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

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Received: 21 September 2012 / Accepted: 4 March 2013 / Published online: 7 April 2013
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Abstract Diel vertical migration is a behavioral antipredator defense that is shaped by a trade-off between higher predation risk in surface waters and reduced growth in deeper waters. The strength of migration of zooplankton increases with a rise in the abundance of predators and their exudates (kairomone). Recent studies span multiple trophic levels, which lead to the concept of coupled vertical migration. The migrations that occur at one trophic level can affect the vertical migration of the next lower trophic level, and so on, throughout the food chain. This is called cascading migration. In this paper, we introduce cascading migration in a well-known model (Hastings and Powell, *Ecology* 73:896–903, 1991). We represent the dynamics of the system as proposed by Hastings and Powell as a phytoplankton–zooplankton–fish (prey–middle predator–top predator) model where fish affect the migrations of zooplankton, which in turn affect the migrations of motile phytoplankton. The system under cascading migration enhances system stability and population coexistence. It is also observed that for a higher rate of cascading migration, the system shows chaotic behavior. We conclude that the observations of Hastings and Powell remain true if the cascading migration rate is high enough.

Keywords Kairomone · Inducible defense · Diel vertical migration · Coexistence · Stability · Hopf-bifurcation · Chaos

The research work is supported by the Council of Scientific and Industrial Research (CSIR), Human Resource Development Group, New Delhi.

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1 Introduction

Diel vertical migration (DVM) is a natural phenomenon of movements of some living organisms living in oceans and lakes. Basically, this is one type of migration. The organisms generally follow a 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. [1], Cohen and Forward [2] and a book by Ringelberg [3]). The migrations that occur at one trophic level can affect the vertical migration of the next trophic level, and so on throughout the food web. In 2011, Bollens et al. for the first time coined the term 'cascading migration' instead of coupled vertical migrations in a multi-trophic food chain and explained the phenomenon with its implications in various scenarios [4].

It has been observed that zooplankton show downward vertical migration in the daytime in the presence of predators who release kairomone or chemical cues to avoid predation [5–13]. However, chemical cues are not the only predator cues that trigger zooplankton DVM (see, [14]). The strength of migration of zooplankton increases with rises in the concentration of fish or fish exudates [11, 15]. Avoidance of predators, such as visually orienting planktivorous fish and carnivorous invertebrates, is the most important factor that regulates DVM in zooplankton [8, 16–18]. Apart from kairomone or chemical cues, there are several reasons for DVM of zooplankton such as light intensity, solar radiation, temperature, dissolved oxygen, UV radiation, and food availability, etc. [1]. However, predation pressure is the most important factor that drives mesozooplankton migrations, which in turn cascade into effects on dinoflagellate migrations [4]. Many species of dinoflagellates have also been observed to undertake vertical migration, residing at the surface during the day and residing at depth at night [19–23]. Although the light intensity at surface water and nutrients at deep water play an important role as drivers of dinoflagellate DVM in laboratory studies [24–30], recent experiments have shown that many of the dinoflagellate species migrate to avoid the predation of copepod and other grazer zooplankton [4, 31]. Therefore, it is clear that the motile phytoplankton (dinoflagellate) and its predator zooplankton (copepod) exhibit opposite migration patterns; the zooplankton undertakes a normal DVM (up at night, down during the day), whereas the dinoflagellate undertake a reverse DVM (down at night, up during the day). It is also known that the migration pattern of zooplankton is opposite to the pattern of fish vertical migration [32–34].

As far as we are aware, mathematical models on a tri-trophic food chain in the presence of cascading migration have not yet been 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 [35] 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 that conclude that the chaos thus observed may be controlled by reasonable biological phenomena. The biological phenomena like imposition of a population floor [36, 37], addition of refugia [38], omnivory [39], intraspecific density dependence [40], toxic inhibition [41], spatial effect [42], density-dependent death of the middle predator, [43], disease in prey and body size of the intermediate predator [44] and, migration in the middle predator [45] can control the chaos. Chowdhury et al. showed that an increase in the migration ratio of the middle predator switches the system from chaos to stable through limit cycles [45], but we theoretically observe that cascading migration can control the chaos predicted in

the Hastings–Powell model. The system becomes stable when the value of the migration ratio of the top-predator remains below a threshold value, but the system shows periodic oscillation, period-doubling and, higher periodic oscillations, respectively, and ultimately, it goes to chaos with an increase in the migration ratio.

In the present paper, we are attempting theoretically to study cascading migration and its effect on complex ecological systems. We study phytoplankton–zooplankton–fish interactions considering the cascading migration through mathematical modeling. In Section 2, we develop a slow–fast model (similar to [46–49]) of cascading migrations of fish, zooplankton, and motile phytoplankton, considering the whole water column as two patches: an upper layer and lower layer that are connected through migrations. The aggregated model has been derived in Section 3. Subsequently, the model analysis and numerical results are explored and explained in Sections 4 and 5 respectively. In Section 6, the paper ends with a brief conclusion.

