Mixed-mode oscillations and chaos in a prey-predator system with dormancy of predators

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Abstract

It is shown that the dormancy of predators induces mixed-mode oscillations and chaos in the population dynamics of a prey-predator system under certain conditions. The mixed-mode oscillations and chaos are shown to bifurcate from a coexisting equilibrium by means of the theory of fast-slow systems. These results may help to find experimental conditions under which one can demonstrate chaotic population dynamics in a simple phytoplankton-zooplankton(-resting eggs) community in a microcosm with a short duration.

keywords: mixed-mode oscillations, chaos, dormancy, prey-predator, fast-slow system

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It is well known that zooplankton mainly produce subitaneous eggs in comfortable environments; however, they produce fertilized eggs (resting eggs, dormant state) to survive periods of harsh living conditions. In this study, we investigate the effects of dormancy on the population dynamics of phytoplankton-zooplankton in freshwater ecosystems through a simple prey-predator model that considers the case in which predators enter dormancy in the event of a shortage of prey. The result is that the dormancy of predators can induce mixed-mode oscillations and chaos in the population dynamics of a prey-predator system under certain conditions. This suggests that the population dynamics of zooplankton species with a long life and a high foraging ability may exhibit complex behavior such as mixed-mode oscillations and chaos in an environment where food deficiency occurs for an extended duration. In this case, the period of mixed-mode oscillations (chaos) has the same order as the average dormancy period. These pieces of information may help to find experimental conditions under which one can demonstrate chaotic population dynamics in a simple phytoplankton-zooplankton(-resting eggs) community in a microcosm with a short duration. In addition, a mechanism of the onset of the mixed-mode oscillations and chaos is revealed by means of the theory of fast-slow systems.

1 Introduction

Many short-lived organisms have ways of coping with variable environmental conditions that significantly impact individual growth, reproduction, and survivorship. In particular, zooplankton mainly produce subitaneous eggs in comfortable environments; however, they produce fertilized eggs (resting eggs, dormant state) to survive periods of harsh living conditions or catastrophic events. The ability to produce resting eggs is most probably an early feature in zooplankton evolution. In addition, the production of resting eggs gives rise to a biotic reservoir, analogous to plant seed banks that preserve genetic material over long periods. Therefore, dormancy has been a central subject in the study of zooplankton, as seen in the review paper by Gyllström and Hansson [15].

In this study, we focus on the effect of dormancy on the population dynamics of phytoplankton-zooplankton in freshwater ecosystems. With regard to this issue, McCauley et al. [27] found that dormancy has a crucial effect on the population dynamics of *Daphnia* and its algal prey; that is, the amplitude of the prey-predator cycles of *Daphnia* and its algal prey in microcosms increases when a portion of females producing resting eggs is replaced by asexually reproducing gravid females. This suggests that the dormancy of predators can stabilize the population dynamics of prey-predator systems. In order to explain these experimental results, a simple prey-predator model was proposed in [22] according to the natural strategy of a predator that produces resting eggs in the event of a shortage of prey. The model is a three-component autonomous ordinary differential equation as follows:

(1.1)
$$\begin{cases} \frac{dp}{dt} = r(1-\frac{p}{K})p - f(p)z\\ \frac{dz}{dt} = k_1\mu(p)f(p)z + \alpha w - d_1z\\ \frac{dw}{dt} = k_2(1-\mu(p))f(p)z - \alpha w - d_2w \end{cases}$$

where p and z denote the population densities of prey and predators, respectively, and w denotes the population density of predators with a dormancy state (resting eggs). r and K denote the intrinsic growth rate and the carrying capacity of prey, respectively. The function f(p) represents the Holling type II functional response defined by

(1.2)
$$f(p) = \frac{bp}{c+p},$$

where b and c denote the maximum foraging rate and the half saturation constant, respectively. k_1 and k_2 denote the increasing rates of predators in the active and dormant states, respectively. A switching function $\mu(p)$ defined as the sigmoid function

(1.3)
$$\mu(p) = \frac{1}{1 + \exp\left(\frac{-2(p-\eta)}{\sigma}\right)} = \frac{1}{2} \left\{ \tanh\left(\frac{p-\eta}{\sigma}\right) + 1 \right\}$$

controls the induction of dormancy, where η and σ denote the switching level and the sharpness of the switching effect, respectively. This function implies that predators produce more resting eggs than subitaneous eggs when the prey density decreases below a certain level η . d_1 and d_2 denote the mortality rates of the active and dormant predators, respectively. α denotes the hatching rate, i.e., resting eggs have a dormancy period with $1/\alpha$ on average. It should be noted that (1.1) is reduced to a classical prey-predator system known as the MacArthur-Rosenzweig model [33]:

(1.4)
$$\begin{cases} \frac{dp}{dt} = r(1-\frac{p}{K})p - f(p)z\\ \frac{dz}{dt} = k_1f(p)z - d_1z, \end{cases}$$

when $\alpha = 0$ and $\mu(p) \equiv 1$. It is well known that as the carrying capacity K increases, the population dynamics of (1.4) is destabilized. In other words, a coexisting equilibrium of (1.4) becomes unstable and a stable periodic orbit (prey-predator limit cycle) appears through the super-critical Hopf bifurcation.

In this study, we show that (1.1) exhibits complex dynamics by means of the theory of fast-slow systems. It is found that the dormancy of predators can induce mixed-mode oscillations and chaos in the population dynamics of the prey-predator system (1.1) under certain conditions. This suggests that the population dynamics of zooplankton species with a long life and a high foraging ability may exhibit complex behavior such as mixed-mode oscillations and chaos in an environment where food deficiency occurs for an extended duration. In this case, the period of mixed-mode oscillations (chaos) has the same order as the average dormancy period. These pieces of information may help to find experimental conditions under which one can demonstrate chaotic population dynamics in a simple phytoplanktonzooplankton community in a microcosm with a short duration (day). On the other hand, in a complex plankton community consisting of many species in a large area with a long duration (year), the existence of chaotic population dynamics has been reported in [5].

The remainder of this paper is organized as follows. In the next section, we show numerical results of (1.1); this set of equations exhibits mixed-mode oscillations and chaos for certain parameter values. In section 3, we introduce a fast-slow system related to (1.1) to understand the mechanism of the onset of mixed-mode oscillations and chaos in (1.1) in the framework of the bifurcation theory [23] and the geometric singular perturbation theory [19, 20].

	Definitions	Values	Units
Variables			
p	phytoplankton density		${ m mg}~{ m L}^{-1}$
z	zooplankton density		${ m mg}~{ m L}^{-1}$
w	resting-egg density		${ m mg}~{ m L}^{-1}$
Parameters			
r	intrinsic growth rate of phytoplakton	0.5	day^{-1}
K	carrying capacity of phytoplakton	variable	${ m mg}~{ m L}^{-1}$
b	maximum foraging rate	2.0	day^{-1}
c	half-saturation constant	2.0	${ m mg}~{ m L}^{-1}$
d_1	mortality rate of zooplankton	0.2	day^{-1}
d_2	mortality rate of resting eggs	0.0001	day^{-1}
k_1	increasing rate of zooplankton	0.6	dimensionless
k_2	increasing rate of resting eggs	0.12	dimensionless
lpha	hatching rate	0.02	day^{-1}
σ	sharpness of switching effect	0.1	dimensionless
η	level of switching effect	1.0	${ m mg}~{ m L}^{-1}$

Table 1: Definitions of variables and parameters and default parameter values used in simulations.

It is shown that a mixed-mode oscillation bifurcates from a coexisting equilibrium in the fast-slow system and it induces chaotic dynamics according to the theory described in [7]. Section 4 presents the concluding remarks.

2 Numerical results: mixed-mode oscillations and chaos

In this section, we numerically investigate the bifurcation structure of (1.1) with respect to K, and show that (1.1) exhibits mixed-mode oscillations and chaos under certain conditions.

2.1 Parametrization

Based on our previous work [22], we choose default parameter values for the numerical simulations in this paper. As seen in [13, 14, 34, 36], these values, listed in Table 1, are not inconsistent with experimental results. They can be considered as a reference to study the qualitative properties of the population dynamics of phytoplankton-zooplankton communities under the model (1.1), although they do not correspond to one identical species.

A few remarks on some parameters are in order: k_1 and k_2 are dimensionless constants satisfying $0 < k_1 < 1$ and $0 < k_2 < 1$, respectively. They are defined by the efficiency at which a predator converts food into reproduction energy divided by the costs of producing subitaneous and resting eggs, respectively. Because the ratio of the costs for producing subitaneous and resting eggs is estimated to be 1 : 5 by [15], we set $k_2 = k_1/5$. Because the mortality rate of resting eggs d_2 is suggested to be very small in [17], we choose $d_2 = 0.0001$. This implies that the decrease in resting eggs is essentially caused by the hatching of resting eggs, i.e., $d_2 \ll \alpha$. Hence, the death of resting eggs does not affect the dynamics of (1.1) because $-\alpha w - d_2 w = -\alpha (1 + d_2/\alpha) w \approx -\alpha w$ holds in the right-hand side of the third equation of (1.1).

