Memorial University of Newfoundland

Dynamics on a General Stage Structured n Parallel Food Chains

Isam Al-Darabsah and Yuan Yuan

November 4, 2013

Outline:

- Propose a general model with n parallel food chains through the stage structured maturation time delay.
- Discuss dynamical properties of the system with single patch, including the existence of equilibrium points and their local and global stabilities.
- Discuss dynamical properties of the system with multiple patches.
- Numerical simulations.

Introduction

- Plankton is the productive base of both marine and freshwater ecosystems and provides food for larger animals. *Armstrong 1999* studied a model structure with n parallel food chains, each consisting of a phytoplankton species P_i and its dedicated zooplankton predator Z_i, proposed the following system

$$
\begin{aligned}
P_i' &= P_i \left[\mu_i(N) - Z_i h_i(P_i) \right] \\
Z_i' &= Z_i \left[\gamma_i P_i h_i(P_i) - \epsilon_i \left(\sum_{j=1}^{n} Z_j \right) \right],
\end{aligned}
\tag{1}
$$

for $i = 1, \ldots, n$ and $N = T - \sum_{i=1}^{n} P_i - \sum_{i=1}^{n} Z_i$, with the growth rate $\mu_i(N)$ of P_i which is a function of nutrient concentration N, the per-phytoplankton-per-zooplankton harvest rate $h_i(P_i)$ of P_i by Z_i, predation on the zooplankton $\epsilon_i \left(\sum_{j=1}^{n} Z_j \right)$ by higher trophic levels. The constant parameter T is the nutrient supply, γ_i is the growth efficiency of Z_i.
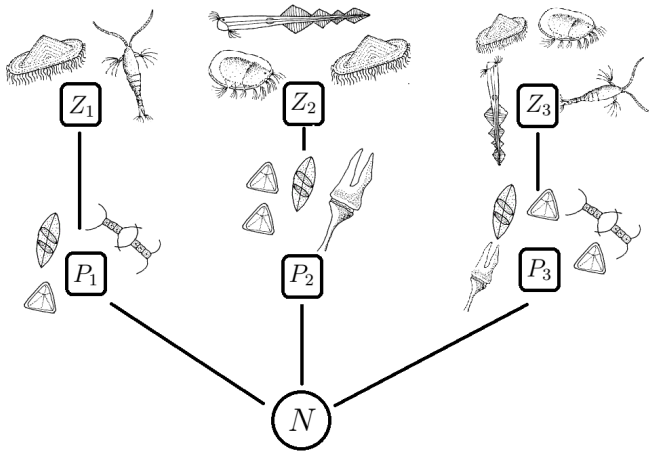
Three parallel food chains.

- *Gourley and Kuang 2004* formulated a general prey-predator model with stage structure with constant maturation time delay, because, in reality, the growth of species is a combined result of birth and death processes, which is closely linked to the resource supply.

- We adopt the idea of stage structure and modify the model (1) to the following:

$$
\begin{aligned}
\frac{dP_i}{dt} &= P_i[\mu_i(\mathcal{N}) - Z_i h_i(P_i)], \quad (2)\\
\frac{dZ_i}{dt} &= b_i e^{-d_i \tau_i} P_i(t - \tau_i) Z_i(t - \tau_i) h_i(P_i(t - \tau_i)) - Z_i \epsilon_i \left(\sum_{k=1}^{n} Z_k \right),
\end{aligned}
$$

where $\mathcal{N} = T - \sum_{k=1}^{n} \alpha_k P_k - \sum_{k=1}^{n} \beta_k Z_k$ is the nutrient concentration with the coefficients $\alpha_k, \beta_k, (k = 1, \cdots, n)$ related to the efficiency of nutrient consuming for each species. We assume that, only the adult predators are capable of preying on the prey species, so Z_i is the adult zooplankton taxon feeding on the phytoplankton P_i,

b_i denotes the adult predator's birth rate, d_i is the mortality death rate of the juvenile (through-stage death rate), τ_i is the unit of time to mature. We omit the equation of juvenile since it is decoupled. All the parameters are positive.

- From the view points in biology and analysis, we assume that all the functions $\mu_i(\mathcal{N})$, $h_i(P_i)$ and $\epsilon_i(\sum_{k=1}^{n} Z_k)$ are continuous and differentiable, and satisfy the following hypothesis for $i = 1, \ldots, n$:

  (C_1) $\mu_i(0) = 0$, $\frac{d\mu_i}{d\mathcal{N}} > 0$ when $\mathcal{N} \in [0, T]$;

  (C_2) $h_i(P_i) \geq 0$, $\frac{d(P_i h_i(P_i))}{dP_i} > 0$, $0 \leq P_i h_i(P_i) \leq M_i$, M_i is a constant;

  (C_3) $\frac{\partial \epsilon_i(Z)}{\partial Z_j} \geq 0$ for each Z_j in $Z = \sum_{k=1}^{n} Z_k$.

One Phytoplankton and One Zooplankton Model

- We start with the simplest case when $n = 1$ which is rewritten as

$$\frac{dP}{dt} = P[\mu(\mathcal{N}) - Zh(P)],$$

$$\frac{dZ}{dt} = be^{-d\tau}P(t-\tau)Z(t-\tau)h(P(t-\tau)) - Z\epsilon(Z), \quad (3)$$

with $\mathcal{N} = T - \alpha P - \beta Z$.

