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Analysis of a mathematical model arising from Barnacle-Algae-Mussel interactions[*]

Sze-Bi Hsu[*], Yi Wang[†], and Hui Zhou [†]

Abstract. In this paper we focus on a patch occupancy 4-dimensional model of barnacle-algae-mussel interactions with external periodic seasonal forcing proposed by Benincà et al. [PNAS-2015]. In order to understand the mechanism of the species fluctuation sustained by a cyclic succession at the edge of chaos, we investigate the corresponding system without seasonal forcing. When the mussel is absent, we give a complete description of the global asymptotic behavior of the solutions. If the mussel is present, we provide an amenable sufficient and necessary condition for the uniform persistence for the 4-dimensional system. Our analytic results on the uniform persistence provide useful necessary information for the chaotic dynamics of the periodically forced system in [1].

Keywords: global asymptotic stability, orbital stability, second compound matrix, positive periodic solution, uniform persistence, coexistence

MSC[2010]: 37C75, 92D25, 37N25, 34D05

1. Introduction and the model.

It is a challenge to test the chaos in a natural ecological system, although there are many mathematical models ([3, 10, 15, 25, 26, 29]) and laboratory experiments ([2, 7]) for which species interactions can generate chaotic behavior. In a recent paper [1], Benincà et al. have reported the recorded data of 20-year time series of populations of barnacle, crustose algae and mussel in a rocky intertidal community located in the Cape Rodney-Okakari Point Marine Reserve on the North Island of New Zealand. The data displays a complex cycle succession for many years at the edge of chaos. First, bare rock was colonized by barnacles and crustose algae, then they were overgrown by mussel and subsequent detachment of the mussels returned bare rock again. The data exhibits irregular species fluctuation.

According to the data, Benincà et al. [1] constructed a patch occupancy model based on the species interaction in the intertidal community. Let B_0 be the fraction of the patches occupied by barnacles without crustose algae, and let B_A be the fraction occupied by barnacles overgrown with crustose algae. Furthermore, let A be the fraction occupied by crustose algae, which includes crustose algae on barnacles B_A and crustose algae on bare rock, let M be the fraction occupied by mussels, and R be the fraction of bare rock. The model takes form as

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[*] Department of Mathematics and The National Center for Theoretical Science, National Tsing Hua University, Hsinchu 300, Taiwan.

[†] School of Mathematical Science, University of Science and Technology of China, Hefei, Anhui 230026, P. R. China

follows (see [1, p.6391]):

$$\begin{cases} \dot{B}_0 = c_{BR}(B_0+B_A)R - c_{AB}AB_0 - c_M MB_0 - m_B B_0 + F(t)m_A B_A, \\ \dot{B}_A = c_{AB}AB_0 - c_M MB_A - m_B B_A - F(t)m_A B_A, \\ \dot{A} = c_{AR}AR + c_{AB}AB_0 - c_M MA - F(t)m_A A, \\ \dot{M} = c_M M(B_0 + A) - F(t)m_M M, \\ R = 1 - B_0 - A - M, \end{cases} \tag{1.1}$$

where

- c_{BR}: the colonization rate of barnacles on bare rock;
- c_{AB}: the colonization rates of crustose algae on barnacles;
- c_{AR}: the colonization rates of crustose algae on bare rock;
- c_M: the colonization rate of mussels on barnacles and crustose algae;
- m_B, m_A, m_M: mortality rates of barnacles, crustose algae, and mussels, respectively;
- $F(t)$: seasonal temperature fluctuations as

$$F(t) = 1 + \alpha \cdot (T_{\max} - T_{\text{mean}}) \cos(\frac{2\pi(t-32)}{365}). \tag{F_*}$$

It is observed that crustose algae and mussels are sensitive to the temperature fluctuation and their mortality rate were forced by seasonal temperature variation with high mortality in summer and low mortality rate in the winter. In the expression of $F(t)$, α represents the strength of seasonal forcing, T_{mean} is the mean annual sea surface temperature 17.1°C and $T_{\max} = 20.5$°C measured at the warming day of the year, namely February 1 with delay 32 days. However, barnacle mortality is not affected by seasonal temperature variation.

In the B_0-equation of (1.1), the first term $c_{BR}(B_0 + B_A)R$ represents the colonization of barnacles on bare rock; in the second term $c_{AB}AB_0$ describes the overgrowth of barnacles by crustose algae; the third term $c_M MB_0$ is the overgrowth of barnacles by mussels; while the fourth term $m_B B_0$ is the mortality of barnacles; and the last term $F(t)m_A B_A$ is the mortality of crustose algae growing on barnacles. In B_A-equation of (1.1), the first term $c_{AB}AB_0$ and fourth term $F(t)m_A B_A$ have already been introduced above. They describe the colonization and mortality of crustose algae on barnacles; the second term $c_M MB_A$ is the overgrowth of barnacles and their crustose algae by mussel population; the third term $m_B B_A$ is the mortality of barnacles covered by crustose algae. In the A-equation of (1.1), the first and second term $c_{AR}AR, c_{AB}AB_0$ describe the colonization of crustose algae on bare rock and on barnacles, respectively; the third term $c_M MA$ is the overgrowth of crustose algae by mussel; and the last term $F(t)m_A A$ is the mortality of crustose algae. In the M-equation of (1.1), we note that the mussel cannot settle on bare rock, only settle on top of barnacles and crustose algae. The first term $c_M M(B_0 + A)$ represents the colonization of mussels on barnacles and crustose algae, and second term $F(t)m_M M$ is mussel mortality. For more detail of the model (1.1), we refer to the SI Appendix in the supplemental material of [1].

To the best of our knowledge, Benincà et al. [1] is perhaps the first article to present evidences that, for the real-world ecological community, erratic fluctuations in an intertidal rock-pool ecosystem are caused by competitive interactions that cause chaotic dynamics. In fact, the extensive numerical simulations in [1] illustrated that a complex cycle succession for many years at the edge of chaos is indeed possible for the model (1.1) under some parameters ranges.

To understand the mechanism of the species fluctuation sustained by a cyclic succession at the edge of chaos, the *first step* appears to be the study of the corresponding system without seasonal forcing, that is, $\alpha = 0$ (hence $F(t) = 1$),

$$\begin{cases} \dot{B}_0 = c_{BR}(B_0 + B_A)R - c_{AB}AB_0 - c_M MB_0 - m_B B_0 + m_A B_A, \\ \dot{B}_A = c_{AB}AB_0 - c_M MB_A - m_B B_A - m_A B_A, \\ \dot{A} = c_{AR}AR + c_{AB}AB_0 - c_M MA - m_A A, \\ \dot{M} = c_M M(B_0 + A) - m_M M, \\ R = 1 - B_0 - A - M. \end{cases} \tag{1.2}$$

The present paper is devoted to investigating the global dynamics of system (1.2). Our work turns out to be *the first attempt* to initiate the research on rigorously analyzing this new model (1.1) of barnacle-algae-mussel interactions.

