Hopf Bifurcation and Dynamical Behavior of a Stage–Structured Predator Sharing a Prey

Suwicha Boonrangsiman and Kornkanok Bunwong

***Abstract*—**In this paper, we divide the predator’s life cycle into two stages of foliage maturity, namely immature and mature. Both types of predators have hunting ability and compete for the same prey. Naturally, their consumption rates and growth rates are limited by the presence of the prey population. Therefore, a stage–structured model with Holling type II response function is proposed. The objective of this paper is to investigate the existence of a local Hopf bifurcation. Bifurcation diagrams of one–parameter family and two–parameter family are also expressed into several regions of different dynamical behaviors. Finally, numerical simulations are carried out in support of the theoretical results.

***Keywords*—**Hopf bifurcation, predator–prey interaction, qualitative behavior, stage–structured model.

I. INTRODUCTION

Understanding the predator–prey relationship within ecological communities should lead to interaction strength and ecosystem stability. One of the most powerful tools for this investigation is mathematical modeling. From the last century, it has been intensively studied and continuously developed in many ecological problems. Among, mathematical models, predator–prey models have been widely modified not only to various loss–win situations in ecology [1] and in epidemiology [2] but also to numerous aspects, in terms of the multispecies interactions [3] and the stage–structure in a certain population. In recent years, the state–structured models have become more popular. Authors in [4]–[6] used the state–structure in the prey population whereas authors in [7]–[15] used the state–structure in the predator population. Besides, researchers in [16]–[17] considered the state–structure in both prey and predator populations. Previously, the major assumption of models with the state–structure in the predator population is that only mature predator has the hunting ability [7]–[15]. Of course, it is a good example for mammals because the immature predator is raised by parents.

In general, the following formula was studied as the stage-structured model in the predator population with the stated assumption.

$$\dot{x} = U(x) - F(x, y_2),$$
$$\dot{y}_1 = \gamma F(x, y_2) - \delta_1 T(y_1),$$
$$\dot{y}_2 = \delta_2 T(y_1) - V(y_2),$$

where $x(t), y_1(t), y_2(t)$ denote the densities of prey, immature predator, and mature predator at time t respectively. $U(x)$ is the intrinsic growth rate of prey in the absence of the predator population. $F(x, y_2)$ represents the relationship between the prey population and the mature predator population. γ is the reproduction rate. $\delta_1 T(y_1)$ describes the movement of the immature predator population outside the immature class. $\delta_2 T(y_1)$ is the conversion of the immature to the mature predator. $V(y_2)$ represents the intrinsic decrease rate of the predator population. For varieties of its application, we refer the reader to Wang [9], Xiao and Chen [10], Georgescu et al. [11]–[13], Wang et al. [14], and Shi et al. [15].

Unlike the previous model, the parents of various marine species abandon their newborn babies; therefore, the newborn babies have to capable to support themselves as quickly as they can. Consequently, the marine predator–prey model with stage–structure in predator population should be investigated differently.

In the work of Boonrangsiman and Bunwong [18], they proposed the following suitable fish population model with the hunting ability of the immature predator and applying Holling type II as the respond function for both types of the predator population.

$$\dot{x} = x(r - ax) - \frac{b_1 x y_1}{1 + m_1 x} - \frac{b_2 x y_2}{1 + m_2 x} \tag{1}$$

$$\dot{y}_1 = \frac{k_2 b_2 x y_2}{1 + m_2 x} - d_1 y_1 \tag{2}$$

$$\dot{y}_2 = \frac{k_1 b_1 x y_1}{1 + m_1 x} - d_2 y_2 \tag{3}$$

where $x(t)$, $y_1(t)$, $y_2(t)$ represent the biomasses of prey, immature predator, and mature predator at time t. All parameters are positive. For each type of the predator

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population, $i = 1,2$, b_i are the searching rates, m_i are the products of the searching rate and the handling time, and d_i are the mortality rates. r is the intrinsic growth rate of prey. k_1 is the conversion rate of the immature predator into the mature predator while k_2 is the reproduction rate of the mature predator. In theoretical results, they established the uniformly boundedness, the existence of positive equilibrium point, the local stability and the permanent of system (1)–(3). In numerical results, after changing the value of parameter d_1, they plotted maximum and minimum values of the biomasses on prey, immature predator and mature predator, respectively. Moreover, the local Hopf bifurcations were numerically discovered, unlike the work of Ajraldi and Venturino [19]. The aim of this paper is to analyze the condition of the existence of a local Hopf bifurcation for Boonrangsiman’ model.