Let $C = C([-\tau, 0), R)$, $C^+ = C([-\tau, 0), R^+)$.

Theorem [positivity and boundedness]

Given the initial condition $P(0), Z(0) \in C^+$, then under the hypothesis $(C_1 - C_3)$, the solutions of (3) are nonnegative in $X = C \times C$. In addition, if $\epsilon(0) > 0$ then all the solutions are ultimately bounded in X.

Existence and Stability of Boundary Equilibrium Points

- It is easy to see that in the system (3), there is a trivial equilibrium point $(0,0)$ and one-species equilibrium point $(\frac{T}{\alpha}, 0) := (\mathcal{T}, 0)$.

Theorem

(i) $(0,0)$ is always an unstable saddle point;

(ii) $(\mathcal{T}, 0)$ is locally asymptotically stable if $\epsilon(0) > b\mathcal{T}h(\mathcal{T})e^{-\tau d}$ and it is unstable if $\epsilon(0) < b\mathcal{T}h(\mathcal{T})e^{-\tau d}$.

- To discuss the global attractivity of the equilibrium point $(\mathcal{T}, 0)$, we introduce the result given in *Gourley and Kuang 2004*

Lemma [*Gourley and Kuang 2004*]

If $a < b$, then the solution of the equation

$$u'(t) = au(t - \tau) - bu(t)$$

where $a, b, \tau > 0$, and $u(t) > 0$ for $-\tau \leq t \leq 0$, satisfies $\lim_{t \to \infty} u(t) = 0$.

With the hypothesis (C_1 - C_3). When $bMe^{-d\tau} < \epsilon(0)$, the solutions of (3) satisfy $P(t) \longrightarrow \mathcal{T}, Z(t) \longrightarrow 0$ as $t \longrightarrow \infty$.

- Since $Ph(P)$ is bounded by M, we can see the condition for the local stability at $(\mathcal{T}, 0)$ is included in the global stability condition.

Existence and Stability of Positive Equilibrium (P^*, Z^*)

- When a positive equilibrium point (P^*, Z^*) exists, P^*, Z^* must satisfy

$$\begin{aligned}
\mu(\mathcal{N}^*) &= Z^* h(P^*), \\
be^{-d\tau} P^* h(P^*) &= \epsilon(Z^*),
\end{aligned} \tag{4}$$

with $\mathcal{N}^* = T - \alpha P^* - \beta Z^*$.

- τ must be less than $\tau_{\max} = \frac{1}{d} \ln \left(\frac{bM}{\epsilon(0)} \right)$. The condition $\tau < \tau_{max}$ is necessary for the existence of such P^* and Z^* in (4), but is not a sufficient condition in general.
- The existence of such P^*, Z^* and the number of solutions in (4) are uncertain which depends on the choice of the functions $\mu(\mathcal{N}), h(P)$ and $\epsilon(Z)$.
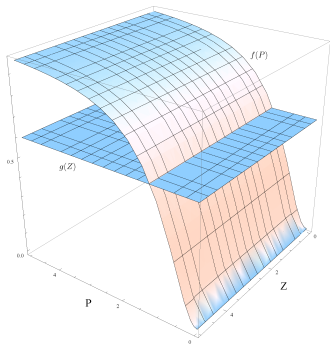
$$\epsilon(Z) = 0.15, \ h(P) = \frac{P}{P^2+1}$$
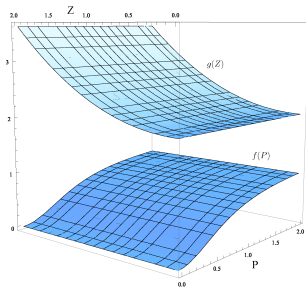
$$\epsilon(Z) = 0.5 + 0.1Z^2, \ h(P) = \frac{P}{P^2+0.5}$$

$$f(P) = Ph(P) \text{ and } g(Z) = \frac{\epsilon(Z)e^{d\tau}}{b}$$

- Let $\tilde{\tau} = \sup\{\tau \in (0, \tau_{\max}) \,|\, \text{the second equation of (4) has at least a solution}\}$.
- When $\tau < \tilde{\tau}$, we can obtain
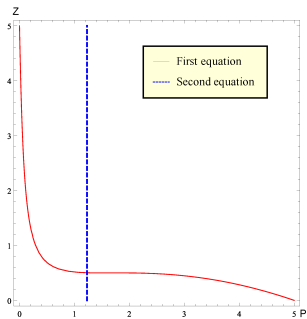
$$Z^* = \epsilon^{-1}(be^{-d\tau}P^*h(P^*)),$$

while P^* is determined by

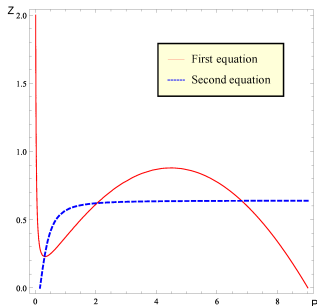$$\mu(T - \alpha P^* - \beta\epsilon^{-1}(be^{-d\tau}P^*h(P^*))) = h(P^*)\epsilon^{-1}(be^{-d\tau}P^*h(P^*)),$$

it is impossible to find an analytical solution in general.

Theorem

When $\epsilon(Z) = c$ is a constant and $bMe^{-d\tau} > c$, there exists a unique positive equilibrium point (P^*, Z^*) in (3).

a) One equilibrium point

b) Three equilibrium points

Existence of (P^*, Z^*) with $b = 0.25$, $d = 0.01$, $\alpha = \beta = 1$ and functions in the following table .