For this purpose, we first consider the crucial case of (1.2) for which mussel is absent, i.e., $M = 0$. System (1.2) is then reduced to the following three-dimensional system:

$$\begin{cases} \dot{B}_0 = c_{BR}(B_0 + B_A)R - c_{AB}AB_0 - m_B B_0 + m_A B_A, \\ \dot{B}_A = c_{AB}AB_0 - m_B B_A - m_A B_A, \\ \dot{A} = c_{AR}AR + c_{AB}AB_0 - m_A A, \\ R = 1 - B_0 - A. \end{cases} \tag{1.3}$$

In the first part of this paper, we will give a complete description of the global dynamics of system (1.3). Based on this, we will present in the second part of this paper an amenable sufficient and necessary condition for the uniform persistence, i.e., the coexistence of the species, for the 4-dimensional barnacle-algae-mussel system (1.2).

The paper will be organized as follows. In Section 2, we state our main results, mention the main difficulties for the proofs and give the biological interpretations of the results. We defer to Section 3 all the detailed proofs. Section 4 is the Discussion Section.

2. Main Results.

We mainly focus on the autonomous system (1.2) of Barnacle-Algae-Mussel interactions. For this purpose, we rewrite (1.2) as the following new system

$$\begin{cases} \dot{B}_0 = B_0[c_{BR}(1 - B_0 - A - M) - c_{AB}A - c_M M - m_B] \\ \qquad + B_A[c_{BR}(1 - B_0 - A - M) + m_A], \\ \dot{B}_A = c_{AB}AB_0 - (c_M M + m_B + m_A)B_A, \\ \dot{A} = A[(c_{AR} - m_A) - c_{AR}A - (c_{AR} + c_M)M + (c_{AB} - c_{AR})B_0], \\ \dot{M} = M[c_M(B_0 + A) - m_M]. \end{cases} \tag{BAM}$$

Let $B = B_0 + B_A$ be the total barnacles. Then B satisfies

$$\dot{B} = B[c_{BR}(1 - B_0 - A) - (c_{BR} + c_M)M - m_B]. \tag{2.1}$$

Since B, A, M are the fractions of the patches occupied by barnacle, crustose algae and mussel in a rocky intertidal community, biologically, it is reasonable to see that $0 \leq B, A, M \leq 1$. Note also that B_A is the fraction occupied by barnacles overgrown with crustose algae. Then it is biologically reasonable to expect $B_A(t) \leq A(t)$ for all $t \geq 0$. Motivated by this, we define in the present paper our working domain Σ as

$$\Sigma = \{(B_0, B_A, A, M) \in \mathbb{R}_+^4 : B_0 + A + M \leq 1, \ \textit{and} \ B_A \leq A\}, \tag{2.2}$$

where $\mathbb{R}_+^4$ is the first orthant in $\mathbb{R}^4$. The following proposition confirms the validity of the choice of Σ from mathematical point of view.

Proposition 2.1. *Σ is positively invariant with respect to system* (BAM)*. Moreover, let $(B_0(t), B_A(t), A(t), M(t))$ be a solution of* (BAM) *in Σ. If $A(0) > 0, M(0) > 0$ and $B(0) = B_0(0) + B_A(0) > 0$, then $B_0(t), B_A(t), A(t)$ and $M(t)$ are all positive for all $t > 0$.*

Next we present our *standing assumption* throughout this paper:

(H1) $c_{AB} > c_{AR}$ and $c_{BR} > m_B$.

Here, $c_{AB} > c_{AR}$ is due to the biological observation that the crustose algae settle more firmly on barnacles than on the bare rock; while $c_{BR} > m_B$ indicates that the colonization rate of barnacles on the bare rock is greater than the mortality rate of barnacles. Note that if $c_{BR} \leq m_B$, then from (2.1) the total population of barnacles becomes extinct as time becomes large.

In order to investigate the dynamics of system (BAM) arising from barnacle-algae-mussel interactions, one needs to analyze a crucial case for which mussel is absent, i.e., $M = 0$. For such particular case, (BAM) turns out to be

$$\begin{cases} \dot{B}_0 = B_0[c_{BR}(1 - B_0 - A) - m_B - c_{AB}A] + B_A[c_{BR}(1 - B_0 - A) + m_A], \\ \dot{B}_A = c_{AB}AB_0 - (m_B + m_A)B_A, \\ \dot{A} = A[(c_{AR} - m_A) - c_{AR}A + B_0(c_{AB} - c_{AR})]. \end{cases} \tag{BA}$$

Clearly, system (BA) is equivalent to system (1.3). Moreover, (2.1) is reduced to

$$\dot{B} = B[c_{BR}(1 - B_0 - A) - m_B]. \tag{2.3}$$

Σ in (2.2) is then reduced to

$$\Gamma = \{(B_0, B_A, A) \in \mathbb{R}_+^3 : B_0 + A \leq 1, B_A \leq A\}, \tag{2.4}$$

which is positively invariant with respect to system (BA).

In the first part of this paper, we will give a complete description of the global dynamics of the 3-dimensional system (BA). More precisely, let

$$\tilde{E}_0 = (0, 0, 0), \ \tilde{E}_B = (B_0^*, 0, 0), \ \tilde{E}_A = (0, 0, A^*),$$

where $B_0^* = 1 - \frac{m_B}{c_{BR}}$, $A^* = 1 - \frac{m_A}{c_{AR}}$. Under assumption (H1), $\tilde{E}_0, \tilde{E}_B$ always exist, while $\tilde{E}_A$ may or may not exist in Γ.

Theorem 2.2. *Assume* (H1). *Let* $\lambda_* = (c_{AR} - m_A) + B_0^*(c_{AB} - c_{AR})$. *Then, for system* (BA),

- (i) *When* $\lambda_* < 0$, $\tilde{E}_B$ *is globally asymptotically stable (G.A.S.) with respect to* $\Gamma \setminus \tilde{E}_0$*;*
- (ii) *When* $\lambda_* > 0$,
  - (a) *if* $\frac{m_B}{c_{BR}} > \frac{m_A}{c_{AR}}$ *(i.e.,* $B_0^* < A^*$*), then* $\tilde{E}_A$ *exists and is G.A.S.with respect to* $\Gamma \setminus \{A = 0\}$*;*
  - (b) *if* $\frac{m_B}{c_{BR}} < \frac{m_A}{c_{AR}}$ *(i.e.,* $B_0^* > A^*$*), there is a unique positive equilibrium* $\tilde{E}_c$ *that is G.A.S. with respect to* $\Gamma \cap \mathrm{Int}\mathbb{R}^3_+$. *Moreover,* $\tilde{E}_c = (\bar{B}_0, \bar{B}_A, \bar{A})$ *satisfying*

$$c_{AR}\bar{A} = (c_{AR} - m_A) + \bar{B}_0(c_{AB} - c_{AR}), \tag{2.5}$$

$$c_{BR}(\bar{B}_0 + \bar{A}) = c_{BR} - m_B, \tag{2.6}$$

$$\bar{B}_A = \frac{c_{AB}}{m_A + m_B}\bar{A}\bar{B}_0. \tag{2.7}$$

Remark 1. (i). Theorem 2.2(i) says if the mortality rate m_A of crustose algae is too large such that $\lambda_* < 0$, then only barnacles survive.

