Chapter 4

Mathematical modeling on cascading migration in a tri-trophic food chain system

4.1 Introduction

Diel vertical migration (DVM) is a natural phenomena of movements of some living organisms living in the oceans and in lakes. Basically, this is one type of migration. The organisms generally follow the DVM movement pattern to avoid predation. There are literally hundreds of well documented articles on DVM of many organisms (we just cite the excellent review by Williamson et al. (2011), Cohen and Forward (2009) and a book by Ringelberg (2010)). The

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migrations that occur at one trophic level can affect the vertical migration of
the next trophic level, and so on throughout the food web. Bollens et al. (2011)
first time coined the term 'cascading migration' instead of coupled vertical
migrations in multi-trophic food chain and explained the phenomena with its
implications in various scenarios.

It has been observed that zooplankton showed downward vertical migration
in the daytime in the presence of predators those release kairomone or chemi-
cal cues to avoid predation (DeMeester et al., 1999; Dodson, 1988b; Gliwicz,
1986; Lampert, 1989, 1993; Lass and Spaak, 2003; Loose and Dawidowicz,
1994; Neill, 1990; Stich and Lampert, 1981), however chemical cues are not
the only predator cues that trigger zooplankton DVM (see, (Bollens et al.,
1994)). The strength of migration of zooplankton increased with increases in
concentration of fish or fish-exudates (Loose and Dawidowicz, 1994; Cayelan
et al., 2011). Avoidance of predators such as visually orienting planktivorous
fish and carnivorous invertebrates is the most important factor which regu-
lates DVM in zooplankton (Lampert, 1989; Bollens and Frost, 1989a,b; Hays,
2003). Apart from kairomone or chemical cues, there are several reasons for
DVM of zooplankton such as light intensity, solar radiation, temperature, dis-
solved oxygen, UV radiation, food availability, etc. (Williamson et al., 2011).
However, predation pressure is the most important factor which drives the
mesozooplankton migrations, which in turn cascade into effects on dinoflag-
ellate migrations (Bollens et al., 2011). Many species of dinoflagellates have
also been observed to undertake vertical migration, residing at the surface dur-
ing the day and residing at depth at night (Eppley et al., 1968; Blasco, 1978;
As far our knowledge concern, mathematical models on a tri-trophic food chain in the presence of cascading migration are not yet explored. However, we believe that this study may open many windows in population dynamics and demand in-depth research in this aspect. In this work, we use the model of Hastings and Powell (Hastings and Powell, 1991) as a starting point to construct a model that includes cascading migration. They observed chaos in a tri-trophic food chain model. The objective of this paper is to observe the role of cascading migration in a well-known model. There are ample of studies on this model and observed that the chaos thus observed may be controlled by reasonable biological phenomena. The biological phenomena like imposition
of a population floor (Ruxton, 1994, 1996), addition of refugia (Eisenberg and Maszle, 1995), omnivory (McCann and Hastings, 1997), intraspecific density dependence (Xu and Li, 2002), toxic inhibition (Chattopadhyay and Sarkar, 2003), spatial effect (Maionchi et al., 2005), density-dependent death of middle predator, (Bandyopadhyay et al., 2008), disease in prey and body size of intermediate predator (Das et al., 2009), migration in middle predator (Chowdhury et al., 2010) can control the chaos. Chowdhury et al. (2010) showed that increase in the migration ratio of middle predator switches the system from chaos to stable through limit cycles. But, we theoretically observe that cascading migration can control the chaos thus predicted in Hastings-Powell model. The system becomes stable when the value of the migration ratio of top-predator remains below a threshold value, but the system shows periodic oscillation, period-doubling, higher periodic oscillations respectively, and ultimately, it goes to chaos with the increase in the migration ratio.
4.2 Model Development

First, we consider the tri-trophic food chain model proposed by Hastings and Powell (1991)

\[
\begin{align*}
\frac{dX}{dt} &= RX\left(1 - \frac{X}{K}\right) - \frac{A_1XY}{B_1+X} \\
\frac{dY}{dt} &= \frac{C_1A_1XY}{B_1+X} - \frac{A_2YZ}{B_2+Y} - D_1Y, \quad (4.1) \\
\frac{dZ}{dt} &= \frac{C_2A_2YZ}{B_2+Y} - D_2Z.
\end{align*}
\]

Where \( X, Y \) and \( Z \) be the concentration of prey, middle predator and top predator population respectively. The other parameter values are interpreted as follows: \( R \) is the intrinsic growth rate of prey population; \( K \) is the carrying capacity of prey population; \( A_1 \) is the maximum predation rate of middle predator on prey; \( A_2 \) is the maximum predation rate of top predator on middle predator; \( B_1 \) is the half-saturation constant of middle predator; \( B_2 \) is the half-saturation constant of top predator; \( C_1 \) is the conversion efficiency of middle predator; \( C_2 \) is the conversion efficiency of top predator; \( D_1 \) is the natural mortality rate of middle predator, and \( D_2 \) is the natural mortality rate of top predator.

Now, we introduce the concept of cascading migration in the system (4.1). According to light penetration into the water, we split the whole pelagic water mass into two layers: upper layer and lower layer. The water column above the secchi depth is referred to as upper layer, where light is available at daytime; whereas, bellow the secchi depth, the water column, where light availability is very low (almost unavailable) during day hours, is refereed to as lower layer. Population densities within each layer are considered to be homogeneous. We
assume that phytoplankton (P) grows logistically in the upper layer. Top predator (fish or other vertebrate) migrates vertically downward and upward frequently for food. Whenever the fish enters into the upper layer, the middle predator (zooplankton) migrates vertically downward to avoid fish predation at day time and it enters into the surface water again at night to graze phytoplankton. Similarly, motile phytoplankton (Dinoflagellate) migrates vertically downward to avoid predation by herbivore and mesozooplankton at night by entering into the lower layer from upper layer. It also returns to the surface water at daytime for nutrient uptake and photosynthesis. Therefore, motile phytoplankton shows reverse DVM along with the DVM of zooplankton and the migration pattern of zooplankton is also reverse to the migration pattern of fish. Such phenomenon is well known as cascading migration in a tri-trophic food chain.