2 Model development

First, we consider the tri-trophic food-chain model proposed by Hastings and Powell [35]

$$\begin{aligned}\frac{dX}{dT} &= RX\left(1 - \frac{X}{K}\right) - \frac{A_1XY}{B_1 + X}, \\ \frac{dY}{dT} &= \frac{C_1A_1XY}{B_1 + X} - \frac{A_2YZ}{B_2 + Y} - D_1Y, \\ \frac{dZ}{dT} &= \frac{C_2A_2YZ}{B_2 + Y} - D_2Z.\end{aligned}\quad (1)$$

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

Now, we introduce the concept of cascading migration into the system (1). According to light penetration into water, we split the whole pelagic water mass into two layers: an upper and lower layer. The water column above the Secchi depth is referred to as the upper layer, where light is available at day-time; whereas, below the Secchi depth, the water column, where light availability is very low (almost unavailable) during day hours, is referred to as the lower layer. Population densities within each layer are considered to be homogeneous. We assume that phytoplankton (P) grow logistically in the upper layer. The top predator (fish or other vertebrates) 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 enters into the surface water again at night to graze phytoplankton. Similarly, motile phytoplankton (Dinoflagellates)

migrate vertically downward to avoid predation by herbivores and mesozooplankton at night by entering into the lower layer from the upper layer. They also return to the surface water at daytime for nutrient uptake and photosynthesis. Therefore, motile phytoplankton show reverse DVM along with the DVM of zooplankton and the migration pattern of zooplankton is reversed with respect to the migration pattern of fish. Such a 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 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 the top predator between two layers is very high and the 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 interactions with prey and predators. Therefore, two different time scales have been considered here: the fast one corresponds to migration, and 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), respectively, in the upper layer, and X_2 , Y_2 , and Z_2 the concentrations of prey, middle predator, and top predator, respectively, in the lower layer. Here we have considered that the migration of the top predator is constant, whereas the migrations of prey and middle predator are assumed to be predator-dependent only. The middle predator migrates into the upper layer when the top predator density is large in the lower layer and enters into the lower layer leaving the upper layer when the presence of a top predator is very high in the upper layer, whereas the prey population (motile phytoplankton) migrate into the lower layer when the density of the middle predator in surface water is high and return to surface water when the density of the middle predator in the lower layer is very high. We also assume that the predation rate of the middle predator remains the same in both layers, whereas the predation rate of the top predator varies for different layers depending on light availability, as most of the top predators (fish) show visually orienting predation.

The coupled system of equations can be written as follows:

$$\begin{aligned}
 \frac{dX_1}{dT} &= (F_2 Y_2 X_2 - F_1 Y_1 X_1) + \epsilon \left[RX_1 \left(1 - \frac{X_1}{K} \right) - \frac{A_1 X_1 Y_1}{B_1 + X_1} \right], \\
 \frac{dX_2}{dT} &= (F_1 Y_1 X_1 - F_2 Y_2 X_2) + \epsilon \left[-\frac{A_1 X_2 Y_2}{B_1 + X_2} - DX_2 \right], \\
 \frac{dY_1}{dT} &= (K_2 Z_2 Y_2 - K_1 Z_1 Y_1) + \epsilon \left[\frac{C_1 A_1 X_1 Y_1}{B_1 + X_1} - \frac{A_2 Y_1 Z_1}{B_2 + Y_1} - D_1 Y_1 \right], \\
 \frac{dY_2}{dT} &= (K_1 Z_1 Y_1 - K_2 Z_2 Y_2) + \epsilon \left[\frac{C_1 A_1 X_2 Y_2}{B_1 + X_2} - \frac{\bar{A}_2 Y_2 Z_2}{B_2 + Y_2} - D_1 Y_2 \right], \\
 \frac{dZ_1}{dT} &= (M_2 Z_2 - M_1 Z_1) + \epsilon \left[\frac{C_2 A_2 Y_1 Z_1}{B_2 + Y_1} - D_2 Z_1 \right], \\
 \frac{dZ_2}{dT} &= (M_1 Z_1 - M_2 Z_2) + \epsilon \left[\frac{C_2 \bar{A}_2 Y_2 Z_2}{B_2 + Y_2} - D_2 Z_2 \right].
 \end{aligned} \tag{2}$$

where, F_1, F_2 are the vertically downward and upward migration rates of the prey population, respectively; K_1 , and 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 predators, respectively. A_2 and $\bar{A}_2$ are the predation rates of the top predator in the upper and lower layers, respectively. ϵ 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 ϵT is the slow time scale.