(ii). Theorem 2.2(ii) says if $\lambda_* > 0$, only crustose algae survives if its mortality rate in comparison with colonization rate on the bare rock, $\frac{m_A}{c_{AR}}$ is smaller than that of barnacles. However, if on the contrary, the species B_0, B_A and A will coexist.

Among others, the most difficult part in proof of Theorem 2.2 is the global asymptotic stability of $\tilde{E}_c$. For this purpose, it is known that the Lyapunov function approach is frequently used in ecology systems with mostly terms of mass action form (see, e.g. [17, 18] or [14] and references therein). Unfortunately, several typical types of Lyapunov functions do not work for the system (BA). As a consequence, one has to try some alternative approach. Motivated by the definition of Γ, we present our approach by introducing some new variables and transform the original system (BA) to a new 3-dimensional system that is of so-called K-competitive (see [8,9,12,23,31,32] and references therein). Since 3-dimensional K-competitive systems have the Poincaré-Bendixson Property (c.f. [12, Theorem 3.23], see also [11,30,31]), the challenging task of the global asymptotic stability of $\tilde{E}_c$ can be reduced to show the orbital stability of any possible positive periodic solutions in Γ. We accomplish this approach by constructing a Lyapunov function and utilizing the stability criterion in term of the second compound equations which was developed by Muldowney [27, 28] (see also [20–22]).

Based on Theorem 2.2, we will provide in the second part of this paper an amenable sufficient and necessary condition for the uniform persistence for the 4-dimensional barnacle-algae-mussel system (BAM).

More precisely, let

$$\sigma \triangleq \frac{c_M}{m_M}\frac{c_{AR} + c_M}{c_{AB}}(M^* - \hat{M}),$$

where

$$M^* = \frac{c_{BR}(c_M - m_M) - c_M m_B}{c_M(c_M + c_{BR})} \quad \text{and} \quad \hat{M} = \frac{c_{AR}(c_M - m_M) - c_M m_A}{c_M(c_M + c_{AR})}.$$

Then, we have the following

Theorem 2.3. *Assume* (H1). *Then, for system* (BAM)*,*

(i) *The positive equilibrium* $E_c \in \Sigma \cap \mathrm{Int}\mathbb{R}^4_+$ *exists if and only if*

$$0 < \sigma < 1 \quad \text{and} \quad \frac{m_B}{c_{BR}} + \frac{m_M}{c_M} < 1.$$

Moreover, if E_c *exists, then it must be unique.*

(ii) (BAM) *is uniformly persistent if and only if* E_c *exists. In other words, system* (BAM) *is uniformly persistent if and only if* $0 < \sigma < 1$ *and* $\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} < 1$.

Remark 2. (i) According to the data reported in Benincà et al. [1], $c_{BR} = 0.018\ \text{day}^{-1}$, $c_{AB} = 0.049\ \text{day}^{-1}$, $c_{AR} = 0.021\ \text{day}^{-1}, c_M = 0.078\ \text{day}^{-1}, m_A = 0.011\ \text{day}^{-1}, m_B = 0.003\ \text{day}^{-1}, m_M = 0.017\ \text{day}^{-1}$, one has $\sigma \approx 0.561388$ and $\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} \approx 0.384615$, which entails that E_c exists and (BAM) is uniformly persistent.

(ii) Actually, we will give in Subsection 3.3 a tedious explicit expression of E_c as

$$E_c = (\frac{m_M}{c_M}\sigma,\ \frac{m_M^2 c_{AB}\sigma(1-\sigma)}{c_M^2(c_M M^* + m_A + m_B)},\ \frac{m_M}{c_M}(1-\sigma),\ M^*).$$

Clearly, $M^* > 0$ if and only if $\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} < 1$. Moreover, if $\sigma = 1$ then E_c is reduced to $E_1(\frac{m_M}{c_M}, 0, 0, M^*)$; while if $\sigma = 0$ (hence $M^* = \hat{M}$) then E_c is reduced to $E_2(0, 0, \frac{m_M}{c_M}, \hat{M})$. As we will see (3.23) in Subsection 3.3, E_1, E_2 are two important extinction equilibria (with mussel non-vanishing) on the boundary of Σ. Furthermore, we will also show that the quantity "σ" essentially describes the biological invasion from E_1 and E_2; while the quantity "$\frac{m_B}{c_{BR}} + \frac{m_M}{c_M}$" characterizes the biological invasion from $\bar{E}_c$. We will discuss this, as well as the biological meaning of uniform persistence, in details in the Discussion Section.

3. Proof of the Main Results.

3.1. Invariant Domain Σ.

In this subsection, we will prove Proposition 2.1 that describes the positively invariant domain $\Sigma \subset \mathbb{R}^4_+$, defined in (2.2), which is motivated from biological point of view.

Proof of Proposition 2.1: Let $(B_0(t), B_A(t), A(t), M(t))$ be any solution of (BAM) with the initial value $(B_0(0), B_A(0), A(0), M(0)) \in \Sigma$. By the form of (A, B, M)-equations in (BAM) and (2.1), it is not difficult to see that $(B(t), A(t), M(t)) \in \mathbb{R}^3_+$ for any $t \geq 0$. The form of (B_0, B_A)-equations in (BAM) also implies that $(B_0(t), B_A(t)) \in \mathbb{R}^2_+$ as long as $(A + B_0 + M)(t) \leq 1$. Furthermore, we note that

$$\frac{d}{dt}(A + B_0 + M) = c_{AR}AR + c_{BR}BR - m_B B_0 - m_A(A - B_A) - m_M M, \tag{3.1}$$

$$\frac{d}{dt}(A - B_A) = c_{AR}AR + m_B B_A - m_A(A - B_A) - c_M(A - B_A)M, \tag{3.2}$$

where $R = 1 - (A + B_0 + M)$.

In order to show $(A+B_0+M)(t)\le 1$ and $B_A(t)\le A(t)$ for all $t\ge 0$, it suffices to show that $(A+B_0+M)(t)<1$ and $B_A(t)<A(t)$ for all $t\ge 0$ provided that $(A+B_0+M)(0)<1$ and $B_A(0)<A(0)$.

