Plankton Model with Time Delayed Nutrient Recycling

Sue Ann Campbell, Matthew Kloosterman and Francis Poulin

Department of Applied Mathematics
University of Waterloo

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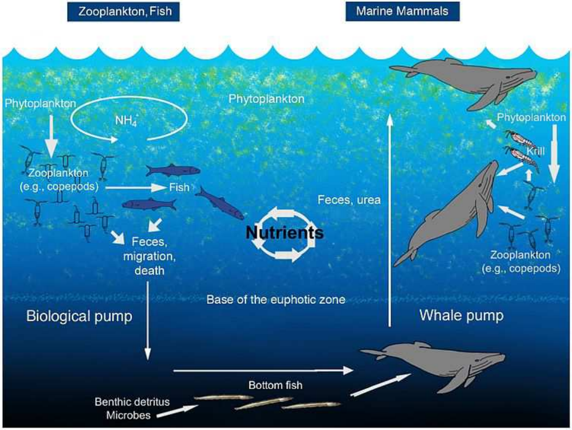
Outline

1. Introduction/Background
2. Existence of Equilibrium Points
3. Stability of Equilibrium Points
   - No Delay
   - With Delay
4. Conclusions and Implications

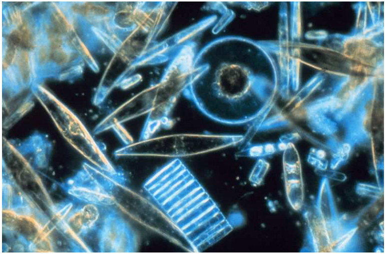
Introduction

Plankton are free floating organisms found in oceans and lakes which form the bottom of the food chain.

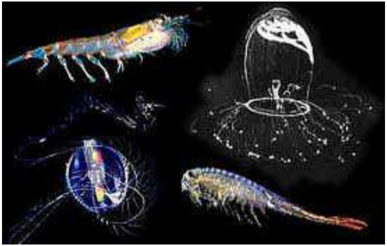


Introduction

Phytoplankton are plankton which carry out photosynthesis
examples: diatoms, golden algae, green algae and cyanobacteria



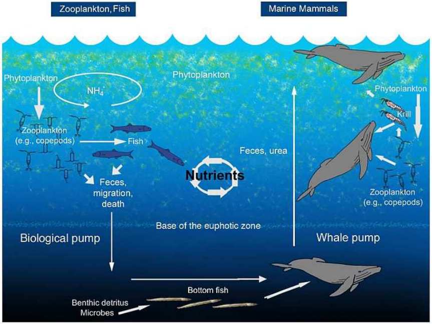
Zooplankton are plankton that feed on phytoplankton
examples: jelly fish, small crustaceans and insect larvae



Motivation

Why study plankton?

- Plankton form the bottom of the ocean food chain.



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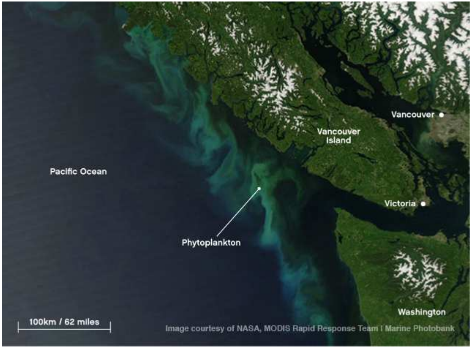
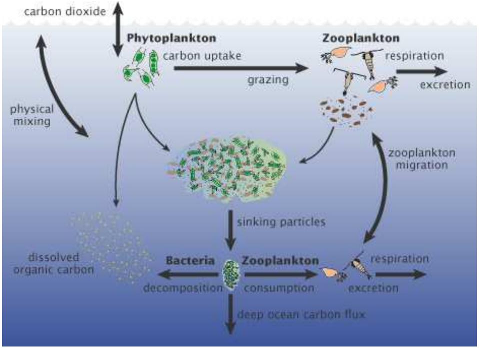
- Plankton form the bottom of the ocean food chain.
- Phytoplankton can exhibit **blooms** which can be harmful to ecosystem and humans.



