A Closed NPZ Model with Delayed Nutrient Recycling

Matt Kloosterman, Sue Ann Campbell, Francis Poulin

Department of Applied Mathematics, University of Waterloo

AMMCS 2013

Introduction

- Plankton is at the bottom of many oceanic food webs, so it is important to understand its structure and dynamics.
- We look at a simple Nutrient-Phytoplankton-Zooplankton (NPZ) model that describes the first two trophic levels of an oceanic ecosystem.
- The model conserves biomass in time.
- We assume there is a delay in nutrient recycling.
- The effect that the total nutrient in the system and the delay distribution together have on the stability and properties of equilibrium solutions is studied.

Model Equations

- The ecosystem is governed by the delay differential equations:

$$\begin{aligned}
\frac{dN(t)}{dt} &= \lambda \int_0^\infty P(t-u)\eta(u)\,du + \delta \int_0^\infty Z(t-u)\eta(u)\,du \\
&+ (1-\gamma)g \int_0^\infty Z(t-u)h(P(t-u))\eta(u)\,du - \mu P(t) f(N(t)), \\
\frac{dP(t)}{dt} &= \mu P(t) f(N(t)) - gZ(t)h(P(t)) - \lambda P(t), \\
\frac{dZ(t)}{dt} &= \gamma g Z(t) h(P(t)) - \delta Z(t).
\end{aligned}$$

- When plankton dies, it is not immediately in a form that is ready to be uptaken by phytoplankton.
- Generally, it will take some time τ to be recycled according to a distribution of possible delays: $\eta(\tau)$.
- The functional form of the phytoplankton nutrient uptake is assumed to have the following properties:

$$f(0) = 0, \qquad f'(N) \geq 0, \qquad f''(N) \leq 0, \qquad \lim_{N\to\infty} f(N) = 1.$$

- The Michaelis-Menten formulation satisfies these properties:

$$f(N) = \frac{N}{N+k}.$$

- The functional form of the zooplankton grazing on phytoplankton is often characterized by type.
- We assume it is Type II or Type III and assume the following properties.

$$h(0) = 0, \qquad h'(P) \geq 0, \qquad \lim_{P\to\infty} h(P) = 1.$$

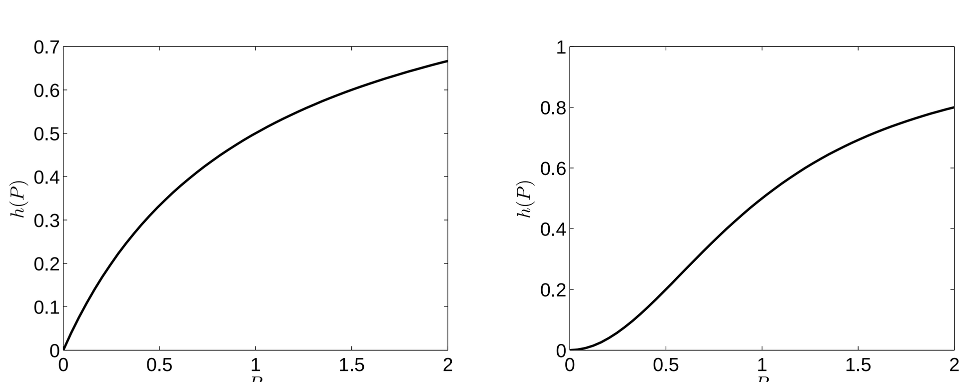

Figure 1: Graphs of Type II (left) and Type III (right) functional forms for zooplankton grazing on phytoplankton.

Conservation Law

- The following quantity is conserved in time:

$$\begin{aligned}
N_T &= N(t) + P(t) + Z(t) \\
&+ \int_0^\infty \int_{t-u}^{t} [\lambda P(v) + \delta Z(v) + (1-\gamma) g Z(v) h(P(v))]\eta(u)\,dv\,du.
\end{aligned}$$

- The constant N_T is the total biomass in the system and is important to the behaviour of the system.