Throughout this paper, we use the parameter values and units listed in Table 1, and do not mention these again unless any ambiguity occurs.

2.2 Bifurcation analysis

In this subsection, we study the bifurcation structure of (1.1) with respect to K, and consider conditions under which (1.1) exhibits mixed-mode oscillations and chaos. We observe how the bifurcation structure changes if the maximum foraging rate b and the mortality rate of active predators d_1 vary. In addition, we numerically estimate the ratio between the period of mixed-mode oscillations (chaos) and the average dormancy period given by $1/\alpha$. The parameters b, d_1 , and α have the same dimension (day⁻¹) and they play important roles in directly controlling the dynamics of active and/or dormant predators.

First, we consider the non-negative equilibria of (1.1). It is easy to verify that (1.1) has two equilibria (K, 0, 0) and (p^*, z^*, w^*) except for the trivial one (0, 0, 0), where p^*, z^* , and w^* are defined by

(2.1)
$$k_1 \mu(p^*) f(p^*) + \frac{k_2 \alpha}{\alpha + d_2} (1 - \mu(p^*)) f(p^*) = d_1,$$

and

(2.2)
$$z^* = \frac{r(1-p^*/K)p^*}{f(p^*)}, \quad w^* = \frac{k_2}{\alpha + d_2}(1-\mu(p^*))f(p^*)z^*.$$

It has been shown in [22] that (p^*, z^*, w^*) transcritically bifurcates from (K, 0, 0) as K increases from a sufficiently small positive value. That is, (K, 0, 0) is stable for $0 < K < K^{tc}$ whereas it is unstable for $K > K^{tc}$, where K^{tc} is a transcritical bifurcation point. Such transcritical bifurcation is also observed in the MacArthur-Rosenzweig model (1.4). Moreover, (p^*, z^*, w^*) is stable for $K^{tc} < K < K^H$ whereas it is unstable for $K > K^H$, where K^H is the Hopf bifurcation point. In this case, we call (p^*, z^*, w^*) a coexisting equilibrium of (1.1).

By using AUTO [11], a software package used for studying the bifurcation structure of differential equations, we can capture the bifurcation structure of (1.1) with respect to K under the parameter values listed in Table 1. In this case, the coexisting equilibrium (p^*, z^*, w^*) bifurcating from (K, 0, 0)becomes unstable as K increases and a periodic orbit appears through the sub-critical Hopf bifurcation at $K^H \approx 5.76$, the bifurcation diagram for which is shown in Fig.1 (a). Moreover, almost every solution of (1.1) converges to a stable periodic orbit on the bifurcating branch for $K > K^H$ (see [22] for details).

Next, we focus on the maximum foraging rate b, and study how the bifurcation structure with respect to K and the dynamics of (1.1) change when we increase b from b = 2.0 and other parameter values are fixed as listed in Table 1. Fig.1 (b) shows a numerical result of the bifurcation diagram of (1.1) with respect to K for b = 7.0. In this case, a stable periodic orbit bifurcates from the coexisting equilibrium through the Hopf bifurcation at $K^H \approx 2.98$. However, the periodic orbit becomes unstable through the period doubling bifurcation at $K^D \approx 4.05$. In fact, AUTO detects the multiplier -1 of the linearization of the Poincaré map around the bifurcating periodic orbit, and numerical simulations show that almost every solution converges to the periodic solution shown in Fig.2.

As K increases considerably, numerical simulations show that the attractor of (1.1) for b = 7.0 exhibits more complex dynamics. For example, when K = 5.0, an attracting mixed-mode oscillatory solution appears as shown in Fig.3, and almost every solution of (1.1) converges to it. As K increases further, the mixed-mode oscillation undergoes a succession of bifurcations and a chaotic attractor appears. Fig.4 shows a chaotic solution for K = 6.0. In fact, the maximum Lyapunov exponent is numerically obtained as $\lambda \approx 0.0042 > 0$. Similar numerical results can be obtained when we decrease the mortality rate of zooplankton d_1 from $d_1 = 0.2$ and other parameter values are fixed as listed in Table 1. In fact, when $d_1 = 0.05$, we can obtain a mixed-mode oscillation for K = 2.7 and chaos for K = 3.0.