Motivation

Why study plankton?

- Plankton form the bottom of the ocean food chain.
- Phytoplankton can exhibit **blooms** which can be harmful to ecosystem and humans.
- Phytoplankton are very important in the transfer of carbon dioxide from the atmosphere to the ocean.



Model

Closed model with three compartments:
dissolved nutrient - $N(t)$
phytoplankton - $P(t)$
zooplankton - $Z(t)$
(measured by amount of limiting nutrient/nitrogen)

P.J.S. Franks (2002) *J Oceanogr.* 58:379-387.

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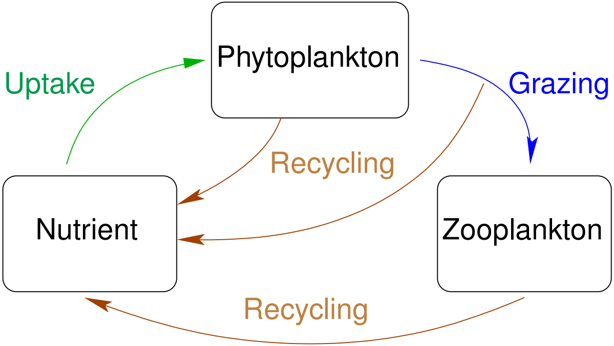

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phytoplankton nutrient uptake

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zooplankton grazing on phytoplankton

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Model Parameters

Parameter	Meaning	Units
μ	phytoplankton maximum growth rate	day^{-1}
λ	phytoplankton death rate	day^{-1}
g	zooplankton maximum grazing rate	day^{-1}
γ	zooplankton assimilation efficiency	
δ	zooplankton death rate	day^{-1}

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Functional Response

Nutrient uptake by phytoplankton: $\mu P(t) f(N(t))$

$f(0) = 0,\ f'(N) \geq 0, f''(N) \leq 0, \lim_{N \to \infty} f(N) = 1$ (Michaelis-Menten/Type II)

W.C. Gentleman & A.B. Neuheimer (2008)
J. Plankton Research 30(11) 1215-1231.

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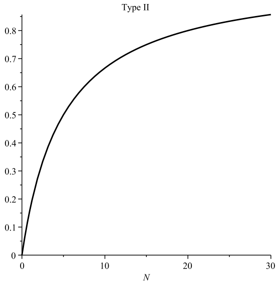

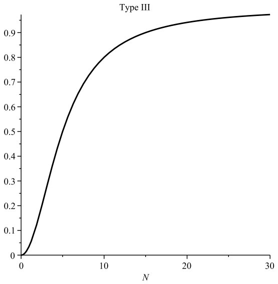

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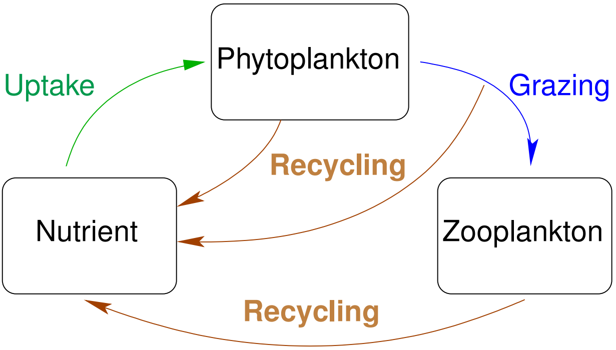

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Include distributed time delay in recycling

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N'(t) &= \int_0^\infty [\lambda P(t-u) + \delta Z(t-u) + (1-\gamma) g Z(t-u) h(P(t-u))] \eta(u)\, du \\
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where $\int_0^\infty \eta(u)\, du = 1, \quad \tau = \int_0^\infty u\, \eta(u)\, du$ (mean delay)

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Recycling time is $u \in [0, \infty)$ with probability $\eta(u)$.