	$h(P)$	$\mu(N)$	$\epsilon(Z)$	T
Fig. a	$\frac{P}{P^2+1}$	$\frac{N}{N+10}$	0.15	5
Fig. b	$\frac{P}{P^2+0.1}$	$\frac{N}{N+15}$	$0.05 + 0.31Z$	9

- We linearize (3) at (P^*, Z^*), by setting $x = P - P^*, y = Z - Z^*$, which is,

$$\frac{dx}{dt} = -P^*(\alpha\mu_*' + Z^* h_*')x(t) - P^*(\beta\mu_*' + h_*)y(t),$$

$$\frac{dy}{dt} = -(\epsilon_* + Z^* \epsilon_*')y(t) + be^{-d\tau}Z^*(h_* + P^* h_*')x(t-\tau) + be^{-d\tau}P^* h_* y(t-\tau),$$

- The characteristic equation is

$$\Delta(\lambda, \tau) = \lambda^2 + a_1\lambda + a_2 + b_1\lambda e^{-\tau\lambda} + b_2 e^{-\tau\lambda} = 0, \qquad (5)$$

with

$$a_1 = P^*(\alpha\mu_*' + Z^* h_*') + (\epsilon_* + Z^* \epsilon_*'),$$
$$a_2 = P^*(\beta\mu_*' + Z^* h_*')(\epsilon_* + Z^* \epsilon_*'),$$
$$b_1 = -be^{-d\tau}P^* h_* < 0,$$
$$b_2 = -be^{-d\tau}(P^*)^2 h_*(\alpha\mu_*' + Z^* h_*') + be^{-d\tau}Z^* P^*(\beta\mu_*' + h_*)(h_* + P^* h_*').$$

- All the roots of $\Delta(\lambda, \tau)$ with $Re(\lambda) \geq 0$ lie in a bounded domain, *F. Wang et al. 2013.*

- When $\tau = 0$ Eq. (5) becomes

$$\Delta(\lambda, 0) = \lambda^2 + (a_1 + b_1)\lambda + (a_2 + b_2) = 0,$$

where

$$
\begin{aligned}
a_1 + b_1 &= P^*(\alpha\mu'_* + Z^*h'_*) + Z^*\epsilon'_*, \\
a_2 + b_2 &= P^*(\alpha\mu'_* + Z^*h'_*)Z^*\epsilon'_* + be^{-d\tau}P^*Z^*(\beta\mu'_* + h_*)\left.\frac{dPh}{dP}\right|_{P=P^*}.
\end{aligned}
$$

- Following the Routh-Hurwitz stability criterion we have

Proposition

At $\tau = 0$, the equilibrium point (P^*, Z^*) is locally asymptotically stable if and only if

$$h'_* > -\left(R + \frac{\mu'_*}{Z^*}\right), \qquad (\mathbf{H_0})$$

where $R = \min\left\{\frac{\epsilon'_*}{P^*}, \frac{be^{-d\tau}}{Z^*\epsilon'_*}(\beta\mu'_* + h_*)\left(\left.\frac{dPh}{dP}\right|_{P=P^*}\right)\right\}$.

- Let $\tau > 0$ and suppose $\lambda = i\omega$ $(\omega > 0)$ is a purely imaginary root of (5). Separating the real and imaginary parts, we obtain:

$$
\begin{aligned}
-\omega^2 + a_2 &= -b_1\omega \sin\omega\tau - b_2 \cos\omega\tau \\
a_1\omega &= -b_1\omega \cos\omega\tau + b_2 \sin\omega\tau.
\end{aligned} \tag{6}
$$

- Squaring and adding both equations

$$
F(\omega, \tau) = \omega^4 + q(\tau)\omega^2 + \ell(\tau) = 0,
$$

where

$$
\begin{aligned}
q(\tau) &= a_1^2 - 2a_2 - b_1^2, \\
\ell(\tau) &= a_2^2 - b_2^2.
\end{aligned}
$$

- Let $u = \omega^2$. In seek of the positive real roots in

$$
F(u, \tau) = u^2 + q(\tau)u + \ell(\tau) = 0,
$$

at first we need

$$
\Theta = q(\tau)^2 - 4\ell(\tau) = \left(a_1^2 - b_1^2\right)\left(a_1^2 - b_1^2 - 4a_2\right) + 4b_2^2 \geq 0. \quad \textbf{(H}_1\textbf{)}
$$

$F(u, \tau) = 0$

- has no positive roots when

$$\ell(\tau) = a_2^2 - b_2^2 \geq 0 \quad \& \quad q(\tau) = a_1^2 - 2a_2 - b_1^2 \geq 0 \qquad \textbf{(H_2)}$$

- has exactly one positive root if

$$\ell(\tau) = a_2^2 - b_2^2 < 0; \qquad \textbf{(H_3)}$$

or when

$$\ell(\tau) = a_2^2 - b_2^2 = 0 \quad \& \quad q(\tau) = a_1^2 - 2a_2 - b_1^2 < 0; \qquad \textbf{(H_4)}$$

- has two positive roots when

$$\ell(\tau) = a_2^2 - b_2^2 > 0 \quad \& \quad q(\tau) = a_1^2 - 2a_2 - b_1^2 < 0. \qquad \textbf{(H_5)}$$