Relation to an NPZD Model

- An NPZD model contains a detritus compartment, which represents dead biomass and zooplankton faecal pellets.
- By taking $\eta(u) = \alpha e^{-\alpha u}$, the system can be shown to be equivalent to the following system of ODE's.

$$\begin{aligned}
\frac{dN}{dt} &= \alpha D - \mu P f(N), \\
\frac{dP}{dt} &= \mu P f(N) - gZh(P) - \lambda P, \\
\frac{dZ}{dt} &= \gamma g Z h(P) - \delta Z, \\
\frac{dD}{dt} &= \lambda P + \delta Z + (1-\gamma) g Z h(P) - \alpha D.
\end{aligned}$$

- Hence, we are studying systems analogous to an NPZD model, but in a more general setting by considering other delay distributions.

Equilibrium Solutions

- Taking the total biomass, N_T, to be a fixed parameter, equilibrium solutions satisfy,

$$\begin{aligned}
\mu P^* f(N^*) - gZ^* h(P^*) - \lambda P^* &= 0, \\
\gamma g Z^* h(P^*) - \delta Z^* &= 0, \\
N^* + P^* + Z^* + [\lambda P^* + \delta Z^* + (1-\gamma) g Z^* h(P^*)]\tau &= N_T,
\end{aligned}$$

where τ is the mean delay.

- There are three types of equilibria:

$$E_0 = (N_T, 0, 0), \qquad E_1 = (\hat{N}, \hat{P}, 0), \qquad E_2 = (N^*, P^*, Z^*).$$

- There are two critical values of total biomass:

$$N_{T1} = f^{-1}\left(\frac{\lambda}{\mu}\right), \qquad N_{T2} = f^{-1}\left(\frac{\lambda}{\mu}\right) + (1+\lambda\tau) h^{-1}\left(\frac{\delta}{\gamma g}\right).$$

- E_1 does not exist for $N_T < N_{T1}$ and E_2 does not exist for $N_T < N_{T2}$.

Stability of Solutions without Delay

	$N_T < N_{T1}$	$N_{T1} < N_T < N_{T2}$	$N_T > N_{T2}$
E_0	Globally Stable	Unstable	Unstable
E_1	Does Not Exist	Globally Stable	Unstable
E_2	Does Not Exist	Does Not Exist	Stability depends on h and N_T.

- For a Type II response, there is a $N_{T3} > N_{T2}$ where a Hopf bifurcation occurs and the E_2 solution becomes unstable.
- For a Type III response, E_2 can be stable for any value of total biomass.

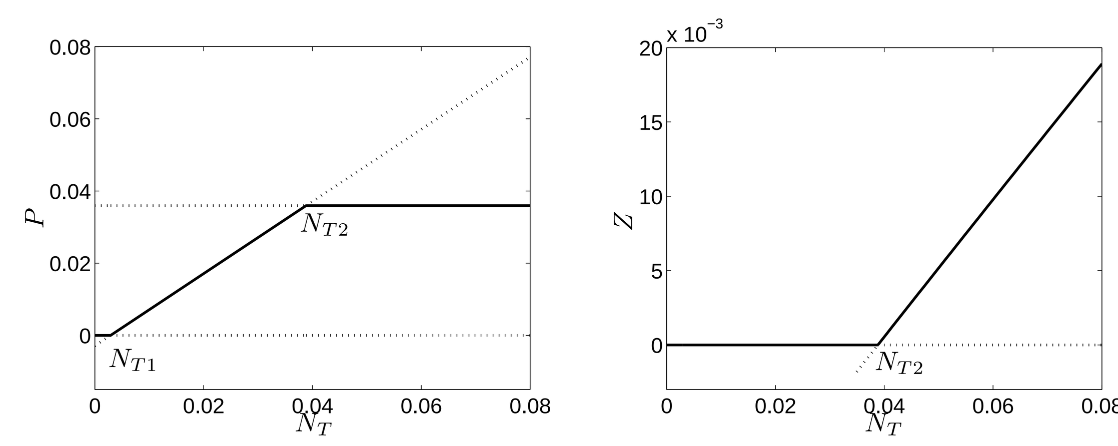

Figure 2: Equilibrium values of phytoplankton and zooplankton as a function of total nutrient. The solid lines represent stable points, while the dotted lines show unstable points.