Distributions

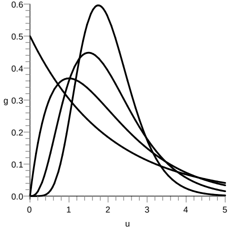
Gamma distribution: $\eta(u) = \dfrac{u^{p-1}\left(\frac{p}{\tau}\right)^{p} e^{-pu/\tau}}{\Gamma(p)}$

Uniform distribution: $\eta(u) = \begin{cases} \frac{1}{2W}, & \tau - W \leq u \leq \tau + W \\ 0, & \text{elsewhere} \end{cases},$

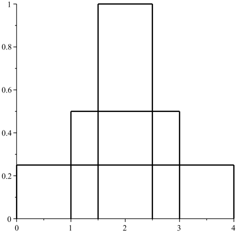
Tent distribution: $\eta(u) = \begin{cases} \frac{u+W-\tau}{W^2}, & \tau - W \leq u \leq \tau \\ \frac{-u+W+\tau}{W^2}, & \tau \leq u \leq \tau + W \\ 0, & \text{elsewhere} \end{cases}.$

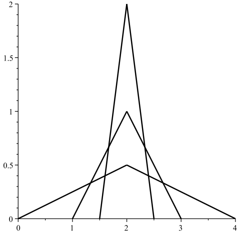
Discrete delay: $\eta(u) = \delta(u - \tau)$

Distributions ($\tau = 2$)



Gamma ($p = 1, 2, 4, 8$)





Uniform ($W = 0.5, 1, 2$) Tent ($W = 0.5, 1, 2$)

Conservation Laws

Model with no delay:

$$\begin{aligned}
N'(t) &= \lambda P(t) + \delta Z(t) + (1-\gamma) g Z(t) h(P(t)) - \mu P(t) f(N(t)) \\
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Total nutrient in system is conserved.

$$N(t) + P(t) + Z(t) = N_T \text{ (constant)}$$

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Total nutrient in system is conserved.

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

Equilibrium Points

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$$
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Must satisfy

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\begin{aligned}
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Must satisfy

$$\begin{aligned} \mu P^* f(N^*) - g Z^* h(P^*) - \lambda P^* &= 0 \\ \gamma g Z^* h(P^*) - \delta Z^* &= 0 \end{aligned}$$

and conservation law:

$$N_T = N^* + P^* + Z^* + [\lambda P^* + \delta Z^* + (1-\gamma) g Z^* h(P^*)]\tau$$

Equilibrium Points - Existence and Uniqueness

For each value of N_T there exists a unique equilibrium point of each of the following types:

- **Trivial**: $(N_T, 0, 0)$ - lies in positive orthant if $N_T > 0$

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- **Phytoplankton**: $(\hat{N}, \hat{P}, 0)$ where

$$\hat{N} = f^{-1}(\lambda/\mu), \quad \hat{P} = \frac{N_T - f^{-1}(\lambda/\mu)}{1 + \lambda\tau}$$

  lies in positive orthant if $N_T > N_{T1} = f^{-1}\left(\frac{\lambda}{\mu}\right)$

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  lies in positive orthant if $N_T > N_{T1} = f^{-1}\left(\frac{\lambda}{\mu}\right)$

- **Coexistence**: (N^*, P^*, Z^*) where

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

  lies in positive orthant if $N_T > N_{T2} = f^{-1}\left(\frac{\lambda}{\mu}\right) + (1 + \lambda\tau)h^{-1}\left(\frac{\delta}{\gamma g}\right)$

Equilibrium Points - Stability with No Delay

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Using linearization and invariance of axes can show, for fixed N_T

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$N(t) + P(t) + Z(t) = N_T$

Using linearization and invariance of axes can show, for fixed N_T

- If $0 < N_T < N_{T1}$ then $(N_T, 0, 0)$ is globally (asymptotically) stable.
- If $N_{T1} < N_T < N_{T2}$ then $(\hat{N}, \hat{P}, 0)$ is globally (asymptotically) stable, $(N_T, 0, 0)$ is unstable.
- If $N_{T2} < N_T$, then $(N_T, 0, 0)$ and $(\hat{N}, \hat{P}, 0)$ are unstable.