The organization of this paper is as follows. Theoretical results including all possible eigenvalues of characteristic equation and the existence criteria of local Hopf bifurcation are analyzed in section II. The bifurcation diagrams of one–parameter family are illustrated in section III while the bifurcation diagrams of two–parameter family are considered in section IV. The conclusion is provided in the final section.

II. THEORITICAL RESULTS

In this section, we first review the useful Lemmas and Theorems which were proven in [18].

Lemma 1 Suppose

$$\Omega := \left\{ (x, y_1, y_2) \in \mathrm{R}_+^3 : 0 \le x \le \frac{r}{a}, 0 \le x + \frac{y_1}{k_2} + \frac{y_2}{k_1} \le M \right\},$$

where $M := r(r+\eta)/\eta a$ and $0 < \eta \le \min\{d_1, d_2\}$. Then all solutions of system (1)–(3) starting in R_+^3 are uniformly bounded and Ω is the region of attraction.

Lemma 2 Suppose $H := a^2 d_1 d_2 + arB - r^2 A$ where $A := b_1 b_2 k_1 k_2 - d_1 d_2 m_1 m_2$ and $B := d_1 d_2 m_1 + d_1 d_2 m_2$. Then we have the following:

1) The trivial equilibrium point $N_0(0,0,0)$ always exists.

2) The predator–free equilibrium point $N_1(r/a, 0, 0)$ always exists.

3) If the inequality $H < 0$ holds then the coexistence equilibrium point $N_2(\bar{x}, \bar{y}_1, \bar{y}_2)$ exists, where

$$\bar{x} = \frac{B + \sqrt{B^2 + 4d_1 d_2 A}}{2A},$$

$$\bar{y}_1 = \frac{d_2(r - a\bar{x})(1 + m_1\bar{x})(1 + m_2\bar{x})}{b_1 d_2(1 + m_2\bar{x}) + b_1 b_2 k_1 \bar{x}}, \text{ and}$$

$$\bar{y}_2 = \frac{b_1 k_1 \bar{x}(r - a\bar{x})(1 + m_2\bar{x})}{b_1 d_2(1 + m_2\bar{x}) + b_1 b_2 k_1 \bar{x}}.$$

Theorem 1 The Jacobian matrix of system (1)–(3) is given by

$$J(x, y_1, y_2) = \begin{bmatrix} J_{11} & -\dfrac{b_1 x}{1 + m_1 x} & -\dfrac{b_2 x}{1 + m_2 x} \\ \dfrac{b_2 k_2 y_2}{(1 + m_2 x)^2} & -d_1 & \dfrac{b_2 k_2 x}{1 + m_2 x} \\ \dfrac{k_1 b_1 y_1}{(1 + m_1 x)^2} & \dfrac{b_1 k_1 x}{1 + m_1 x} & -d_2 \end{bmatrix}$$

where $J_{11} := r - 2ax - \dfrac{b_1 y_1}{(1 + m_1 x)^2} - \dfrac{b_2 y_2}{(1 + m_2 x)^2}$.

Suppose

$$\alpha_1 := -J_{11} + d_1 + d_2,$$

$$\alpha_2 := -J_{11}(d_1 + d_2) + D_1 + D_2,$$

$$\alpha_3 := \frac{b_1 d_1 d_2 y_1}{(1 + m_1 x)^2} + \frac{b_2 d_1 d_2 y_2}{(1 + m_2 x)^2} + d_1 D_2 + d_2 D_1,$$

where $D_1 := \dfrac{b_1 d_1 \, y_1}{(1 + m_1 x)(1 + m_2 x)}$,

$$D_2 := \frac{b_2 d_2 \, y_2}{(1 + m_1 x)(1 + m_2 x)},$$

then we obtain the following

1) The equilibrium point $N_0(0,0,0)$ is always unstable.

2) The predator–free equilibrium point $N_1(r/a, 0, 0)$ is locally asymptotically stable if $H > 0$ and unstable if $H < 0$.

3) The coexistence equilibrium point $N_2(\bar{x}, \bar{y}_1, \bar{y}_2)$, if it exists, is locally asymptotically stable if $\alpha_1 > 0$ and $\alpha_1 \alpha_2 > \alpha_3$.

Obviously, there are only two equilibrium points while the predator–free equilibrium point is stable. As it begins to lose its stability, the coexistence equilibrium point starts to appear in the system. For further analysis, the possibility of occurrence of a local Hopf bifurcation is explored. In fact, it requires two conditions. One is the presence of an equilibrium point with a pair of purely imaginary eigenvalues for a particular value of the bifurcation parameter and another one is the change in its stability for a variation of the bifurcation parameter. Here, we will focus on the coexistence equilibrium point only.