These mixed-mode oscillations and chaos cannot be observed for sufficiently small α because the dynamics of (1.1) is almost decoupled to those of the (p, z)- and w-components. Similarly, we cannot observe mixed-mode oscillations and chaos for sufficiently large α because w decays exponentially fast; hence, the asymptotic dynamics of (1.1) can be reduced to the dynamics of the (p, z)-component. Thus, (1.1) has mixed-mode oscillations and chaos only for intermediate (slightly small) values of α under conditions that the maximum foraging rate b is large and/or the mortality rate of active predators d_1 is small (as compared to the reference values listed in Table 1).

From numerical simulations for various parameter values, the period of a mixed-mode oscillation T is roughly estimated as 1 < T/s < 10, where $s = 1/\alpha$ is the average dormancy period; that is, T has the same order as the average dormancy period.



Fig. 1: The bifurcation diagrams of (1.1) with respect to K for (a) b = 2.0and (b) b = 7.0. Other parameter values are as listed in Table 1. Here, the horizontal and vertical axes indicate K and the size (in the L^2 -sense) of solutions of (1.1), respectively. The solid line indicates asymptotically stable solutions, whereas the dashed line indicates unstable ones. The white and black squares indicate the transcritical and the Hopf bifurcation points, respectively. The circle indicates the period doubling bifurcation point.



Fig. 2: An attracting solution of (1.1) for K = 4.05 when b = 7.0. Other parameter values are as listed in Table 1. The solution orbit in the phase space (p, z, w) is represented.



Fig. 3: An attracting mixed-mode oscillation of (1.1) for K = 5.0 when b = 7.0. Other parameter values are as listed in Table 1. The graphs of p, z, and w in t (on the left) and the solution orbit in the phase space (p, z, w) (on the right) are represented.

It should be noted that the prey density satisfies $p < \eta$ in Figs.3 and 4, where η is the level of switching of the dormancy. Numerical simulations for various parameter values show that $p(t) \leq \eta$ holds for a rather wide range of values of t ($p(t) > \eta$ holds for some t under certain parameter values). This suggests that mixed-mode oscillations and chaos of the population of zooplankton can be observed in an environment where food deficiency occurs for an extended duration.

Figs.3 and 4 show that the derivatives dw/dt along the orbits are smaller than dp/dt and dz/dt on average. We expect that the onset of mixed-mode oscillations and chaos may be well explained by using the fast-slow system (3.1) described below. Indeed, the shapes of the orbits shown in Figs.3 and 4 are typical for a three-dimensional fast-slow system, as reported in [7].

3 An approach to mixed-mode oscillations and chaos via a fast-slow system

In this section, we investigate a possible mathematical mechanism to generate the mixed-mode oscillations and chaos of (1.1). Our approach is based on standard arguments of the bifurcation theory and the geometric singular perturbation theory with the aid of numerical computations [9, 12, 19, 20,



Fig. 4: A chaotic attractor of (1.1) for K = 6.0 when b = 7.0. Other parameter values are as listed in Table 1. The graphs of p, z, and w in t (on the left) and the solution orbit in the phase space (p, z, w) (on the right) are represented. The maximum Lyapunov exponent is numerically obtained as $\lambda \approx 0.0042 > 0$.

23, 24, 29].

In Sec.3.1, we introduce a fast-slow system related to (1.1) and investigate its bifurcation diagram with respect to K. In this system, a small parameter ε is introduced to apply a singular perturbation method. The mathematical method has a limitation in that the value of ε must be sufficiently small, although $\varepsilon = 1.0$ in the original system (1.1). However, it is often the case that the dynamic structure found by the singular perturbation method qualitatively persists even for an ε value that is not so small. This appears to be true in our case as well as demonstrated by the numerical simulations in the previous section. We further confirm this point by numerically showing that solution orbits (Fig.4) on the chaotic attractor for (1.1) move along the critical manifold (introduced in Sec.3.2) of the fast-slow system (Fig.9). Although the fast-slow system (3.1) does not have a direct physical relevance, it is a useful mathematical procedure for investigating the dynamical behavior of the original system (1.1). In Sec.3.3, the bifurcation diagram of the fastslow system with respect to b is investigated and it is shown that a mixedmode oscillation bifurcates from a coexisting equilibrium. In Sec.3.4, the bifurcation diagram of the fast-slow system with respect to ε is investigated and a chaotic attractor is shown to bifurcate from the mixed-mode oscillation.