Stability of (N^*, P^*, Z^*) depends on form of $h(P)$.

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Using linearization and invariance of axes can show, for fixed N_T

- $h(P)$ type II: Exists N_{T3} such that.
  - If $N_{T2} < N_T < N_{T3}$ then (N^*, P^*, Z^*) is asymptotically stable.
  - When $N_{T3} = N_T$ then characteristic equation has a pair of pure imaginary roots.
  - If $N_{T3} < N_T$ then (N^*, P^*, Z^*) is unstable.
- $h(P)$ type III: Stability depends $P^* = h^{-1}(\frac{\delta}{\gamma g})$
  - If $h(P^*) \leq P^* h'(P^*)$ and $N_{T2} < N_T$ then (N^*, P^*, Z^*) asymptotically stable.
  - If $h(P^*) > P^* h'(P^*)$ then stability of (N^*, P^*, Z^*) is as for Type II.

Model Parameters

Parameter	Meaning	Value
μ	phytoplankton maximum growth rate	5.9 day^{-1}
λ	phytoplankton death rate	0.017 day^{-1}
K_N	half saturation constant for N uptake	1.0 μM N
g	zooplankton maximum grazing rate	7 day^{-1}
γ	zooplankton assimilation efficiency	0.7
δ	zooplankton death rate	0.17 day^{-1}
K_P	half saturation constant for Z grazing on P	1.0 μM N

Functional response for phytoplankton nutrient uptake: $f(N) = \frac{N}{N+K_N}$

Functional response for zooplankton grazing:

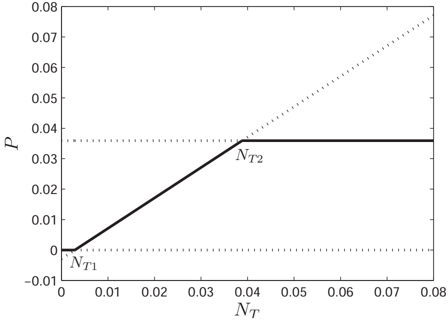
$$h(P) = \frac{P}{P+K_P} \text{ (Type II)} \qquad \text{or} \qquad h(P) = \frac{P^2}{P^2+K_P^2} \text{ (Type III)}$$

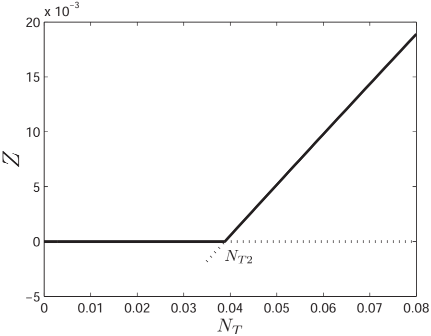
References:

F.J. Poulin & P.J.S. Franks *J. Plankton Research* 32(8) (2010) 1121-1130.

A.E. Edwards *J. Plankton Research* 23(4) (2001) 389-413.