Lemma 3 Suppose

$$M := \sqrt[3]{-\frac{q}{2}+\sqrt{D}}\ ,\ N := \sqrt[3]{-\frac{q}{2}-\sqrt{D}}\ ,$$

$$D := \frac{q^2}{4}+\frac{p^3}{27},\ p := \alpha_2 - \frac{\alpha_1^2}{3},\ \text{and}\ q := \frac{2\alpha_1^3}{27}-\frac{\alpha_1\alpha_2}{3}+\alpha_3 .$$

If $D > 0$ then the eigenvalues of the Jacobian matrix evaluated at the coexistence equilibrium point $N_2\left(\bar{x},\bar{y}_1,\bar{y}_2\right)$ are as follows:

1) If $M+N > -\frac{2\alpha_1}{3}$ then there are one real eigenvalue and two complex eigenvalues with negative real parts.

2) If $M+N = -\frac{2\alpha_1}{3}$ then there are one real eigenvalue and two complex eigenvalues with purely imaginary parts.

3) If $M+N < -\frac{2\alpha_1}{3}$ then there are one real eigenvalue and two complex eigenvalues with positive real parts.

Proof The characteristic equation generated by the Jacobian matrix of system (1)–(3) evaluated at an equilibrium point $N\left(x,y_1,y_2\right)$ can be written in the form:

$$\lambda^3+\alpha_1\lambda^2+\alpha_2\lambda+\alpha_3=0. \tag{4}$$

where $\alpha_1 := -J_{11}+d_1+d_2$,

$$\alpha_2 := -J_{11}\left(d_1+d_2\right)+D_1+D_2,$$

$$\alpha_3 := \frac{b_1d_1d_2y_1}{\left(1+m_1x\right)^2}+\frac{b_2d_1d_2y_2}{\left(1+m_2x\right)^2}+d_1D_2+d_2D_1.$$

$$D_1 := \frac{b_1d_1\ y_1}{\left(1+m_1x\right)\left(1+m_2x\right)},$$

$$D_2 := \frac{b_2d_2\ y_2}{\left(1+m_1x\right)\left(1+m_2x\right)},$$

$$J_{11} := r-2ax-\frac{b_1y_1}{\left(1+m_1x\right)^2}-\frac{b_2y_2}{\left(1+m_2x\right)^2}.$$

Performing the change of variable, we let $\lambda = z-\alpha_1/3$.

Then (4) becomes

$$z^3+p\lambda+q=0. \tag{5}$$

where $p := \alpha_2-\frac{\alpha_1^2}{3}$, and $q := \frac{2\alpha_1^3}{27}-\frac{\alpha_1\alpha_2}{3}+\alpha_3$.

Again we transform $z = r-\left(p/3r\right)$. Consequently, (5) can be written as follows

$$\left(r^3\right)^2+qr^3-\frac{1}{27}p^3=0. \tag{6}$$

Hence, $r^3 = -\frac{q}{2}\pm\sqrt{D}$. Next, we apply finding 3th root in a complex number to obtain the roots of r. Hence $MN = -\frac{p}{3}$.

Therefore, three eigenvalues of (4) are

$$\lambda_1 = M+N-\frac{\alpha_1}{3},$$

$$\lambda_2 = M\mu+N\mu^2-\frac{\alpha_1}{3},\ \text{and}$$

$$\lambda_3 = M\mu^2+N\mu-\frac{\alpha_1}{3},$$

where $\mu = -\frac{1}{2}+\frac{\sqrt{3}}{2}i$. More detail can be seen in [20].

From [21], we can conclude that if $D>0$ then λ_1 is a real eigenvalue of (4) while $\lambda_{2,3}$ are complex eigenvalues which can be written as follows

$$\lambda_1 = M+N-\frac{\alpha_1}{3}, \tag{7}$$

$$\lambda_{2,3} = -\left[\frac{1}{2}\left(M+N\right)+\frac{\alpha_1}{3}\right]\pm\frac{\sqrt{3}}{2}\left(M-N\right)i. \tag{8}$$

Obviously, the coexistence equilibrium point $N_2\left(\bar{x},\bar{y}_1,\bar{y}_2\right)$ is locally asymptotically stable if $M+N<\alpha_1/3$ and $M+N>-2\alpha_1/3$ because of one negative real eigenvalue and two complex eigenvalues with negative real parts. In addition, the coexistence equilibrium point $N_2\left(\bar{x},\bar{y}_1,\bar{y}_2\right)$ is unstable if $M+N>\alpha_1/3$ or $M+N<-2\alpha_1/3$. The real parts of two complex eigenvalues become zeros when $M+N=-2\alpha_1/3$.