Throughout this section, we perform numerical computations by using the parameter values related to the chaotic attractor shown in Fig.4. However, the results in this section are applicable to understand the chaos of (1.1) for other parameter values.

3.1 Fast-slow system

Motivated by the argument presented at the end of Section 2, we introduce a small parameter $\varepsilon > 0$ and define the fast-slow system related to (1.1) to be

(3.1)
$$\begin{cases} \frac{dp}{dt} = r(1-\frac{p}{K})p - f(p)z\\ \frac{dz}{dt} = k_1\mu(p)f(p)z + \alpha w - d_1z\\ \frac{dw}{dt} = \varepsilon(k_2(1-\mu(p))f(p)z - \alpha w - d_2w). \end{cases}$$

Our purpose is to study the bifurcation structure of (3.1) with respect to K and b for small ε .

First, we set b = 7.0, $\varepsilon = 0.2$, and other parameter values as listed in Table 1, and investigate the bifurcation diagram of (3.1) with respect to Kby using AUTO to compare it with that of (1.1) obtained as shown in Fig.1 (b). The result is shown in Fig.5. The left-hand side of Fig.5 shows that the bifurcation diagram of (3.1) is similar to that of (1.1) (see Fig.1 (b)) when K is smaller than the Hopf bifurcation point ($K < K^H$). However,



Fig. 5: The bifurcation diagram of (3.1) with respect to K (on the left) and the phase portrait (on the right) for $\varepsilon = 0.2$ and b = 7.0, where b = 7.0 is the same as that in Fig.4. Other parameter values are as listed in Table 1. Here, the horizontal and vertical axes indicate K and the size (in the L^2 sense) of solutions of (3.1), respectively. The solid line in the left-hand side indicates asymptotically stable solutions, whereas the dashed line indicates unstable ones. The white and black squares indicate the transcritical and the Hopf bifurcation points, respectively. Periodic orbits corresponding to the numbered points in the bifurcation diagram are respectively drawn in the projected phase plain (p, w) on the right-hand side.

it is remarkable that as K increases, a periodic orbit grows and becomes a mixed-mode oscillation along the stable branch bifurcating from a coexisting equilibrium, as shown in the right-hand side of Fig.5. This suggests that the fast-slow system (3.1) is suitable for studying the bifurcation structure of mixed-mode oscillations of (1.1). In the following subsections, we clarify the mechanism of the onset of mixed-mode oscillations and chaos using the theory described in [7].

3.2 Critical manifold

It is well known [7, 19, 20, 29] that the dynamics of the fast-slow system (3.1) can be explained by the critical manifold of (3.1) and the dynamics on it as follows.



Fig. 6: The critical manifold of (3.1) for b = 7.0 and K = 6.0. These values are the same as those in Fig.4, and other parameter values are as listed in Table 1.

Setting $\varepsilon = 0$ in (3.1), we have the unperturbed system of (3.1):

(3.2)
$$\begin{cases} \frac{dp}{dt} = r(1-\frac{p}{K})p - f(p)z\\ \frac{dz}{dt} = k_1\mu(p)f(p)z + \alpha w - d_1z\\ \frac{dw}{dt} = 0. \end{cases}$$

The critical manifold of (3.1) is defined by the set of fixed points of (3.2) as (3.3)

$$M = \{ (p, z, w) \in \mathbf{R}^3 \mid r(1 - \frac{p}{K})p - f(p)z = 0, \ k_1\mu(p)f(p)z + \alpha w - d_1z = 0 \}.$$

We consider M in the region $p \ge 0, z \ge 0$, and $w \ge 0$ because p, z, and w denote population densities. In this region, the critical manifold Mfor b = 7.0 and K = 6.0 is numerically calculated and the result is shown in Fig.6. It is found that M consists of the line $M_1 = \{p = 0, \alpha w - d_1 z = 0\}$ and the parabola-like curve M_2 . When regarding w as a bifurcation parameter, the red points on M_2 (branch N_1) in Fig.6 indicate unstable focuses; that is, the linearized matrix of the right-hand side of (3.2) corresponding to each red point on M_2 has two complex eigenvalues with positive real parts. The green branch on M_2 (branch N_2) consists of stable focuses and it is connected to the red branch at the Hopf bifurcation point. On the other hand, the blue and purple branches on M_2 (branches N_3 and N_4 , respectively) consist of stable nodes and saddle points, respectively. The purple branch connects to the green branch at the fold point of M_2 , which is the saddle-focus bifurcation point. Similarly, the purple and blue branches on M_1 consist of saddle points and stable nodes, respectively. The intersection of M_1 and M_2 is the transcritical bifurcation point. It should be noted that the critical manifold of (3.1) has the same structure as that shown in Fig.6 for a rather wide range of values of b and K.