Our model deals with two major components of the aquatic system. The first one describes the phytoplankton, zooplankton and fish growth and their interactions in each layer, whereas the second component describes the dispersal (through migration) of fish, zooplankton and motile phytoplankton between upper and lower layers. We assume that the migration rate of top predator between two layers is very high and corresponding cascading migrations in zooplankton and phytoplankton are also high. As a result, the change in concentrations of fish, zooplankton and phytoplankton due to cascading migration are much higher compared to the change in concentration due to birth, death and the interactions with prey and predator. Therefore, two different time scales have been considered here: the fast one corresponds to migration, and
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the comparatively slow one is for birth, death and predator-prey interactions.

Let, $X_1$, $Y_1$ and $Z_1$ be the concentrations of prey (phytoplankton), middle predator (zooplankton) and top predator (fish) in upper layer respectively and $X_2$, $Y_2$ and $Z_2$ be the concentrations of prey, middle predator and the top predator in the lower layer respectively. Here we have considered that the migration of top predator is constant whereas, the migrations of prey and middle predator are assumed to be predator dependent only. Middle predator migrates into the upper layer when top predator density is large in the lower layer and enter into the lower layer leaving the upper layer when the presence of top predator is very high in the upper layer. Whereas, the prey population (motile phytoplankton) migrates into the lower layer when the density of middle predator in surface water is high and return to surface water when the density of middle predator in the lower layer is very high. We also assume that the predation rate of middle predator remains same in both layers, whereas the predation rate of top predator varies for different layer depending on the light availability as most of the top predator (fish) shows visually orienting predation.

The coupled system of equations can be written as follows:
\[
\begin{align*}
\frac{dX_1}{dt} &= (F_2 Y_2 X_2 - F_1 Y_1 X_1) + \epsilon \left[ RX_1 \left(1 - \frac{X_1}{K_1}\right) - \frac{A_1 X_1 Y_1}{B_1 + X_1}\right], \\
\frac{dX_2}{dt} &= (F_1 Y_1 X_1 - F_2 Y_2 X_2) + \epsilon \left[ -\frac{A_1 X_1 Y_1}{B_1 + X_1} - DX_2\right], \\
\frac{dY_1}{dt} &= (K_2 Z_2 Y_2 - K_1 Z_1 Y_1) + \epsilon \left[ \frac{A_1 X_1 Y_1}{B_1 + X_1} - \frac{A_2 Y_2 Z_2}{B_2 + Y_2} - D_1 Y_1\right], \\
\frac{dY_2}{dt} &= (K_1 Z_1 Y_1 - K_2 Z_2 Y_2) + \epsilon \left[ \frac{A_1 X_1 Y_1}{B_1 + X_1} - \frac{A_2 Y_2 Z_2}{B_2 + Y_2} - D_1 Y_2\right], \\
\frac{dZ_1}{dt} &= (M_2 Z_2 - M_1 Z_1) + \epsilon \left[ \frac{A_2 Y_2 Z_2}{B_2 + Y_2} - D_2 Z_1\right], \\
\frac{dZ_2}{dt} &= (M_1 Z_1 - M_2 Z_2) + \epsilon \left[ \frac{A_2 Y_2 Z_2}{B_2 + Y_2} - D_2 Z_2\right].
\end{align*}
\]

Where, \(F_1, F_2\) are the vertically downward and upward migration rates of prey population respectively; \(K_1, K_2\) are the vertically downward and upward migration rates of middle predators respectively and \(M_1, M_2\) are the downward and upward migration rates of top predator respectively. \(A_2, \bar{A}_2\) are the predation rate of top predators in upper layer, and lower layer respectively. \(\epsilon\) is a small dimensionless parameter meaning that biotic processes are assumed to be slow \((0 < \epsilon \ll 1)\). Here, \(T\) is the fast time scale and \(\epsilon T\) is the slow time scale.

Now, introducing dimensionless variables \(X_1 = \frac{X_1}{K_1}, X_2 = \frac{X_2}{K_1}, Y_1 = \frac{Y_1}{Y_1}, Y_2 = \frac{Y_2}{Y_1}, Z_1 = \frac{Z_1}{C_1 K}, Z_2 = \frac{Z_2}{C_2 K}\) and \(\tau = RT\) we obtain the following dimensionless system

\[
\begin{align*}
\frac{d\bar{x}_1}{d\tau} &= (f_2 \bar{y}_2 \bar{x}_2 - f_1 \bar{y}_1 \bar{x}_1) + \epsilon \left[ \bar{x}_1 (1 - \bar{x}_1) - \frac{\bar{a}_1 \bar{y}_1}{1 + \bar{b}_1 \bar{x}_1}\right], \\
\frac{d\bar{x}_2}{d\tau} &= (f_1 \bar{y}_1 \bar{x}_1 - f_2 \bar{y}_2 \bar{x}_2) + \epsilon \left[ -\frac{\bar{a}_1 \bar{y}_1}{1 + \bar{b}_1 \bar{x}_2} - d\bar{x}_2\right], \\
\frac{d\bar{y}_1}{d\tau} &= (k_2 \bar{z}_2 \bar{y}_2 - k_1 \bar{z}_1 \bar{y}_1) + \epsilon \left[ \frac{\bar{a}_1 \bar{y}_1}{1 + \bar{b}_1 \bar{x}_1} - \frac{\bar{a}_2 \bar{y}_2 \bar{z}_2}{1 + \bar{b}_2 \bar{y}_2} - d\bar{y}_1\right], \\
\frac{d\bar{y}_2}{d\tau} &= (k_1 \bar{z}_1 \bar{y}_1 - k_2 \bar{z}_2 \bar{y}_2) + \epsilon \left[ \frac{\bar{a}_1 \bar{y}_1}{1 + \bar{b}_1 \bar{x}_2} - \frac{\bar{a}_2 \bar{y}_2 \bar{z}_2}{1 + \bar{b}_2 \bar{y}_2} - d\bar{y}_2\right], \\
\frac{d\bar{z}_1}{d\tau} &= (m_2 \bar{z}_2 - m_1 \bar{z}_1) + \epsilon \left[ \frac{\bar{a}_1 \bar{y}_1}{1 + \bar{b}_1 \bar{y}_1} - d\bar{z}_1\right], \\
\frac{d\bar{z}_2}{d\tau} &= (m_1 \bar{z}_1 - m_2 \bar{z}_2) + \epsilon \left[ \frac{\bar{a}_2 \bar{y}_2 \bar{z}_2}{1 + \bar{b}_2 \bar{y}_2} - d\bar{z}_2\right].
\end{align*}
\]
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The system has to be analyzed with the initial conditions \( x_1(0) = x_{10} > 0 \), \( x_2(0) = x_{20} > 0 \), \( y_1(0) = y_{10} > 0 \), \( y_2(0) = y_{20} > 0 \), \( z_1(0) = z_{10} > 0 \), and \( z_2(0) = z_{20} > 0 \).

