Chapter 6

Effect of vertical migration of middle predator in a tri-trophic food chain: a non-autonomous system

6.1 Introduction

The diel vertical migration (DVM) of zooplankton in the water column is a well documented but poorly understood biological phenomenon. Diel vertical migration of zooplankton is a behavioral antipredator defense that is regulated by the trade off between higher predation risk in surface water and reduced growth rate in deep water. It has been observed that zooplankton migrates vertically downward during day hours in the presence of predator (or predator
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kairomone) and it enters into the surface water again at night to graze phytoplankton (Dodson, 1988b; Gliwicz, 1986; Lampert, 1989; Lass and Spaak, 2003; Loose and Dawidowicz, 1994; Neill, 1990; Stich and Lampert, 1981; Tollrian and Dodson, 1999). Avoidance of predators such as visually orienting planktivorous fish and carnivorous invertebrates is the most important factor which regulates DVM in zooplankton (Bollens and Frost, 1989a,b, 1991; Hardy and Gunther, 1935; Hays, 2003; Lampert, 1989; Zaret and Suffern, 1976; Stich and Lampert, 1981; Gliwicz, 1986; Pearre, 2003). Predator avoidance is generally thought to be the most important factor driving vertical migration in zooplankton (Zaret and Suffern, 1976). The strength of downward migration of zooplankton increased with increases in concentration of fish or fish-exudates (Cayelan et al., 2011; Loose and Dawidowicz, 1994). Zooplankton take daytime refuge from fish in the hypolimnion and areas of vegetation where food concentrations are lower than in the pelagic epilimnion (Davies, 1985; Lampert, 1989). Zooplankton, those migrating downward experience lower temperature and food deficiency, which force them to migrate vertically upward into the upper layer of the water column to predate phytoplankton. This upward migration of zooplankton from lower layer to upper layer is proportional to available phytoplankton density in the upper layer. Increase in phytoplankton density increases the strength of upward vertical migration of zooplankton by leaving the lower layer entering into the upper layer (Morozov et al., 2007).

The vertical gradient of light conditions decisively determines the predation pressure from visually orientated planktivorous fish. Concurrently, the development of the phytoplankton, the main food source for zooplankton, is highest...
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in the warm and well-lit upper layers, where predation by visual planktivores is most intensive. Facing these two contradictory environmental factors, most of zooplankton species have been found to exhibit different strategies regarding their position in the water column. These strategies usually exhibit a trade-off between meeting their food requirements and decreasing the threat of predation. One possibility, well characterized as "better hungry than dead" (Kremer and Kremer, 1988; Lampert, 1989), is seen in animals that perform diel vertical migrations. They spend the daylight period in the relatively safe but cold and food-poor hypolimnion, and ascend to the warm and food-rich epilimnion only during the night. The contrasting "better dead than unfed" strategy is adopted by animals staying in the epilimnion until they feed sufficient amount of food to tolerate the metabolic cost and the cost of vertical migration, in spite of the greater danger of predation (Huntley and Brooks, 1982; Flik and Ringelberg, 1993; Johnsen and Jakobsen, 1987).

Experimental and field data revealed that besides biotic factors (predation pressure and food availability), abiotic factors such as light intensity (George, 1983), thermal stratification (Tappa, 1965; Carter and Goudie, 1986; McLaren, 1963), dissolved oxygen (Hanazato et al., 1989; Weider and Lampert, 1985) and salinity (Rothlisberg, 1982) stimulate the vertical distribution of zooplankton. Food availability, predation pressure and light are the major control variables of DVM (Enright, 1977; Enright and Honegger, 1977; Iwasa, 1982; Clark and Levy, 1988; Han and Straskraba, 1998, 2001). Light, among the abiotic factor is the most important factors inducing diurnal vertical migrations of zooplankton in the upper water layer (Williamson et al., 1994; Ringelberg, 1999; Hans-
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son et al., 2007). Light (sunlight and moonlight) acts as a visual cue which mediate strong effects on such avoidance behavior (Gliwicz, 1986; Ringelberg, 1995).

Changes in light intensity have been proposed as the main exogenous factor causing vertical migrations of zooplankton at dawn and dusk, in both marine and freshwater environments (Cushing, 1951; Ringelberg, 1995). Although light induced swimming of Daphnia was found to be enhanced in the presence of a predator kairomone (Ringelberg, 1991; Van Gool and Ringelberg, 1995). Food concentration and predator kairomone level influence the swimming velocity of zooplankton in response to light changes (Van Gool and Ringelberg, 1998a,b). Usually, zooplankton migrate to deeper water to escape predation by visually hunting fish during the day, and return to the food-rich surface water to eat and profit from warmer water at night (DeMeester et al., 1999).

6.2 Mathematical model

Depending on the light availability into the water column we split the whole pelagic water mass into two layers: surface water and deep water. The water column above the secchi depth is referred as surface water or upper layer, where light is available at daytime; whereas, bellow the secchi depth, the water column, where light is not available (or available light intensity is very low) during day hours, is refereed as lower layer (deep water). We assume that phytoplankton (P) are present only in the upper layer and its density is homogenous throughout the layer. Let, $Z_1$ and $Z_2$ be the abundance of
zooplankton in the upper layer and lower layer respectively. We assume that zooplankton in the upper layer graze on phytoplankton and zooplankton in the lower layer cannot predate until they enter into surface water.

Most of the fishes show visually oriented predation (light-dependent predation) on zooplankton. Thus, we assume that fish predate zooplankton only in the upper layer. Zooplankton of upper layer migrates vertically downward to escape from the light-dependent mortality imposed by visually orienting predator (fish) during day hours. This down-ward migration of zooplankton from upper layer to lower layer is directly proportional to predation pressure (i.e., predator abundance). In the presence of kairomones (predator and/or predator exudates) a portion of zooplankton become invulnerable to predator through the prey refuge (via downward vertical migrations). On the other hand, zooplankton of lower layer experience lower temperature and food deficiency, which force them to migrate vertically upward into the upper layer of the water column to predate phytoplankton. This upward migration of zooplankton from lower layer to upper layer is also proportional to available phytoplankton density in the upper layer. Thus, zooplankton population makes the transition from vulnerable to invulnerable state through inducible defense mechanisms (vertical migration) in presence of predators. We also assume that zooplankton living in the lower layer cannot reproduce.

Keeping the above facts in mind the dynamics of the system is governed by the following systems of nonlinear differential equations:
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\[\begin{align*}
\frac{dP}{dt} &= rP\left(1 - \frac{P}{K}\right) - \frac{a_1 P Z_1}{b_1 + P}, \\
\frac{dZ_1}{dt} &= \frac{c_1 a_1 P Z_1}{b_1 + P} - \frac{a_2 Z_1^2 F}{b_2 + Z_1^2} - m_1 Z_1 F + m_2 P Z_2 - \mu Z_1, \\
\frac{dZ_2}{dt} &= m_1 Z_1 F - m_2 P Z_2 - \mu Z_2, \\
\frac{dF}{dt} &= \frac{c_2 a_2 Z_2^2 F}{b_2 + Z_2^2} - \phi F.
\end{align*}\]  

(6.1)

Where phytoplankton population follows the logistic growth with maximum intrinsic growth rate \(r\) and carrying capacity \(K\) in the absence of predation. We assume that, predation of zooplankton on phytoplankton in the upper layer follows holling type-II functional response with half saturation constant \(b_1\), whereas the fish predation on zooplankton in the upper layer follows holling type-III functional response (Scheffer, 1991) with half saturation constant \(b_2\). Zooplankton of the upper layer migrate downward at the rate \(m_1\) and that of the upward migration rate of zooplankton of the lower layer is \(m_2\). Let, \(c_1\) and \(c_2\) are the conversion efficiency of zooplankton and fish respectively. Let, \(\mu\) be the natural mortality rate of zooplankton.

6.3 Model Analysis

6.3.1 Boundedness of the system

Theorem 6.1 All the solution of (6.1) with positive initial conditions are bounded.