To this end, we first note that if $B(0)=0$ then we have done. In fact, for such situation, we have $B_0(t)=B_A(t)=0$ for all $t\ge 0$. Moreover, due to A-equation in (BAM), it is clear that $A(t)>0=B_A(t)$, because $A(0)>B_A(0)=0$; and hence, from (3.1), one has $(A+B_0+M)'(t_0)\le -m_AA(t_0)<0$ whenever $(A+B_0+M)(t_0)=1$ for some $t_0>0$. Consequently, we have obtained $(A+B_0+M)(t)<1$ for all $t\ge 0$.

So, we now assume that $B(0)>0$. By (2.1) and A-equation in (BAM) again, one has $B(t)>0$ and $A(t)>0$ for all $t\ge 0$, Since $(A+B_0+M)(0)<1$ and $B_A(0)<A(0)$, we define $t_1=\sup\{t>0:(A+B_0+M)(t)<1\}$ and $t_2=\sup\{t>0:B_A(t)<A(t)\}$. Let $t_*=\min\{t_1,t_2\}$. Clearly, $t_*>0$. If $t_*=+\infty$, then we have done. Suppose that $t_*<+\infty$. Then, we will have the following three alternatives, respectively.

Case (i): $t_*=t_1<t_2$. Then one has $R(t_*)=0$ and $(A-B_A)(t_*)>0$; and moreover, $B_0(t_*)\ge 0$ (since $(A+B_0+M)(t)\le 1$ for all $t\in[0,t_*]$). It then follows from (3.1) that $(A+B_0+M)'(t_*)\le -m_A(A-B_A)(t_*)<0$. Hence, $(A+B_0+M)(t)>(A+B_0+M)(t_*)=1$, for any $t<t_*$ close to t_*, contradicting the definition of $t_*(=t_1)$.

Case (ii): $t_*=t_2<t_1$. Then one has $(A-B_A)(t_*)=0$ and $R(t_*)>0$; and moreover, $B_A(t_*)\ge 0$ (since $(A+B_0+M)(t)\le 1$ for all $t\in[0,t_*]$). It then follows from (3.2) that $(A-B_A)'(t_*)\ge c_{AR}A(t_*)R(t_*)>0$ (because $A(t_*)>0$ as well). So, $(A-B_A)(t)<(A-B_A)(t_*)<0$ for any $t<t_*$ close to t_*, a contradiction to the definition of t_* again.

Case (iii): $t_*=t_1=t_2$. Then $(A-B_A)(t_*)=0$ and $R(t_*)=0$. Noticing that $A(t_*)>0$ and $B(t_*)>0$ (hence, either $B_0(t_*)>0$ or $B_A(t_*)>0$), it again follows from (3.1) and (3.2) that either $(A+B_0+M)'(t_*)<0$ or $(A-B_A)'(t_*)>0$. So either $(A+B_0+M)(t)>1$ or $(A-B_A)(t)<0$, hfor any $t<t_*$ close to t_*, a contradiction to the definition of $t_*(=t_1=t_2)$. Thus, we have proved $t_*=+\infty$, that is, $(A+B_0+M)(t)<1$ and $B_A(t)<A(t)$ for all $t\ge 0$. Therefore, we have proved the positive invariance of Σ with respect to system (BAM).

Finally, assume further that $A(0)>0, M(0)>0$ and $B(0)=B_0(0)+B_A(0)>0$. Then $A(t),M(t),B(t)$ are clearly positive for all $t>0$. If $B_A(t)=0$ for some $t>0$, we let $\tilde t$ be the first time such that $B_A(\tilde t)=0$. Then $B_A'(\tilde t)\le 0$ and $B_0(\tilde t)=B(\tilde t)>0$; and hence, from the B_A-equation in (BAM) one has $B_A'(t)>0$, a contradiction. Similarly, if $B_0(\tilde t)=0$ then $B_0'(\tilde t)\le 0$ and $B_A(\tilde t)=B(\tilde t)>0$; and hence, from B_0-equation in (BAM) one has $B_0'(\tilde t)>0$, a contradiction. Thus, $B_0(t),B_A(t),A(t)$ and $M(t)$ are all positive for all $t>0$. □

3.2. Global Dynamics for System (BA) without Mussels.

In this subsection, we will focus on the 3-dimensional system (BA) for which mussel is absent. We will prove Theorem 2.2 which describes the global dynamics of system (BA) on $\Gamma\subset\mathbb{R}^3_+$ defined in (2.4).

3.2.1. Preliminary.

As in Section 2, we denote the boundary equilibria for system (BA) by

$$\tilde E_0=(0,0,0),\ \tilde E_B=(B_0^*,0,0),\ \tilde E_A=(0,0,A^*),$$

on $\Gamma \cap \partial\mathbb{R}^3_+$, with $B_0^* = 1 - \frac{m_B}{c_{BR}}$, $A^* = 1 - \frac{m_A}{c_{AR}}$, and denote the positive equilibrium

$$\tilde{E}_c = (\bar{B}_0, \bar{B}_A, \bar{A}) \in \Gamma \cap \mathrm{Int}\mathbb{R}^3_+,$$

with $(\bar{B}_0, \bar{B}_A, \bar{A})$ satisfies (2.5)-(2.7). Here, $\partial\mathbb{R}^3_+$ and $\mathrm{Int}\mathbb{R}^3_+$ denote the boundary and interior of $\mathbb{R}^3_+$, respectively.

Due to the assumption (H1), $\tilde{E}_0, \tilde{E}_B$ always exist; while $\tilde{E}_A$ exists if and only if $c_{AR} > m_A$. In order to guarantee the existence of $\tilde{E}_c$, we introduce

$$\lambda_* = (c_{AR} - m_A) + B_0^*(c_{AB} - c_{AR}), \tag{3.3}$$

$$\Delta_1 = c_{BR}A^* - (c_{BR} - m_B). \tag{3.4}$$

Remark 3. Obviously, $\Delta_1 < 0$ if and only if $\frac{m_B}{c_{BR}} < \frac{m_A}{c_{AR}}$.

Lemma 3.1. *$\tilde{E}_c$ exists if and only if $\lambda_* > 0$ and $\Delta_1 < 0$. Moreover, if $\tilde{E}_c$ exists, then it is unique and satisfies* (2.5)-(2.7).