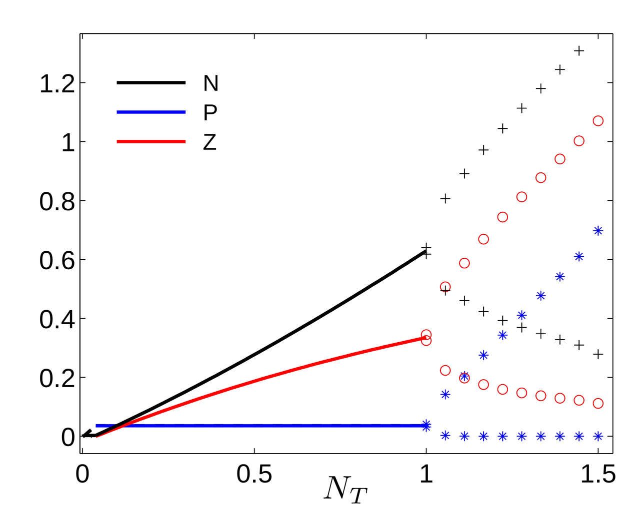

Figure 3: Stable equilibrium values against total biomass (solid lines) and minimum and maximum values of limit cycles after the Hopf bifurcation. This is for a Type II functional response.

Stability of Solutions with Delay

- We linearize the equations and compute curves in the $\tau - N_T$ plane where there is an eigenvalue with zero real part.

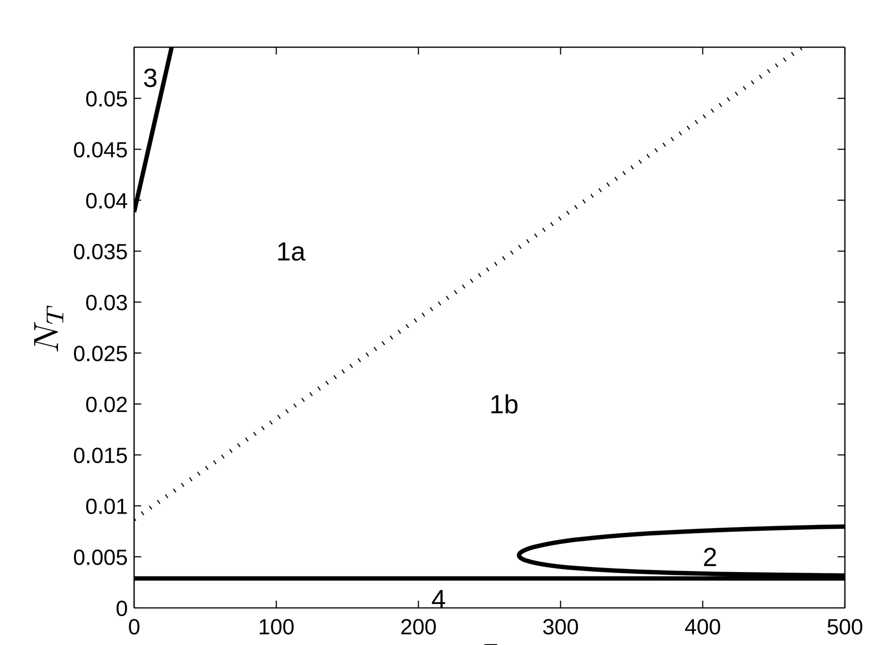

Figure 4: Regions in the $\tau - N_T$ plane that exhibit different properties for the E_1 equilibrium. Region 1a is stable regardless of delay distribution. Region 1b can be stable for some delay distributions. Region 2 is where instability occurs for a discrete delay. Region 3 is always unstable and is where E_2 exists. Region 4 is where E_1 does not exist and E_0 is stable.