- From (6), we have

$$
\begin{aligned}
\sin \omega(\tau)\tau &= \frac{a_1 b_2 \omega(\tau) - b_1 \omega(\tau)\left(a_2 - \omega(\tau)^2\right)}{b_1^2 \omega(\tau)^2 + b_2^2}, \\
\cos \omega(\tau)\tau &= \frac{b_2\left(\omega(\tau)^2 - a_2\right) - a_1 b_1 \omega(\tau)^2}{b_1^2 \omega(\tau)^2 + b_2^2}.
\end{aligned}
\tag{7}
$$

- Define the function $\theta(\tau) \in [0, 2\pi)$ such that $\sin \theta(\tau)$ and $\cos \theta(\tau)$ are given by (7). Following *E. Beretta, Y. Kuang 2002*, let

$$
S_n(\tau) = \tau - \frac{\theta(\tau) + 2n\pi}{\omega(\tau)}, \quad n \in \mathbb{N}, \quad \tau \in (0, \tau_{\max}),
\tag{8}
$$

then $i\omega(\tau^*)$ is a root in (5) if and only if τ^* is a zero of a function S_n for some $n \in \mathbb{N}$.

Proposition

If $\tau^* \in (0, \tau_{\max})$ is a positive root of S_n given in (8) for some $n \in \mathbb{N}$, then a pair of purely imaginary roots $i\omega(\tau^*)$ of (5) exist which crosses the imaginary axis from left to right if $S_n'(\tau^*) > 0$ and crosses the imaginary axis from right to left if $S_n'(\tau^*) < 0$, and

$$\text{Sign}\left\{\left.\frac{d\text{Re}\,(\lambda)}{d\tau}\right|_{\lambda = i\omega(\tau^*)}\right\} = \text{Sign}\left\{\left.\frac{dS_n(\tau)}{d\tau}\right|_{\tau = \tau^*}\right\}.$$

- When the positive equilibrium point (P^*, Z^*) exists, the stability of (P^*, Z^*) is given in the following:

Theorem

(i) When $(\mathbf{H_0})$, $(\mathbf{H_1})$ and $(\mathbf{H_2})$ hold, (P^*, Z^*) is locally asymptotically stable for any feasible time delay τ;

(ii) When $(\mathbf{H_0})$, $(\mathbf{H_1})$ with either $(\mathbf{H_3})$, $(\mathbf{H_4})$ or $(\mathbf{H_5})$ hold, (P^*, Z^*) is locally asymptotically stable for small time delay τ, say $\tau < \min\{\tau_n^*\}$;

(iii) When $(\mathbf{H_0})$ does not hold and $(\mathbf{H_1})$ with either $(\mathbf{H_3})$, $(\mathbf{H_4})$ or $(\mathbf{H_5})$ hold, (P^*, Z^*) is unstable for small time delay τ. If there exists a τ_n^*, such that $S_n'(\tau_n^*) < 0$, (P^*, Z^*) can become stable with $\tau > \tau_n^*$.

n Parallel Phytoplankton Zooplankton Patches

- Rewrite the system (2) as

$$
\begin{aligned}
P_1' &= P_1\left[\mu_1(\mathcal{N}) - Z_1 h_1(P_1)\right] \\
Z_1' &= b_1 e^{-d_1\tau_1} P_1(t-\tau_1) Z_1(t-\tau_1) h_1(P_1(t-\tau_1)) - Z_1\epsilon_1\left(\sum_{k=1}^{n} Z_k\right) \\
&\ \ \vdots \\
P_n' &= P_n[\mu_n(\mathcal{N}) - Z_n h_n(P_n)] \\
Z_n' &= b_n e^{-d_n\tau_n} P_n(t-\tau_n) Z_n(t-\tau_n) h_n(P_n(t-\tau_n)) - Z_n\epsilon_n\left(\sum_{k=1}^{n} Z_k\right).
\end{aligned}
\tag{9}
$$

Theorem [positivity and boundedness]

Given the initial condition $P_i(0), Z_i(0) \in C^+$, for all $i = 1, \ldots, n$, then under the hypothesis (C_1 - C_3), the solutions of (9) are nonnegative in $\mathcal{X} = C^n \times C^n$. In addition, if each $\epsilon_i(0) > 0$, then the solutions are ultimately bounded in $\mathcal{X}$.

- System (9) has a trivial equilibrium point $E_0 = \underbrace{(0, 0, \ldots, 0, 0)}_{2n}$ and

  infinite number of predator-free equilibrium points with the form

  $$\tilde{E} = \underbrace{\left(\alpha_1 \tilde{P}_1, 0, \alpha_2 \tilde{P}_2, 0, \ldots, \alpha_n \tilde{P}_n, 0 \right)}_{2n}$$

  such that $\sum_{k=1}^{n} \alpha_k \tilde{P}_k = T$, and it is also possible to have the co-existed positive equilibrium point $(P_1^*, Z_1^*, P_2^*, Z_2^* \ldots, P_n^*, Z_n^*)$ under the hypothesis $(C_1 - C_3)$ and certain conditions.