Now, introducing dimensionless variables $x_1 = \frac{X_1}{K}, x_2 = \frac{X_2}{K}, y_1 = \frac{Y_1}{C_1 K}, y_2 = \frac{Y_2}{C_1 K}, z_1 = \frac{Z_1}{C_1 C_2 K}, z_2 = \frac{Z_2}{C_1 C_2 K}$ and $\tau = RT$, we obtain the following dimensionless system

$$\begin{aligned}\frac{dx_1}{d\tau} &= (f_2 y_2 x_2 - f_1 y_1 x_1) + \epsilon \left[x_1(1 - x_1) - \frac{a_1 x_1 y_1}{1 + b_1 x_1} \right], \\ \frac{dx_2}{d\tau} &= (f_1 y_1 x_1 - f_2 y_2 x_2) + \epsilon \left[-\frac{a_1 x_2 y_2}{1 + b_1 x_2} - d x_2 \right], \\ \frac{dy_1}{d\tau} &= (k_2 z_2 y_2 - k_1 z_1 y_1) + \epsilon \left[\frac{a_1 x_1 y_1}{1 + b_1 x_1} - \frac{a_2 y_1 z_1}{1 + b_2 y_1} - d_1 y_1 \right], \\ \frac{dy_2}{d\tau} &= (k_1 z_1 y_1 - k_2 z_2 y_2) + \epsilon \left[\frac{a_1 x_2 y_2}{1 + b_1 x_2} - \frac{\bar{a}_2 y_2 z_2}{1 + b_2 y_2} - d_1 y_2 \right], \\ \frac{dz_1}{d\tau} &= (m_2 z_2 - m_1 z_1) + \epsilon \left[\frac{a_2 y_1 z_1}{1 + b_1 y_1} - d_2 z_1 \right], \\ \frac{dz_2}{d\tau} &= (m_1 z_1 - m_2 z_2) + \epsilon \left[\frac{\bar{a}_2 y_2 z_2}{1 + b_2 y_2} - d_2 z_2 \right].\end{aligned}\quad (3)$$

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 $f_1 = \frac{F_1 C_1 K}{R}, f_2 = \frac{F_2 C_1 K}{R}, k_1 = \frac{K_1 C_1 C_2 K}{R}, k_2 = \frac{K_2 C_1 C_2 K}{R}, m_1 = \frac{M_1}{R}, m_2 = \frac{M_2}{R}, a_1 = \frac{A_1 C_1 K}{R B_1}, a_2 = \frac{A_2 C_1 C_2 K}{R B_2}, \bar{a}_2 = \frac{\bar{A}_2 C_1 C_2 K}{R B_2}, b_1 = \frac{K}{B_1}, b_2 = \frac{C_1 K}{B_2}, d = \frac{D}{R}, d_1 = \frac{D_1}{R}$, and $d_2 = \frac{D_2}{R}$.

Now, we perform a perturbation technique to aggregate the variables corresponding to the asymptotically stable fast equilibrium point, and obtain a global (or aggregated) model easier to handle (at a slow time scale), which approximates the initial one [46–49].

3 Aggregation of the model

As we see, system (3) is mainly driven by the migration part, and the demographic part is only a small perturbation. We are now interested in fast dynamics, and the corresponding fast model is obtained by neglecting the slow part, i.e., taking $\epsilon = 0$,

$$\begin{aligned}\frac{dx_1}{d\tau} &= (f_2 y_2 x_2 - f_1 y_1 x_1), \\ \frac{dx_2}{d\tau} &= (f_1 y_1 x_1 - f_2 y_2 x_2),\end{aligned}$$

$$\begin{aligned}
\frac{dy_1}{d\tau} &= (k_2 z_2 y_2 - k_1 z_1 y_1), \\
\frac{dy_2}{d\tau} &= (k_1 z_1 y_1 - k_2 z_2 y_2), \\
\frac{dz_1}{d\tau} &= (m_2 z_2 - m_1 z_1), \\
\frac{dz_2}{d\tau} &= (m_1 z_1 - m_2 z_2).
\end{aligned} \tag{4}$$

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 system (4).

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

$$\begin{aligned}
f_1 y_1 x_1 - f_2 y_2 x_2 &= 0, \\
x_1 + x_2 &= x, \\
k_1 z_1 y_1 - k_2 z_2 y_2 &= 0, \\
y_1 + y_2 &= y, \\
m_1 z_1 - m_2 z_2 &= 0, \\
z_1 + z_2 &= z,
\end{aligned} \tag{5}$$

which is equivalent to

$$\begin{aligned}
x_1 &= \frac{kx}{fm + k}, \\
x_2 &= \frac{fmx}{fm + k}, \\
y_1 &= \frac{my}{k + m}, \\
y_2 &= \frac{ky}{k + m}, \\
z_1 &= \frac{z}{1 + m}, \\
z_2 &= \frac{mz}{1 + m},
\end{aligned} \tag{6}$$

where $f = \frac{f_1}{f_2}$, $k = \frac{k_1}{k_2}$ and $m = \frac{m_1}{m_2}$ are the migration ratios of the prey, middle predator, and top predator, respectively.