Proof: Let us define a function

\[W = P + \frac{1}{c_1} Z_1 + \frac{1}{c_2} Z_2 + \frac{1}{c_1 c_2} F.\]  

(6.2)
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The time derivative of the Equation (6.2) along with the solution of (6.1) is

\[
\frac{dw}{dt} = \frac{dP}{dt} + \frac{1}{c_1} \frac{dZ_1}{dt} + \frac{1}{c_1 c_2} \frac{dZ_2}{dt} + \frac{1}{c_1 c_2} \frac{dF}{dt}
= rP \left( 1 - \frac{P}{K} \right) \left[ \frac{\mu}{c_1} Z_1 - \frac{\mu}{c_1} Z_2 - \frac{\phi}{c_1 c_2} F \right]
\]

\[
\frac{dw}{dt} + qW = \left( rP + qP - \frac{rP^2}{K} \right) - \left( \frac{\mu}{c_1} - q \right) Z_1 - \left( \frac{\mu}{c_1} - q \right) Z_2 - \left( \frac{\phi}{c_1 c_2} - q \right) F
\]

Now if \( q < \min \{ \frac{\mu}{c_1}, \frac{\phi}{c_1 c_2} \} \) then

\[
\frac{dw}{dt} + qW \leq \left( rP + qP - \frac{rP^2}{K} \right)
\]

\[
\frac{dw}{dt} + qW \leq \frac{(r + q)^2 K}{4r} = B \text{ (say)}
\]

Applying the theorem of differential inequality (Birkhoff and Rota, 1989), we obtain

\[
0 \leq W(P(t), Z_1(t), Z_2(t), F(t)) \leq \frac{B}{q} (1 - e^{-qt}) + W(P(0), Z_1(0), Z_2(0), F(0)) e^{-qt}
\]

, which implies that \( 0 \leq W \leq \frac{B}{q} \) as \( t \to \infty \). Hence, all the solution of (6.1), are bounded.

6.3.2 Equilibria and their existence

The above model (6.1) has at most four non-negative equilibrium points. The trivial equilibrium point \( E_0(0, 0, 0, 0) \) and the axial equilibrium point
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$E_1(K, 0, 0, 0)$ exist for all parameter values. The top predator free equilibrium point is $E_2(P, Z_1, 0, 0)$, where

$$
\bar{P} = \frac{\mu b_1}{c_1 a_1 - \mu}, \quad Z_1 = \frac{r}{a_1} (b_1 + \bar{P}) \left(1 - \frac{P}{K}\right).
$$

The top predator free equilibrium point $E_2$ exists if $\mu < \frac{c_1 a_1 K}{1 + b_1}$.

The interior equilibrium is given by $E^*(P^*, Z_1^*, Z_2^*, F^*)$, where

$$
Z_1^* = \sqrt{\frac{\phi b_2}{c_2 a_2 - \phi}}, \quad P^* = \frac{1}{2} \left( (K - b_1) + \sqrt{(K - b_1)^2 + 4 \left( b_1 K - \frac{a_1 K Z_1^*}{r} \right)} \right),
$$

$$
Z_2^* = \frac{m_1 (b_2^2 + Z_1^{2*}) (c_1 a_1 P^* Z_1^* - \mu Z_1^* (b_1 + P^*))}{(b_1 + P^*) (a_2 * Z_1^* (m_1 P^* + \mu) + \mu m_1 (b_2^2 + Z_1^{2*}))}, \quad F^* = \frac{(m_2 P^* + \mu) Z_2^*}{m_1 Z_1^*}.
$$

The interior equilibrium $E^*$ exists if the following conditions hold

$c_2 a_2 > \phi$, $\frac{c_1 a_1 P^*}{b_1 + P^*} > \mu$, $K > b_1$ and $(K + b_1)^2 - \frac{4 a_1 K Z_1^*}{r} > 0$.

6.3.3 Local stability of equilibria

**Theorem 6.2**

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

(ii) The axial equilibrium point $E_1(K, 0, 0, 0)$ is locally asymptotically (LAS) if $R_{01} < 1$, where $R_{01} = \frac{1}{\mu} \left( \frac{c_1 a_1 K}{(b_1 + K)} \right)$,

(iii) The predator free equilibrium point $E_2(P, Z_1, 0, 0)$ is LAS if $R_{02} < 1$, where $R_{02} = \frac{1}{\phi} \left( \frac{c_2 a_2 Z_2^2}{(b_2 + Z_1^*)} \right)$ and $\frac{r}{K} > \frac{a_1 Z_1^*}{(b_1 + P^*)^2}$.
(iv) The interior equilibrium point \( E^*(P^*, Z^*_1, Z^*_2, F^*) \) for the system (6.1) is locally asymptotically stable if \( \sigma_1, \sigma_3, \sigma_4 > 0 \) and \( \sigma_1 \sigma_2 \sigma_3 > \sigma_2^2 + \sigma_1^2 \sigma_4 \), where \( \sigma_1, \sigma_2, \sigma_3, \sigma_4 \) are given below.

**Proof.** The local stability of the system (6.1) around each of the equilibria is obtained by computing the Jacobian matrix corresponding to each equilibrium point. The Jacobian matrix around arbitrary equilibrium point \( E = (P, Z_1, Z_2, F) \) for the system (6.1) is given by

\[
J(P, Z_1, Z_2, F) =
\begin{pmatrix}
 r - \frac{2rP}{K} - \frac{a_1 Z_1}{(b_1 + P)} + \frac{a_1 P Z_1}{(b_1 + P)^2} & -\frac{a_1 P}{(b_1 + P)} & 0 & 0 \\
\frac{a_1 b_1 Z_1}{(b_1 + P)^2} + m_2 Z_2 & \frac{a_1 P}{(b_1 + P)} - \frac{2a_2 b_2 Z_1 P}{(b_2 + Z_2)^2} - m_1 F - \mu & m_2 P & -\frac{a_2 Z_1^2}{(b_2 + Z_2)^2} - m_1 Z_1 \\
-m_2 Z_2 & m_1 F & -m_2 P - \mu & m_1 Z_1 \\
0 & \frac{2a_2 b_2 Z_1 P}{(b_2 + Z_2)^2} & 0 & \frac{c_2 Z_1^2}{(b_2 + Z_2)^2} - \phi
\end{pmatrix}
\]

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

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

The eigenvalues of the Jacobian matrix at \( E_0 \) are \( r, -\mu, -\mu, -\phi \). One of the eigenvalues \( (r) \) is always positive. Therefore, \( E_0 \) is always unstable.

(ii) The Jacobian matrix at the equilibrium point \( E_1(K,0,0,0) \) is

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\[ J(E_1) = \begin{pmatrix} -r - \frac{a_1 K}{b_1 + K} & 0 & 0 \\ 0 & \frac{a_1 K}{b_1 + K} - \mu & 0 \\ 0 & 0 & -m_2 K - \mu \end{pmatrix}. \]

The eigenvalues are \(-r\), \(-\frac{a_1 K}{b_1 + K} - \mu\), and \(-\phi\). Therefore, the equilibrium point \(E_1\) is stable if \(-\frac{a_1 K}{b_1 + K} - \mu < 0\) which implies \(R_{01} < 1\).