- To study the stability of any equilibrium point $(x_1, y_1, x_2, y_2, \ldots, x_n, y_n)$, we need to know the general form of the characteristic equation, which is,

  $$\Delta(\lambda) = \det\left(\lambda I - J^0 - \sum_{k=1}^{n} J^k e^{-\lambda \tau_k} \right) = 0$$

  where $J^0 = (a_{ij})$ and $J^k = \left(c_{ij}^k \right)$ are $2n \times 2n$ matrices with

$$a_{ij} = \begin{cases} -x_{\frac{i+1}{2}}\left[\alpha_{\frac{i+1}{2}}\mu'_{\frac{i+1}{2}}\left(\bar{\mathcal{N}}\right) + y_{\frac{i+1}{2}}h'_{\frac{i+1}{2}}\left(x_{\frac{i+1}{2}}\right)\right] & , & i \text{ odd}, j = i; \\ -x_{\frac{i+1}{2}}\left[\beta_{\frac{i+1}{2}}\mu'_{\frac{i+1}{2}}\left(\bar{\mathcal{N}}\right) + h_{\frac{i+1}{2}}\left(x_{\frac{i+1}{2}}\right)\right] & , & i \text{ odd}, \ j = i+1; \\ -\alpha_{\frac{i+1}{2}}x_{\frac{i+1}{2}}\mu'_{\frac{i+1}{2}}\left(\bar{\mathcal{N}}\right) & , & i,j \text{ odd}, i \neq j; \\ -\beta_{\frac{j}{2}}x_{\frac{i+1}{2}}\mu'_{\frac{i+1}{2}}\left(\bar{\mathcal{N}}\right) & , & i \text{ odd}, j \text{ even } j \neq i+1; \\ -\epsilon_{\frac{i}{2}}\left(\sum\limits_{k=1}^{n}y_k\right) - y_{\frac{i}{2}}\epsilon'_{\frac{i}{2}}\left(\sum\limits_{k=1}^{n}y_k\right) & , & i \text{ even}, j = i; \\ -y_{\frac{i}{2}}\epsilon'_{\frac{i}{2}}\left(\sum\limits_{k=1}^{n}y_k\right) & , & i,j \text{ even}, i \neq j; \\ 0 & , & i \text{ even}, j \text{ odd}, \end{cases}$$

where $\bar{\mathcal{N}} = T - \sum\limits_{k=1}^{n}\alpha_k x_k - \sum\limits_{k=1}^{n}\beta_k y_k$ and

$$c_{ij}^k = \begin{cases} 0 & , & i \text{ odd, any } j; \text{ or } i \text{ even}, j \neq 2k, j \neq 2k-1; \\ b_k e^{-d_k\tau_k}y_k\left(h_k(x_k) + x_k h'_k(x_k)\right) & , & i = 2k, \ j = 2k-1; \\ b_k e^{-d_k\tau_k}x_k h_k(x_k) & , & i = 2k, \ j = 2k; \end{cases}$$

Theorem

(i) E_0 is always an unstable saddle point;

(ii) All $\tilde{E}$ are locally asymptotically stable if
$b_k \tilde{P}_k h_k(\tilde{P}_k) e^{-d_k \tau_k} < \epsilon_k(0)$ for all $k = 1, 2, \ldots, n$ and they are
unstable if $b_k \tilde{P}_k h_k(\tilde{P}_k) e^{-d_k \tau_k} > \epsilon_k(0)$ for some $k = 1, 2, \ldots, n$.

- Although we cannot show the global attractivity of each equilibrium
  point $\tilde{E}$, we have the following "group" property.

Theorem

When $b_i M_i e^{-d_i \tau_i} < \epsilon_i(0)$ for all $i = 1, \ldots, n$, the solutions of (9) satisfy
$\sum\limits_{i=1}^{n} \alpha_i P_i(t) \longrightarrow T$ and $Z_i(t) \longrightarrow 0$ for all $i = 1, \ldots, n$ as $t \longrightarrow \infty$.

- If $E^* = (P_1^*, Z_1^*, P_2^*, Z_2^*, \ldots, P_n^*, Z_n^*)$ exists then τ_i must be less than

$$\tau_{\max} = \min\left\{ \frac{1}{d_i} \ln\left(\frac{b_i M_i}{\epsilon_i(0)}\right) : i = 1, 2, \ldots, n \right\}.$$

- The condition $\tau < \tau_{\max}$ is necessary for the existence of such E^* in (9).
- The existence and the number of positive equilibrium point E^* are uncertain which depend on the choices of the functions, parameters and time delay, but with some particular choice of the functions, we maybe able to obtain some better result.

Case I: When the total predation terms from higher trophic level from higher trophic level $\epsilon_i \left(\sum\limits_{k=1}^{n} Z_k \right)$ are constants for all $i = 1, 2, \ldots, n$.

Theorem

When $\epsilon_i \left(\sum\limits_{k=1}^{n} Z_k \right) = c_i$ are constants and $b_i M_i e^{-d_i \tau_i} > c_i$ for $i = 1, 2, \ldots, n$, there exists a unique positive equilibrium point E^* in (9).