Where, the dimensionless parameters are \( f_1 = \frac{F_1 C K}{R} \), \( f_2 = \frac{F_2 C K}{R} \), \( k_1 = \frac{K_1 C_1 C_2 K}{R} \), \( k_2 = \frac{K_2 C_1 C_2 K}{R} \), \( m_1 = \frac{M_1}{R} \), \( m_2 = \frac{M_2}{R} \), \( a_1 = \frac{A_1 C_1 K}{R B_1} \), \( a_2 = \frac{A_2 C_1 C_2 K}{R B_2} \), \( b_2 = \frac{C_2 K}{B_2} \), \( d = \frac{D}{R} \), \( d_1 = \frac{D_1}{R} \) and \( d_2 = \frac{D_2}{R} \).

Now, we perform the perturbation technique to aggregate variables corresponding to the asymptotically stable fast equilibrium point, and obtain a global (or aggregated) model easier to handle (in slow time scale), which approximates the initial one (Auger and Benoit, 1993; Auger and Poggiale, 1996; Auger and Bravo de la Parra, 2000; Auger et al., 2000).

4.3 Aggregation of the model

As we see, the system (4.3) is mainly driven by the migration part, the demographic one is being only a small perturbation. We are now interested in the fast dynamics, and the corresponding fast model is obtained by neglecting the slow part i.e. taking \( \epsilon = 0 \),
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\[
\begin{align*}
\frac{dx_1}{dt} & = (f_2y_2x_2 - f_1y_1x_1), \\
\frac{dx_2}{dt} & = (f_1y_1x_1 - f_2y_2x_2), \\
\frac{dy_1}{dt} & = (k_2z_2y_2 - k_1z_1y_1), \\
\frac{dy_2}{dt} & = (k_1z_1y_1 - k_2z_2y_2), \\
\frac{dz_1}{dt} & = (m_2z_2 - m_1z_1), \\
\frac{dz_2}{dt} & = (m_1z_1 - m_2z_2).
\end{align*}
\] (4.4)

Let us denote \( x_1 + x_2 = x \), \( y_1 + y_2 = y \) and \( z_1 + z_2 = z \), which are the total population densities. These are the constants of motion of the system (4.4).

The fast equilibrium point is the solution of the following system of equations:

\[
\begin{align*}
f_1y_1x_1 & = f_2y_2x_2, \\
x_1 + x_2 & = x, \\
k_2z_2y_2 & = k_1z_1y_1, \\
y_1 + y_2 & = y, \\
m_1z_1 & = m_2z_2, \\
z_1 + z_2 & = z.
\end{align*}
\] (4.5)

which is equivalent to
\[ x_1 = \frac{kx}{k^m+k} , \]
\[ x_2 = \frac{fx}{k^m+k} , \]
\[ y_1 = \frac{my}{k^m+k} , \]
\[ y_2 = \frac{k^m x}{k^m+k} , \]
\[ z_1 = \frac{z}{k^m+k} , \]
\[ z_2 = \frac{z}{k^m+k} . \]

where \( f = \frac{f_x}{f_z} \), \( k = \frac{k_1}{k_2} \) and \( m = \frac{m_1}{m_2} \) are the migration ratio of prey, middle predator and top predator respectively.

Now,

\[ \frac{dz_1}{dt} = f_2 y_2 x_2 - f_1 y_1 x_1 , \]
\[ = f_2 y_2 (x - x_1) - f_1 y_1 x_1 , \]
\[ = f_2 y_2 x - (f_2 y_2 + f_1 y_1) x_1 . \]

Therefore, \( g_1(x_1) = -(f_2 y_2 + f_1 y_1) < 0 \). Similarly, \( g_2(y_1) = - (k_2 z_2 + k_1 z_1) < 0 \) and \( g_3(z_1) = -(m_1 + m_2) < 0 \). Therefore, the fast equilibrium is always asymptotically stable. By aggregating the variables corresponding to the same population, the following global model at slow time scale is obtained:

\[ \frac{dx}{dt} = x_1 \frac{1}{1+\gamma_1^1 x_1} - \frac{a_1 (1+\beta_1^1 x_1) x_1}{(1+\gamma_1^1 x_1)(1+\delta_1^1 x_1)} , \]
\[ \frac{dy}{dt} = \frac{a_2 (1+\beta_2^2 y_2) y_2}{(1+\gamma_2^1 y_2)(1+\delta_2^1 y_2)} - \frac{a_3 (1+\beta_3^3 y_3) y_3}{(1+\gamma_3^1 y_3)(1+\delta_3^1 y_3)} - d_1 y , \]
\[ \frac{dz}{dt} = \frac{a_4 (1+\beta_4^4 z_4) z_4}{(1+\gamma_4^1 z_4)(1+\delta_4^1 z_4)} - d_2 z , \]

where \( r = \frac{k^m+k}{k^m+k} \), \( \tilde{K} = \frac{(m+k)(k-d m)}{k^2} \), \( \alpha_1 = \frac{a_1 km (m+k)(1+f)}{(m+k)(m+k)^2} \), \( \beta_1 = \frac{b_1 f (m+k)}{(m+k)(1+f)} \),
\( \gamma_1 = \frac{b_1^2 (m+k)}{(m+k)^2} \), \( \delta_1 = \frac{b_1 f m}{(m+k)} \), \( \alpha_2 = \frac{m (a_1 + \alpha_1 k)}{(1+m)(m+k)} \), \( \beta_2 = \frac{b_2 k (a_1 + \alpha_1 k)}{(m+k)(a_2 + \alpha_2 k)} \), \( \gamma_2 = \frac{b_2 m}{(m+k)} \).
\[ \delta_2 = \frac{b_2}{(m+k)} \] and \[ t = \tau e \] (slow time scale).