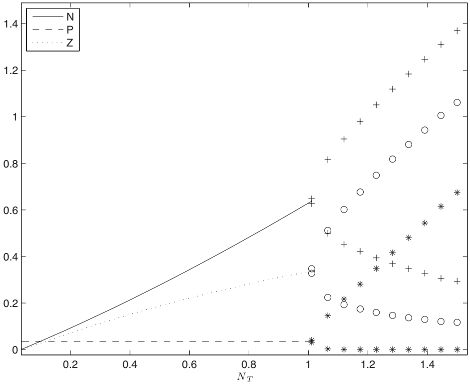
Model without Delay





Transcritical bifurcations at $N_T = N_{T1}$ and $N_T = N_{T2}$

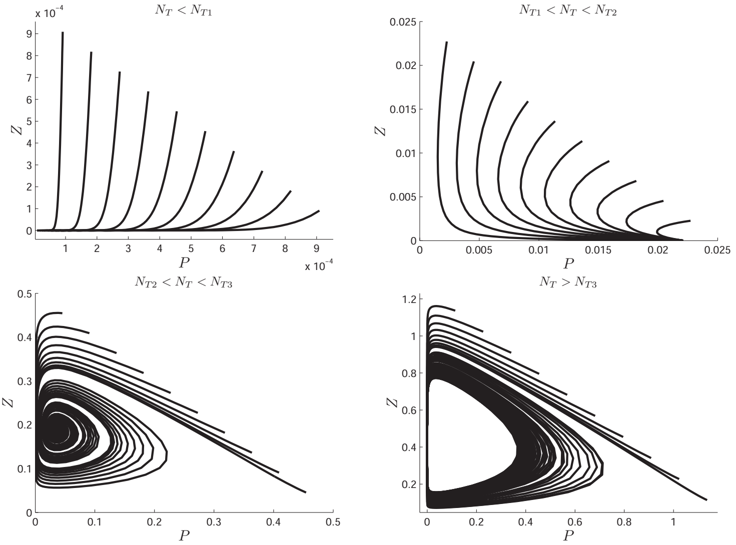
Model without Delay (Type II Functional Response)



Hopf bifurcation at $N_T = N_{T3}$

Model without Delay (Type II Functional Response)

Numerical Simulations



Model with Delay - Stability

Theorem:

- Equilibrium $(N_T, 0, 0)$ is stable/unstable if $N_T \lessgtr N_{T1} = f^{-1}\left(\frac{\lambda}{\mu}\right)$
- Equilibrium $(\hat{N}, \hat{P}, 0)$ is stable for any N_T and distribution satisfying $f^{-1}\left(\frac{\lambda}{\mu}\right) + \frac{2\lambda(1+\tau\lambda)}{\mu a} < N_T < f^{-1}\left(\frac{\lambda}{\mu}\right) + (1+\lambda\tau)h^{-1}\left(\frac{\delta}{\gamma g}\right) = N_{T2}(\tau)$
- Equilibrium $(\hat{N}, \hat{P}, 0)$ is unstable for any N_T and distribution satisfying $N_T > N_{T2}(\tau)$

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Proof. Characteristic equation of linearization about $(N_T, 0, 0)$:

$$s\,(s+\delta)\,(s-\mu f(N_T)+\lambda) = 0.$$

Characteristic equation of linearization about $(\hat{N}, \hat{P}, 0)$:

$$(s-\gamma g d+\delta)[s^2+\mu\hat{P}as+\mu\hat{P}a\lambda(1-\hat{\eta}(s))] = 0.$$

where $a = f'(\hat{N}),\ d = h(\hat{P})$. Apply Rouché's Theorem.

Model with Delay - Stability

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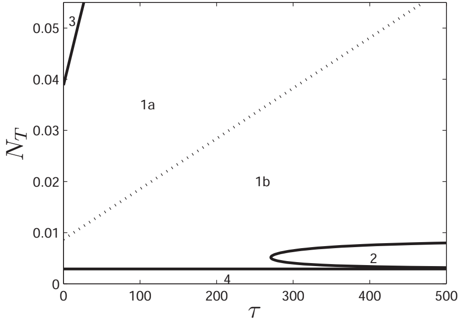

Model with Delay - Stability of $(\hat{N}, \hat{P}, 0)$

Characteristic equation for $(\hat{N}, \hat{P}, 0)$:

$$(s - \gamma g d + \delta)[s^2 + \mu \hat{P} a s + \mu \hat{P} a \lambda (1 - \hat{\eta}(s))] = 0.$$

Boundary of stability region corresponds to points in parameter space where characteristic equation has a pair of pure imaginary roots.