Step for determining a local Hopf bifurcation

Step 1: Find α_1, M, and N as the function of the interesting bifurcation parameter, c.

Step 2: Solve the equation $M+N=-2\alpha_1/3$ for a critical value (c^*) of the interesting bifurcation parameter. This condition implies the occurrence of a pair of purely imaginary eigenvalues.

Step 3: Choose a critical value that also satisfies the inequality $H<0$, the existence criterion of the coexistence equilibrium point $N_2\left(\bar{x},\bar{y}_1,\bar{y}_2\right)$.

Step 4: Verify the transversality condition by differentiating the real part of two complex eigenvalues with respect to the interesting bifurcation parameter and substituting a critical value, i.e.,

$$\left.\frac{d\,\mathrm{Re}\left(\lambda_{2,3}\right)}{dc}\right|_{c=c^*}. \tag{9}$$

Step 5: Determine the occurrence of a local Hopf bifurcation by considering the sign of (9).

If (9) is equal to zero then a local Hopf bifurcation does not occur.

If (9) is nonzero then a local Hopf bifurcation occurs. In addition, if (9) is positive, the system behavior changes from equilibrium state to oscillatory. In contrast, if (9) is negative then the system behavior changes from oscillatory to equilibrium state.

III. ONE–PARAMETER FAMILY

In this section, numerical simulations are carried out to illustrate the theoretical results with the same set of parameter values, $r = 3$, $a = 2.3$, $b_1 = 0.95$, $b_2 = 1.5$, $m_1 = 1$, and $m_2 = 1.8$. The initial condition, used in this work, is $(1,1,1)$.

Case 1 k_1–bifurcation parameter

The additional values of parameters are $k_2 = 1$, $d_1 = 0.3$, and $d_2 = 0.4$. Here, k_1 is treated as a bifurcation parameter. Following the five–step procedure outlined in the previous section, we obtain the following results.

1) Two critical values of k_1 are $k_1^* = 2.02306$ and $k_1^{**} = 133.636$.
2) The coexistence equilibrium point $N_2(\bar{x}, \bar{y}_1, \bar{y}_2)$ exists for both critical values since $H = -21.0486 < 0$ for k_1^* and $H = -1708.98 < 0$ for k_1^{**}.
3) The transversality condition at each critical value is shown as follows

$$\left.\frac{d\,\mathrm{Re}(\lambda_{2,3})}{dk_1}\right|_{k_1 = k_1^*} = 0.06789 \quad \text{and}$$

$$\left.\frac{d\,\mathrm{Re}(\lambda_{2,3})}{dk_1}\right|_{k_1 = k_1^{**}} = -0.00012\,.$$

As a conclusion, the local Hopf bifurcation occurs twice. Firstly, the coexistence equilibrium point loses its stability as k_1 increases from 1 to 3 and the system undergoes a local Hopf bifurcation at $k_1 = 2.02306$ as shown in Fig. 1(a). Secondary, the coexistence equilibrium point becomes stable as k_1 increases from 132 to 135 and the system undergoes a local Hopf bifurcation at $k_1 = 133.636$ as displayed in Fig. 1(b).

We also plot various dynamical behaviors of the solution depending on the values of the parameter k_1. The chosen value of k_1, less than k_1^{**}, can be associated with either a non–oscillatory solution in Fig. 2(a) or a damped oscillatory behavior in Fig. 2(b). Next, $k_1 = 2.3$, greater than k_1^{**}, is chosen to satisfy the condition under which a limit cycle will occur as shown in Fig. 2(c).

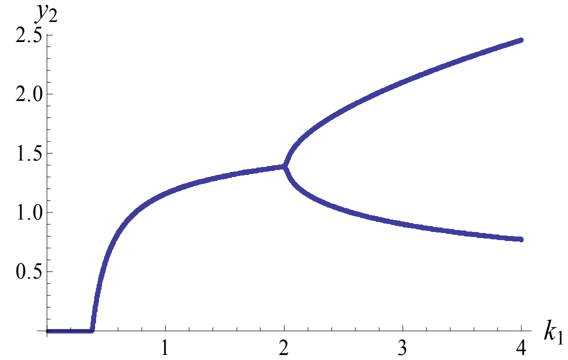
Case 2 d_1–bifurcation parameter

The interesting bifurcation parameter is d_1.