Now,

$$\begin{aligned}
\frac{dx_1}{d\tau} &= f_2 y_2 x_2 - f_1 y_1 x_1, \\
&= f_2 y_2 (x - x_1) - f_1 y_1 x_1, \\
&= f_2 y_2 x - (f_2 y_2 + f_1 y_1) x_1, \\
&= g_1(x_1).
\end{aligned} \tag{7}$$

Then, $g'_1(x_1) = -(f_2 y_2 + f_1 y_1) < 0$. 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 point is always asymptotically stable. By aggregating the variables corresponding to the same population, the following global model at a slow time scale is obtained:

$$\begin{aligned}\frac{dx}{dt} &= rx \left(1 - \frac{x}{\tilde{K}}\right) - \frac{\alpha_1(1 + \beta_1 x)xy}{(1 + \gamma_1 x)(1 + \delta_1 x)}, \\ \frac{dy}{dt} &= \frac{\alpha_1(1 + \beta_1 x)xy}{(1 + \gamma_1 x)(1 + \delta_1 x)} - \frac{\alpha_2(1 + \beta_2 y)yz}{(1 + \gamma_2 y)(1 + \delta_2 y)} - d_1 y, \\ \frac{dz}{dt} &= \frac{\alpha_2(1 + \beta_2 y)yz}{(1 + \gamma_2 y)(1 + \delta_2 y)} - d_2 z,\end{aligned}\quad (8)$$

where $r = \frac{k-d\bar{f}m}{\bar{f}m+k}$, $\tilde{K} = \frac{(\bar{f}m+k)(k-d\bar{f}m)}{k^2}$, $\alpha_1 = \frac{a_1 km(\bar{f}m+k)(1+\bar{f})}{(m+k)(\bar{f}m+k)^2}$, $\beta_1 = \frac{b_1 \bar{f}(m+k)}{(\bar{f}m+k)(1+\bar{f})}$, $\gamma_1 = \frac{b_1 k}{(\bar{f}m+k)}$, $\delta_1 = \frac{b_1 \bar{f}m}{(\bar{f}m+k)}$, $\alpha_2 = \frac{m(a_2+\bar{a}_2 k)}{(1+m)(m+k)}$, $\beta_2 = \frac{b_2 k(a_2+\bar{a}_2 m)}{(m+k)(a_2+\bar{a}_2 k)}$, $\gamma_2 = \frac{b_2 m}{(m+k)}$, $\delta_2 = \frac{b_2 k}{(m+k)}$ and $t = \tau\epsilon$ (slow time scale).

We are now in a position to state the following theorem corresponding to the boundedness of the aggregated system.

Theorem 1 *All the solutions of (8) that originate in R_+^3 are confined in the region*

$$B = \left\{ (x, y, z) \in R_+^3 : x + y + z = \frac{L}{\mu} + \epsilon, \forall \epsilon > 0 \right\}.$$

Proof of Theorem 1 is given in Appendix A.

Since

- 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 (8), are always bounded,

aggregated system (8) is an approximation of system (3) and the accumulated error is negligible [50]

4 Local stability analysis of the equilibrium points

There are four equilibrium points of aggregated system (8), a trivial equilibrium point $E_0 = (0, 0, 0)$, an axial equilibrium point $E_1 = (\tilde{K}, 0, 0)$, planar equilibrium point $E_2 = (\bar{x}, \bar{y}, 0)$ and an interior equilibrium point $E^* = (x^*, y^*, z^*)$.

Here, $\bar{x}$ and $\bar{y}$ are the solutions of

$$\begin{aligned}r \left(1 - \frac{x}{\tilde{K}}\right) - \frac{\alpha_1(1 + \beta_1 x)y}{(1 + \gamma_1 x)(1 + \delta_1 x)} &= 0, \\ \frac{\alpha_1(1 + \beta_1 x)x}{(1 + \gamma_1 x)(1 + \delta_1 x)} - d_1 &= 0,\end{aligned}\quad (9)$$

which gives $\bar{x} = \frac{-[d_1(\gamma_1 + \delta_1) - \alpha_1] \pm \sqrt{[d_1(\gamma_1 + \delta_1) - \alpha_1]^2 - 4(d_1 \gamma_1 \delta_1 - \alpha_1 \beta_1 d_1)}}{2(d_1 \gamma_1 \delta_1 - \alpha_1 \beta_1 d_1)}$, and $\bar{y} = \frac{r(1 - \frac{\bar{x}}{\tilde{K}})(1 + \gamma_1 \bar{x})(1 + \delta_1 \bar{x})}{\alpha_1(1 + \beta_1 \bar{x})}$. If $b_1 d_1 - a_1 < 0$ and $\bar{x} < \tilde{K}$, then the system has a unique top predator free equilibrium (E_2).

Again, (x^*, y^*, z^*) is the solution of

$$\begin{aligned} r \left(1 - \frac{x}{\tilde{K}} \right) - \frac{\alpha_1(1 + \beta_1 x)y}{(1 + \gamma_1 x)(1 + \delta_1 x)} &= 0, \\ \frac{\alpha_1(1 + \beta_1 x)x}{(1 + \gamma_1 x)(1 + \delta_1 x)} - \frac{\alpha_2(1 + \beta_2 y)z}{(1 + \gamma_2 y)(1 + \delta_2 y)} - d_1 &= 0, \\ \frac{\alpha_2(1 + \beta_2 y)z}{(1 + \gamma_2 y)(1 + \delta_2 y)} - d_2 &= 0, \end{aligned} \quad (10)$$