Proof. Necessity. Let $\tilde{E}_c = (\bar{B}_0, \bar{B}_A, \bar{A}) \in \Gamma$ be a positive equilibrium of (BA). Then the right hand side of (BA) must vanishes at $\tilde{E}_c$. By (2.3) and the A-equation in (BA), we obtain (2.5)-(2.6); and hence obtain (2.7) by B_A-equation. This implies that $\tilde{E}_c$ must be unique. Moreover, by (2.6), we have $\bar{B}_0 + \bar{B}_A = B_0^*$, and hence, $\bar{B}_0 < B_0^*$, which implies that $\lambda_* > (c_{AR} - m_A) + \bar{B}_0(c_{AB} - c_{AR})$. By (2.5), one has $\lambda_* > c_{AR}\bar{A} > 0$. Furthermore, again by (2.5)-(2.6), we have $0 < \bar{B}_0 = (\frac{m_A}{c_{AR}} - \frac{m_B}{c_{BR}}) \cdot \frac{c_{AR}}{c_{AB}}$. Thus, $\frac{m_B}{c_{BR}} < \frac{m_A}{c_{AR}}$, that is, $\Delta_1 < 0$.

Sufficiency. If $\lambda_* > 0$ and $\frac{m_B}{c_{BR}} < \frac{m_A}{c_{AR}}$, then we consider the function $g(B_0) := \frac{c_{AB}}{c_{AR}}B_0 - (\frac{m_A}{c_{AR}} - \frac{m_B}{c_{BR}})$. Clearly, $g(0) < 0$ and $g(B_0^*) = \frac{\lambda_*}{c_{AR}} > 0$. Then there is a unique $\bar{B}_0 \in (0, B_0^*)$ such that $g(\bar{B}_0) = 0$, so back to formula (2.5), we can obtain $\bar{A}$ by defining $c_{AR}\bar{A} = (c_{AR} - m_A) + \bar{B}_0(c_{AB} - c_{AR})$. Together with $g(\bar{B}_0) = 0$, one can easily check that the obtained $(\bar{B}_0, \bar{A})$ also satisfies (2.6). Finally, we use (2.7) to obtain $\bar{B}_A$ so that $(\bar{B}_0, \bar{B}_A, \bar{A}) \in \mathrm{Int}\mathbb{R}^3_+ \cap \Gamma$ is the unique positive equilibrium. We have completed the proof. ■

Before going further, we note that the Jacobian of the vector field for (BA) is as

$$\begin{pmatrix} L_1 & c_{BR}(1 - B_0 - A) + m_A & -c_{AB}B_0 - c_{BR}(B_0 + B_A) \\ c_{AB}A & -(m_B + m_A) & c_{AB}B_0 \\ (c_{AB} - c_{AR})A & 0 & L_2 \end{pmatrix}, \tag{3.5}$$

where $L_1 = [c_{BR}(1 - 2B_0) - m_B] - c_{BR}B_A - (c_{AB} + c_{BR})A$ and $L_2 = [c_{AR}(1 - 2A) - m_A] + B_0(c_{AB} - c_{AR})$.

The following two lemmas give a complete classification of the stability of the equilibria of (BA) according to the sign of λ_* and Δ_1.

Lemma 3.2. (i) *If $\lambda_* < 0$, then $\tilde{E}_B$ is globally asymptotically stable (G.A.S.) for $\Gamma \setminus \tilde{E}_0$;*

(ii) *If $\lambda_* > 0$ and $\Delta_1 > 0$, then $\tilde{E}_A$ exists and is G.A.S. for $\Gamma \setminus \{A = 0\}$.*

Proof. (i). Together with Lemma 3.1 and (H1), $\lambda_* < 0$ implies that neither $\tilde{E}_c$ nor $\tilde{E}_A$ exists; and moreover, the Jacobian (3.5) at $\tilde{E}_B$ is

$$\begin{pmatrix} -c_{BR}B_0^* & m_B + m_A & -c_{AB}B_0^* - c_{BR}B_0^* \\ 0 & -(m_B + m_A) & c_{AB}B_0^* \\ 0 & 0 & \lambda_* \end{pmatrix},$$

with all the eigenvalues are negative. We now show the global stability of $\tilde{E}_B$ for $\Gamma \setminus \tilde{E}_0$. In fact, by virtue of (2.3), we have $\dot{B} \le B(c_{BR}(1-B) - m_B)$. So, for any small $\varepsilon > 0$, there exists a $T_\varepsilon > 0$ such that $B(t) \le B_0^* + \varepsilon$ for $t \ge T_\varepsilon$. Then, the A-equation in system (BA) implies that

$$\begin{aligned} \tfrac{1}{A}\dot{A} \quad &\le (c_{AR} - m_A) + B_0(c_{AB} - c_{AR}) \\ &\le (c_{AR} - m_A) + (B_0^* + \varepsilon)(c_{AB} - c_{AR}) = \lambda_* + \varepsilon(c_{AB} - c_{AR}) < 0, \end{aligned}$$

for $t \ge T_\varepsilon$ and ε sufficiently small. Consequently, $A(t) \to 0$; and hence, $B_A(t) \to 0$ and $B_0(t) \to B_0^*$, as $t \to +\infty$. Thus, $\tilde{E}_B$ is G. A. S. for $\Gamma \setminus \tilde{E}_0$.

(ii). If $\lambda_* > 0$ and $\Delta_1 > 0$, then (H1) and Lemma 3.1 implies that $\tilde{E}_A$ exists, but $\tilde{E}_c$ does not exist. We now show the global stability of $\tilde{E}_A$ for $\Gamma \setminus \{A = 0\}$. Note that

$$A' \quad = A[(c_{AR} - m_A) - c_{AR}A + B_0(c_{AB} - c_{AR})] \ge A[(c_{AR} - m_A) - c_{AR}A].$$

Then, for any small $\eta > 0$, there exists a $T_\eta > 0$ such that $A(t) \ge A^* - \eta$, for $t \ge T_\eta$. Since $\Delta_1 > 0$, one has $\frac{m_B}{c_{BR}} > \frac{m_A}{c_{AR}}$ by Remark 3. Hence, $B_0^* < A^*$. Therefore,

$$B' \le B[c_{BR}(1 - (A^* - \eta)) - m_B] \le c_{BR}B[B_0^* - (A^* - \eta)] < 0,$$

for $t \ge T_\eta$ and η sufficiently small. Hence, $B(t) \to 0$ and $A(t) \to A^*$, as $t \to +\infty$. Thus, $\tilde{E}_A$ is G.A.S.. ■

Lemma 3.3. *If $\lambda_* > 0$ and $\Delta_1 < 0$ (i.e., $\tilde{E}_c$ exists by Lemma 3.1), then*

(i) *$\tilde{E}_c$ is always locally asymptotically stable (L.A.S);*

(ii) *$\tilde{E}_A$ is always unstable, whenever it exists. Furthermore, any orbit with initial value in $\Gamma \setminus$ (A-axis) will move away from $\tilde{E}_A$.*

Proof. If $\lambda_* > 0$ and $\Delta_1 < 0$, then Lemma 3.1 implies that $\tilde{E}_c$ always exists; while $\tilde{E}_A$ may exist or not.