Case II: When the n parallel food chains are symmetric, that is, the growth functions for all taxa at the same trophic level have the same functional forms and the same parameter values, the maturation delay for each predator is the same, then the system has at least a positive equilibrium point E^* with $P_1^* = P_2^* = \ldots = P_n^* := P^*$, and $Z_1^* = Z_2^* = \ldots = Z_n^* := Z^*$ and the characteristic equation $\Delta(\lambda) = 0$ has the form,

$$
\begin{vmatrix}
\lambda + l_1 + l_2\alpha & l_3 + l_2\beta & l_2\alpha & l_2\beta & l_2\alpha & l_2\beta & \cdots \\
m_1 e^{-\tau\lambda} & \lambda + m_2 e^{-\tau\lambda} + m_3 + m_4 & 0 & m_4 & 0 & m_4 & \cdots \\
l_2\alpha & l_2\beta & \lambda + l_1 + l_2\alpha & l_3 + l_2\beta & l_2\alpha & l_2\beta & \cdots \\
0 & m_4 & m_1 e^{-\tau\lambda} & \lambda + m_2 e^{-\tau\lambda} + m_3 + m_4 & 0 & m_4 & \cdots \\
l_2\alpha & l_2\beta & l_2\alpha & l_2\beta & \lambda + l_1 + l_2\alpha & l_3 + l_2\beta & \cdots \\
0 & m_4 & 0 & m_4 & m_1 e^{-\tau\lambda} & \lambda + m_2 e^{-\tau\lambda} + m_3 + m_4 & \cdots \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \ddots
\end{vmatrix} = 0,
$$

which is equal to

$$
\Delta(\lambda) = \det\left(A_1 A_2^{n-1}\right) = 0,
$$

where

$$A_1 = \begin{pmatrix} \lambda + l_1 + n\alpha l_2 & l_3 + n l_2 \beta \\ m_1 e^{-\tau\lambda} & \lambda + m_3 + n\beta m_4 + m_2 e^{-\tau\lambda} \end{pmatrix}$$

and

$$A_2 = \begin{pmatrix} \lambda + l_1 & l_3 \\ m_1 e^{-\tau\lambda} & \lambda + m_3 + m_2 e^{-\tau\lambda} \end{pmatrix},$$

with

$$\begin{aligned}
l_1 &= P^* Z^* h'_*, \quad l_2 = P^* \mu'_*, \quad l_3 = P^* h_*, \\
m_1 &= -be^{-d\tau} Z^*(h_* + P^* h'_*), \quad m_2 = -be^{-d\tau} l_3, \quad m_3 = \epsilon_*, \quad m_4 = Z^* \epsilon'_*.
\end{aligned}$$

- Comparing with the result in *Armstrong 1999*, without the maturation delay, the effect from A_2 does not affect the stability of the system if the predator functional response is stabilizing.

- With the delay in the maturation time, the system becomes much more involved, we can expect the system to exhibit rich dynamics, especially when the system owns some symmetry.

- We leave the theoretical analysis for future research, and give some numerical simulations.

Numerical Simulations

Example

$n = 1$. We take the functions and the parameters in system (3) as,

$$\mu(\mathcal{N}) = \frac{\mathcal{N}}{15 + \mathcal{N}}, \; h(P) = \frac{7}{P+1}, \; \epsilon(Z) = 0.05 + 0.8Z$$
$$d = 0.13, \; b = 0.05, \; T = 7, \; \alpha = 0.9, \; \beta = 0.4.$$

- $\tau_{max} = 14.968$ and $\tilde{\tau} \approx 9.248$.
- At $\tau = 0$, the positive equilibrium is $E_1 = (0.393, 0.061)$. By checking the condition ($\mathbf{H_0}$), we know E_1 is unstable.
- The curve of $S_1(\tau) = 0$ has one root $\tau^* = 4.347$ and is decreasing from positive to negative.
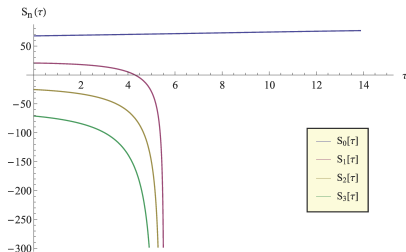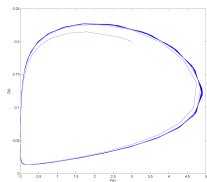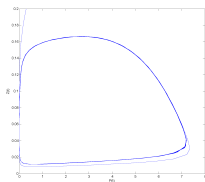
$\tau = 0.1$ $\tau = 2.9$
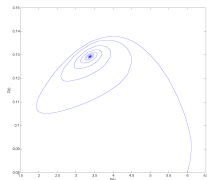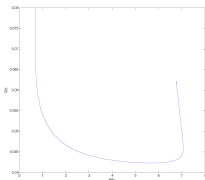
$\tau = 4.5$ $\tau = 8.6$

Phase portrait with different values of time delay τ.

- Biologically, when the maturation process is short, the concentration of phytoplankton and zooplankton are oscillated regularly; when this process is a little long, all the species move to a certain level with constant concentration; but if the maturation time is too long, the zooplankton cannot survive without enough prey–phytoplankton. Therefore, the maturation time control the dynamical behavior of the system.

Example

$n = 1$. Let

$$\mu(\mathcal{N}) = \frac{\mathcal{N}}{15 + \mathcal{N}}, \ h(P) = \frac{P}{P^2 + 0.1}, \ \epsilon(Z) = 0.05 + 0.31Z$$
$$\alpha = \beta = 1, \ d = 0.01, \ b = 0.25, \ T = 9$$

in system (3)

- $\tau_{\max} = 160.944$ and $\tilde{\tau} \approx 160.819$.