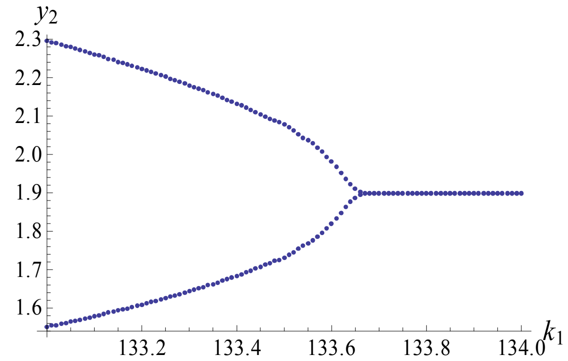
Case 2A

In this case, the additional values of parameter are $k_1 = 1$, $k_2 = 3$, and $d_2 = 0.4$. Again following five–step procedure and, then, we obtain the following results

1) Three critical values of d_1 are the following $d_1^* = 0.0672456$, $d_1^{**} = 0.413786$, and $d_1^{***} = 16.2152$.



(a) Critical value $k_1^* = 2.02306$.



(b) Critical value $k_1^{**} = 133.636$.

Fig. 1 Maximum and minimum values of the biomass of mature predator around the critical values as k_1 changes.

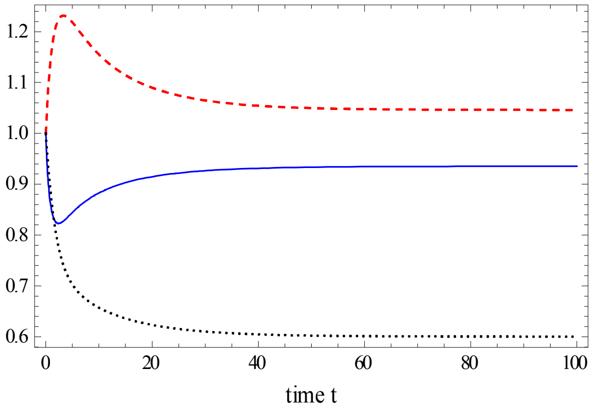
2) The coexistence equilibrium point $N_2(\bar{x}, \bar{y}_1, \bar{y}_2)$ exists for d_1^* and d_1^{**} only since
   $H = -37.3773 < 0$ for d_1^*,
   $H = -31.7204 < 0$ for d_1^{**}, and
   $H = 226.222 > 0$ for d_1^{***}.

3) The transversality condition at each critical value is shown as follows

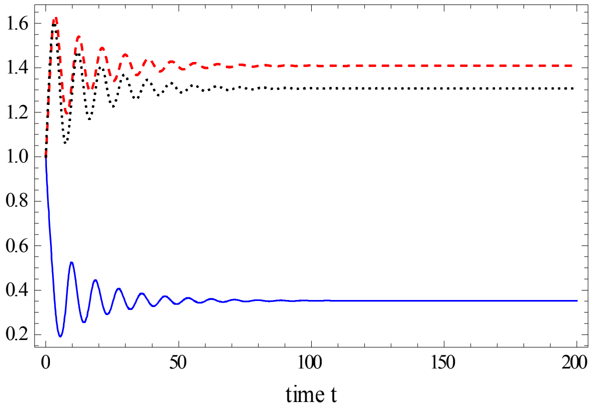
$$\left.\frac{d\,\mathrm{Re}(\lambda_{2,3})}{dd_1}\right|_{d_1 = d_1^*} = 0.656343 \quad \text{and}$$

$$\left.\frac{d\,\mathrm{Re}(\lambda_{2,3})}{dd_1}\right|_{d_1 = d_1^{**}} = -0.27823\,.$$

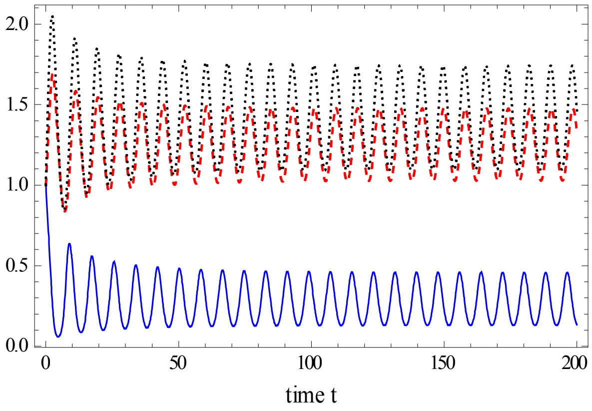
Consequently, the local Hopf bifurcation occurs twice. As d_1 increases and passes through the critical value $d_1^* = 0.0672456$ then the coexistence equilibrium point loses its stability and the system undergoes a local Hopf bifurcation. Later on the coexistence equilibrium point becomes stable as d_1 increases from 0.3 to 0.5 and the system undergoes a local Hopf bifurcation at $d_1 = 0.413786$ as represented in Fig. 3(a).