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Set $s = \pm i\omega$ in second factor:

$$-\omega^2 + \mu \hat{P} a i \omega + \mu \hat{P} a \lambda (1 - \hat{\eta}(i\omega))] = 0.$$

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$$-\omega^2 + \mu \hat{P} a i \omega + \mu \hat{P} a \lambda (1 - \hat{\eta}(i\omega))] = 0.$$

Parameterizing distribution, $\eta(u)$, in terms of mean delay, τ, define

$$\mathcal{C}(\omega, \tau) = \mathrm{Re}[\hat{\eta}(i\omega)], \quad \mathcal{S}(\omega, \tau) = -\mathrm{Im}[\hat{\eta}(i\omega)]$$

then boundary is determined by

$$\begin{array}{rcl} -\omega^2 + \mu \hat{P} a \lambda [1 - C(\omega, \tau)] & = & 0 \\ \omega + \lambda S(\omega, \tau) & = & 0 \end{array} \quad \Rightarrow \quad \begin{array}{rcl} \tau & = & \tau_c(\hat{P}) \\ \omega & = & \omega_c(\hat{P}) \end{array}$$

and

$$N_T = f^{-1}(\lambda/\mu) + [1 + \lambda \tau_c(\hat{P})]\hat{P}$$

Model with Delay - Stability of $(\hat{N}, \hat{P}, 0)$

Gamma distribution with $p = 1, 2$: no solution for τ_c, ω_c
$(\hat{N}, \hat{P}, 0)$ stable for any N_T and τ satisfying $N_T < N_{T2}(\tau)$

Model with Delay - Stability of $(\hat{N}, \hat{P}, 0)$

Gamma distribution with $p = 1, 2$: no solution for τ_c, ω_c
$(\hat{N}, \hat{P}, 0)$ stable for any N_T and τ satisfying $N_T < N_{T2}(\tau)$

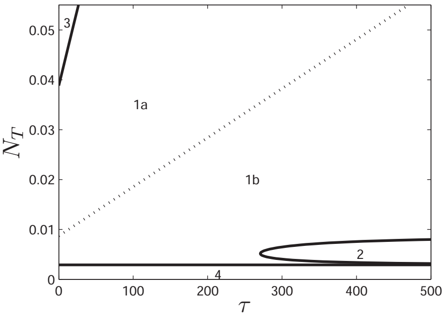
Discrete delay:
boundary of stability region is given by

$$\begin{aligned} \tau_c(\hat{P}) &= \begin{cases} \frac{1}{\omega_c}\left[\pi - \sin^{-1}\left(-\frac{\omega_c}{\lambda}\right)\right] & \text{if } 0 < \mu\hat{P}a \leq \lambda \\ \frac{1}{\omega_c}\left[2\pi + \sin^{-1}\left(-\frac{\omega_c}{\lambda}\right)\right] & \text{if } \lambda < \mu\hat{P}a < 2\lambda. \end{cases} \\ N_{Tc}(\hat{P}) &= f^{-1}\left(\frac{\lambda}{\mu}\right) + [1 + \lambda\tau_c(\hat{P})]\hat{P} \end{aligned}$$

where $\omega_c = \sqrt{2\mu\hat{P}a\lambda - (\mu\hat{P}a)^2}$.

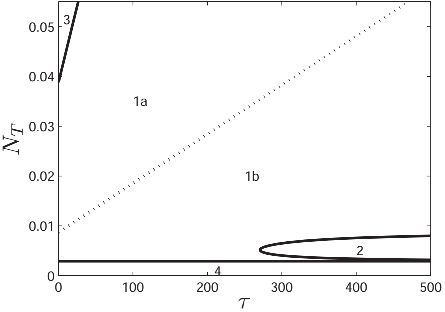
Model with Delay - Stability of $(\hat{N}, \hat{P}, 0)$

Exact region of stability



Model with Delay - Stability of $(\hat{N}, \hat{P}, 0)$

Exact region of stability



Parameter values: as before (Poulin & Franks (2010)
Other parameters: $\tau \sim 5 - 250$ days; $N_T \sim 1 - 15$ mmol N m^{-3}
(A.E. Edwards *J. Plankton Research* 23(4) (2001) 389-413).