(i). The Jacobian (3.5) at $\tilde{E}_c$ is

$$\begin{pmatrix} -c_{BR}\bar{B}_0 - c_{BR}\bar{B}_A - c_{AB}\bar{A} & m_B + m_A & -c_{AB}\bar{B}_0 - c_{BR}(\bar{B}_0 + \bar{B}_A) \\ c_{AB}\bar{A} & -(m_B + m_A) & c_{AB}\bar{B}_0 \\ (c_{AB} - c_{AR})\bar{A} & 0 & -c_{AR}\bar{A} \end{pmatrix}. \tag{3.6}$$

We will prove local asymptotic stability of $\tilde{E}_c$ by Routh-Hurwitz approach (c.f. [6,13]). In fact, a direct calculation yields that the characteristic equation of (3.6) is $\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0 = 0$ with

$$\begin{aligned} a_2 &= c_{AR}\bar{A} + m_B + m_A + c_{BR}\bar{B}_0 + c_{BR}\bar{B}_A + c_{AB}\bar{A} > 0, \\ a_1 &= (m_B + m_A)c_{BR}(\bar{B}_0 + \bar{B}_A) + c_{AR}\bar{A}(m_B + m_A + c_{BR}\bar{B}_0 + c_{BR}\bar{B}_A + c_{AB}\bar{A}) \\ &\quad + (c_{AB} - c_{AR})\bar{A}(c_{AB}\bar{B}_0 + c_{BR}(\bar{B}_0 + \bar{B}_A)) > 0, \\ a_0 &= (m_B + m_A)\bar{A}c_{AB}c_{BR}(\bar{B}_0 + \bar{B}_A) > 0. \end{aligned}$$

A direct insight (by noticing the product of the last term of a_2 and the first term of a_1) yields that $a_1a_2 - a_0 > 0$. This then implies all the eigenvalues of (3.6) are negative, which entails that the locally asymptotic stability of $\tilde{E}_c$.

(ii). When $\tilde{E}_A$ exists, the Jacobian (3.5) at $\tilde{E}_A$ is

$$\begin{pmatrix} (c_{BR}-m_B)-(c_{AB}+c_{BR})A^* & c_{BR}(1-A^*)+m_A & 0 \\ c_{AB}A^* & -(m_B+m_A) & 0 \\ (c_{AB}-c_{AR})A^* & 0 & -c_{AR}A^* \end{pmatrix}. \tag{3.7}$$

So, $\tilde{E}_A$ possesses three eigenvalues μ_1, μ_2 and $-c_{AR}A^*$, where $\mu_1\mu_2 = \Delta_1 \cdot (m_A + m_B + c_{AB}A^*)$ and $\mu_1 + \mu_2 = -c_{AB}A^* - (m_A + m_B) - \Delta_1$. Since $\Delta_1 < 0$, one has $\mu_1\mu_2 < 0$ (hence, $\tilde{E}_A$ is a saddle). We may assume without loss of generality that $\mu_1 < 0 < \mu_2$. Clearly, the vector $(0, 0, 1)$ is the corresponding eigenvector with respect to $-c_{AR}A^*$. We further assert that the eigenvector associated with $\mu_1 < 0$ has the component-sign as $(+, -, 0)$. Indeed, it is not difficult to see that $(a, b, 0)$ is the eigenvector associated with $\mu_1 < 0$; and moreover, we have

$$b[\mu_1 + (m_A + m_B)] = ac_{AB}A^*$$
$$a[\mu_1 - (c_{BR} - m_B - c_{AB}A^* - c_{BR}A^*)] = (c_{BR}(1 - A^*) + m_A)b.$$

Suppose that $ab > 0$. Then one has

$$0 > \mu_1 > c_{BR} - m_B - c_{AB}A^* - c_{BR}A^* \quad \text{and} \quad \mu_1 > -(m_A + m_B).$$

Together with (3.7), one has $\mu_1 + \mu_2 = [c_{BR} - m_B - c_{AB}A^* - c_{BR}A^*] - (m_A + m_B) < 2\mu_1$. So, $\mu_2 < \mu_1 < 0$, a contradiction (because $\mu_2 > 0$). Thus, one has $ab < 0$. Thus, we have proved the assertion, which implies that any initial value in $\Gamma \setminus (A\text{-axis})$ will move away from $\tilde{E}_A$. ■

Remark 4. By Lemma 3.2(ii) and the Jocobian (3.5) at $\tilde{E}_0$ and $\tilde{E}_B$, it is easy to see that if $\tilde{E}_c$ exists (i.e., $\lambda_* > 0$ and $\Delta_1 < 0$), then none of $\tilde{E}_0, \tilde{E}_B, \tilde{E}_A$ can be the omega limit point of any orbit starting in $\Gamma \cap \mathrm{Int}\mathbb{R}^3_+$.

By virtue of Lemma 3.3, it is now clear that $\tilde{E}_c$ *is always L.A.S. whenever it exists.* However, it is a challenging task to prove the *global asymptotic stability of* $\tilde{E}_c$. This will be done in the next Subsection 3.2.2.

3.2.2. An alternative viewpoint with K-competitive property . Now, we will focus on the global asymptotic stability of $\tilde{E}_c$. Our approach is essentially motivated from the biological point of view. More precisely, based on this model, we will introduce several new variables and transform the original system (BA) to a new system which is of so-called K-competitive systems (see [8, 9, 12, 23, 31, 32] and references therein) with respect to the partial ordering defined by a convex cone K in $\mathbb{R}^3$. It is well-known that 3-dimensional K-competitive systems have the Poincaré-Bendixson Property (see [12, Theorem 3.23] or [11, 30, 31]). So, in order to prove the global asymptotic stability of $\tilde{E}_c$, one needs to show the orbital stability of any possible periodic solutions in $\Gamma \cap \mathrm{Int}\mathbb{R}^3_+$. We will accomplish this approach by utilizing the stability criterion in term of the second compound equations which was developed by Muldowney [27, 28] (see also [20–22]).