(a) $k_1 = 0.5$.

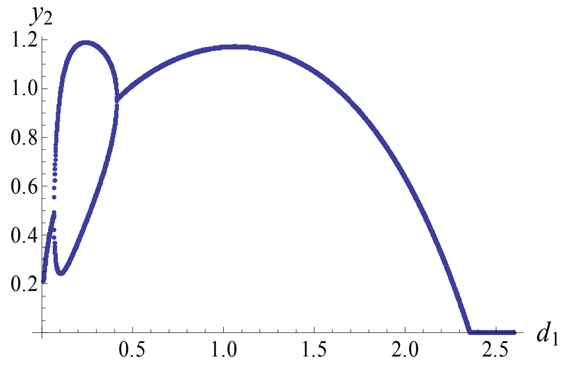


(b) $k_1 = 1.5$.

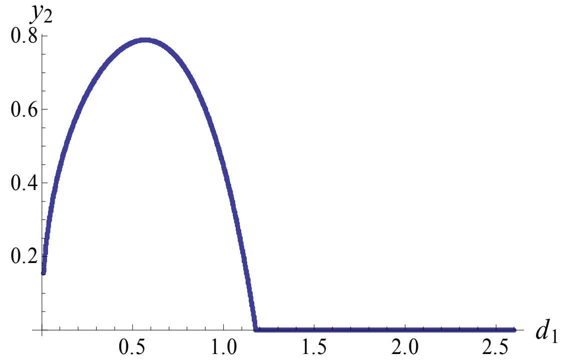


(c) $k_1 = 2.3$.

Fig. 2 The time series of the solution to system (1)–(3) with (a) $k_1 = 0.5$, (b) $k_1 = 1.5$, and (c) $k_1 = 2.3$. The symbols for the curves in this figure are $(-): x$, $(--): y_1$ and $(\cdot): y_2$.



(a) $d_2 = 0.4$.



(b) $d_2 = 0.8$.

Fig. 3 Maximum and minimum values of the biomass of mature predator as d_1 changes with (a) $d_2 = 0.4$ and (b) $d_2 = 0.8$.

Case 2B

In this case, the additional parameter which are $k_1 = 1$, $k_2 = 3$, and $d_2 = 0.8$. After repeating the five–step procedure, we obtain a single critical value $d_1^* = 17.8556$. However, the coexistence equilibrium point $N_2(\bar{x}, \bar{y}_1, \bar{y}_2)$ does not exist since $H = 544.473 > 0$. Hence, the local Hopf bifurcation does not occur as displayed in Fig. 3(b).

IV. TWO–PARAMETER FAMILY

In this section, we perform the bifurcation diagram with two bifurcation parameters to investigate the different system behavior in each region. The parameter space is delineated by the graphs of the following equations,

$$H := a^2 d_1 d_2 + arB - r^2 A = 0, \tag{10}$$

$$M + N = -\frac{2\alpha_1}{3}, \tag{11}$$

$$D := \frac{q^2}{4} + \frac{p^3}{27} = 0, \tag{12}$$

with the same fixed values of parameters $r = 3$, $a = 2.3$, $b_1 = 0.95$, $b_2 = 1.5$, $m_1 = 1$, and $m_2 = 1.8$.

Case 1 (k_1,k_2) –bifurcation parameter

In this case, the additional values of parameter are $d_1 = 0.3$ and $d_2 = 0.4$. We demonstrate the (k_1,k_2) parameter space in Fig. 4.

In Region I, $H>0$. Consequently, the coexistence equilibrium point $N_2(\bar{x},\bar{y}_1,\bar{y}_2)$ does not exist. Also, the solution converges to the predator–free equilibrium point $N_1(r/a,0,0)$.

In Region II$_0$ and II^0, $H<0$ and $M+N>-2\alpha_1/3$. The coexistence equilibrium point $N_2(\bar{x},\bar{y}_1,\bar{y}_2)$ exists and is asymptotically stable. The difference between two regions is that the coexistence equilibrium point $N_2(\bar{x},\bar{y}_1,\bar{y}_2)$ in Region II$_0$ generates one real eigenvalue and a pair of complex eigenvalues since $D>0$ while the coexistence equilibrium point $N_2(\bar{x},\bar{y}_1,\bar{y}_2)$ in Region II$_0$ generates three real eigenvalues since $D<0$.

In Region III, $H<0$ and $M+N<-2\alpha_1/3$. Thus, the coexistence equilibrium point $N_2(\bar{x},\bar{y}_1,\bar{y}_2)$ exists and it unstable since the complex eigenvalues have positive real parts.