Model with Delay - Stability of (N^*, P^*, Z^*)

Recall: $P^* = h^{-1}\left(\frac{\delta}{\gamma g}\right)$, $Z^* = \frac{\gamma P^*}{\delta}[\mu f(N^*) - \lambda]$

$$N_T = N^* + h^{-1}\left(\frac{\delta}{\gamma g}\right)\left[1 - \frac{\gamma\lambda}{\delta} + \left(\frac{\gamma}{\delta} + \tau\right)\mu f(N^*)\right]$$

Characteristic equation:

$$s^3 + a_2(N^*)s^2 + a_1(N^*)s + a_0(N^*) + [b_1(N^*)s + b_0(N^*)]\hat{\eta}(s) = 0$$

Model with Delay - Stability of (N^*, P^*, Z^*)

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$$N_T = N^* + h^{-1}\left(\frac{\delta}{\gamma g}\right)\left[1 - \frac{\gamma\lambda}{\delta} + \left(\frac{\gamma}{\delta} + \tau\right)\mu f(N^*)\right]$$

Characteristic equation:

$$s^3 + a_2(N^*)s^2 + a_1(N^*)s + a_0(N^*) + [b_1(N^*)s + b_0(N^*)]\hat{\eta}(s) = 0$$

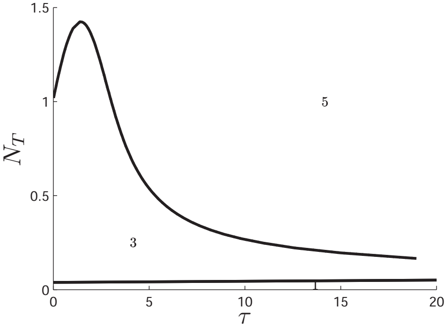
Characteristic equation with $s = \pm i\omega$ is equivalent to

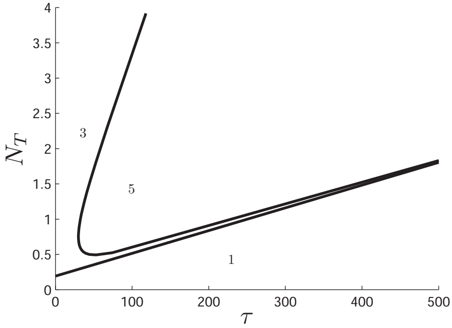
$$\mathbf{B}(\omega, N^*)\left(\begin{array}{c} \mathcal{C}(\omega,\tau) \\ \mathcal{S}(\omega,\tau) \end{array}\right) = \mathbf{y}(\omega, N^*) \quad \Rightarrow \quad \omega = \omega_c(N^*),\ \tau = \tau_c(N^*)$$

Determines boundary of region of stability in $\tau,\ N_T$ parameter space

Model with Discrete Delay - Stability of (N^*, P^*, Z^*)

$$\mathcal{C}(\omega,\tau) = \cos(\omega\tau),\ \mathcal{S}(\omega,\tau) = \sin(\omega\tau)$$