(iii) The Jacobian matrix at the equilibrium point \(E_2(\bar{P}, \bar{Z}_1, 0, 0)\) is LAS if \(R_{02} < 1\) is

\[ J(E_2) = \begin{pmatrix} -\frac{r\bar{P}}{K} + \frac{a_1 P\bar{Z}_1}{(b_1 + \bar{P})^2} & -\frac{a_1 \bar{P}}{b_1 + \bar{P}} & 0 & 0 \\ \frac{a_1 b_1 c_1 \bar{Z}_1}{(b_1 + \bar{P})^2} & 0 & m_2 \bar{P} & -\frac{a_2 \bar{Z}_1^2}{(b_2^2 + \bar{Z}_1^2)} - m_1 \bar{Z}_1 \\ 0 & 0 & -m_2 \bar{P} - \mu & m_1 \bar{Z}_1 \\ 0 & 0 & 0 & a_2 c_1 \bar{Z}_1^2 \end{pmatrix}. \]

The characteristic equation of the Jacobian matrix is

\[
\lambda^2 - \left( -\frac{r\bar{P}}{K} + \frac{a_1 P\bar{Z}_1}{(b_1 + \bar{P})^2} \right) \left( -m_2 \bar{P} - \mu - \lambda \right) \left( \frac{a_2 c_1 \bar{Z}_1^2}{(b_2^2 + \bar{Z}_1^2)} - \phi - \lambda \right) = 0
\]

and the corresponding eigenvalues are

\[
\lambda_{1,2} = \frac{1}{2} \left( \frac{r\bar{P}}{K} - \frac{a_1 P\bar{Z}_1}{(b_1 + \bar{P})^2} \right) \pm \sqrt{\left( \frac{r\bar{P}}{K} - \frac{a_1 P\bar{Z}_1}{(b_1 + \bar{P})^2} \right)^2 - 4\frac{a_2 c_1 P\bar{Z}_1}{(b_1 + \bar{P})^4}},
\]

\[
\lambda_3 = -m_2 \bar{P} - \mu,
\]

\[
\lambda_4 = \frac{c_2 a_2 \bar{Z}_1^2}{b_2^2 + \bar{Z}_1^2} - \phi.
\]

Hence, \(E_2\) is LAS if \(\frac{c_2 a_2 \bar{Z}_1^2}{b_2^2 + \bar{Z}_1^2} - \phi < 0\) and \(\frac{r\bar{P}}{K} - \frac{a_1 P\bar{Z}_1}{(b_1 + \bar{P})^2} > 0\) which implies the conditions \(R_{02} < 1\) and \(\frac{r}{K} > \frac{a_1 \bar{Z}_1}{(b_1 + \bar{P})^2}\).
(iii) The Jacobian matrix $J(E^*) = J_{ij}$ ($i,j=1,2,3,4$) at the interior point $E^*(P^*, Z_1^*, Z_2^*, F^*)$ has the components

$$
J_{11} = \frac{a_1 P^* Z_1^*}{(b_1 + P^*)^2} - \frac{r P^*}{K},
J_{12} = -\frac{a_1 P^*}{(b_1 + P^*)},
J_{13} = 0,
J_{14} = 0,
$$

$$
J_{21} = \frac{c_1 a_1 b_1 Z_1^*}{(b_1 + P^*)^2} + m_2 Z_2^*,
J_{22} = \frac{c_1 a_1 P^*}{(b_1 + P^*)^2} - 2a_2 b_2 Z_1^* F^* - m_1 F^* - \mu,
$$

$$
J_{23} = m_2 P^*,
J_{24} = \frac{a_2 Z_1^*}{(b_2 + Z_1^*)^2} - m_1 Z_1^*,
J_{31} = m_2 Z_2^*,
J_{32} = m_1 F^*,
$$

$$
J_{33} = -m_2 P^* - \mu,
J_{34} = m_1 Z_1^*,
J_{41} = 0,
J_{42} = \frac{2c_2 a_2 b_2 Z_1^* F^*}{(b_2 + Z_1^*)^2},
J_{43} = 0,
J_{44} = 0.
$$

The characteristic equation of the Jacobian matrix is given by

$$
\rho^4 + \sigma_1 \rho^3 + \sigma_2 \rho^2 + \sigma_3 \rho + \sigma_4 = 0
$$

where

$$
\sigma_1 = -J_{11} - J_{22} + J_{33}
$$

$$
\sigma_2 = J_{11} J_{22} + J_{11} J_{33} + J_{22} J_{33} - J_{23} J_{32} - J_{24} J_{42} - J_{12} J_{21}
$$

$$
\sigma_3 = -J_{11} J_{22} J_{33} + J_{11} J_{23} J_{32} + J_{11} J_{24} J_{42} - J_{23} J_{34} J_{42} + J_{24} J_{34} J_{43} + J_{24} J_{33} J_{42} + J_{12} J_{21} J_{33} - J_{12} J_{23} J_{31}
$$

$$
\sigma_4 = J_{11} J_{23} J_{34} J_{42} - J_{11} J_{24} J_{33} J_{42}.
$$

Using the Routh-Hurwitz criteria we observe that the system (6.1) is stable around the interior equilibrium point $E^*$ if $\sigma_1 > 0$, $\sigma_3 > 0$, $\sigma_4 > 0$ and $\sigma_1 \sigma_2 \sigma_3 > \sigma_3^2 + \sigma_1^2 \sigma_4$.

Hence the prove.
6.4 Seasonally forced system

Light and temperature, modified by other physical and biological factors, seem usually to be important in initiating, controlling, and orienting migration. Light is assumed to act on the migration not only by its absolute value but also by its relative intensity variation (Forward, 1988). Zooplankton usually shows light dependent migration in the presence of predators. The benefit of downward migration at dawn is the escape from the light-dependent mortality imposed by visually orienting predators, mostly fish, during daylight hours. The zooplankton of deep water enters into the surface water at night to graze phytoplankton when the predation risk is negligible. Most species migrated upward as the surface light intensity decreased and downward with an increase in light intensity. Therefore, migration rates of zooplankton and the predation rate of fish are strongly influenced by light. To include the effect of the seasonal cycle of light and temperature in the model (6.1), we impose a sinusoidal variation of the value of the relevant model parameters over the year.

Considering the rate parameters of the system (6.1) to be periodic function, we propose a non-autonomous model given below

\[
\frac{dP(t)}{dt} = r(t)P(1 - \frac{P}{K(t)}) - \frac{a_1(t)PZ_1}{b_1 + P},
\]

\[
\frac{dZ_1(t)}{dt} = \frac{c_1(t)a_1(t)PZ_1}{b_1 + P} - \frac{a_2(t)Z_1^2F}{b_2^2 + Z_1^2} - m_1(t)Z_1F + m_2(t)PZ_2 - \mu(t)Z_1,
\]

\[
\frac{dZ_2(t)}{dt} = m_1(t)Z_1F - m_2(t)PZ_2 - \mu(t)Z_2,
\]

\[
\frac{dF(t)}{dt} = \frac{c_2(t)a_2(t)Z_2^2F}{b_2^2 + Z_2^2} - \phi(t)F.
\]

We assume that the carrying capacity \((K)\) to be a function of light. The parameters related with metabolism of phytoplankton, zooplankton and fish
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$(r, a_1, a_2, c_1, c_2, \mu, \phi)$ depend upon temperature. The daily average migration rate, both downward migration and upward migration also depend on light. Therefore, $r(t)$, $K(t)$, $a_1(t)$, $a_2(t)$, $c_1(t)$, $c_2(t)$, $m_1(t)$, $m_2(t)$, $\mu(t)$, $\phi(t) \in C(\mathbb{R}, \mathbb{R}^+)$, $\mathbb{R}^+ = (0, +\infty)$ are $\omega$-periodic functions; $b_1$, $b_2$ are positive constants.

It is to be noted that the summer maximum in the temperature is usually delayed compared to the maximum in irradiation. For simplicity, we neglect this phase shift and simply incorporate the effect of seasons by considering the periodic rate parameters with period of one year.

6.5 Existence of periodic solution

In this section, we use Gaines and Mawhin's continuation theorem to establish the sufficient conditions for the existence of positive periodic solutions of the system (6.3). To derive the sufficient conditions for the existence of positive periodic solution, we first summarize some important results from (Gaines and Mawhin, 1977) that will be basic for this section.

Let $X, Y$ be real Banach spaces, $L : \text{Dom}L \subset X \to Y$ a linear mapping, and $N : X \to Y$ a continuous mapping. The mapping $L$ is called a Fredholm mapping of index zero if $\dim \text{Ker}L = \text{codim} \text{Im}L < +\infty$ and $\text{Im}L$ is closed in $Y$. If $L$ is a Fredholm mapping of index zero and there exist continuous projectors $P : X \to Y$, and $Q : Y \to Y$ such that $\text{Im}P = \text{Ker}L$, $\text{Ker}Q = \text{Im}(I - Q)$, then the restriction $L_P$ of $L$ to $\text{Dom}L \cap \text{Ker}P : (I - Q)X \to \text{Im}L$ is invertible. Denote the inverse of $L_P$ by $K_P$. If $\Omega$ is an open bounded subset of $X$, the mapping $N$ will be called $L$-compact on $\bar{\Omega}$ if $QN(\bar{\Omega})$ is bounded and
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$K_p(I - Q)N : \tilde{\Omega} \to X$ is compact. Since $\text{Im} Q$ is isomorphic to $\text{Ker} L$, there exists isomorphism $J : \text{Im} Q \to \text{Ker} L$.