The dynamics of w of (3.1) on the critical manifold M is given by the slow system

(3.4)
$$\frac{dw}{dt} = \varepsilon (k_2(1-\mu(p))f(p)z - \alpha w - d_2 w)\Big|_{(p,z,w)\in M}$$

that is, the dynamics of (3.1) on M is reduced to the dynamics defined by the one-dimensional equation (3.4).

3.3 Bifurcation from a coexisting equilibrium to a mixedmode oscillation

In this subsection, we investigate the behavior of a coexisting equilibrium on the critical manifold M and study the bifurcation structure of (3.1) with respect to b in order to reveal the onset of mixed-mode oscillations. It will be shown that a mixed-mode oscillation bifurcates from a coexisting equilibrium through the Hopf bifurcation at the fold point of M (cf. [19]). Throughout this subsection, we set $\varepsilon = 0.2$, K = 6.0, and we increase b from b = 2.0 to b = 7.0, where b = 2.0 is the reference value listed in Table 1 and b = 7.0 is the same as that in Fig.4.

Setting b = 2.0, we have an unstable equilibrium (coexisting equilibrium) near the red branch of M_2 (branch N_1) and a stable periodic orbit (preypredator cycle) of (3.1) in a region p > 0, z > 0, and w > 0 (see Fig.7).

As we increase b from b = 2.0, the coexisting equilibrium moves upward along M_2 and into the green branch on M_2 (the branch N_2). This implies that the coexisting equilibrium becomes stable, and an unstable periodic orbit appears through the Hopf bifurcation at $b \approx 2.16$ (See Fig.8).

As b increases considerably, the stable coexisting equilibrium continues to move upward and approaches the fold point of M_2 . On the other hand, the stable periodic orbit (prey-predator cycle) collides with the unstable periodic orbit and disappears through the saddle-node bifurcation at $b \approx 3.14$ (see Fig.8).

As we further increase b, the coexisting equilibrium becomes unstable near the fold point of M_2 , and a stable periodic orbit appears through the Hopf bifurcation at $b \approx 6.46$. The bifurcating periodic orbit grows and turns into a mixed-mode oscillation as b increases (see Figs.8 and 9 (a)).

Thus, we see that the mixed-mode oscillations of (3.1) bifurcate from a coexisting equilibrium when we increase b from the reference value b = 2.0 listed in Table 1. Moreover, it is found that (3.1) exhibits mixed-mode oscillations when we choose parameter values such that a coexisting equilibrium is near the fold point of the critical manifold. For example, taking large



Fig. 7: The critical manifold, a stable periodic orbit, and an unstable equilibrium of (3.1) for K = 6.0, $\varepsilon = 0.2$, and b = 2.0, where K = 6.0 is the same as that in Fig.4 and b = 2.0 is the reference value of b listed in Table 1. Other parameter values are as listed in Table 1. The black curve and cross point denote a periodic orbit and an equilibrium, respectively.



Fig. 8: The bifurcation diagram of (3.1) with respect to b (on the left) and phase portrait (on the right) for K = 6.0 and $\varepsilon = 0.2$, where K = 6.0 is the same as that in Fig.4. Other parameter values are as listed in Table 1. Here, the horizontal and vertical axes indicate b and the size (in the L^2 sense) of solutions of (3.1), respectively. The solid line in the left-hand side indicates asymptotically stable solutions, whereas the dashed line indicates unstable ones. The black square indicates the Hopf bifurcation point. Periodic orbits on the stable branch bifurcating from a coexisting equilibrium at b = 6.5, 6.6, 6.7, and 7.0 are respectively drawn in the projected phase plain (p, w) on the right, where b = 7.0 is the same as that in Fig.4.



Fig. 9: The critical manifold and an attractor of (3.1) when b = 7.0 and K = 6.0; (a) a mixed-mode oscillation for $\varepsilon = 0.2$ and (b) a chaotic attractor for $\varepsilon = 1.0$. Other parameter values are as listed in Table 1.