Now, we are in a position to state the following theorem corresponding to the boundedness of the aggregated system.

**Theorem 4.1** All the solution of (4.8) which originate in \( \mathbb{R}^3_+ \) are confined in the region

\[ B = \{(x, y, z) \in \mathbb{R}^3_+ : x + y + z = \frac{L}{\mu} + e \forall e > 0 \}. \]

**Proof:** Let us define a function

\[ W = x + y + z. \]  \hspace{1cm} (4.9)

The time derivative of the Equation (4.9) along with the solution of (4.8) is

\[ \frac{dW}{dt} = \frac{dx}{dt} + \frac{dy}{dt} + \frac{dz}{dt} = r(1 - \frac{z}{K}) - d_1 y - d_2 z \]

\[ \Rightarrow \frac{dW}{dt} + \mu W = r x (1 + \frac{\mu}{r} - \frac{z}{K}) - (d_1 - \mu) y - (d_2 - \mu) z \leq \frac{(r+\mu)^2 K}{4r} = L \text{ (say)}, \]

where \( \mu \leq \min\{d_1, d_2\} \).

Applying the theorem of differential inequality (Birkhoff and Rota, 1989) we obtain \( 0 \leq W(x, y, z) \leq L/\mu(1 - e^{-\mu t}) + W(x_0, y_0, z_0)e^{-\mu t} \), which implies that \( 0 \leq W \leq L/\mu \) as \( t \to \infty \). Hence, all the solution of (4.8), that initiate in \( \mathbb{R}^3_+ \setminus \{0\} \), are confined in the region \( B = \{(x, y, z) \in \mathbb{R}^3_+ : W = L/\mu + e\} \).

Since,
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1. the fast equilibrium points are hyperbolically stable, i.e. they are asymptotically stable solutions of the linearized equations,

2. the global variables $x$, $y$ and $z$, whose dynamics are described by (4.8), are always bounded,

the aggregated system (4.8) is an approximation of the system (4.3) and the accumulated error is negligible (Michalski, 1997).

4.4 Local stability analysis of the equilibrium points

There are four equilibrium points of the aggregated system (4.8), (i) trivial equilibrium point $E_0 = (0, 0, 0)$, (ii) axial equilibrium point $E_1 = (K, 0, 0)$, (iii) planer equilibrium point $E_2 = (x, y, 0)$ and (iv) interior equilibrium point $E^* = (x^*, y^*, z^*)$.

Here, $x$ and $y$ are the solution of

$$r(1 - \frac{x}{K}) - \frac{\alpha_1(1+\beta_1)x}{(1+\gamma_x)(1+\delta_1x)} = 0,$$
$$\frac{\alpha_1(1+\beta_1)x}{(1+\gamma_x)(1+\delta_1x)} - d_1 = 0,$$

which gives $x = \frac{-d_1(\gamma_1+\delta_1)-\alpha_1 \pm \sqrt{(d_1(\gamma_1+\delta_1)-\alpha_1)^2-4(d_1\gamma_1\delta_1-\alpha_1\beta_1)d_1}}{2(d_1\gamma_1\delta_1-\alpha_1\beta_1)}$, and $y = \frac{r(1 - \frac{x}{K})(1+\gamma_x)(1+\delta_1x)}{\alpha_1(1+\beta_1x)}$. If $b_2d_1 - \alpha_1 < 0$ and $x < K$ then the system has unique top predator free equilibrium ($E_2$).
Again, \((x^*, y^*, z^*)\) is the solution of

\[
\begin{align*}
    r(1 - \frac{x}{K}) - \frac{a_1(1 + \beta x)y}{(1 + \gamma_1 x)(1 + \delta_1 x)} &= 0, \\
    \frac{a_1(1 + \beta x)x}{(1 + \gamma_1 x)(1 + \delta_1 x)} - \frac{a_2(1 + \beta y)x}{(1 + \gamma_2 y)(1 + \delta_2 y)} - d_1 &= 0, \\
    \frac{a_2(1 + \beta y)x}{(1 + \gamma_2 y)(1 + \delta_2 y)} - d_2 &= 0,
\end{align*}
\]

where \(y^* = \frac{-(d_2(\gamma_2 + \delta_2) - a_2) \pm \sqrt{(d_2(\gamma_1 + \delta_1) - a_2)^2 - 4(d_2(\gamma_2 + a_2) - a_2)}d_2}{2(d_2(\gamma_2 + \delta_2) - a_2)}\),

\(x^*\) is the positive root of the of the third order polynomial

\[
\frac{r(\gamma_1 \delta_1 + \delta_1) - r\gamma_1 \delta_1}{K} x^3 + \frac{\{\frac{r}{K}(\gamma_1 + \delta_1) - r\gamma_1 \delta_1\}}{K} x^2 + \{\alpha_1 \beta y^* - r(\gamma_1 + \delta_1) + \frac{r}{K}\} x + (\alpha_2 y^* - r) = 0,
\]

and \(z^* = \frac{(1 + \beta_1 x^*)}{a_2(1 + \beta y^*)} \left[\frac{a_2(1 + \beta y^*)x^*}{(1 + \gamma_2 y^*)(1 + \delta_1 x^*)} - d_1\right]\).

**Theorem 4.2**

(i) The trivial equilibrium point \(E_0(0, 0, 0)\) is always unstable,

(ii) The axial equilibrium point \(E_1 = (\bar{K}, 0, 0)\) is Locally Asymptotically Stable (LAS) iff \(\frac{a_1(1 + \beta x)}{1 + \gamma_1 x(1 + \delta_1 x)} < d_1\),

(iii) The planer equilibrium point \(E_2 = (\bar{x}, \bar{y}, 0)\) is LAS if \(\Omega_1 < 0, \Omega_3 > 0\) and \(\Omega_5 < 0\), where \(\Omega_i\)'s \((i = 1, 2, \ldots, 5)\) are defined later,

(iv) The positive interior equilibrium \(E^* = (x^*, y^*, z^*)\) is LAS if \(\Sigma_1 > 0, \Sigma_3 > 0, \Sigma_1 \Sigma_2 > \Sigma_3\), where, \(\Sigma_i\)'s \((i = 1, 2, 3)\) are defined later.