**Lemma 6.1.** Let $Q \subset X$ be an open bounded set. Let $L$ be a Fredholm mapping of index zero and $N$ be $L -$ compact on $\tilde{\Omega}$. Assume

(a) for each $\lambda \in (0, 1)$, $x \in \partial \Omega \cap \text{Dom} L$, $Lx \neq \lambda Nx$;

(b) for each $x \in \partial \Omega \cap \text{Ker} L$, $QNx \neq 0$;

(c) $\deg \{Q, \Omega \cap \text{Ker} L, 0\} \neq 0$.

Then $Lx = Nx$ has at least one solution in $\tilde{\Omega} \cap \text{Dom} L$.

**Lemma 6.2.** If function $f$ is nonnegative, intergal and uniformly continuous on $[0, +\infty)$, then $\lim_{t \to \infty} f(t) = 0$ (Gopalsamy, 1992).

**Definition 6.1.** If $\bar{x}(t)$ is a $\omega -$ periodic solution of system (6.3), and $x(t)$ is an any solution of (6.3) satisfying $\lim_{t \to \infty} |\bar{x}(t) - x(t)| = 0$, we call $\bar{x}(t)$ globally attractive.

Throughout this paper, we denote

$$\bar{f} = \frac{1}{\omega} \int_0^\omega f(t) dt, \quad f^L = \min_{t \in [0, \omega]} f(t), \quad f^M = \max_{t \in [0, \omega]} f(t).$$

**Remark:** Following the boundedness of the system (6.1) we have,

$$W(P(t), Z_1(t), Z_2(t), F(t)) \leq \frac{(r^M + q)^2 K^M}{4r L} = \tilde{B} \ (\text{say}).$$

Therefore, the system (6.3) is also bounded.
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Theorem 6.3 The system (6.3) has at least one positive \( \omega \)-periodic solution if the following condition hold:

\[
[A_1] \text{ the algebraic equation set set:}
\]

\[
\begin{align*}
\bar{f} - \frac{\bar{r}e^{u_1}}{K} - \frac{\bar{a}_1 e^{u_2}}{b_1 + e^{u_1}} &= 0, \\
\bar{c}_1 \bar{a}_1 e^{u_1} - \frac{\bar{a}_2 e^{u_2+u_4}}{b_2 + e^{2u_2}} - \bar{m}_1 e^{u_4} + \bar{m}_2 e^{u_1-u_2+u_3} - \bar{\mu} &= 0, \\
\bar{m}_1 e^{u_4+u_2-u_3} - \bar{m}_2 e^{u_1} - \bar{\mu} &= 0, \\
\bar{c}_2 \bar{a}_2 e^{2u_2} - \bar{\phi} &= 0,
\end{align*}
\]

has finite real-valued solutions \((u_1^*, u_2^*, u_3^*, u_4^*), i = 1, 2, ..., n, such that

\[
\sum_{(u_1^*, u_2^*, u_3^*, u_4^*)} \det G(u_1^*, u_2^*, u_3^*, u_4^*) \prod_{i=1}^{n} u_1^* \prod_{i=1}^{n} u_2^* \prod_{i=1}^{n} u_3^* \prod_{i=1}^{n} u_4^* \neq 0,
\]

where, \( G(u_1, u_2, u_3, u_4) \) is a \( 4 \times 4 \) matrix and \( G \) has the components

\[
\begin{align*}
G_{11} &= -\frac{\bar{r}e^{u_1}}{K} + \frac{\bar{a}_1 e^{u_1+u_2}}{(b_1 + e^{u_1})^2},
G_{12} &= -\frac{\bar{a}_1 e^{u_2}}{b_1 + e^{u_1}},
G_{13} &= 0,
G_{14} &= 0, \\
G_{21} &= \frac{\bar{c}_1 \bar{a}_1 e^{u_1}}{b_1 + e^{u_1}} - \frac{\bar{c}_1 \bar{a}_1 e^{u_1}}{(b_1 + e^{u_1})^2} + \bar{m}_2 e^{u_1-u_2+u_3},
G_{22} &= -\frac{\bar{a}_2 e^{u_4+u_4}}{b_2^2 + e^{2u_2}} + \frac{2\bar{a}_2 e^{3u_2+u_4}}{(b_2^2 + e^{2u_2})^2},
G_{23} &= \bar{m}_1 e^{u_4-u_2+u_3},
G_{24} &= -\frac{\bar{a}_2 e^{u_2+u_4}}{b_2^2 + e^{2u_2}} - \bar{m}_1 e^{u_4},
G_{31} &= \bar{m}_1 e^{u_2-u_3+u_4},
G_{32} &= \bar{m}_2 e^{u_2-u_3+u_4},
G_{33} &= -\bar{m}_1 e^{u_2-u_3+u_4},
G_{34} &= \bar{m}_1 e^{u_2-u_3+u_4},
G_{41} &= 0, \\
G_{42} &= \bar{m}_1 e^{u_2-u_3+u_4},
G_{43} &= 0,
G_{44} &= 0.
\end{align*}
\]

Then system (6.3) has at least one positive \( \omega \)-periodic solutions.

Proof. Suppose \((P(t), Z_1(t), Z_2(t), F(t))\) ia an arbitraty positive solution
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of the system (6.3). Making change of variables

\[ u_1(t) = \ln\{P(t)\}, \]
\[ u_2(t) = \ln\{Z_1(t)\}, \]
\[ u_3(t) = \ln\{Z_2(t)\}, \]
\[ u_4(t) = \ln\{F(t)\}, \]

then equation (6.3) becomes,

\[ \begin{align*}
\frac{du_1(t)}{dt} &= r(t) - \frac{r(t) e^{u_1(t)}}{K(t)} - \frac{a_1(t) e^{u_1(t)}}{b_1 + e^{u_1(t)}}, \\
\frac{du_2(t)}{dt} &= \frac{c_1(t) a_1(t) e^{u_1(t)}}{b_1 + e^{u_1(t)}} - \frac{a_2(t) e^{u_2(t) - u_1(t)}}{b_2 + e^{u_2(t)}} - \frac{m_1(t) e^{u_4(t)}}{b_2 + e^{u_2(t)}} + \frac{m_2(t) e^{u_1(t) - u_2(t) + u_3(t)}}{b_2 + e^{u_2(t)}} - \mu(t), \\
\frac{du_3(t)}{dt} &= \frac{m_1(t) e^{u_1(t) - u_2(t) + u_3(t)}}{b_2 + e^{u_2(t)}} - \frac{m_2(t) e^{u_1(t) - u_2(t) - u_3(t)}}{b_2 + e^{u_2(t)}} - \mu(t), \\
\frac{du_4(t)}{dt} &= \frac{c_2(t) a_2(t) e^{u_2(t)}}{b_2 + e^{u_2(t)}} - \phi(t).
\end{align*} \]

Obviously, if the system (6.5) has one \( \omega \)-periodic solution \((u^*_1(t), u^*_2(t), u^*_3(t), u^*_4(t))\)^T, then \( z^*(t) = (P^*(t), Z_1^*(t), Z_2^*(t), F^*(t))^T = (\exp\{u^*_1(t)\}, \exp\{u^*_2(t)\}, \exp\{u^*_3(t)\}, \exp\{u^*_4(t)\})^T \) is a positive \( \omega \)-periodic solution of the system (6.1). Hence to complete the proof, it suffices to verify that system (6.5) has at least one \( \omega \)-periodic solution.