Fig. 10: A schematic view of the Poincaré section Σ .

values of b (as compared to the reference value listed in Table 1) is one of conditions under which a coexisting equilibrium is near the fold point of the critical manifold.

3.4 Bifurcation from the mixed-mode oscillation to chaos

According to the parameter values related to the chaotic attractor shown in Fig.4, we set b = 7.0, K = 6.0, $\varepsilon = 0.2$, and other parameter values as listed in Table 1. Then, we obtain the critical manifold and a mixed-mode oscillation of (3.1), as shown in Fig.9 (a). Next, when we increase ε from 0.2 to 1.0, the mixed-mode oscillation becomes chaotic (Fig.9 (b)) through the cascade bifurcation, as seen in Section 2. Based on the theory described in [7], the mechanism of the onset of mixed-mode oscillations and chaos can be explained as follows.

Let us define a Poincaré section Σ that transversally intersects an attrac-



Fig. 11: Positional relationship of the rectangle R and $\Pi(R)$.

tor (the mixed-mode oscillation or the chaotic attractor) of (3.1) denoted by \mathcal{A} , as shown in Fig.10. Take a small open set $U \subset \Sigma$ including $\Sigma \cap \mathcal{A}$ and consider a solution of (3.1) starting from $y \in U$. Since the green branch on M_2 (branch N_2) consists of stable focuses of (3.2), the orbit approaches this branch. Since the right-hand side of the slow dynamics (3.4) is positive on the green branch on M_2 , the orbit moves upward rotating around M_2 and reaches the fold point of M_2 . Then, the orbit leaves the fold point and approaches the blue branch on M_1 (branch N_3) consisting of stable nodes of (3.2). Since the right-hand side of (3.4) is negative on M_1 , the orbit moves downward along M_1 and reaches the transcritical point. Then, the orbit leaves the transcritical point and returns to Σ . In this manner, we can define a Poincaré map $\Pi: U \to \Sigma$.

In order to investigate the properties of the Poincaré map Π , take a rectangle R on $U \subset \Sigma$ and consider how it behaves when it runs along the flow of (3.1). The rectangle R is folded into a ring-shaped domain R' when moving upward around the green branch on M_2 , and the radius of R' is decreasing. If ε is sufficiently small, then R' stays near the green branch of M_2 for a long duration because the dynamics of w defined by (3.4) is very slow. In this case, R' sufficiently shrinks when passing through the vicinity of M_2 , and hence, $\Pi(R) \subset R$ holds (Fig.11(a)). This implies that Π is a contraction map, and thus, (3.1) has a stable periodic orbit (Fig.9 (a)). In contrast, when ε is not so small, R' cannot shrink sufficiently. Therefore, $\Pi(R)$ transversally intersects R and a horseshoe is formed, as shown in Fig.11(b). Therefore, the dynamics of (3.1) becomes chaotic through the cascade bifurcation as ε increases (see [7] for the proof).

In this section, we introduced the small parameter ε to apply the theory described in [7] and revealed the mechanism of the onset of mixed-mode oscillations and chaos of the fast-slow system. Nevertheless, we emphasize that the mechanism of the onset of mixed-mode oscillations and chaos for the original system (1.1) (i.e. $\varepsilon = 1.0$) is similar to that of the fast-slow system. In fact, Figs.3 and 4 show that dw/dt is much smaller than dp/dt and dz/dt along the orbits. This implies that (1.1) can be regarded as the fast-slow system without introducing the small parameter ε . Furthermore, dw/dt along the chaotic attractor of (1.1) (see Fig.4) is larger than that along the mixed-mode oscillation of (1.1) (see Fig.3) on average. Thus, the mixed-mode oscillation of (1.1) becomes chaotic by the same mechanism discussed above.

4 Concluding remarks

In this study, we show that the dormancy of predators can induce mixedmode oscillations and chaos in the population dynamics of a prey-predator system under certain conditions. Noting that the time derivative of the density of dormant predators is smaller than those of prey and active predators, we introduced the fast-slow system to show that a mixed-mode oscillation and a chaotic attractor bifurcate from a coexisting equilibrium. This approach enables us to understand the mechanism of the onset of mixed-mode oscillations and chaos in a prey-predator system with dormancy of predators.