where $y^* = \frac{-\{d_2(\gamma_2 + \delta_2) - \alpha_2\} \pm \sqrt{\{d_2(\gamma_2 + \delta_2) - \alpha_2\}^2 - 4(d_2\gamma_2\delta_2 - \alpha_2\beta_2)d_2}}{2(d_2\gamma_2\delta_2 - \alpha_2\beta_2)}$, x^* is the positive root of the third-order polynomial $\frac{r\gamma_1\delta_1}{\tilde{K}}x^3 + \left\{ \frac{r}{\tilde{K}}(\gamma_1 + \delta_1) - r\gamma_1\delta_1 \right\}x^2 + \left\{ \alpha_1\beta_1y^* - r(\gamma_1 + \delta_1) + \frac{r}{\tilde{K}} \right\}x + (\alpha_1y^* - r) = 0$, and $z^* = \frac{(1 + \gamma_2y^*)(1 + \delta_2y^*)}{\alpha_2(1 + \beta_2y^*)} \left[\frac{\alpha_2(1 + \beta_1x^*)x^*}{(1 + \gamma_1x^*)(1 + \delta_1x^*)} - d_1 \right]$.

The local stability of system (8) around each of the equilibria is obtained by computing the variational matrix corresponding to each equilibrium point. The results thus obtained are stated below.

Lemma 1 System (8) around $E_0 = (0, 0, 0)$ is always unstable.

Lemma 2 System (8) around $E_1 = (\tilde{K}, 0, 0)$ is locally asymptotically stable (LAS) iff $\frac{\alpha_1(1 + \beta_1\tilde{K})}{(1 + \gamma_1\tilde{K})(1 + \delta_1\tilde{K})} < d_1$.

Lemma 3 System (8) around $E_2 = (\bar{x}, \bar{y}, 0)$ is LAS if $\Omega_1 < 0$, $\Omega_3 > 0$ and $\Omega_5 < 0$, where,

$$\begin{aligned} \Omega_1 &= -\frac{r\bar{x}}{\tilde{K}} - \frac{\alpha_1\beta_1\bar{x}\bar{y}}{(1 + \gamma_1\bar{x})(1 + \delta_1\bar{x})} + \frac{\alpha_1\gamma_1(1 + \beta_1\bar{x})\bar{x}\bar{y}}{(1 + \gamma_1\bar{x})^2(1 + \delta_1\bar{x})} + \frac{\alpha_1\delta_1(1 + \beta_1\bar{x})\bar{x}\bar{y}}{(1 + \gamma_1\bar{x})(1 + \delta_1\bar{x})^2}, \\ \Omega_3 &= \frac{\alpha_1(1 + \beta_1\bar{x})\bar{y}}{(1 + \gamma_1\bar{x})(1 + \delta_1\bar{x})} + \frac{\alpha_1\beta_1\bar{x}\bar{y}}{(1 + \gamma_1\bar{x})(1 + \delta_1\bar{x})} - \frac{\alpha_1\gamma_1(1 + \beta_1\bar{x})\bar{x}\bar{y}}{(1 + \gamma_1\bar{x})^2(1 + \delta_1\bar{x})} \\ &\quad - \frac{\alpha_1\delta_1(1 + \beta_1\bar{x})\bar{x}\bar{y}}{(1 + \gamma_1\bar{x})(1 + \delta_1\bar{x})^2}, \end{aligned}$$

$$\text{and } \Omega_5 = \frac{\alpha_2(1 + \beta_2\bar{y})\bar{y}}{(1 + \gamma_2\bar{y})(1 + \delta_2\bar{y})} - d_2.$$

Lemma 4 System (8) around $E^* = (x^*, y^*, z^*)$ is LAS if the root of the characteristic equation $\lambda^3 + \Sigma_1\lambda^2 + \Sigma_2\lambda + \Sigma_3 = 0$ of the Jacobian matrix $(J(E^*))$ satisfies the Routh–Hurwitz criteria, i.e., $\Sigma_1 > 0$, $\Sigma_3 > 0$, and $\Sigma_1\Sigma_2 > \Sigma_3$, where,

$$J(E^*) = \begin{bmatrix} \Pi_1 & -\Pi_2 & 0 \\ \Pi_3 & \Pi_4 & -\Pi_5 \\ 0 & \Pi_6 & 0 \end{bmatrix}$$

and

$$\begin{aligned} \Sigma_1 &= -\Pi_1 - \Pi_4 \\ \Sigma_2 &= \Pi_1\Pi_4 + \Pi_2\Pi_3 + \Pi_5\Pi_6, \\ \Sigma_3 &= -\Pi_1\Pi_5\Pi_6, \end{aligned}$$