Set

\[ X = Y = \{(u_1(t), u_2(t), u_3(t), u_4(t))^T : u_i(t + \omega) = u_i, i = 1, 2, 3, 4\} \]

and

\[ \|(u_1(t), u_2(t), u_3(t), u_4(t))^T\| = \sum_{i=1}^{4} \max_{t \in [0, \omega]} |u_i(t)|, \]

where \( |.| \) denotes the Euclidian norm. Then \( X \) and \( Y \) are both Banach spaces when they are endowed with the norm \( \|\| \).

Let

\[ L : \text{Dom}L \cap X, L(u_1(t), u_2(t), u_3(t), u_4(t))^T = \left( \frac{du_1(t)}{dt}, \frac{du_2(t)}{dt}, \frac{du_3(t)}{dt}, \frac{du_4(t)}{dt} \right)^T, \]

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where, \( \text{Dom}\ L = \{ (u_1(t), u_2(t), u_3(t), u_4(t))^T \in C^1(R, R^4) \} \) and \( N : X \rightarrow X \),

\[
N\begin{pmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \end{pmatrix} = \begin{pmatrix}
\frac{\tau(t) - \tau(t)e^{u_1(t)}}{b_1 + e^{u_1(t)}} - \frac{a_1(t)e^{u_2(t)}}{b_1 + e^{u_1(t)}} \\
\frac{a_2(t)e^{u_2(t)} + u_4(t)}{b_2^2 + e^{2u_2(t)}} - m_1(t)e^{u_1(t)} + m_2(t)e^{u_1(t) - u_2(t) + u_3(t)} - \mu(t) \\
m_2(t)e^{u_1(t) - u_2(t) - u_3(t)} - m_2(t)e^{u_1(t)} - \mu(t) \\
\frac{c_2(t)a_2(t)e^{2u_2(t)}}{b_2^2 + e^{2u_2(t)}} - \phi(t)
\end{pmatrix}
\]

Define

\[
P \begin{pmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \end{pmatrix} = Q \begin{pmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \end{pmatrix} = \begin{pmatrix} \frac{1}{\omega} \int_0^\omega u_1(t)dt \\ \frac{1}{\omega} \int_0^\omega u_2(t)dt \\ \frac{1}{\omega} \int_0^\omega u_3(t)dt \\ \frac{1}{\omega} \int_0^\omega u_4(t)dt \end{pmatrix}, \quad \begin{pmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \end{pmatrix} \in X = Y.
\]

Obviously, we have

\[
\text{Ker}\ L = \{ x \mid x \in X, \ x = h, \ h \in R^4 \},
\]

\[
\text{Im}\ L = \{ y \mid y \in Y, \ \int_0^\omega y(t)dt = 0 \},
\]

and \( \text{dim Ker}\ L = \text{codim} L = 4 \).

Since \( \text{Im}\ L \) is closed in \( Y \), \( L \) is a Fredholm mapping of index zero. It is easy to show that \( P \) and \( Q \) are continuous projectors such that

\[
\text{Im}\ P = \text{Ker}\ L, \ \text{Ker}\ Q = \text{Im}\ L = \text{Im}\ (I - Q).
\]

Furthermore, through an easy computation, we can verify that the inverse \( K_P \) of \( L_P \) has the form

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\[ K_P : \text{Im } L \to \text{Dom } L \cap \text{Ker } P, \quad K_P(y) = \int_0^t y(s)\,ds - \frac{1}{\omega} \int_0^\omega \int_0^t y(s)\,ds\,dt. \]

Accordingly, \( QN : X \to Y \) and \( K_P(I - Q)N : X \to X \) lead
\[
QN_x = \left\{ \begin{array}{l}
\frac{1}{\omega} \int_0^\omega \left[ \frac{1}{\omega} \int_0^\omega \left[ \frac{r(t) - \frac{r(t) e^{u_1(t)}}{K(t)} - \frac{a_1(t) e^{u_2(t)}}{b_1 + e^{u_3(t)}}}{m_1(t) e^{u_4(t)} + m_2(t) e^{u_1(t) - u_2(t) + u_3(t) - u_4(t) - \mu(t)}} \right] dt \\
\frac{1}{\omega} \int_0^\omega \left[ \frac{c_2(t) e^{u_4(t)}}{b_2 + e^{2u_2(t)}} - \phi(t) \right] dt \\
\end{array} \right. 
\]

\[ K_P(I - Q)N_x = \int_0^t Nx(s)\,ds - \frac{1}{\omega} \int_0^\omega \int_0^t Nx(s)\,ds\,dt - \left( \frac{t - \frac{1}{2} \int_0^\omega Nx(s)\,ds}{\omega} \right) \]

Obviously, \( QN \) and \( K_P(I - Q)N \) are continuous by Lebesgue theorem. Moreover, \( QN(\Omega) \) and \( K_P(I - Q)N(\Omega) \) are relatively compact for any open bounded set \( \Omega \subset X \). Therefore, \( N \) is \( L \)-compact on \( \Omega \) for any open bounded set \( \Omega \subset X \).

In order to apply Lemma 2.1, we need to search for a suitable open, bounded subset \( \Omega \).

Corresponding to the operator equation \( Lx = \lambda Nx, \ \lambda \in (0, 1) \), one has

\[
\frac{du_1(t)}{dt} = \lambda \left[ \frac{r(t) e^{u_1(t)}}{K(t)} - \frac{a_1(t) e^{u_2(t)}}{b_1 + e^{u_3(t)}} \right], \\
\frac{du_2(t)}{dt} = \lambda \left[ \frac{c_2(t) e^{u_4(t)}}{b_2 + e^{2u_2(t)}} - \frac{a_2(t) e^{u_3(t) + u_4(t)}}{b_1 + e^{u_3(t)}} \right] - m_1(t) e^{u_4(t)} + m_2(t) e^{u_1(t) - u_2(t) + u_3(t) - u_4(t) - \mu(t)} \\
\frac{du_3(t)}{dt} = \lambda \left[ m_1(t) e^{u_4(t) + u_2(t) - u_3(t)} - m_2(t) e^{u_1(t)} - \mu(t) \right], \\
\frac{du_4(t)}{dt} = \lambda \left[ \frac{c_2(t) e^{u_4(t)}}{b_2 + e^{2u_2(t)}} - \phi(t) \right].
\]

Suppose that \( (u_1(t), u_2(t), u_3(t), u_4(t))^T \in X \), is a solution of (6.6) for cer-
tain $\lambda \in (0, 1)$. Then from (6.6) we have

$$ r(t) = \frac{r(t)e^{u_1(t)}}{K(t)} + \frac{a_1(t)e^{u_2(t)}}{b_1 + e^{u_1(t)}}, $$

(6.7)

$$ \frac{c_1(t)a_1(t)e^{u_1(t)}}{b_1 + e^{u_1(t)}} + m_2(t)e^{u_2(t) - u_3(t) + u_4(t)} = \frac{a_2(t)e^{u_2(t) + u_4(t)}}{b_2 + e^{2u_2(t)}} + m_1(t)e^{u_2(t)} + \mu(t), $$

(6.8)

$$ m_1(t)e^{u_2(t) + u_3(t) - u_3(t)} = m_2(t)e^{u_1(t)} + \mu(t), $$

(6.9)

$$ \frac{c_2(t)a_2(t)e^{2u_2(t)}}{b_2 + e^{2u_2(t)}} = \phi(t), $$

(6.10)

From (6.7) we have

$$ r(t) \geq \frac{r(t)e^{u_1(t)}}{K(t)} $$

$$ \implies u_1(t) \leq \ln \{K(t)\} = H_1 $$

and

$$ \frac{r(t)e^{u_1(t)}}{K(t)} \geq r(t) - \frac{a_1(t)e^{u_2(t)}}{b_1} $$

$$ \implies e^{u_1(t)} \geq K(t) - \frac{K(t)a_1(t)e^{u_2(t)}}{b_1r(t)} $$

$$ \implies u_1(t) \geq \ln \left\{ K - \frac{K(t)a_1(t)e^{u_2(t)}}{b_1r(t)} \right\} = L_1. $$