To the best of our knowledge, mixed-mode oscillations and chaos have not yet been experimentally demonstrated in a simple phytoplankton-zooplankton(resting eggs) community in a microcosm with a short duration. We expect that such complex behavior will be experimentally demonstrated in the future based on our theory. In fact, as reported in [26], the period of a prey-predator cycle in *Daphnia*-algal systems was 21.4 days on average under certain experimental conditions. On the other hand, the period of a prey-predator cycle in our model (1.1) is approximately 20.9 (day) under the parameter values listed in Table 1 and $K \approx 5.17$ (this value corresponds to the limiting point on the bifurcating branch of periodic orbits in the bifurcation diagram of (1.1)shown in Fig. 1(a)). This suggests that the experimental prey-predator cycle in *Daphnia*-algal systems corresponds to the theoretical one in our model. Thus, it is expected that the *Daphnia*-algal prey-predator cycle will become unstable and the systems will exhibit mixed-mode oscillations and chaos if the experimental conditions are varied because in our model, mixed-mode oscillations and chaos bifurcate from the prey-predator cycle. Our model may serve as a reference for empirical researchers to find a good example of chaos in plankton communities, and it may contribute toward understanding the ecological implications of dormancy for short-lived organisms such as zooplankton, though it should be emphasized that our theoretical prediction concerns the qualitative properties of population dynamics in a simple phytoplankton-zooplankton(-resting eggs) community.

Complex dynamics such as mixed-mode oscillations and chaos has also been reported in many literatures concerning food webs consisting of three or more species (prey-predator is a basic building block of a food web). Roughly speaking, they are concerned with chaotic dynamics in (extensions of) a three-species model of the food-prey-predator type known as the Hastings-Powell model [18]. The reader should consult classical and recent papers [9, 12, 18, 25, 30, 31] and the references therein. [9, 12, 24] introduced fastslow systems to investigate bifurcation structures. However, the mechanism of generating mixed-mode oscillations and chaos in our system is different from those in [9, 12, 24]. For example in [9, 12], the dimension of the fast direction is one whereas it is two in our system. Our analysis of the fastslow system is based on the theory described in [7], in which the existence of mixed-mode oscillations and chaos is proved for a three-dimensional fast-slow system with a two-dimensional fast direction.

Our model requires some extensions in order to reflect more realistic conditions. For example, to consider intraspecies interaction (density-dependent inhibition) among active predators, we propose the system

(4.1)
$$\begin{cases} \frac{dp}{dt} = r(1 - \frac{p}{K})p - f(p)z \\ \frac{dz}{dt} = k_1\mu(p)f(p)z + \alpha w - d_1z - \gamma z^2 \\ \frac{dw}{dt} = k_2(1 - \mu(p))f(p)z - \alpha w - d_2w, \end{cases}$$

where γ is a positive constant. The effects of intraspecies interaction among predators for the MacArthur-Rosenzweig model and the Hastings-Powell model have been studied by [4, 28] and [10, 30, 37], respectively (an extension of the MacArthur-Rosenzweig model with intraspecies interaction among predators is called the Bazykin model). From [10, 30, 37], it appears that (4.1) have chaotic attractors for a narrow range of parameter values due to a stabilizing effect of intraspecies interaction. Combining singular perturbation methods and scaling arguments, the difference between (1.1) and (4.1) should be clarified by detailed bifurcation analysis with the aid of numerical computations. It is one of the important problems to be considered in further studies.

It may also be profitable to seek other possibilities to generalize the model (1.1) and explore their bifurcation structures. This provides many pieces of useful information for understanding how the dormancy of predators affects the population dynamics of prey-predator systems.

Dormancy has begun attracting considerable interest among freshwater ecologists, and recent empirical studies have provided fundamental and profound knowledge about the dormancy of zooplankton [2, 6, 15, 16, 27, 32]. Moreover, dormancy appears to have evolved independently among a wide variety of living organisms [1, 3, 8, 21, 35]. It is an important adaptive response to selective pressures that are common to a large number of organisms. Therefore, theoretical approaches such as those presented in this paper are indispensable for understanding the ecological implications of dormancy. Acknowledgments The authors express their sincere gratitude to Dr. Takefumi Nakazawa, Professors Toshiyuki Ogawa and Kunimochi Sakamoto for their useful advice and comments. Moreover, the authors would like to appreciate the referees for their useful suggestions and comments, which have improved the original manuscript. The first author was supported in part by the Grant-in-Aid for Scientific Research (C) No.18540120 JSPS, and the second author by JSPS Fellowships for Young Scientists.

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