We start with introducing new variables $T := A - B_A$ and $S := A + B_0$ for $(B_0, B_A, A) \in \Gamma$. Clearly, $0 \le T \le A \le S \le 1$, and

$$B_0 = S - A; \; B_A = A - T; \; B = S - T; \; R = 1 - S.$$

Let $\Lambda = \{(S, A, T) : 0 \le T \le A \le S \le 1\}$. Then, the original system (BA) on Γ is transformed to a new system on Λ as

$$\begin{cases} \dot{S} = c_{AR}A(1-S) + c_{BR}(S-T)(1-S) - m_B(S-A) - m_A T, \\ \dot{A} = c_{AR}A(1-S) + c_{AB}A(S-A) - m_A A, \\ \dot{T} = c_{AR}A(1-S) + m_B(A-T) - m_A T. \end{cases} \tag{SAT}$$

Denote by F the vector field of (SAT). Then the Jacobian matrix $DF(T, A, S)$ is

$$\begin{pmatrix} a_{11} & c_{AR}(1-S)+m_B & -c_{BR}(1-S)-m_A \\ (c_{AB}-c_{AR})A & a_{22} & 0 \\ -c_{AR}A & c_{AR}(1-S)+m_B & a_{33} \end{pmatrix}, \tag{3.8}$$

where

$$\begin{aligned} a_{11} &= -c_{AR}A + c_{BR}(1-S) - c_{BR}(S-T) - m_B, \\ a_{22} &= c_{AR}(1-S) - 2c_{AB}A + c_{AB}S - m_A, \\ a_{33} &= -(m_B + m_A). \end{aligned}$$

Due to the standing assumption (H1), we have $c_{AB} > c_{AR}$. So, our key viewpoint from (3.8) is that *system* (SAT) *is a K-competitive system* with respect to the partial ordering defined by the special convex cone $K = \{S, A, T) \in \mathbb{R}^3 : S \ge 0, A \le 0, T \ge 0\}$. So, system (SAT) has the Poincaré-Bendixson Property (see, e.g. [12, Theorem 3.23]), i.e., *any compact limit set of system (SAT) that contains no equilibrium points is a periodic orbit.*

We will show that any possible periodic orbit of (SAT) is orbitally stable. This will be done by utilizing the stability criterion in term of the second compound equations.

Based on such insight, we consider the second compound matrix $DF^{[2]}(S, A, T)$ of (3.8) as

$$DF^{[2]}(S,A,T) = \begin{pmatrix} a_{11}+a_{22} & 0 & c_{BR}(1-S)+m_A \\ c_{AR}(1-S)+m_B & a_{11}+a_{33} & c_{AR}(1-S)+m_B \\ c_{AR}A & (c_{AB}-c_{AR})A & a_{22}+a_{33} \end{pmatrix}, \tag{3.9}$$

where

$$\begin{aligned} a_{11}+a_{22} &= [-c_{AR}A + c_{BR}(1-S) - c_{BR}(S-T) - m_B] + [c_{AR}(1-S) - 2c_{AB}A + c_{AB}S - m_A]; \\ a_{11}+a_{33} &= [-c_{AR}A + c_{BR}(1-S) - c_{BR}(S-T) - m_B] - (m_B + m_A); \\ a_{22}+a_{33} &= [c_{AR}(1-S) - 2c_{AB}A + c_{AB}S - m_A] - (m_B + m_A). \end{aligned}$$

One may refer to more details on compound matrices and differential equations in [20,21,27,28] and references therein.

For the sake of convenience, we rewrite

$$a_{11} + a_{22} = -c_{AR}A - c_{BR}(S-T) + \gamma_1 + \gamma_2 - c_{AB}A; \tag{3.10}$$

$$a_{11} + a_{33} = -c_{AR}A - c_{BR}(S-T) + \gamma_1 - m_B - m_A; \tag{3.11}$$

$$a_{22} + a_{33} = \gamma_2 - c_{AB}A - m_B - m_A, \tag{3.12}$$

with $\gamma_1 = c_{BR}(1-S) - m_B$ and $\gamma_2 = c_{AR}(1-S) + c_{AB}(S-A) - m_A$.

Lemma 3.4. *Both* γ_1 *and* γ_2 *have average* 0 *along any periodic-solution of* (SAT)*.*

Proof. By (2.3), we have $\dot{B} = B[c_{BR}(1-S) - m_B]$. Moreover, the A-equation in (SAT) entails that $\dot{A} = A[c_{AR}(1-S) + c_{AB}(S-A) - m_A]$. This concludes the proof. ■

The main result in this subsection is the following:

Proposition 3.5. *Any nonconstant periodic solution of* (SAT) *is, if it exists, asymptotically orbitally stable.*

Proof. Given any periodic solution $(S(t), A(t), T(t))$ to (SAT) with a least period $\omega > 0$, we consider the ω-periodic linear equation

$$\frac{dX}{dt} = DF^{[2]}(S, A, T)X \tag{3.13}$$

along the ω-periodic solution $(S(t), A(t), T(t))$, where $X = (X_1, X_2, X_3)^T$ and $DF^{[2]}(S, A, T)$ is as in (3.9).

Now we introduce the function $W(S, A, T; X) = \sum_{i=1}^{3} p_i(S, A, T) \cdot |X_i|$, where $p_i(S, A, T)$ for $i = 1, 2, 3$, are *auxiliary positive smooth* functions, which will be determined later. Let $W(t) := W(S(t), A(t), T(t); X(t))$. Then, the right-hand derivative $D_+W(t)$ of $W(t)$ with respect to t exists (see, e.g. [21, 24]), and has the form

$$D_+W(t) = \sum_{i=1}^{3} p_i'(t)|X_i(t)| + p_i(t) \cdot D_+(|X_i(t)|), \tag{3.14}$$

where $p_i(t) = p_i(S(t), A(t), T(t))$ and $p_i'(t)$ is the derivative of $p_i(t)$. Note that $DF^{[2]}(S, A, T)_{ij} \geq 0$ for $i \neq j$. Then a direct calculation yields that $D_+(|X_i(t)|) \leq \sum_{j=1}^{3} DF^{[2]}(S, A, T)_{ij} \cdot |X_j(t)|$, for $i = 1, 2, 3$. For brevity, we write the element $Q_{ij} = DF^{[2]}(S, A, T)_{ij}$ of the matrix $DF^{[2]}(S, A, T)$. Then, together with (3.14), we have

$$\begin{aligned} D_+W(t) &\leq \sum_{i=1}^{3} p_i'|X_i(t)| + \sum_{i,j=1}^{3} Q_{ij} \cdot p_i \cdot |X_j(t)| \\ &= \sum_{i=1}^{3} \left[p_i' + \sum_{j=1}^{3} Q_{ji} \cdot p_j \right] \cdot |X_i(t)| = \sum_{i=1}^{3} \left[p_i'/p_i + \sum_{j=1}^{3} Q_{ji} \cdot p_j/p_i \right] \cdot (p_i|X_i(t)|). \end{aligned} \tag{3.15}$$

By (3.9) and (3.10)-(3.12), one can obtain that

$$\begin{aligned} \sum_{j=1}^{3} Q_{j1} \cdot p_j/p_1 &= \gamma_1 + \gamma_2 - C_{AB}A - c_{BR}(S-T) \\ &\quad + [c_{AR}(1-S) + m_B] \cdot p_2/p_1 + c_{AR}A(p_3/p_1 - 1), \\ \sum_{j=1}^{3} Q_{j2} \cdot p_j/p_2 &= [\gamma_1 - c_{AR}A - c_{BR}(S-T) - m_B - m_A] + [(c_{AB} - c_{AR})A] \cdot p_3/p_2, \\ \sum_{j=1}^{3} Q_{j3} \cdot p_j/p_3 &= [\gamma_2 - c_{AB}A - m_B - m_A] \\ &\quad + [\gamma_1 + m_B + m_A] \cdot p_1/p_3 + [c_{AR}(1-S) + m_B] \cdot p_2/p_3. \end{aligned}$$

