished predators of the starfish. The formulation of this hypothesis was prompted by the overfishing of the giant triton (*Charonia tritonis*), a large marine snail they preys upon the crown-of-thorns starfish, prior to the first outbreaks of the starfish on the Great Barrier Reef.

The predator removal hypothesis has evolved, in recent years, and now places greater emphasis on piscine (fishlike) predators of starfish. On the Great Barrier Reef, Sweatman (2008) showed that reefs open to fishing were several times more likely to experience outbreaks of starfish than reefs closed to fishing because of no-take marine reserves. Dulvy et al. (2004), in turn, examined fish densities, starfish densities, and coral reef structure along a 13-island gradient of increasing fishing effort in Fiji. Fish (predator) densities declined by 61% and starfish densities increased by three orders of magnitude along this gradient. These studies lend support to the predator removal hypothesis.

One of the earliest models to look at the effects of predators on starfish populations took the simple form

$$\frac{dN}{dT} = r\,N\left(1 - \frac{N}{K}\right) - \frac{c\,N\,P}{a + N}\,, \tag{1.1a}$$

$$\frac{dP}{dT} = s\,P\left(1 - \frac{P}{L + b\,N}\right). \tag{1.1b}$$

N is the density of starfish, P is the density of predators, and T is time. All parameters (a, b, c, K, L, r, and s) are nonnegative. The predators are generalist predators that feed on a variety of species.

1. Basic interpretation

Describe the biological meaning of the terms and parameters in this predator-prey model. Be succinct but accurate. If there are names or if there is standard terminology associated with particular terms or parameters, be sure to state these.

2. Nondimensionalization and simplification

In order to simplify the above differential equations, introduce the dimensionless variables

$$x \equiv \frac{N}{a}\,, \quad y \equiv \frac{P}{L}\,, \quad t \equiv r\,T \tag{1.2}$$

and reduce your differential equations to a system of the form

$$\frac{dx}{dt} = f(x)\,[\,g(x,\alpha) - \beta\, y\,]\,, \tag{1.3a}$$

$$\frac{dy}{dt} = \gamma\, y \left[1 - \frac{y}{h(x,\delta)} \right], \tag{1.3b}$$

for appropriate functions $f(x)$, $g(x, \alpha)$, and $h(x, \delta)$. Here, α, β, δ, and γ are dimensionless parameters.

Identify (write out) the functions $f(x)$, $g(x, \beta)$, $h(x, \delta)$. What are (write out) your dimensionless parameters (α, β, γ, and δ) in terms of the original model parameters (a, b, c, K, L, r, and s)?

3. Zero-growth isoclines

Find and draw the prey and predator zero-growth isoclines in the first quadrant of the predator-prey plane. Draw all *reasonable* (qualitatively different, biologically plausible) configurations for your zero-growth isoclines. (I am looking for several configurations that differ with respect to (a) the number of intersections between the isoclines and/or (b) the sign(s) of the slope of the prey zero-growth isocline at these intersections.) What are the directions of the vector fields in each portion of your subdivided phase planes?

4. Equilibria and bifurcations

Characterize your equilibria. How may equilibria are there and where are they? What bifurcations do you expect to occur as you change the various (nondimensionalized) parameters in your model?

5. Easy stability analysis

Determine the stability and the nature of the equilibrium at $(0, 1)$, corresponding to extinction of the starfish but survival of the predators, using a linearized stability analysis. Be sure to state your community matrix (Jacobian) and eigenvalues. Keep your analysis lean and clean. (I don't want to see lots of ugly algebra.)

6. Coexistence

The original analysis for this model made two interesting claims regarding equilibria where predators and prey coexist:

(i) Any equilibrium where the predator zero-growth isocline intersects a descending part of the prey zero-growth isocline is stable.

(ii) Any equilibrium where the (ascending) prey zero-growth isocline is steeper than the predator zero-growth isocline is unstable.

Prove one or the other (or, better yet, both) of these two claims. Again, keep your analysis lean and clean and avoid ugly algebra.

7. Summary

Draw phase portraits and briefly summarize the behavior of your system for each of the various, qualitatively different, configurations of your isoclines.