**Proof:** The local stability of the system (4.8) around each of the equilibria is obtained by computing the Jacobian matrix corresponding to each equilibrium point. The Jacobian matrix around arbitrary equilibrium point \(E = (x, y, z)\) for the system (4.8) is given by
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\[ J(x, y, z) = \begin{pmatrix} J_{11} & J_{12} & J_{13} \\ J_{21} & J_{22} & J_{23} \\ J_{31} & J_{32} & J_{33} \end{pmatrix}, \]

where,

\[ J_{11} = r - \frac{2 \pi x}{K} - \frac{a_1 \beta_1 x}{(1 + \gamma_1)(1 + \gamma_1)} - \frac{a_1(1 + \beta_1)x}{(1 + \gamma_1)(1 + \gamma_1)} + \frac{a_1 \gamma_1(1 + \beta_1)x}{(1 + \gamma_1)(1 + \gamma_1)} + \frac{a_1 \beta_1(1 + \beta_1)x}{(1 + \gamma_1)(1 + \gamma_1)}, \]

\[ J_{12} = \frac{a_1(1 + \beta_1)x}{(1 + \gamma_1)(1 + \gamma_1)}, \quad J_{13} = 0, \quad J_{21} = \frac{a_1 \beta_1 x}{(1 + \gamma_1)(1 + \gamma_1)} + \frac{a_1(1 + \beta_1)x}{(1 + \gamma_1)(1 + \gamma_1)} - \frac{a_1 \gamma_1(1 + \beta_1)x}{(1 + \gamma_1)(1 + \gamma_1)} - \frac{a_1 \beta_1(1 + \beta_1)x}{(1 + \gamma_1)(1 + \gamma_1)}, \]

\[ J_{22} = \frac{a_1(1 + \beta_1)x}{(1 + \gamma_1)(1 + \gamma_1)} - \frac{a_1 \beta_1 y z}{(1 + \gamma_1)(1 + \gamma_1)} - \frac{a_1 \gamma_1(1 + \beta_1)x}{(1 + \gamma_1)(1 + \gamma_1)} + \frac{a_1 \beta_1(1 + \beta_1)x}{(1 + \gamma_1)(1 + \gamma_1)}, \]

\[ J_{23} = -\frac{a_1(1 + \beta_1)y}{(1 + \gamma_1)(1 + \gamma_1)} - \frac{a_2 \beta_2 y z}{(1 + \gamma_1)(1 + \gamma_1)} - \frac{a_2 \gamma_2(1 + \beta_2)y}{(1 + \gamma_1)(1 + \gamma_1)} + \frac{a_2 \beta_2(1 + \beta_2)y}{(1 + \gamma_1)(1 + \gamma_1)} - \frac{a_2 \gamma_2(1 + \beta_2)y z}{(1 + \gamma_1)(1 + \gamma_1)}, \quad J_{31} = 0, \quad J_{32} = \frac{a_2 \beta_2 y z}{(1 + \gamma_1)(1 + \gamma_1)}, \]

\[ J_{33} = \frac{a_2(1 + \beta_2)y}{(1 + \gamma_1)(1 + \gamma_1)} - \frac{a_2 \gamma_2(1 + \beta_2)y}{(1 + \gamma_1)(1 + \gamma_1)} + \frac{a_2 \beta_2(1 + \beta_2)y}{(1 + \gamma_1)(1 + \gamma_1)} - \frac{a_2 \gamma_2(1 + \beta_2)y z}{(1 + \gamma_1)(1 + \gamma_1)}, \]

(i) The Jacobian matrix at the trivial equilibrium point \( E_0(0, 0, 0) \) is

\[ J(E_0) = \begin{pmatrix} r & 0 & 0 \\ 0 & -d_1 & 0 \\ 0 & 0 & -d_2 \end{pmatrix}. \]

The eigenvalues are \( r, -d_1 \) and \( -d_2 \). One of the eigenvalues (\( r \)) is always positive. Hence \( E_0 \) is always unstable.

(ii) The Jacobian matrix at the trivial equilibrium point \( E_1 = (\tilde{K}, 0, 0) \) is

\[ J(E_1) = \begin{pmatrix} -r & -\frac{a_1(1 + \beta_1 \tilde{K})}{(1 + \gamma_1)(1 + \gamma_1)} & 0 \\ 0 & -\frac{a_1(1 + \beta_1 \tilde{K})}{(1 + \gamma_1)(1 + \gamma_1)} - d_1 & 0 \\ 0 & 0 & -d_2 \end{pmatrix}. \]
The eigenvalues are $-r$, $-\frac{\alpha_1(1+\beta_1\epsilon)}{(1+r_\eta)(1+\delta_1 \kappa)}$, $-\frac{\alpha_2(1+\beta_2\epsilon)}{(1+r_\eta)(1+\delta_2 \kappa)}$ and $-d_2$, which implies that $E_1$ is LAS if $\frac{\alpha_1(1+\beta_1\epsilon)}{(1+r_\eta)(1+\delta_1 \kappa)} < 1$. (iii) The Jacobian matrix at the trivial equilibrium point $E_2 = (\bar{x}, \bar{y}, 0)$ is

$$J(E_2) = \begin{pmatrix} \Omega_1 & -\Omega_2 & 0 \\ \Omega_3 & 0 & -\Omega_4 \\ 0 & 0 & \Omega_5 \end{pmatrix}$$

where, $\Omega_1 = -\frac{\alpha_1(1+\beta_1\epsilon)}{(1+r_\eta)(1+\delta_1 \kappa)}$, $\Omega_2 = -\frac{\alpha_2(1+\beta_2\epsilon)}{(1+r_\eta)(1+\delta_2 \kappa)}$, $\Omega_3 = \frac{\alpha_1(1+\beta_1\epsilon)}{(1+r_\eta)(1+\delta_1 \kappa)}$, $\Omega_4 = \frac{\alpha_2(1+\beta_2\epsilon)}{(1+r_\eta)(1+\delta_2 \kappa)}$, $\Omega_5 = \frac{\alpha_1(1+\beta_1\epsilon)}{(1+r_\eta)(1+\delta_1 \kappa)}$. The characteristic equation of the system is