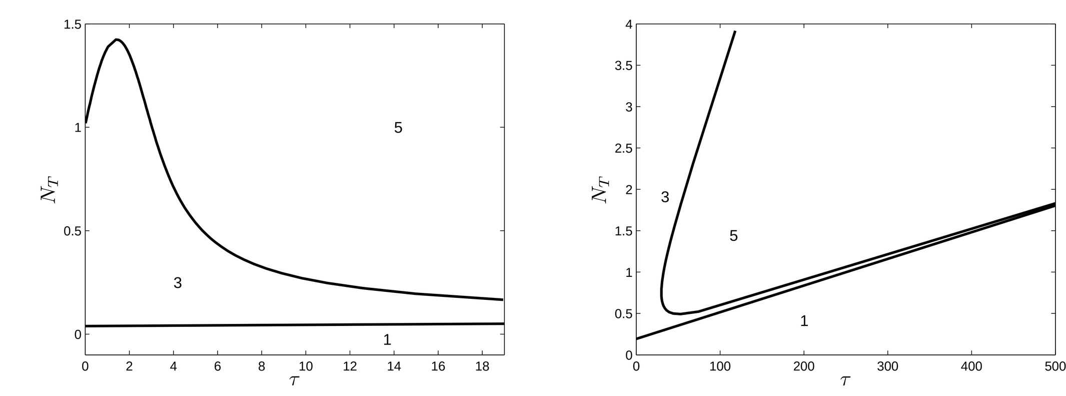

Figure 5: Regions in the $\tau - N_T$ plane that exhibit different properties for the E_2 equilibrium for a discrete delay with Type II functional response (left) and Type III response (right). Region 1 is where E_2 does not exist. Region 3 is where it exists and is stable. Region 5 is where the assurance of stability is lost.

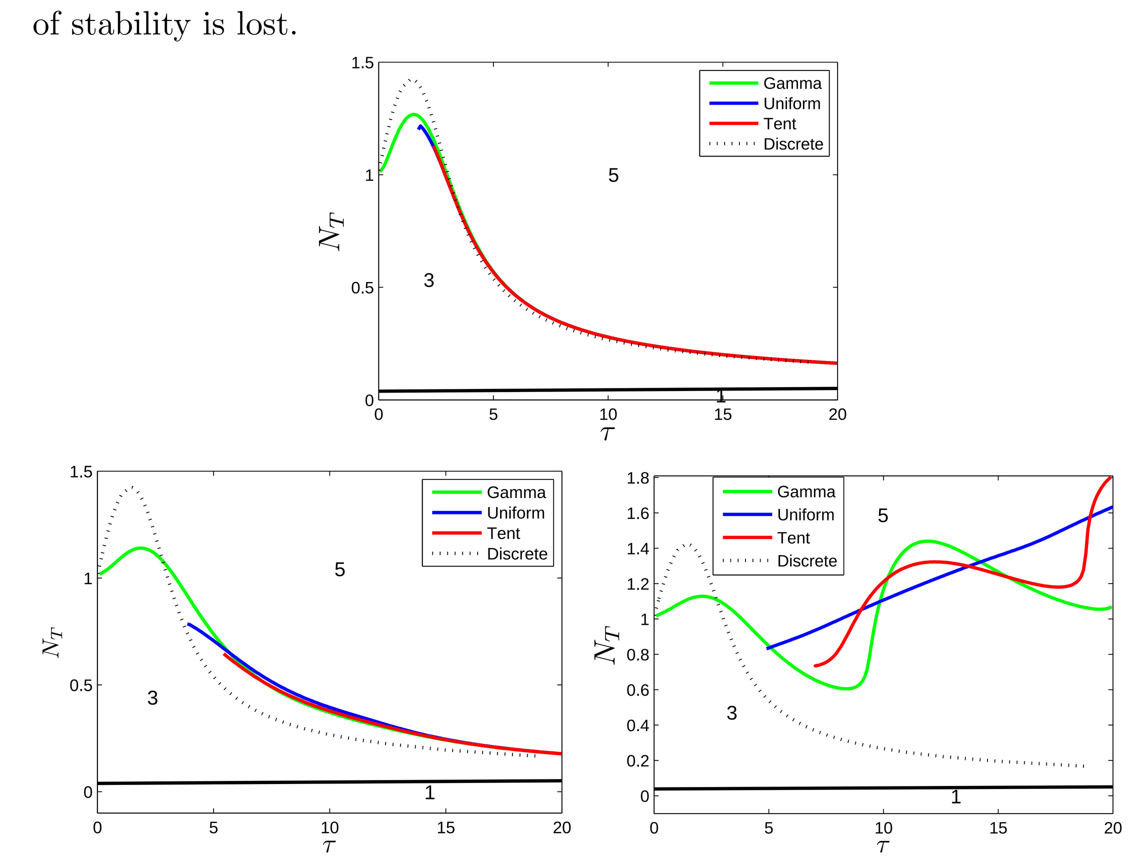

Figure 6: Stability regions for E_2 with a Type II response for different types of distributions with fixed variances. The top has variance fixed at 1 day^2, the bottom left has it fixed at 5 day^2, and the bottom right has it fixed at 8 day^2.