8. Discussion

What insights does your analysis of the above model give you regarding the ability of generalist predators to control or exclude starfish populations. What factors or combinations of factors are likely to have the biggest effects. Please discuss.

References

De'ath, G., Fabricius, K. E., Sweatman, H., and Puotinen, M. 2012. The 27–year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 17995−17999.

Dulvy, N. K., Freckleton, R. P., and Polunin, N. V. C., 2004. Coral reef cascades and indirect effects of predator removal by exploitation. *Ecology Letters*, **7**, 410−416.

Kayal, M., Vercelloni, J., Lison de Loma, T., Bosserelle, P., Chancerelle, Y., Geoffrey, S., Stievenart, C., Michonneau, F., Penin, L., Planes, S., Adjeroud, M. 2010. Predator crown-of-thorns starfish (*Acanthaster planci*) outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. *PLoS One*, **7**, e47363.

Sweatman, H. 2008. No-take reserves protect coral reefs from predatory starfish. *Current Biology*, **18**, 598−599.

Question 2

Consider the starfish-generalist-predator model from Question 1.

(a) Using population counts, N_t and P_t, formulate a stochastic version of this model, using a continuous-time Markov chain (CTMC) framework. Make sure you specify all instantaneous transitions and their corresponding rates.

(b) Using your interpretation of model parameters in Question 1, set these parameters and initial conditions, N_0 and P_0, to some biologically reasonable values. Simulate 10 trajectories of the CTMC using the chosen parameters over a time interval $[0, t]$. Make sure your counts don't grow too high (say above 10,000). You can adjust either the model parameters or the length of the observation period t to prevent large population sizes.

(c) Use one of the simulated trajectories as data to estimate model parameters in a Bayesian framework, pretending you don't know the underlying true values of these parameters that went into your simulation. Use your knowledge of true parameters (yes, I know, it is cheating big time) to specify relatively informative priors for all model parameters so they do not wander too far off into crazy land during MCMC. I recommend using univariate random walk proposals on the log scale for all parameters. Report prior densities **and** posterior histograms for all model parameters.

(d) Comment on convergence and mixing of your MCMC.

(e) Comment on identifiability of model parameters by comparing priors and their corresponding posteriors.

Question 3: Statistical Inference
Bleaching occurs when water temperature exceeds threshold values, causing corals to eject zooxanthellae. This has been occurring for decades (and likely occurs naturally) but the frequency and intensity of bleaching events has been growing. For instance, in 2016, a massive bleaching event in the Great Barrier Reef, where over 2/3 of the entire ecosystem was affected. Recently, scientists have warned that the reef may never recover.

Bleaching is also a concern in the Caribbean Ocean. Because the Caribbean is sub-tropical, there is likely a pronounced seasonal signal of temperature that governs the likelihood of bleaching. A recent compilation of data from monitoring programs provides information on the intensity/severity of bleaching events (1) throughout the world. That database has information on the country in which the surveyed reef resides, broad locations within countries, and sometimes the specific reef or stations within reefs. The samples vary considerably in the specificity information on sample location. In addition, some samples are part of routine monitoring surveys, some are ad hoc samples, while others were part of research projects not intended to judge coral bleaching.

I have used this larger database to select most Caribbean nations, and summarized the data by country. The data file called "CoralBleachByCountry" contains for each year and season the number of samples, the number of samples with severe (>50%) bleaching, and number of samples with moderate (11-50%) or severe bleaching. The latter two are termed N_SEVERE_BLEACH and N_MOD_BLEACH, respectively. The mean latitude of samples in each country that were samples is also included (MEANLAT). YEAR and COUNTRY are self explanatory.

You seek to know whether the frequency of bleaching has increased over the time period that the database covers, and whether are southern reefs experiencing greater change than northern reefs. You will answer this for both SEVERE bleaching only, as well as MODERATE or SEVERE bleaching.

Grading Rubric
1. Explain the model(s) used, and justify why they are appropriate
2. Choose a method of making inference, and justify why that approach is appropriate
3. Report on the model results, including relevant diagnostics on model fit (hint: you should be making several plots!)
4. A brief (3-4 paragraph) synthesis of your conclusions and interpretation of the models

1. Donner SD, Rickbeil GJM, & Heron SF (2017) A new, high-resolution global mass coral bleaching database. *PLoS One* 12(4):e0175490.