with

$$\begin{aligned}\Pi_1 &= -\frac{rx^*}{\tilde{K}} - \frac{\alpha_1\beta_1x^*y^*}{(1+\gamma_1x^*)(1+\delta_1x^*)} + \frac{\alpha_1\gamma_1(1+\beta_1x^*)x^*y^*}{(1+\gamma_1x^*)^2(1+\delta_1x^*)} + \frac{\alpha_1\delta_1(1+\beta_1x^*)x^*y^*}{(1+\gamma_1x^*)(1+\delta_1x^*)^2}, \\ \Pi_2 &= \frac{\alpha_1(1+\beta_1x^*)x^*}{(1+\gamma_1x^*)(1+\delta_1x^*)}, \\ \Pi_3 &= \frac{\alpha_1(1+2\beta_1x^*)y^*}{(1+\gamma_1x^*)(1+\delta_1x^*)} - \frac{\alpha_1\gamma_1(1+\beta_1x^*)x^*y^*}{(1+\gamma_1x^*)^2(1+\delta_1x^*)} - \frac{\alpha_1\delta_1(1+\beta_1x^*)x^*y^*}{(1+\gamma_1x^*)(1+\delta_1x^*)^2}, \\ \Pi_4 &= -\frac{\alpha_2\beta_2y^*z^*}{(1+\gamma_2y^*)(1+\delta_2y^*)} + \frac{\alpha_2\gamma_2(1+\beta_2y^*)y^*z^*}{(1+\gamma_2y^*)^2(1+\delta_2y^*)} + \frac{\alpha_2\delta_2(1+\beta_2y^*)y^*z^*}{(1+\gamma_2y^*)(1+\delta_2y^*)^2}, \\ \Pi_5 &= \frac{\alpha_2(1+\beta_2y^*)y^*}{(1+\gamma_2y^*)(1+\delta_2y^*)}, \\ \Pi_6 &= \frac{\alpha_2(1+2\beta_2y^*)z^*}{(1+\gamma_2y^*)(1+\delta_2y^*)} - \frac{\alpha_2\gamma_2(1+\beta_2y^*)y^*z^*}{(1+\gamma_2y^*)^2(1+\delta_2y^*)} - \frac{\alpha_2\delta_2(1+\beta_2y^*)y^*z^*}{(1+\gamma_2y^*)(1+\delta_2y^*)^2}.\end{aligned}$$

Theorem 2 When the migration ratio (m) of the top predator crosses a critical value, the system (8) undergoes a Hopf bifurcation around the positive equilibrium point. The necessary and sufficient conditions for this Hopf bifurcation to occur are that there exist $m = m^*$ such that

- (a) $H(m^*) \equiv \Sigma_1(m^*)\Sigma_2(m^*) - \Sigma_3(m^*) = 0$,
- (b) $\frac{d}{dm}(Re(\lambda(m)))|_{m=m^*} \neq 0$,

where λ is the root of the characteristic equation corresponding to the interior equilibrium point.

Proof See Appendix B. □

5 Numerical results

In this section, we perform numerical experiments to observe the dynamics of system (8) with the following set of parameter values, taken for the most part from [35]. The parameter values are

$$\begin{aligned}a_1 = 5, a_2 = 0.2, \bar{a}_2 = 0.18, b_1 = 5, b_2 = 2, d_1 = 0.4, d_2 = 0.01, d = 0.05, \\ m = 0.1, k = 0.2, f = 0.2.\end{aligned}$$

This parameter set is kept fixed throughout the numerical experiments except for b_1 , m , k , and f . Although aggregated system (8) has the parameters r , $\tilde{K}$, α_1 , β_1 , γ_1 , δ_1 , α_2 , β_2 , γ_2 , and δ_2 , we are not concerned about these parameter values because all of these parameters are functions of the dimensionless parameters given earlier. We perform numerical experiments using these 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 $\Sigma_1 = 0.7755$, $\Sigma_3 = 5.7682 \times 10^{-4}$, $\Sigma_1\Sigma_2 - \Sigma_3 = 0.0059$, which means that system (8) is locally asymptotically stable around the positive interior equilibrium E^* .

In absence of cascading migration, system (8) becomes the dimensionless system of the Hastings–Powell model.

Hastings and Powell observed the stability, limit cycle, and chaotic dynamics of the system by changing the half-saturation constant (b_1). We first observe the exchange of states (stability-limit, cycle-period, period-doubling route to chaos) keeping the parameter values the same as [35] except for the parameter a_2 . We observed that for $0 < b_1 < 1.2$ the system is stable around the positive steady state (Fig. 1a) and for $1.2 < b_1 < 1.63$ it shows limit cycle oscillation (Fig. 1b). Period doubling is observed at $b_1 = 1.63$ (Fig. 1c). Finally, chaotic dynamics is observed for $1.63 < b_1 \leq 9.4$ (Fig. 1d).

To observe the effect of cascading migration in system (8), we fix the migration ratio of prey ($f = 0.2$) and the migration ratio of the middle predator ($k = 0.2$) and vary the migration ratio of the top-predator (m) where the other parameter values are kept the same as in Fig 1(d). For $0.072 < m < 0.15$, the system is stable around the positive steady state (Fig. 2a), which indicates that cascading migration has the potential to stabilize the chaotic system, but a further increment in m leads the system from stable fixed point to limit cycle (with Hopf bifurcation occurring at $m = 0.15$), limit cycle to period doubling and period doubling to chaos. The system shows limit cycle oscillation for $0.15 < m < 0.4$ (Fig. 2b) and period doubling observed at $m = 0.4$ (Fig. 2c). The system shows chaotic behavior for $0.4 < m \leq 1.29$ (Fig. 2d), and the system collapses if the migration ratio (m) is increased further.