$$(\xi^2 - \Omega_1\xi + \Omega_2\Omega_3)(\Omega_5 - \xi) = 0$$

The eigenvalues are $\xi_{1,2} = \frac{-\Omega_1 \pm \sqrt{\Omega_1^2 - 4\Omega_2\Omega_3}}{2}$ and $\xi = \Omega_5$. The eigenvalues $\xi_1$ and $\xi_2$ are negative or have negative real part if $\Omega_1 < 0$ and $\Omega_3 > 0$. Therefore, the planer equilibrium point $E_2 = (\bar{x}, \bar{y}, 0)$ is LAS if $\Omega_1 < 0$, $\Omega_3 > 0$ and $\Omega_5 < 0$. (iv) The Jacobian matrix at the trivial equilibrium point $E_2 = (\bar{x}, \bar{y}, 0)$ is

$$J(E_2) = \begin{pmatrix} \Pi_1 & -\Pi_2 & 0 \\ \Pi_3 & \Pi_4 & -\Pi_5 \\ 0 & \Pi_6 & 0 \end{pmatrix}$$
The characteristic equation of the Jacobian matrix is

$$\lambda^3 + \Sigma_1 \lambda^2 + \Sigma_2 \lambda + \Sigma_3 = 0$$

where, $\Sigma_1 = -\Pi_1 - \Pi_4$

$\Sigma_2 = \Pi_1 \Pi_4 + \Pi_2 \Pi_3 + \Pi_5 \Pi_6,$

$\Sigma_3 = -\Pi_1 \Pi_5 \Pi_6.$

The interior equilibrium point $E^* = (x^*, y^*, z^*)$ is LAS if the coefficients of the characteristic equation satisfies the Routh-Hurwitz criteria i.e.

$\Sigma_1 > 0, \Sigma_3 > 0,$ and $\Sigma_1 \Sigma_2 > \Sigma_3.$

**Theorem 4.3** When the migration ratio $(m)$ of top predator crosses a critical value, the system (4.8) enters into Hopf bifurcation around the positive equilibrium. The necessary and sufficient conditions for Hopf bifurcation to occur is that there exist $m = m^*$ such that,

(a) $H(m^*) \equiv \Sigma_1(m^*) \Sigma_2(m^*) - \Sigma_3(m^*) = 0,$

(b) $\left. \frac{d}{dm}(Re(\lambda(m))) \right|_{m=m^*} \neq 0,$
where $\lambda$ is the root of the characteristic equation corresponding to the interior equilibrium point.

**Proof:** For $m = m^*$, we can write the characteristic equation
\[
\lambda^3 + \Sigma_1 \lambda^2 + \Sigma_2 \lambda + \Sigma_3 = 0
\]
as
\[
(\lambda^2 + \Sigma_2)(\lambda + \Sigma_1),
\]
which has three roots $\lambda_1 = i\sqrt{\Sigma_2}$, $\lambda_2 = -i\sqrt{\Sigma_2}$ and $\lambda_3 = -\Sigma_1$.

For all $m$, the roots are in general of the form
\[
\lambda_j(m) = \phi_l(m) + i\phi_2(m),
\]
\[
\lambda_2(m) = \phi_l(m) - i\phi_2(m),
\]
\[
\lambda_3(m) = -\Sigma_1.
\]

Now, we shall verify the transversality condition
\[
\frac{d}{dm}(\operatorname{Re}(\lambda(m))) \mid_{m=m^*} \neq 0, \quad j = 1, 2.
\]
Substituting $\lambda_j(m) = \phi_l(m) + i\phi_2(m)$ into the characteristic equation and calculating the derivative, we have
\[
P(m)\phi'_l(m) - Q(m)\phi'_2(m) + U(m) = 0,
\]
\[
Q(m)\phi'_l(m) + P(m)\phi'_2(m) + V(m) = 0,
\]
where,
\[
P(m) = 3\phi'_l(m) + 2\Sigma_1(m)\phi_1(m) + \Sigma_2(m) - 3\phi'_2(m),
\]
\[
Q(m) = 6\phi_1(m)\phi_2(m) + 2\Sigma_1(m)\phi_2(m),
\]
\[
U(m) = \phi'_l(m)\Sigma'_1(m) + \Sigma'_2(m)\phi_1(m) + \Sigma'_3(m) - \Sigma'_1(m)\phi'_2(m),
\]
\[
V(m) = 2\phi_1(m)\phi_2(m)\Sigma'_1(m) + \Sigma'_2(m)\phi_2(m).
\]

Noticing that $\phi_1(m^*) = 0$, $\phi_2(m^*) = \sqrt{\Sigma_2(m^*)}$, we have
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\[ P(m^*) = -2\Sigma_2(m^*) \]
\[ Q(m^*) = 2\Sigma_1(m^*)\sqrt{\Sigma_2(m^*)} \]
\[ U(m^*) = \Sigma_3(m^*) - \Sigma_1(m^*)\Sigma_2(m^*) \]
\[ V(m^*) = \Sigma_2(m^*)\sqrt{\Sigma_2(m^*)} \]

and \[ F(m^*) = \Sigma_5(m^*)^2 \]

Now,

\[ \frac{d}{dm} \left( Re(\lambda(m)) \right) \bigg|_{m=m^*} = \frac{Q(m^*)V(m^*)+P(m^*)U(m^*)}{P(m^*)^2+Q(m^*)^2} \]

\[ = \frac{2\Sigma_1(m^*)\sqrt{\Sigma_2(m^*)}\times\Sigma_4(m^*)\sqrt{\Sigma_2(m^*)}+(-2\Sigma_2(m^*))^{\Sigma_5(m^*)}-(\Sigma_3(m^*)^2)}{(-2\Sigma_2(m^*))^2+(2\Sigma_5(m^*)\sqrt{\Sigma_2(m^*)})^2} \]

\[ = \frac{\Sigma_1(m^*)\Sigma_4(m^*)-\Sigma_3(m^*)^2+\Sigma_4(m^*)\Sigma_2(m^*)}{2(\Sigma_2(m^*))^2+(\Sigma_5(m^*))^2} \]

\[ \neq 0, \quad \text{if} \quad \Sigma_1(m^*)\Sigma_4(m^*)-\Sigma_3(m^*)^2+\Sigma_4(m^*)\Sigma_2(m^*) \neq 0, \]

and \[ \lambda_3(m^*) = -\Sigma_1(m^*) \neq 0. \]

Therefore, the transversality conditions hold. This implies that a Hopf-bifurcation occurs at \( m = m^* \). Hence the theorem.