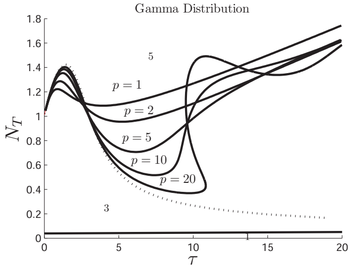


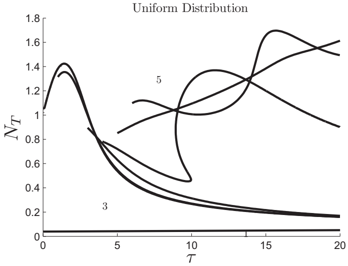


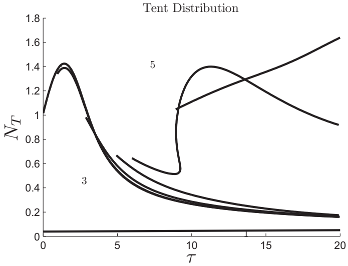
Type II - $h(P) = \dfrac{P}{P + K_P}$ Type III - $h(P) = \dfrac{P^2}{P^2 + K_P^2}$

Physical values: $\tau \sim 5 - 250$ days; $N_T \sim 1 - 15$ mmol N m^{-3}

Model with Distributed Delay - Stability of (N^*, P^*, Z^*)



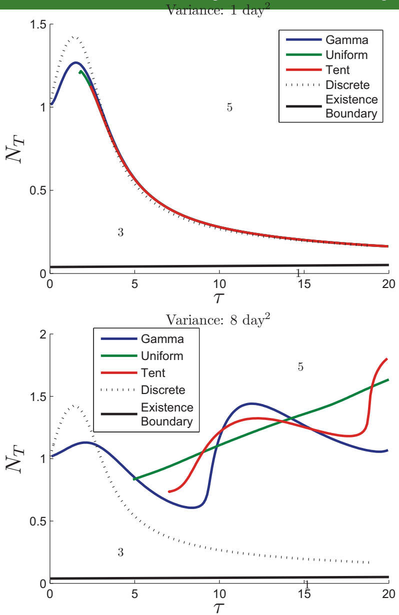




$W = 0.001, 1, 3, 4, 5, 6$

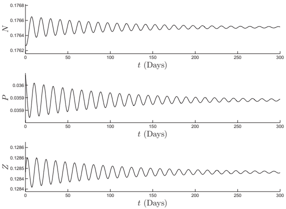
$W = .001, 1, 3, 5, 6, 7$

Model with Distributed Delay - Stability of (N^*, P^*, Z^*)

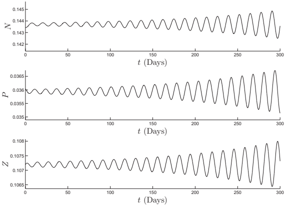


Model with Gamma Distributed Delay - Simulations

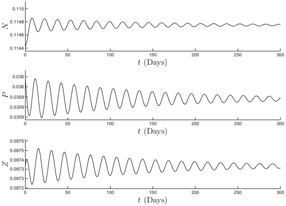
Simulations $p = 20, N_T = 0.5$



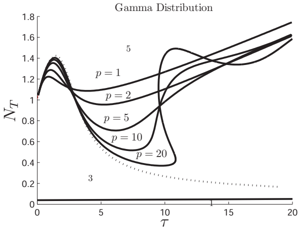
$\tau = 5$



$\tau = 8$



$\tau = 12$



Conclusions

- Characterized total nutrient needed to sustain phytoplankton in isolation and in coexistence with zooplankton ($N_{T1} < N_{T2}$).
- N_{T2} increases as time delay in recycling increases, as less biomass is available to sustain organisms.
- Type II functional response for phytoplankton grazing is "less stable" than type III in the following sense:
  - With type II coexistence equilibrium can be destabilized for sufficiently large total nutrient ($N_T > N_{T3}$), leading to oscillations
  - If $N_T < N_{T3}$ type III needs larger delay to destabilize coexistence equilibrium.
- Small delay can be stabilizing - coexistence equilibrium is stable for larger values of N_T.
- If variance in distribution of delays is small, then actual distribution not important in determining stability.

Kloosterman, Campbell & Poulin *J. Mathematical Biology* (2013).

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Matt Kloosterman, Francis Poulin

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