From (6.8) we have

$$ \mu(t)e^{u_2(t)} \leq \frac{c_1(t)a_1(t)e^{u_1(t)} + u_3(t)}{b_1 + u_1(t)} + m_2(t)e^{u_2(t) + u_3(t)} $$

$$ \implies \mu(t)e^{u_2(t)} \leq c_1(t)a_1(t)e^{u_2(t)} + m_2(t)e^{u_2(t) + u_3(t)} $$

$$ \implies e^{u_2(t)}[\mu(t) - c_1(t)a_1(t)] \leq m_2(t)e^{u_2(t) + u_3(t)} $$

$$ \implies e^{u_2(t)} \leq \frac{m_2(t)e^{u_2(t) + u_3(t)}}{\mu(t) - c_1(t)a_1(t)} $$

$$ \implies u_2(t) \leq \ln \left\{ \frac{m_2(t)e^{u_2(t) + u_3(t)}}{\mu(t) - c_1(t)a_1(t)} \right\} = H_2, $$

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and

\[
\frac{a_2(t)e^{u_2(t) + u_4(t)}}{b_2(t)e^{u_2(t)}} + m_1(t)e^{u_2(t) + u_4(t)} + \mu(t)e^{u_2(t)} \geq m_2(t)e^{u_1(t) + u_3(t)}
\]

\[\Rightarrow a_2(t)e^{u_4(t)} + m_1(t)e^{u_2(t) + u_4(t)} + \mu(t)e^{u_2(t)} \geq m_2(t)e^{u_1(t) + u_3(t)}
\]

\[\Rightarrow \left(\frac{m_1(t)}{q} + \mu(t)\right)e^{u_2(t)} \geq m_2(t)e^{H_1 - a_2(t)\hat{B}}
\]

\[\Rightarrow u_2(t) \geq \ln \left\{ \frac{m_2(t)e^{H_1 - a_2(t)\hat{B}}}{\left(m_1(t)e^{H_1} + \mu(t)\right)} \right\}
\]

From (6.9) we have

\[\mu(t)e^{u_3(t)} \leq m_1(t)e^{u_2(t) + u_4(t)}
\]

\[\Rightarrow e^{u_3(t)} \leq \frac{m_1(t)}{\mu(t)}e^{H_2\hat{B}}
\]

\[m_2(t)e^{u_2(t) + u_3(t)} \leq m_1(t)e^{u_2(t) + u_4(t)}
\]

\[\Rightarrow m_2(t)e^{u_3(t)}e^{L_1} \leq m_1(t)e^{H_2\hat{B}}
\]

\[\Rightarrow e^{u_3(t)} \leq \frac{m_1(t)}{m_2(t)}e^{H_2-L_1\hat{B}}.
\]

Therefore,

\[e^{u_3(t)} \leq \min \left\{ \frac{m_1(t)}{\mu(t)}e^{H_2\hat{B}}, \frac{m_1(t)}{m_2(t)}e^{(H_2-L_1)\hat{B}} \right\}
\]

\[u_3(t) \leq \ln \left[ \min \left\{ \frac{m_1(t)}{\mu(t)}e^{H_2\hat{B}}, \frac{m_1(t)}{m_2(t)}e^{(H_2-L_1)\hat{B}} \right\} \right] = H_3.
\]

On the other hand,

\[e^{u_3(t)} = \frac{m_1(t)e^{u_2(t) + u_4(t)}}{m_2(t)e^{u_2(t)} + \mu(t)}
\]

\[\Rightarrow e^{u_3(t)} \geq \frac{m_1(t)e^{L_2}}{m_2(t)e^{H_1} + \mu(t)}
\]

\[\Rightarrow u_3(t) \geq \ln \left\{ \frac{m_1(t)e^{L_2}}{m_2(t)e^{H_1} + \mu(t)} \right\} = L_3.
\]

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We have proved earlier that

\[ F(t) \leq \hat{B} \]

\[ \implies e^{u_4(t)} \leq \hat{B} \]

\[ \implies u_4(t) \leq \ln \left\{ \frac{\hat{B}}{B} \right\} = H_4. \]

From (6.9) we also have

\[ e^{u_4(t)} = \frac{(m_2(t)e^{u_1(t)} + \mu(t))e^{u_2(t)}}{m_1(t)e^{u_2(t)}} \]

\[ \implies e^{u_4(t)} \geq \frac{\mu(t)e^{L_3}}{m_1(t)e^{H_2}} \]

\[ \implies u_4(t) \geq \ln \left\{ \frac{\mu(t)e^{L_3}}{m_1(t)e^{H_2}} \right\} = L_4 \]

Therefore, we have

\[ |u_1(t)| < H_1, \quad |u_2(t)| < H_2, \quad |u_3(t)| < H_3, \quad |u_4(t)| < H_4, \quad \forall t \in \mathbb{R}. \]

Clearly, \( H_i \) (\( i = 1, 2, 3, 4 \)) are independent of \( \lambda \). Denote

\[ \hat{M} = H_1 + H_2 + H_3 + H_4 + \varepsilon, \]

where \( \varepsilon \) is taken sufficiently large such that each solution \((u_1^*, u_2^*, u_3^*, u_4^*)^T\) (if the system has at least one solution) of the system of algebraic equations

\[ \begin{align*}
    \frac{\ddot{r}}{K} - \frac{\dddot{e}^{u_1}}{b_1 + e^{u_1}} - \frac{\dddot{a}_1 e^{u_2}}{b_1 + e^{u_1}} - \dddot{a}_2 e^{u_3 + u_4} - m_1 e^{u_4} + m_2 e^{u_1 - u_2 + u_3} - \dddot{\mu} &= 0, \\
    \frac{\dddot{m}_1 e^{u_4 + u_2 - u_3} - \dddot{m}_2 e^{u_1} - \dddot{\mu}}{b_2 + e^{2u_4}} &= 0, \\
    \frac{\dddot{\phi}}{b_2 + e^{2u_4}} &= 0, 
\end{align*} \]

satisfies \( \|(u_1^*, u_2^*, u_3^*, u_4^*)^T\| < \hat{M} \) provided that the system (6.11) has one or a number of solutions.
We now set \( \Omega = \{(u_1(t), u_2(t), u_3(t), u_4(t))^T \in X : \|(u_1(t), u_2(t), u_3(t), u_4(t))^T\| < \tilde{M}\} \).

It is easy to see that the condition (a) of Lemma 2.1 is satisfied. When \((u_1(t), u_2(t), u_3(t), u_4(t))^T \in \partial \Omega \cap \text{Ker} L = \partial \Omega \cap R^4, (u_1(t), u_2(t), u_3(t), u_4(t))^T\) is a constant vector in \(R^4\) with \(|u_1| + |u_2| + |u_3| + |u_4| = \tilde{M}\). If the system (6.11) has at least one solution, then we have

\[
QN \begin{pmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \end{pmatrix} = \begin{pmatrix} \frac{\tilde{p} - \tilde{p} e^{u_1}}{b_1 + e^{u_1}} - \frac{\tilde{a}_1 e^{u_2}}{b_1 + e^{u_1}} \\ \frac{\tilde{a}_1 e^{u_1}}{b_1 + e^{u_1}} - \frac{\tilde{a}_2 e^{u_1 + u_2}}{b_2 + e^{2u_2}} - \tilde{m}_1 e^{u_4} + \tilde{m}_2 e^{u_1 + u_3} - \tilde{\mu} \\ \frac{\tilde{m}_1 e^{u_4 + u_2} - \tilde{m}_2 e^{u_1} - \tilde{\mu}}{b_2 + e^{2u_2}} - \frac{\tilde{a}_2 v_2^{2u_2}}{b_2 + e^{2u_2}} - \tilde{\phi} \\ \tilde{a}_2 e^{2u_2} - \tilde{\phi} \end{pmatrix} \neq \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}.
\]

If the system (6.11) does not have a solution, we can directly derive

\[
QN \begin{pmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \end{pmatrix} \neq \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}.
\]

This proves that condition (b) in Lemma 2.1 is satisfied.