### 4.5 Numerical results

In this section we perform the numerical experiments to observe the dynamics of the system (4.8) with the following set of parameter values and most of the parameter values are taken from Hastings and Powell (1991). The parameter values are

\[ a_1 = 5, \quad a_2 = 0.2, \quad \bar{a}_2 = 0.18, \quad b_1 = 5, \quad b_2 = 2, \quad d_1 = 0.4, \quad d_2 = 0.01, \quad \bar{a}_2 = 0.18, \]
\[ d = 0.05, \quad m = 0.1, \quad k = 0.2, \quad f = 0.2. \]

This parameter set is being kept fixed throughout the numerical experiments except \( b_1, m, k \) and \( f \). Though, the aggregated system (4.8) have
parameters $r$, $K$, $a_1$, $\beta_1$, $\gamma_1$, $\delta_1$, $\alpha_2$, $\beta_2$, $\gamma_2$ and $\delta_2$, but we are not bothered about these parameter values because all of these parameters are functions of dimensionless parameters given earlier. We perform numerical experiments using those dimensionless parameter values. For the above set of parameters we obtain the positive interior equilibrium $E^*(1.0035, 0.1565, 1.2868)$. For the same set of parameter values we have $\Sigma_1 = 0.7755$, $\Sigma_2 = 5.7682 \times 10^{-4}$, $\Sigma_1 \Sigma_2 - \Sigma_3 = 0.0059$, which means that the system (4.8) is locally asymptotically stable around the positive interior equilibrium $E^*$. 


Figure 4.1: The figure depicts the solution of the system (4.8) in the absence of cascading migration. (a) Depicts the steady state stable distribution with \(a_1 = 5, a_2 = 0.2, \alpha_2 = 0.18, b_1 = 1, b_2 = 2, d_1 = 0.4, d_2 = 0.01\). (b) Shows the limit cycle oscillation for \(b_1 = 1.6\). (c) Depicts the period-doubling of the system for \(b_1 = 1.7\). Finally, (d) shows a chaotic oscillation at \(b_1 = 5\).

In the absence of cascading migration, the system (4.8) becomes the dimensionless system of Hastings-Powell model. They observed stability, limit cycle and chaotic dynamics of the system by changing half saturation constant \(b_1\). We first observe the exchange of states (stability-limit cycle-period doubling-chaos) keeping the parameter values same as Hastings and Powell.
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(1991) except the parameter $a_2$. We observed that for $0 < b_1 < 1.2$ the system is stable around the positive steady state (Figure 1(a)) and for $1.2 < b_1 < 1.63$ it shows limit cycle oscillations (Figure 4.1(b)). The period doubling is observed at $b_1 = 1.63$ (Figure 4.1(c)). Finally, chaotic dynamics is observed for $1.63 < b_1 < 9.4$ (Figure 4.1(d)).
Figure 4.2: In the presence of cascading migration, (a) shows the stable coexistence of three species of the system (4.8) for $a_1 = 5$, $a_2 = 0.2$, $\alpha_2 = 0.18$, $b_1 = 5$, $b_2 = 2$, $d_1 = 0.4$, $d_2 = 0.01$, $\alpha_2 = 0.18$, $d = 0.05$, $k = 0.2$, $f = 0.2$, $m = 0.1$. (b) Depicts limit cycle oscillation of the system for $m = 0.39$. (c) Depicts the period-doubling of the system for $m = 0.4$. Finally, (d) depicts the chaotic dynamics of the dynamics for $m = 0.6$.

To observe the effect of cascading migration in the system (4.8) we fix the migration ratio of prey ($f = 0.2$) and the migration ratio of middle predator ($k = 0.2$) and vary the migration ratio of top-predator ($m$) where the other parameter values are kept same as in figure 4.1(d). For $0.072 < m < 0.15$
the system is stable around the positive steady state (Figure 4.2(a)) which indicates that cascading migration has the potential to stabilize the chaotic system. But, further increment in $m$ leads the system from stable to limit cycle (with Hopf-bifurcation occurred at $m = 0.15$), limit cycle to period doubling and period doubling to chaos. The system shows a limit cycle oscillation for $0.15 < m < 0.4$ (Figure 4.2(b)) and period doubling observed at $m = 0.4$ (Figure 4.2(c)). The system shows chaotic behavior for $0.4 < m < 1.29$ (Figure 4.2(d)), and the system collapses if the migration ration ($m$) is increased further.