Obviously, if the value of parameter k_2 is fixed, for example $k_2 = 1$. The stability of the coexistence equilibrium point $N_2(\bar{x},\bar{y}_1,\bar{y}_2)$ changes from stable to unstable as k_1 increases and passes through the critical value $k_1^* = 2.02306$. Similar to Case 1, the illustration is shown in Fig. 1(a).

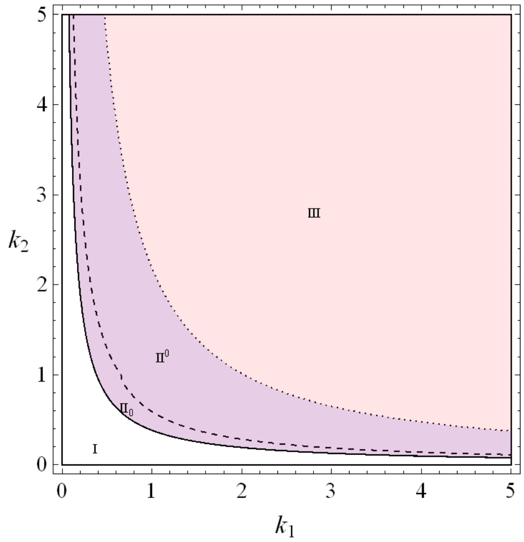
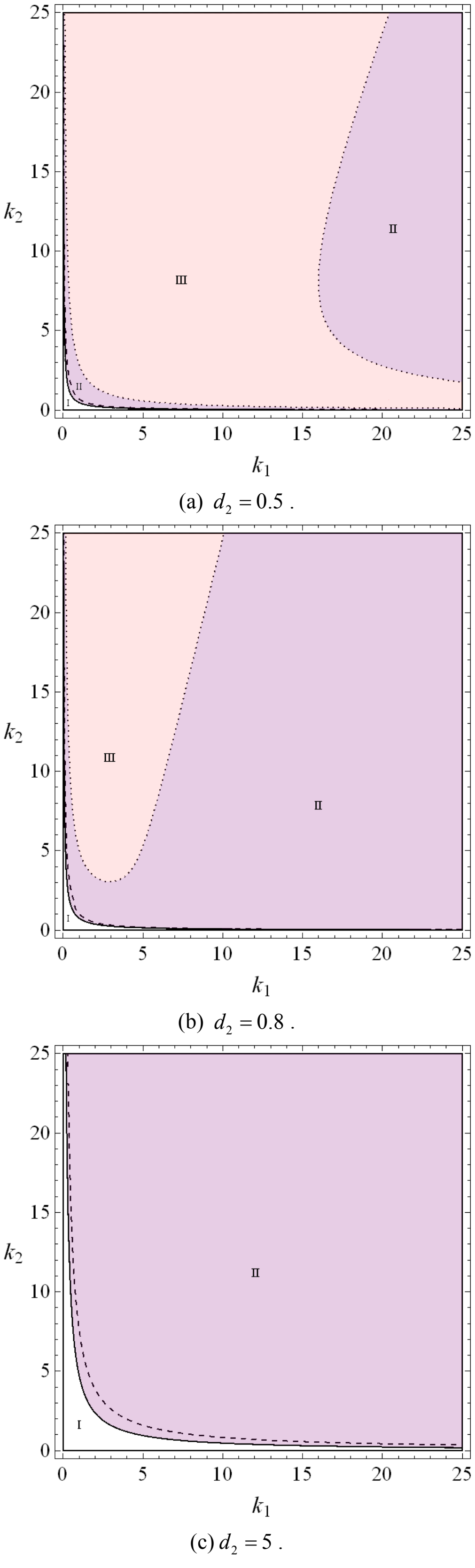


Fig. 4 The (k_1,k_2) parameter space. The symbols for the curves in this figure are as follows $(—): H=0$, $(--): D=0$, and $(\cdot\cdot): M+N=-2\alpha_1/3$.



(a) $d_2 = 0.5$.

(b) $d_2 = 0.8$.

(c) $d_2 = 5$.

Fig. 5 The (k_1,k_2) parameter space. The symbols for the curves in this figure are as follows $(—): H=0$, $(--): D=0$, and $(\cdot\cdot): M+N=-2\alpha_1/3$.

(k_1, k_2) parameter spaces with d_2 = 0.5, 0.8, and d_2 = 5 are displayed in Fig. 5 when the effect of parameter d_2 is also taken into account. Obviously, the higher value of parameter d_2, the larger area of Region I and the smaller area of Region III.