- There are three positive equilibrium points $E_1 = (P_1^*, Z_1^*)$, $E_2 = (P_2^*, Z_2^*)$ and $E_3 = (P_3^*, Z_3^*)$ with $P_1^* < P_2^* < P_3^*$ for $\tau \in (0, \hat{\tau})$ with $\hat{\tau} = 38.836$, two (P_1^*, Z_1^*), (P_2^*, Z_2^*) at $\tau = \hat{\tau}$ and one (P^*, Z^*) for $\tau \in (\hat{\tau}, \tilde{\tau})$.
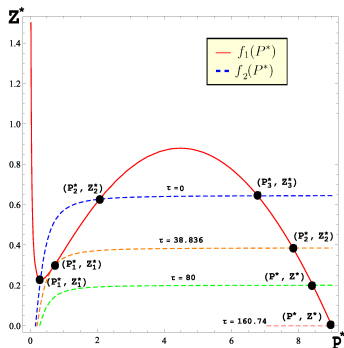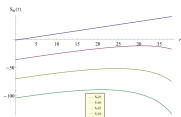
at P_1^*
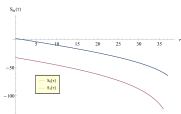
at P_3^*

- When τ is small, E_1 is stable and E_3 is unstable, while E_2 is a saddle point.
- With the increasing of τ, E_1 loses the stability at $\tau^* = 1.826$ and a stable limit cycle is bifurcated, E_3 gains the stability at τ^*.
- Since E_2 is a saddle point, there exists a "basin boundary" which divides the phase plane into two parts with different dynamics in each part.
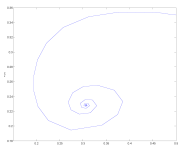
$\tau = 0.2,\ E_1$
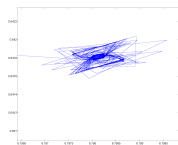
$\tau = 0.2,\ E_3$
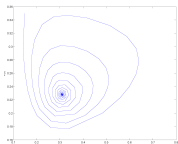
$\tau = 1.5,\ E_1$
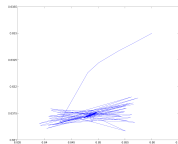
$\tau = 1.5,\ E_3$
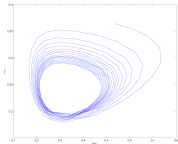
$\tau = 2.1,\ E_1$
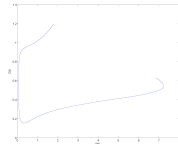
$\tau = 2.1,\ E_3$

Example

$n = 3$. We choose all the functional responses and the parameters in each species are the **same** as,

$$\mu_1(\mathcal{N}) = \mu_2(\mathcal{N}) = \mu_3(\mathcal{N}) = \frac{\mathcal{N}}{10 + \mathcal{N}}, \ h_1(P) = h_2(P) = h_3(P) = \frac{P}{P^2 + 1},$$

$$\epsilon_1(Z) = \epsilon_2(Z) = \epsilon_3(Z) = 0.15, \ d_1 = d_2 = d_3 = 0.01, \ b_1 = b_2 = b_3 = 0.25,$$

$$T = 7, \ \alpha_1 = \alpha_2 = \alpha_3 = 0.8, \ \beta_1 = \beta_2 = \beta_3 = 0.5,$$

in the system (2).

- $\tau_{\max} = 51.083$ and $\tilde{\tau} = 28.122$.
- The condition $b_i M_i e^{-d_i \tau_i} > \epsilon(Z)$ for $i = 1, 2, 3$ is satisfied for small value of delay $\tau_1 = \tau_2 = \tau_3 := \tau$, thus there exists a unique positive equilibrium point.

- Since all the functional responses are the same, it is expected that all the species will be synchronized, i.e., with different initial condition, after a transaction period, each phytoplankton and each zooplankton approach to the same level by group
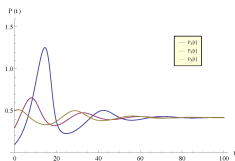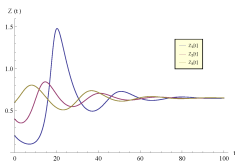
Time series $P_i(t)$, $(i = 1, 2, 3)$. Time series $Z_i(t)$, $(i = 1, 2, 3)$.

$\tau = 0.8$, $P_1(0) = 0.1$, $Z_1(0) = 0.2$, $P_2(0) = 0.3$, $Z_2(0) = 0.4$, $P_3(0) = 0.5$ and $Z_3(0) = 0.6$.

- With the increasing of the maturation time, the steady state loses the stability and the system becomes oscillatory.
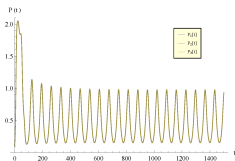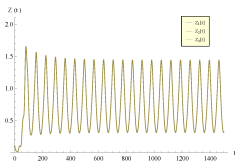
Time series $P_i(t)$, $(i = 1, 2, 3)$. Time series $Z_i(t)$, $(i = 1, 2, 3)$.

$\tau = 20$, $P_1(0) = Z_1(0) = P_2(0) = Z_2(0) = P_3(0) = Z_3(0) = 0.1$.

Example

$n = 3$. We take different functional responses and some parameters, such as,

$$\mu_1(\mathcal{N}) = \frac{\mathcal{N}}{15 + \mathcal{N}}, \mu_2(\mathcal{N}) = \mu_3(\mathcal{N}) = \frac{4\mathcal{N}}{10 + \mathcal{N}}, \; h_1(P) = \frac{P}{P^2 + 0.1},$$

$$h_2(P) = h_3(P) = \frac{1}{P + 1}, \; \epsilon_1(Z) = 0.05 + 0.31Z, \; \epsilon_2(Z) = \epsilon_3(Z) = 0.15,$$

$$T = 9, d_1 = d_2 = d_3 = 0.01, \; b_1 = b_2 = b_3 = 0.25,$$

$$\alpha_1 = \alpha_2 = \alpha_3 = 1, \; \beta_1 = \beta_2 = \beta_3 = 1.$$

in the system (2).