To make it more clear we draw the bifurcation diagram for all the populations with $m$ as the bifurcating parameter (Figure 4.3). We observe that for $m > 0.072$ three species start to coexist and the system shows the steady state solution in the range $0.072 < m < 0.15$, limit cycle for $0.15 < m < 0.4$ and finally the system goes to chaos through period doubling for $m > 0.4$, keeping other parameter same as in Figure 4.2. The system remains chaotic for $0.4 < m < 1.29$, but, for $m > 1.29$ $z$-population extinct from the system and $x$-population and $y$-population shows boom-bust dynamics. Furthermore, all the branching points of the bifurcation diagram are always same for the three populations. To make it clearer, we indicate the branching points by the vertical dashed line in each bifurcation diagram.
Figure 4.3: The bifurcation diagram of the system (4.8) corresponding to the bifurcating parameter $m \in [0, 1.4]$ and $f = 0.2$, $k = 0.2$ showing that the system enters into chaos from order and for higher values of $m$ system collapses. Other parameter values are kept same as in Figure 4.2. The vertical dashed lines indicate the branching points.
In Figure 4.4, for \( f = 0.2 \) and \( m = 0.1 \) the bifurcation diagram is drawn with bifurcation parameter \( k \), the migration ratio of middle predator. For \( 0.0014 < k < 0.0015 \), the system shows stable dynamics, limit cycle for \( 0.0015 < k < 0.016 \), period doubling for \( 0.016 < k < 0.019 \), higher periodic and chaotic for \( 0.019 < k < 0.044 \). Further increase in \( k \) leads the system to period doubling for \( 0.044 < k < 0.054 \), limit cycle for \( 0.054 < k < 0.132 \) and stable for \( 0.132 < k \leq 0.274 \). As we increase \( k \) gradually, the system enters into chaos from order through period doubling bifurcation and the system again return to its stable steady state solution from chaos through period halving bifurcation. Finally, \( z \)-population extinct from the system for \( k > 0.274 \) and \( x \)-population and \( y \)-population shows oscillatory coexistence.
Figure 4.4: The bifurcation diagram of the system (4.8) corresponding to the bifurcating parameter $k \in [0, 0.3]$ and $f = 0.2$, $m = 0.1$, showing that the system enters into order from chaos. The vertical dashed lines indicate the branching points.
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On the other hand, when the value of $k$ and $m$ are kept fixed at 0.2 and 0.1 respectively, the system is stable around the positive steady state for $0.103 < f < 1.14$ and leads to oscillations (with Hopf-bifurcation occurred at $f = 1.14$) for $1.14 < f < 2.357$ (Figure 4.5). However, if the value of $f$ is higher than 2.357 then $z$-population extinct from the system and $x$-population and $y$-population shows boom-bust dynamics.
Figure 4.5: The bifurcation diagram of the system (4.8) corresponding to the bifurcating parameter $f \in [0, 3]$ and $k = 0.2, m = 0.1$, showing that the system enters into a limit cycle oscillation from stable condition. The vertical dashed line indicates the bifurcating point.
It is believed that chaos may arise in tri-trophic food chain systems due to oscillations in predator-prey systems. Hastings and Powell (1991) observed that in a predator-prey subsystem, prey and middle predator, oscillates at one frequency, while another subsystem, middle predator and top predator, oscillates at a different frequency. The frequencies of the oscillations are determined by the model parameters. It is interesting to note that the two subsystems are coupled through middle predator because the predator in one (first trophic level) is the prey in the other (higher trophic level). When the frequency of the oscillation in one subsystem is not commensurate with the frequency of the other one (i.e. period of one subsystem is not some multiple of other subsystem) chaos arises in the tri-trophic food chain system (Hastings and Powell, 1991).

Here, the chaotic behavior of the system (4.8) may be interpreted in terms of $m$, $k$ and $f$, migration ratios of top predator, middle predator and prey populations. If we keep other migration ratios fix, increase in $m$ implies relatively more top predator (fish) migrates downward. As a result, the predation pressure on the zooplankton will be reduced. Ultimately, it will increase the density of zooplankton on surface water and increases the predation pressure on the primary producer or prey population. We observe that up to a certain threshold value of $m$, the predation pressure of fish on zooplankton and the predation pressure of zooplankton on prey (phytoplankton) are mediated, which enhances system stability but above that threshold value, the system shows oscillation and the system become chaotic whenever the frequencies of the oscillations in $x - y$ and $y - z$ subsystem are not commensurate. However,
the migration of phytoplankton and zooplankton are assumed to be inducible defense mechanisms of the respective populations. If the migration ratio of middle predator, $k$ is increased, then within a range of values of $k$, the system shows oscillations and chaotic behavior, whereas below and the above of the range, the system becomes stable. For that range of values of $k$ the trade-off between lower food of zooplankton and higher predation pressure by fish makes the system oscillatory, and chaos arises whenever the frequencies of the oscillations in $x - y$ and $y - z$ are not commensurate. If the migration ratio of prey populations, $f$ is increased, the system shows stable dynamics up to a threshold value as the edibility of prey reduced. On the other hand, the net growth of phytoplankton is reduced and the energy flow from prey to top predator becomes lower. It is to be noted that up to a certain range of $f$ the system shows oscillation whereas above that range, the top predator goes extinct. But the prey and the middle predator populations show boom burst oscillations. Thus, the increase in the migration ratio of top predator makes the system chaotic whereas the increase in migration ratios of middle predator and prey populations make the system more regular.

4.6 Conclusion

Our results suggest that for different set of values of migration rates of each trophic level (i.e. the migration ratio of downward and upward vertical migration of each trophic level), the system shows stable, oscillatory and/or chaotic behavior. Therefore, cascading migrations have a huge impact on the dynamics of a tri-trophic food chain. It is observed that the system seems to have num-
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bers of switching from one state into the other, from chaos to order, from order to chaos. Increasing the value of the migration ratio of prey leads the system to limit cycles from stable steady state (Figure 4.5). The transitions between stable steady state, limit cycles, period doubling, chaos, period halving and ultimately stable steady state occurred for gradual increases in the migration ratio of middle predator (Figure 4.4) whereas, the transitions occurred between stable steady state, limit cycles, period doubling, chaos for increasing the value of the migration ratio of top predator (Figure 4.3). Stabilizing effect (chaos to order) of migrations of middle predator on the Hastings-Powell model already been observed by Chowdhury et al. (2010). Our results clearly indicate that the cascading migration on top predator (naturally other trophic level) enhances the system stability. It is also interesting to note that further increase in the cascading migration on the top predators the considered system again enters in chaotic phase from the order. The results predicted by Hastings and Powell are also true for higher rate of cascading migration than a threshold value.

Before ending the article, we like to mention that as this is the first model in this direction, so there are lots of scope to generalize the model. As a matter of fact, to study DVM in single species or cascading migration in a multi-trophic food chain more attention is needed to articulate the rate of migration rather than observation of changing population peaks in the environment. The relative distribution of populations in the water column may not always represent the actual migration rate of organisms (Hays et al., 2008). The assumptions and hypotheses can be modified according to the future outcomes of labo-
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Laboratory and field experiments on cascading migration. We hope that it will help observationalists and experimentalist to design their own experiments to manipulate the rate of cascading migrations.