In order to prove the condition (c) in Lemma 2.1, we define the homomorphism mapping \( J : \text{Im} Q \rightarrow \text{Ker} L, (u_1, u_2, u_3, u_4)^T \rightarrow (u_1, u_2, u_3, u_4)^T\), a standard and direct calculation shows that

\[
\text{deg}(JQN(u_1, u_2, u_3, u_4)^T, \Omega \cap \text{Ker} L, (0, 0, 0, 0)^T) = \sum_{z_i^* \in QN^{-1}(0)} \text{sgn} JQN(z_i^*)
\]

\[
= \sum_{(u_1^*, u_2^*, u_3^*, u_4^*) \in QN^{-1}(0)} \text{det} G(u_1^*, u_2^*, u_3^*, u_4^*) \prod_{i=1}^{n} u_1^* \prod_{i=1}^{n} u_2^* \prod_{i=1}^{n} u_3^* \prod_{i=1}^{n} u_4^* \neq 0.
\]

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Then the condition (c) in Lemma 2.1 holds. By Lemma 2.1, the system (6.5) has at least one positive \( \omega \)-periodic solution on \( \Omega \cap \text{Dom}(L) \). The proof is now complete.

### 6.6 Global attractivity

**Theorem 6.4** Assume that the assumption \([A_1]\) and the following conditions hold:

\[
\begin{align*}
\text{[A2]} & : 0 < P(0), Z_1(0), Z_2(0), F(0) < +\infty; \\
\text{[A3]} & : \left[ \frac{\mu_1 r(t)}{K(t)} - \frac{\mu_1 a_1(t) e^{H_3}}{(b_1 + e^{L_1})^2} - \frac{2 \mu_2 b_1 c_1(t) a_1(t) e^{H_3}}{(b_1 + e^{L_1})^2} - \mu_2 m_2(t) e^{H_3} + \mu_3 m_2(t) e^{L_3} \right]_{t \in [0,\omega]} > 0; \\
\text{[A4]} & : \left[ -\frac{\mu_1 a_1(t)}{b_1 + e^{L_1}} - \frac{\mu_2 c_1(t) a_1(t) e^{H_1}}{(b_1 + e^{L_1})^2} - \frac{2 \mu_2 a_2(t) e^{3 H_3 + H_4}}{(b_2^2 + e^{2L_2})^2} - \frac{2 \mu_2 a_2(t) e^{H_3 + H_4}}{(b_2^2 + e^{2L_2})^2} + \mu_4 m_1(t) e^{L_4} \\
& \quad + \mu_5 \mu(t) - \mu_5 m_1(t) e^{H_4} - \frac{2 \mu_4 c_2(t) a_2(t) e^{H_2}}{(b_2^2 + e^{2L_2})^2} \right]_{t \in [0,\omega]} > 0; \\
\text{[A5]} & : \left[ -\mu_2 m_2(t) e^{H_1} + \mu_3 m_2(t) e^{L_1} + \mu_3 \mu(t) \right]_{t \in [0,\omega]} > 0; \\
\text{[A6]} & : \left[ -\frac{\mu_2 a_2(t) e^{2H_2}}{(b_2^2 + e^{2L_2})^2} + \mu_2 m_1(t) e^{L_2} - \mu_3 m_1(t) e^{H_2} \right]_{t \in [0,\omega]} > 0.
\end{align*}
\]

Then the system (6.3) has only one positive \( \omega \)-periodic solution which is globally attractive.

**Proof.** From theorem 6.3, we know that the system (6.3) has at least one positive \( \omega \)-periodic solution \((\tilde{P}(t), \tilde{Z}_1(t), \tilde{Z}_2(t), \tilde{F}(t))\) and

\[ e^{L_1} \leq \tilde{P}(t) \leq e^{H_1}, \quad e^{L_2} \leq \tilde{Z}_1(0) \leq e^{H_2}, \quad e^{L_3} \leq \tilde{Z}_2(0) \leq e^{H_3}, \quad e^{L_4} \leq \tilde{F}(0) \leq e^{H_4}. \]
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Suppose \((P(t), Z_1(t), Z_2(t), F(t))\) is any positive periodic solution of (6.3).

Let

\[
V(t) = \mu_1 \ln P(t) - \ln P(t) + \mu_2 |Z_1(t) - \bar{Z}_1(t)| + \mu_3 |Z_2(t) - \bar{Z}_2(t)| + \mu_4 |F(t) - \bar{F}(t)|. \tag{6.12}
\]

By calculating Dini derivative (right hand derivative) of (6.12) along the solution of the system (6.3), we get

\[
V^+(t) = \mu_1 \text{sgn} \left( \frac{P(t) - \bar{P}(t)}{P(t)} \right) \left( \frac{\dot{P}(t)}{P(t)} - \frac{\bar{P}(t)}{\bar{P}(t)} \right) + \mu_2 \text{sgn} \left( \frac{Z_1(t) - \bar{Z}_1(t)}{Z_1(t)} \right) \left( \frac{\dot{Z}_1(t)}{Z_1(t)} - \frac{\bar{Z}_1(t)}{\bar{Z}_1(t)} \right)
\]

\[
+ \mu_3 \text{sgn} \left( \frac{Z_2(t) - \bar{Z}_2(t)}{Z_2(t)} \right) \left( \frac{\dot{Z}_2(t)}{Z_2(t)} - \frac{\bar{Z}_2(t)}{\bar{Z}_2(t)} \right) + \mu_4 \text{sgn} \left( \frac{F(t) - \bar{F}(t)}{F(t)} \right) \left( \frac{\dot{F}(t)}{F(t)} - \frac{\bar{F}(t)}{\bar{F}(t)} \right)
\]

\[
= -\frac{\mu_1 r(t)}{K(t)} |P(t) - \bar{P}(t)| + \frac{\mu_1 a_1(t) \bar{Z}_1(t)}{(b_1 + P(t))(b_1 + \bar{P}(t))} |P(t) - \bar{P}(t)| + \frac{\mu_1 a_1(t) \bar{Z}_1(t)}{(b_1 + P(t))(b_1 + \bar{P}(t))} |P(t) - \bar{P}(t)|
\]

\[
+ \frac{\mu_2 a_2(t) b_1(t) F(t)}{(b_2 + Z_1^2(t))} |Z_1(t) - \bar{Z}_1(t)| + \frac{\mu_2 a_2(t) b_1(t) \bar{Z}_1(t)}{(b_2 + Z_1^2(t))} |F(t) - \bar{F}(t)|
\]

\[
+ \frac{\mu_2 a_2(t) F(t)(Z_1(t) + \bar{Z}_1(t))}{(b_2 + Z_1^2(t))} |Z_1(t) - \bar{Z}_1(t)| - \mu_2 m_1(t) F(t) |Z_1(t) - \bar{Z}_1(t)|
\]

\[
- \mu_2 m_1(t) \bar{Z}_1(t) |F(t) - \bar{F}(t)| + \mu_3 m_2(t) Z_2(t) |P(t) - \bar{P}(t)| + \mu_3 m_2(t) P(t) |Z_2(t) - \bar{Z}_2(t)|
\]

\[
- \mu_2 m_1(t) |Z_1(t) - \bar{Z}_1(t)| + \mu_3 m_1(t) F(t) |Z_1(t) - \bar{Z}_1(t)| + \mu_3 m_1(t) \bar{Z}_1(t) |F(t) - \bar{F}(t)|
\]

\[
- \mu_3 m_2(t) P(t) |Z_2(t) - \bar{Z}_2(t)| - \mu_3 m_2(t) \bar{Z}_2(t) |P(t) - \bar{P}(t)| - \mu_3 m_1(t) |Z_2(t) - \bar{Z}_2(t)|
\]

\[
+ \frac{\mu_4 c_2(t) a_2(t) Z_2(t) + \bar{Z}_1(t)}{(b_2 + Z_1^2(t))} |Z_1(t) - \bar{Z}_1(t)|.
\]
Which implies that

\[ V^+(t) \leq -\Pi_1|P(t) - \bar{P}(t)| - \Pi_2|Z_1(t) - \bar{Z}_1(t)| - \Pi_3|Z_2(t) - \bar{Z}_2(t)| - \Pi_4|F(t) - \bar{F}(t)| \tag{6.13} \]