Question 4: Optimization

Coral reefs provide habitat for some of the most diverse biological systems in the world. They also generate billions of dollars of revenues to local economies through fishing and tourism, and they protect coastal communities from storm surges, erosion and flooding. Unfortunately, coral reefs are threatened around the globe by rising sea surface temperatures, ocean acidification, toxic, nutrient-rich runoffs from urban and agricultural areas and from overfishing. The relationship between fishing and reef health is complex. Coral reefs provide spawning grounds and nurseries for many commercial fishes such as the reef trout, triggerfish, red emperors and snappers. Most of these commercial species are predatory. They eat other fish (*piscivore*) or they eat *echinoderms* (e.g., sea urchins) thereby controlling biological community structures on the reefs (Boaden and Kingsford 2015). Fishing of these predators can cause trophic cascades whereby the abundance of prey species, such as herbivorous, algae-feeding fishes or sea urchins increases. This can compromise algae coverage on reefs or lead to spikes in population levels of filamentous algae that are resistant to grazing (McClanahan and Shafir 1990). In either case, trophic cascades caused by fishing can lead to the biological erosion of reefs because corals depend on a finely tuned, symbiotic relationship with algae. The reefs provide habitat and protection for algae, which in turn supply corals with oxygen. Lastly, commercial fishing of piscivores can inadvertently lead to the removal of herbivorous fishes as well. In either case, the health and integrity of the reefs are compromised if there is too much or too little of the various algae species critical to corals.

One way to protect coral reefs from damaging trophic cascades is to establish marine protected areas (MPAs) where fishing is either prohibited or is highly regulated. Some argue (e.g., Hart 2006) that these protective measures can lead to such a recovery and abundance of commercial fishes in MPAs that their populations inevitably “spill” out to unprotected areas benefiting the bottom line of fishing operators. Can MPAs supply commercial fisheries with higher catch rates and thus more revenues? In this exercise, you will analyze the tradeoffs, if there are any, between the establishment of MPAs to protect coral reefs and the economy of commercial fisheries outside of the reserves. Consider the following hypothetical example somewhere in the Indo-Pacific region:

Assume, for simplicity, that there are 49 candidate MPAs arranged in a 7x7 grid pattern (Fig. 1). Each of the candidate cells are square shaped and 10 km wide. Assume that the current population levels of the primary commercial species (reef trout) in each of the 49 candidate cells is at about one half of carrying capacity due to fishing: 5,000. Carrying capacity is estimated to be 10,000 in each cell. Marine biologists project that the annual population growth of reef trout populations is about 30% until population levels reach carrying capacity after which they stay constant at or oscillate around 10,000. Immigration is projected to occur between adjacent cells based on the probabilities listed in Fig. 1 in blue. For example, 40% of the population found in an internal cell, surrounded by 8 other cells, is predicted to stay in the cell each year. Ten percent are to leave for each of the four adjacent cells that share common boundaries with the source cell, and 5% for each diagonally adjacent cell. Annual immigration rates are slightly different for cells that are on the external boundary of the grid. Assume that reef habitat is restricted to the 49 cells depicted on Fig. 1 and therefore reef trout cannot survive outside of this region.

Assuming that 25% of the estimated population in each unprotected cell can be harvested annually, would it be possible to increase total catch (in terms of number of fish caught) over a 10-year period by setting aside in Year 1 some of the 49 cells as MPAs where fishing is prohibited? To answer this question, formulate the problem as a linear integer program. For an example of how to model exponential population growth with linear, discrete time difference equations, see St. John and Tóth (2015). Once done, conduct a sensitivity analysis with respect to immigration probabilities, harvest quotas and annual population growth rates. Consider at least two other scenarios for each of these three factors. Please submit the following items:

(1) The mathematical formulation with accompanying definitions and explanations. Please make sure that you clearly define the decision and auxiliary variables, parameters, sets and any other mathematical components used in the model. Explain each function and constraint in detail **[20 points]**;
(2) The computer code that automates the formulation of the model for the 49-cell hypothetical problem on Fig. 1 **[20 points]**;
(3) The raw solution outputs for each scenario from CPLEX or whichever solver you used **[5 points]**; and
(4) An analysis of the solutions found complete with visual illustrations. Comment on the spatial structure of your MPA network using the recommendations listed in Table 1 of McLeod et al. (2009) **[20 points]**.