Simulation

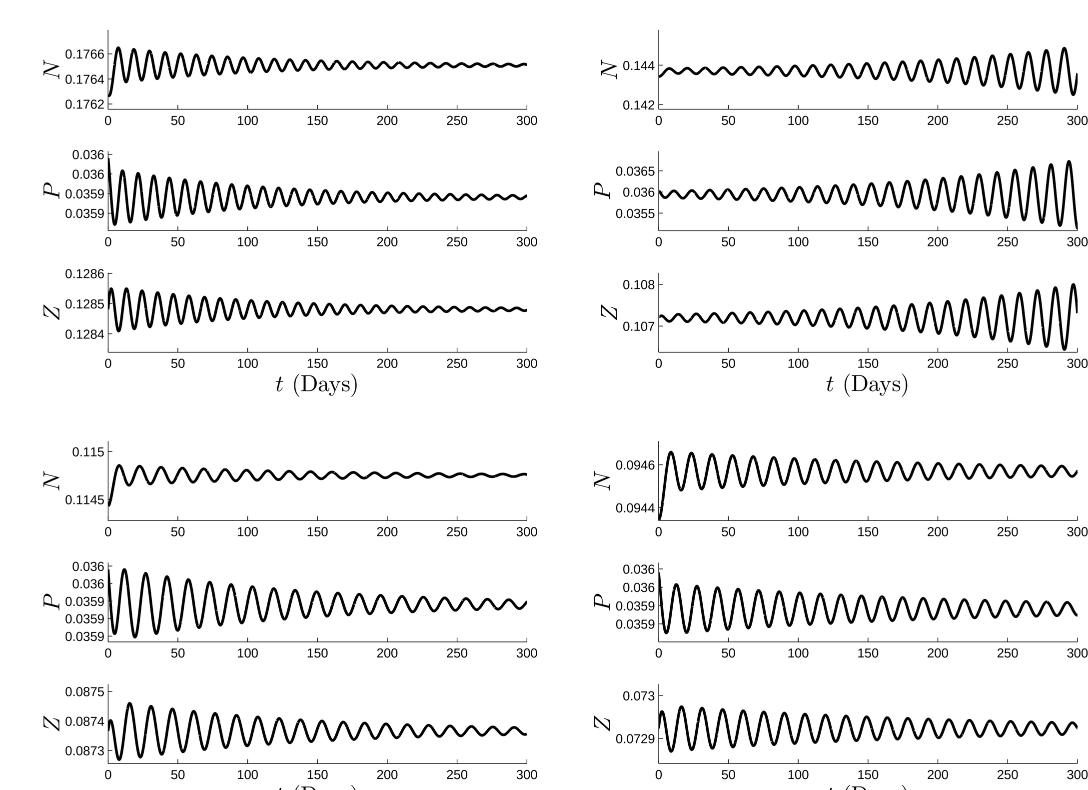

Figure 7: Simulations for the gamma distribution with shape parameter $p = 20$. The top left is for total nutrient $N_T = 0.5$ and mean delay $\tau = 5$. The top right is for $N_T = 0.5$ and $\tau = 8$. The bottom left is for $N_T = 0.5$ and $\tau = 12$. The bottom right is for $N_T = 0.35$ and $\tau = 8$.

Discussion

- There is always a zero eigenvalue in the linearized equations, corresponding to the line of equilibrium solutions.
- If all the other eigenvalues have negative real part, solutions locally approach the line of equilibrium solutions, hence stability.
- A Type III response tends to result in more stable behaviour for E_2 than a Type II response.
- A small variance leads to similar results for different distributions, while the results depend on the shape of the distribution when the variance is large.
- Simulations agree with results predicted from linear theory.
- Total biomass, N_T, plays an important part in existence of equilibrium solutions and their stability.
- Future work assumes state-dependent delay in gestation time.

Acknowledgements

The authors gratefully acknowledge financial support from the Natural Sciences and Engineering Research Council of Canada. M.K. also gratefully acknowledges financial support from the Ontario Graduate Scholarship Program.