To make it clearer, we draw bifurcation diagrams for all the populations with m as the bifurcation parameter (Fig. 3). We observe that for $m > 0.072$, three species start to

Fig. 1 The figure depicts the solution of system (8) in the absence of cascading migration. **a** Steady-state stable distribution with $a_1 = 5$, $a_2 = 0.2$, $\bar{a}_2 = 0.18$, $b_1 = 1$, $b_2 = 2$, $d_1 = 0.4$, $d_2 = 0.01$. **b** Limit cycle oscillation for $b_1 = 1.6$. **c** Period-doubling of the system for $b_1 = 1.7$. Finally, **d** shows chaotic oscillation at $b_1 = 5$

Fig. 2 In the presence of cascading migration, **a** shows stable co-existence of three species of system (8) for $a_1 = 5$, $a_2 = 0.2$, $\bar{a}_2 = 0.18$, $b_1 = 5$, $b_2 = 2$, $d_1 = 0.4$, $d_2 = 0.01$, $d = 0.05$, $k = 0.2$, $f = 0.2$, $m = 0.1$. **b** Limit cycle oscillation of the system for $m = 0.39$. **c** Period-doubling of the system for $m = 0.4$. Finally, **d** depicts the chaotic dynamics of the dynamics for $m = 0.6$

coexist and the system shows a steady-state solution in the range $0.072 < m < 0.15$, a limit cycle for $0.15 < m < 0.4$, and finally the system goes to chaos through period doubling for $m > 0.4$, keeping the other parameters the same as in Fig. 2. The system remains chaotic for $0.4 < m \leq 1.29$, but for $m > 1.29$ the z -population extinct from the system and the x and y -populations show boom-bust dynamics. Furthermore, all the branching points of the bifurcation diagrams are always the same for the three populations. To make it clearer, we indicate the branching points by a vertical dashed line in each bifurcation diagram.

In Fig. 4, for $f = 0.2$ and $m = 0.1$ the bifurcation diagram is drawn with bifurcation parameter k , the migration ratio of the middle predator. The system shows stable dynamics for $0.0014 < k < 0.0015$, limit cycle for $0.0015 < k < 0.016$, period doubling for $0.016 < k < 0.019$, and higher periodicities and chaos for $0.019 < k < 0.044$. A 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 dynamics 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 returns to its stable steady-state solution from chaos through a period halving bifurcation. Finally, the z -population becomes extinct for $k \geq 0.274$ and the x - and y -populations show oscillatory coexistence.

On the other hand, when the value of k and m are kept fixed as 0.2 and 0.1, the system is stable around the positive steady state for $0.103 < f < 1.14$ and leads to oscillation

Fig. 3 The bifurcation diagram of system (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 a higher value of m the system collapses. Other parameter values are kept the same as in Fig. 2. The vertical dashed lines indicate the branching points

(with Hopf bifurcation occurring at $f = 1.14$) for $1.14 < f < 2.357$ (Fig. 5). However, if the value of f is higher than 2.357, then the z -population becomes extinct and the x - and y -populations show boom–bust dynamics.

It is believed that chaos may arise in tri-trophic food-chain systems due to oscillations in predator–prey systems. Hastings and Powell [35] observed that 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

Fig. 4 Bifurcation diagrams of system (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

subsystems are coupled through the 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., the period of one subsystem is not some multiple of the other subsystem), chaos arises in the tri-trophic food-chain system [35].

Here, the chaotic behavior of system (8) may be interpreted in terms of m , k and f , the migration ratios of top predator, middle predator, and prey populations. If we keep other migration ratios fixed, an increase in m implies that relatively more top predators (fish)

Fig. 5 Bifurcation diagrams of system (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 a stable condition. The vertical dashed line indicates the bifurcating point

migrate 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 increase 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 this threshold value, the system shows oscillation and becomes chaotic whenever the frequencies of the oscillations in the $x - y$ and $y - z$ subsystems are not commensurate. However, the migrations of phytoplankton and zooplankton are assumed

to be inducible defense mechanisms of respective populations. If the migration ratio of the middle predator, k , is increased, then within a range of values of k , the system shows oscillations and chaotic behavior, whereas below and above this range, the system becomes stable. For this range of values of k , the trade-off between the lower food of zooplankton and the 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 the prey population, f , is increased, the system shows stable dynamics up to a threshold value as the edibility of prey is 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 this range, the top predator becomes extinct. However, the prey and the middle predator populations show boom–bust oscillations. Thus, an increase in the migration ratio of the top predator makes the system chaotic whereas an increase in the migration ratios of the middle predator and prey populations makes the system more regular.

6 Conclusions

Our results suggest that for different sets of migration rate values of each trophic level (i.e., the migration ratios 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 switch from one state into another, from chaos to order, and from order and to chaos. Increasing the value of the migration ratio of prey leads the system to limit cycle from stable steady state (Fig. 5). The transitions between stable steady state, limit cycle, period doubling, chaos, period halving, and ultimately to a stable steady state occurred for gradual increases in the migration ratio of middle predator (Fig. 4) whereas the transitions occurred between a stable steady state, limit cycle, period doubling, and chaos for increasing values of the migration ratio of top predator (Fig. 3). The stabilizing effect (chaos to order) of migrations of middle predator on the Hastings–Powell model has already been observed by [45]. Our results clearly indicate that the cascading migration on the top predator (naturally other trophic level) enhances the system stability. It is also interesting to note that increasing the cascading migration of the top predator, the system enters into a chaotic phase from the order phase. 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 would like to mention that as this is the first model in this direction, there are lots of scopes to generalize the model. As a matter of fact, to study DVM in a 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 [51]. The assumptions and hypotheses can be modified according to the future outcomes of laboratory and field experiments on cascading migration. We hope that it will help observationalists and experimentalists to design their own experiments to manipulate the rate of cascading migrations.