Where

\[
\Pi_1 = \frac{\mu_1 P(t)}{K(t)} - \frac{\mu_1 a_1(t)e^{H_1}}{(b_1 + e^{H_1})^2} - \frac{\mu_2 b_1 c_1(t)a_1(t)e^{H_2}}{(b_1 + e^{H_1})^2} - \mu_2 m_1(t)e^{H_3} + \mu_3 m_2(t)e^{L_3};
\]

\[
\Pi_2 = -\frac{\mu_2 a_1(t)}{(b_1 + e^{H_1})} - \frac{\mu_2 c_1(t)a_1(t)e^{H_1}}{(b_1 + e^{H_1})} - \frac{2\mu_2 a_2(t)e^{3H_2+H_4}}{(b_2 + e^{2L_2})^2} - \frac{2\mu_2 a_2(t)e^{H_2+H_4}}{(b_2 + e^{2L_2})} + \mu_2 m_1(t)e^{L_4} + \mu_2 a_2(t)e^{H_3};
\]

\[
\Pi_3 = -\mu_2 m_2(t)e^{H_1} + \mu_3 m_2(t)e^{L_1} + \mu_3 \mu(t);
\]

\[
\Pi_4 = -\frac{\mu_2 a_2(t)e^{2H_3}}{(b_2 + e^{2L_2})} + \mu_2 m_1(t)e^{L_2} - \mu_3 m_3(t)e^{H_2}.
\]

If the conditions \([A_2] - [A_6]\) hold then \(P_i > 0\) for \(i = 1, 2, 3, 4\). Therefore, \(V(t)\) is non-increasing on \([0, \infty)\). Integrating the above inequality from 0 to \(t\) and noticing condition \([A_2]\), we obtain that

\[
V(t) + \Pi_1 \int_0^t |P(t) - \bar{P}(t)| + \Pi_2 \int_0^t |Z_1(t) - \bar{Z}_1(t)| + \Pi_3 \int_0^t |Z_2(t) - \bar{Z}_2(t)| \\
+ \Pi_4 \int_0^t |F(t) - \bar{F}(t)| \leq V(0) < +\infty, \ \forall t > 0.
\]

Following Lemma 5.2, we have

\[
\lim_{t \to \infty} |P(t) - \bar{P}(t)| = 0, \ \lim_{t \to \infty} |Z_1(t) - \bar{Z}_1(t)| = 0, \ \lim_{t \to \infty} |Z_2(t) - \bar{Z}_2(t)| = 0, \ \lim_{t \to \infty} |F(t) - \bar{F}(t)| = 0,
\]

so we can claim that \((\bar{P}(t), \bar{Z}_1(t), \bar{Z}_2(t), \bar{F}(t))\) is globally attractive.
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6.7 Numerical results

For the given set of parameter values $r = 2$, $K = 20$, $a_1 = 0.6$, $b_1 = 12$, $c_1 = 0.6$, $a_2 = 0.7$, $b_2 = 12$, $m_1 = 0.2$, $m_2 = 0.2$, $\mu = 0.012$, $\phi = 0.3$, $\phi = 0.01$ we obtain a unique positive interior equilibrium $E^*(19.4887, 2.68328, 2.21961, 16.1707)$ of the system (6.1). We also obtain $\sigma_1 = 9.2329 > 0$, $\sigma_2 = 14.8019 > 0$, $\sigma_3 = 1.5225 > 0$, $\sigma_4 = 0.0301 > 0$ and $\sigma_1\sigma_2\sigma_3 - \sigma_2^2 - \sigma_1^2\sigma_4 = 203.1837 > 0$, which satisfy the Routh-Hurwitz criterion for order 4. Hence the system (6.1) is locally asymptotically stable around the positive interior equilibrium (see Figure 5.1).
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Figure 6.1: The system 6.1 shows stable coexistence of all species

To capture the seasonal variation of phytoplankton growth, diel vertical migration of zooplankton and the predation rate, we consider those rate parameters to be a sinusoidal function with a period of 1 year. We set

\[ r = 2 + 1.5 \sin(\omega_0 t) \]

\[ m_1(t) = 0.2 + 0.15 \sin(\omega_0 t), \]

\[ m_2(t) = 0.2 + 0.15 \cos(\omega_0 t), \]

\[ a_2(t) = 0.2 + 0.1 \sin(\omega_0 t), \text{ and } \omega_0 = \frac{2\pi}{365} \]

to incorporate non-autonomous periodic
functional form of growth rate of phytoplankton, migration rate of zooplankton and predation rate of planktivores with a period of $\omega = 365$ days. Other parameter values are kept fixed as in Figure 6.1. Simulating the non-autonomous system (6.3) we have observed that there exist a positive periodic solution (see Figure 6.2). Figure 6.2 also shows that the positive periodic solutions are globally asymptotically stable, i.e. all the periodic solutions initiating from different initial values converge to a single periodic solution.
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Figure 6.2: The figure depicts the global attractiveness of positive periodic solution of the non-autonomous system (6.3)

Figure 6.2: The figure depicts the global attractiveness of positive periodic solution of the non-autonomous system (6.3)
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6.8 Discussion and conclusion

Diel vertical migration can be understood as an adaptive strategy that optimizes zooplankton growth by minimizing mortality from visual predators through daytime downward migration to the darker region (refuge) and maximizing phytoplankton predation and reproductive rates through night-time upward migration to warm surface water (Lampert, 1993). The benefit of downward migration at dawn is the escape from the light-dependent mortality imposed by visually orienting predators, mostly fish, during daylight hours. This interpretation is strongly supported by the recent finding that DVM in many zooplankton species can be induced by kairomones exuded by predators (Dodson, 1988b; Dawidowicz et al., 1990; Neill, 1990; Loose et al., 1993; Pijanowska, 1993). On the other hand, the upward migration at dusk reflects avoidance of the costs of staying in the deep water refuge and being hungry.

Food availability, predation pressure and light are the major control variables of DVM (Enright, 1977; Enright and Honegger, 1977; Iwasa, 1982; Clark and Levy, 1988; Han and Straskraba, 1998, 2001). It is widely accepted that light plays an important role in the behavioral response of pelagic zooplankton (Forward, 1988). It has been known that zooplankton migrations and consumer induced mortality of zooplankton are driven by light (Clarke, 1934; Duval and Geen, 1976; Pagano et al., 1993; George, 1983; Atkinson et al., 1996; Zaret and Suffern, 1976). Others environmental factors such as temperature (Tappa, 1965; Carter and Goudie, 1986; McLaren, 1963), dissolved oxygen (Hanazato et al., 1989; Weider and Lampert, 1985), ultraviolet radiation (Hunter et al., 1981; Kouwenberg et al., 1999) and salinity (Rothlisberg, 1985).
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1982) also stimulate the vertical distribution of zooplankton.

Though predatory fish are able to migrate, but, they do not simply follow the prey downward because most them are light dependent predators, rely on the contrast between their prey item and the background to see and capture moving prey. A fish that swims downward to locate prey will lose the advantage of seeing the object silhouetted against the light background of the sky, presumably resulting in a greatly reduced predation efficiency (Zaret, 1972; Zaret and Kerfoot, 1975).

In our proposed non-autonomous model, we capture the seasonal variation of the daily average migration rates of zooplankton. Downward migration rate of zooplankton in surface water increases with increase in daily average light intensity and decreases with decrease in the daily average light intensity. Upward migration of zooplankton living in the lower layer follows the reverse pattern of downward avoiding migration. The predation rate of planktivory fish also light dependent as most of the fish are visually oriented predator. We consider periodic function (sinusoidal function) with period 1 year to incorporate the seasonal patterns. We observed that the system (6.3) has a unique positive periodic solution with period 1 year (see Figure 6.2), whereas the autonomous system (6.1) (all the rate parameters are constant) is a stable focus (see Figure 6.1). We also observed that the periodic solution of the non-autonomous system is globally attractive.