- With the same initial condition, when the maturation time is very small, a doubly periodic solution exists, implying a parallel condition given in (H_5) may be satisfied for the feasible value of τ.
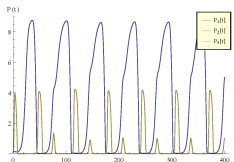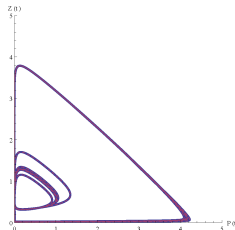
Time series $P_i(t)$, $(i = 1, 2, 3)$.
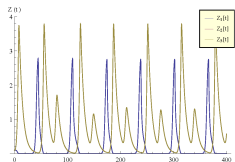
Time series $Z_i(t)$, $(i = 1, 2, 3)$.
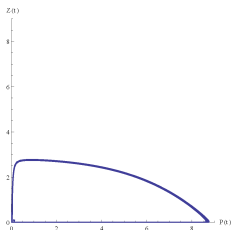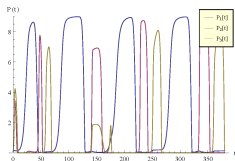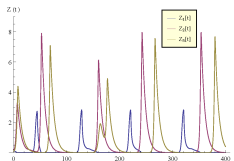
$P_1(t)$ and $Z_1(t)$.

$P_2(t)$, $Z_2(t)$ and $P_3(t)$, $Z_3(t)$.

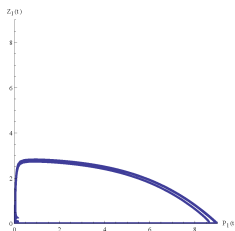$\tau = 0.1$, $P_1(0) = P_2(0) = P_3(0) = Z_1(0) = Z_2(0) = Z_3(0) = 0.1$.

- When we change the initial condition a little bit, then the doubly periodic orbit is disappeared, although a periodic solution still exists and the second and the third patches have almost the same behavior,
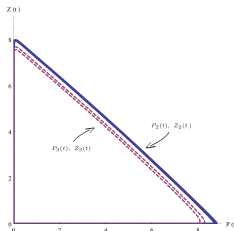

Time series $P_i(t)$, $(i = 1, 2, 3)$.

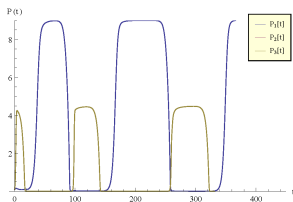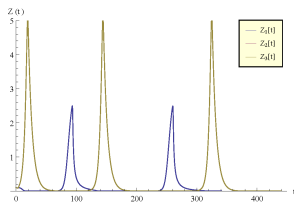Time series $Z_i(t)$, $(i = 1, 2, 3)$.

$P_1(t)$ and $Z_1(t)$.

$P_2(t)$, $Z_2(t)$ and $P_3(t)$, $Z_3(t)$.

$\tau = 0.1$, $P_1(0) = Z_1(0) = 0.1, P_2(0) = 1$, $Z_2(0) = 0.2$, $P_3(0) = Z_3(0) = 0.1$.

- The dynamical behavior is sensitive to the initial condition.
- Is it possible to have chaotic motion and/or does this due to the partial symmetry of the system since we choose two of the three patches have same response?
- As the maturation time is relative large, even with the same initial condition, the double periods disappeared.

Time series $P_i(t)$, $(i = 1, 2, 3)$. Time series $Z_i(t)$, $(i = 1, 2, 3)$.

$\tau = 2.6,\ P_1(0) = P_2(0) = P_3(0) = Z_1(0) = Z_2(0) = Z_3(0) = 0.1.$

Conclusion

- We propose a general model with n parallel food chains through the stage structured maturation time delay. We have carried out mathematical analysis to discuss the existence of the steady states and their stabilities.

- When $n = 1$, we provide the explicit conditions for the local stability of the one-species or the co-existed species equilibrium points and the global stability of the predator-free equilibrium point. Further, we show that the time delay can, not only destroy the existence, but also destabilize the positive equilibrium even it exists.

- We extend some of the results for the single patch to the model with $n > 1$ multiple parallel patches.

- We illustrate some numerical simulation to complement the analytical results and to show the rich dynamics in the system.

Future Work:

Study of:

- a prey-predator system with a single state variable G represents the total biomass of zooplankton grazers.
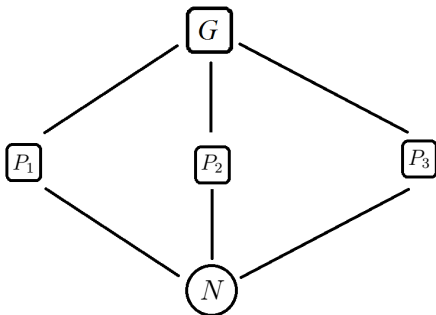
- adding a stage structure on prey, in which the immature prey and the mature prey are preyed by predator.

Thank You