Acknowledgements The authors are grateful to the reviewers for their useful comments on the previous version of the paper.

Appendix

Appendix A: Proof of Theorem 1

Let us define a function

$$W = x + y + z. \quad (11)$$

The time derivative of Eq. (9) along with the solution of (8) is

$$\begin{aligned} \frac{dW}{dt} &= \frac{dx}{dt} + \frac{dy}{dt} + \frac{dz}{dt} = r \left(1 - \frac{x}{\tilde{K}} \right) - d_1 y - d_2 z \\ &\Rightarrow \frac{dW}{dt} + \mu W = rx \left(1 + \frac{\mu}{r} - \frac{x}{\tilde{K}} \right) - (d_1 - \mu)y - (d_2 - \mu)z \\ &\leq \frac{(r + \mu)^2 \tilde{K}}{4r} = L \text{ (say)}, \end{aligned}$$

where $\mu \leq \min\{d_1, d_2\}$.

Applying the theorem of differential inequality [52], 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 $t \rightarrow \infty$. Hence, all the solutions of (8), that initiate in $R_+^3 - \{0\}$, are confined in the region $B = \{(x, y, z) \in R_+^3 : W = L/\mu + \epsilon\}$.

Appendix B: Proof of Theorem 2

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

$$\begin{aligned} \lambda_1(m) &= \phi_1(m) + i\phi_2(m), \\ \lambda_2(m) &= \phi_1(m) - i\phi_2(m), \\ \lambda_3(m) &= -\Sigma_1. \end{aligned}$$

Now, we shall verify the transversality condition

$$\frac{d}{dm}(\operatorname{Re}(\lambda(m)))|_{m=m^*} \neq 0, \quad j = 1, 2.$$

Substituting $\lambda_j(m) = \phi_1(m) + i\phi_2(m)$ into the characteristic equation and calculating the derivative, we have

$$\begin{aligned} P(m)\phi_1'(m) - Q(m)\phi_2'(m) + U(m) &= 0, \\ Q(m)\phi_1'(m) + P(m)\phi_2'(m) + V(m) &= 0, \end{aligned}$$

where

$$\begin{aligned}P(m) &= 3\phi_1^2(m) + 2\Sigma_1(m)\phi_1(m) + \Sigma_2(m) - 3\phi_2^2(m), \\Q(m) &= 6\phi_1(m)\phi_2(m) + 2\Sigma_1(m)\phi_2(m), \\U(m) &= \phi_1^2(m)\Sigma'_1(m) + \Sigma'_2(m)\phi_1(m) + \Sigma'_3(m) - \Sigma'_1(m)\phi_2^2(m), \\V(m) &= 2\phi_1(m)\phi_2(m)\Sigma'_1(m) + \Sigma'_2(m)\phi_2(m).\end{aligned}$$

Noticing that $\phi_1(m^*) = 0$, $\phi_2(m^*) = \sqrt{\Sigma_2(m^*)}$, we have

$$\begin{aligned}P(m^*) &= -2\Sigma_2(m^*), \quad Q(m^*) = 2\Sigma_1(m^*)\sqrt{\Sigma_2(m^*)}, \\U(m^*) &= \Sigma'_3(m^*) - \Sigma'_1(m^*)\Sigma_2(m^*)\end{aligned}$$

and $V(m^*) = \Sigma'_2(m^*)\sqrt{\Sigma_2(m^*)}$. Now,

$$\begin{aligned}&\frac{d}{dm}(Re(\lambda(m)))|_{m=m^*} \\&= \frac{Q(m^*)V(m^*) + P(m^*)U(m^*)}{P(m^*)^2 + Q(m^*)^2} \\&= \frac{2\Sigma_1(m^*)\sqrt{\Sigma_2(m^*)} \times \Sigma'_2(m^*)\sqrt{\Sigma_2(m^*)} + (-2\Sigma_2(m^*))(\Sigma'_3(m^*) - \Sigma'_1(m^*)\Sigma_2(m^*))}{(-2\Sigma_2(m^*))^2 + (2\Sigma_1(m^*)\sqrt{\Sigma_2(m^*)})^2} \\&= \frac{\Sigma_1(m^*)\Sigma'_2(m^*) - \Sigma'_3(m^*) + \Sigma'_1(m^*)\Sigma_2(m^*)}{2(\Sigma_2(m^*) + (\Sigma_1(m^*))^2)} \\&\neq 0, \text{ if } \Sigma_1(m^*)\Sigma'_2(m^*) - \Sigma'_3(m^*) + \Sigma'_1(m^*)\Sigma_2(m^*) \neq 0,\end{aligned}$$

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.

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