No hand-written submissions will be accepted for any of these components.

References:

Boaden, A. E., and M. J. Kingsford. 2015. Predators drive community structure in coral reef fish assemblages. Ecosphere 6(4):46. http://dx.doi.org/10.1890/ES14-00292.1

Hart. D.R. 2006. When do marine reserves increase fishery yield? 2006. Can. J. Fish. Aquat. Sci. 63:1445-1449

McClanahan, T. R. 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity and sea urchins. Coral Reefs 13: 231–241.

McLeod, E., Salm, R., Green, A. and Almany, J. (2009), Designing marine protected area networks to address the impacts of climate change. Frontiers in Ecology and the Environment, 7: 362–370. doi:10.1890/070211

St. John, Rachel and Sándor F. Tóth 2015. Spatially-Explicit Forest Harvest Scheduling with Difference Equations. Annals of Operations Research. 232(1): 235-257.

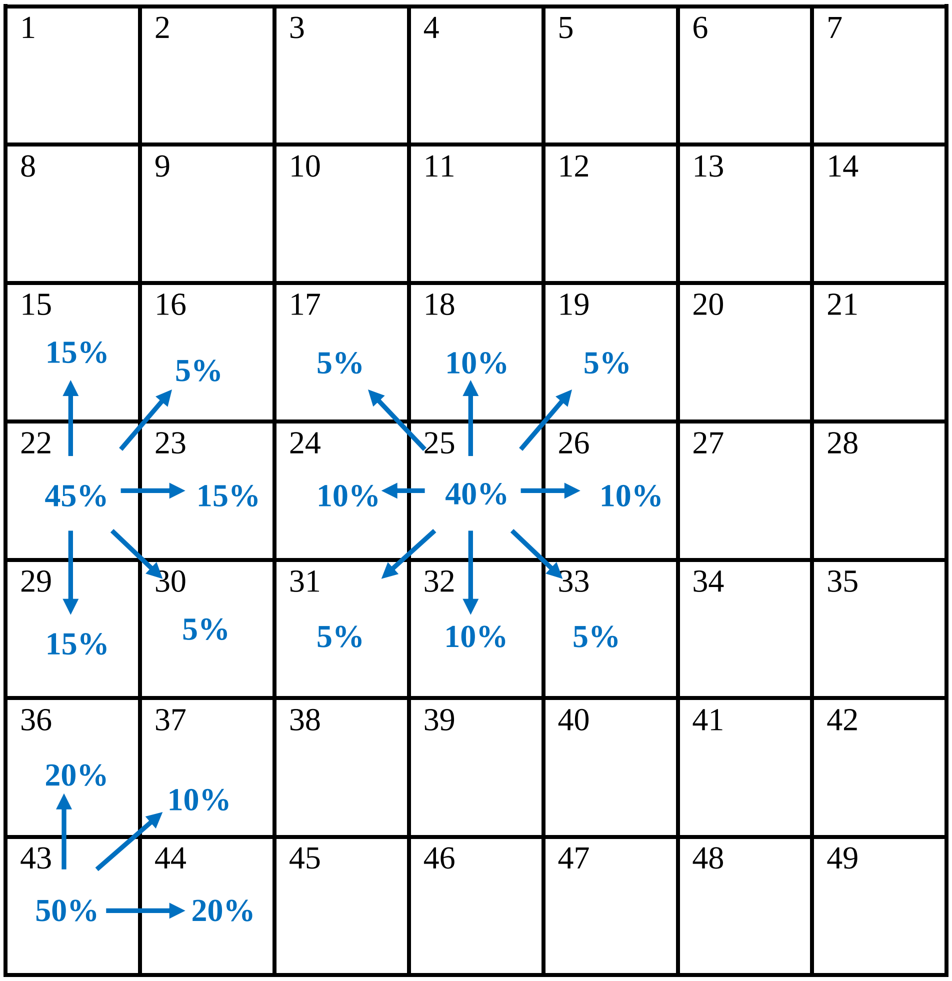


Fig. 1. Hypothetical MPA candidates