Case 2 (d_1, d_2)–bifurcation parameter

In this case, we then investigate parameters d_1 and d_2 as the bifurcation parameters. In Fig. 6(a), we plot the (d_1, d_2) parameter space with the additional values of parameter $k_1 = 1$ and $k_2 = 3$. Region I, II, and III in this case have the same description as that in Case 1.

If the value of parameter d_2 is fixed, for example, $d_2 = 0.4$ or $d_2 = 0.8$. The corresponding bifurcation diagrams are illustrated in Case 2A and Case 2B, respectively.

Furthermore, more (d_1, d_2) parameter spaces with $k_2 = 9$ and $k_2 = 25$ are shown in Figs. 6(b)–6(c). In Region II^0, the coexistence equilibrium point $N_2(\bar{x}, \bar{y}_1, \bar{y}_2)$ has complex eigenvalues with negative real parts while, in Region II_0, the coexistence equilibrium point $N_2(\bar{x}, \bar{y}_1, \bar{y}_2)$ has three real eigenvalues. As a conclusion, the solution in Region II^0 has damped oscillatory behavior while the solution in Region II_0 has non–oscillatory behavior. Obviously, the higher value of parameter d_2, the larger area of Region III and the smaller area of Region I.

V. CONCLUSION

This model is an approximation to the realistic behavior of marine food web where each organism is considered to be in different trophic levels such as primary producers, primary consumers, secondary consumers, and so on. Of course, all populations are assumed to be homogenous and the spatial dependence is ignored. Particularly, the predator's life cycle is taken into account and divided into immature and mature stages. Both types of the predator population have ability to attack prey. In nature, marine animals cannot consume indefinitely with abundant resources. Therefore, their uptake rate is described by the Holling type II functional response. Obviously, the recruitment rate and the mortality of the immature and the mature predator have affected the dynamical behavior of this predator–prey system. It has been theoretically and numerically shown that a local Hopf bifurcation is possible. Therefore, this population dynamics permits a limit cycle behavior.

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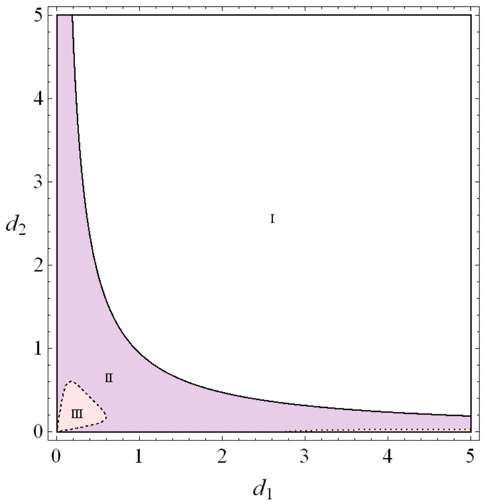
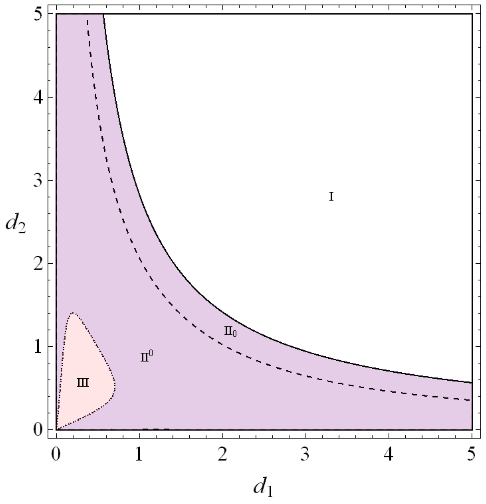
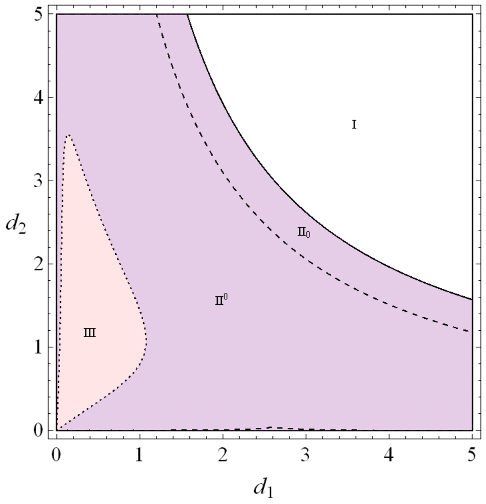


(a) $k_2 = 3$



(b) $k_2 = 9$.



(c) $k_2 = 25$

Fig. 6 The (d_1, d_2) parameter space. The symbols for the curves in this figure are as follows $(-) : H = 0$, $(--) : D = 0$, and $(\cdot\cdot) : M + N = -2\alpha_1/3$.

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