Now, by choosing $p_1 = p_3 := p > 0$, where $p = p(S, A, T)$ is a positive smooth function of the state variables. Then we have

$$\sum_{j=1}^{3} Q_{j1} \cdot p_j/p_1 = \gamma_1 + \gamma_2 - c_{AB}A - c_{BR}(S-T) + [c_{AR}(1-S) + m_B] \cdot p_2/p,$$

$$\sum_{j=1}^{3} (Q)_{j2} \cdot p_j/p_2 = [\gamma_1 - c_{AR}A - c_{BR}(S-T) - m_B - m_A] + [(c_{AB} - c_{AR})A] \cdot p/p_2,$$

$$\sum_{j=1}^{3} (Q)_{j3} \cdot p_j/p_3 = (\gamma_1 + \gamma_2 - c_{AB}A) + [c_{AR}(1-S) + m_B] \cdot p_2/p.$$

Therefore, combining with (3.15), we have

$$D_+W(t) \le [g_1(t) - c_{BR}(S-T)] \cdot p|X_1(t)| + g_2(t) \cdot p_2|X_2(t)| + g_1(t) \cdot p|X_3(t)|,$$

where

$$g_1(t) = p'/p + \gamma_1 + \gamma_2 - c_{AB}A + [c_{AR}(1-S) + m_B] \cdot p_2/p,$$
$$g_2(t) = p_2'/p_2 + \gamma_1 + [-c_{AR}A - c_{BR}(S-T) - m_B - m_A] + [(c_{AB} - c_{AR})A] \cdot p/p_2.$$

Consequently, it entails that

$$D_+W(t) \le \max\{g_1(t), g_2(t)\} \cdot W(t). \tag{3.16}$$

Note that along the ω-periodic solution $(S(t), A(t), T(t)), t \in [0, \omega]$, one has $\int_0^\omega \frac{p'}{p} dt = \int_0^\omega \frac{p_2'}{p_2} dt = 0$; and moreover, by Lemma 3.4, $\int_0^\omega \gamma_i dt = 0$, $i = 1, 2$. So, in order to estimate $D_+W(t)$ in (3.16), it suffices to choose some p and p_2 such that

$$[c_{AR}(1-S) + m_B] \cdot p_2/p \le c_{AB}A$$

and

$$[(c_{AB} - c_{AR})A] \cdot p/p_2 \le c_{AR}A + c_{BR}(S-T) + m_B + m_A.$$

In other words, it suffices to choose some positive functions $p(S, A, T)$ and $p_2(S, A, T)$ such that

$$\frac{(c_{AB} - c_{AR})A}{c_{AR}A + c_{BR}(S-T) + m_B + m_A} \le \frac{p_2}{p} \le \frac{c_{AB}A}{c_{AR}(1-S) + m_B}. \tag{3.17}$$

For this purpose, by recalling that $A^* = 1 - m_A/c_{AR} \le A \le S$ along any periodic solution, one has $\frac{(c_{AB} - c_{AR})}{c_{AR}A + c_{BR}(S-T) + m_B + m_A} \le \frac{(c_{AB} - c_{AR})}{c_{AR}A^* + m_B + m_A}$ and $\frac{c_{AB}}{c_{AR}(1-A^*) + m_B} \le \frac{c_{AB}}{c_{AR}(1-S) + m_B}$. In the following, we will show that

$$\frac{(c_{AB} - c_{AR})}{c_{AR}A^* + m_B + m_A} < \frac{c_{AB}}{c_{AR}(1-A^*) + m_B}. \tag{3.18}$$

Indeed, this can be easily done by plugging $A^* = 1 - m_A/c_{AR}$ into this inequality and simply noticing the fact that $c_{AB}m_A/c_{AR} < c_{AB} + m_A + m_B$. As a consequence, one only needs to choose p, p_2 such that

$$\frac{(c_{AB} - c_{AR})A}{c_{AR} + m_B} \le \frac{p_2}{p} \le \frac{c_{AB}A}{m_A + m_B}. \tag{3.19}$$

To this end, let $p = \sqrt{\dfrac{m_A + m_B}{c_{AB} - c_{AR}}} \cdot \dfrac{A}{S}$ and $p_2 = \sqrt{\dfrac{c_{AB}}{c_{AR} + m_B}} \cdot \dfrac{A^2}{S}$; which satisfies (3.19), and hence, satisfies (3.17) automatically.

By virtue of (3.16)-(3.17), we have obtained that $W(t) \to 0$ as $t \to \infty$. Consequently, the linear system (3.13) is asymptotically stable; and hence, the periodic solution $(S(t), A(t), T(t))$ is asymptotically orbitally stable by [28, Theorem 4.2] (see also [21, Theorem 3.1]). ■

Proposition 3.6. *$\tilde{E}_c$ is globally asymptotically stable in $\Gamma \cap \mathrm{Int}\mathbb{R}^3_+$.*

Proof. First, let Ω be an omega-limit set of (BA) with initial value in $\Gamma \cap \mathrm{Int}\mathbb{R}^3_+$. We first claim that Ω is a locally asymptotically stable periodic orbit if it contains no equilibrium. Indeed, by the transformation $(B_0, B_A, A) \mapsto (S, A, T)$, Ω is transformed to the limit set Ω' of the K-competitive system (SAT) and Ω' does not contain any equilibrium of (SAT). Then, the Poincaré-Bendixson Property for (SAT) (see, e.g. [12, Theorem 3.23]) implies that Ω' is a periodic closed orbit. It then follows from Proposition 3.5 that Ω' is locally asymptotically stable. As a consequence, we obtain that Ω is a periodic closed orbit of (BA) that is locally asymptotically stable. Thus, we have proved the claim.

Now, we will prove $\tilde{E}_c$ is globally asymptotically stable in $\Gamma \cap \mathrm{Int}\mathbb{R}^3_+$. Recall that $\tilde{E}_c$ is locally asymptotically stable (see Lemma 3.3(i)). Then the basin of attraction $\mathcal{A}$ of $\tilde{E}_c$ is a nonempty relatively open subset of Γ. Denote by $\partial_\Gamma \mathcal{A}$ the boundary of $\mathcal{A}$ relative to Γ. Clearly, $\partial_\Gamma \mathcal{A}$ is invariant because $\mathcal{A}$ is invariant. If $\partial_\Gamma \mathcal{A}$ does not intersect $\mathrm{Int}\mathbb{R}^3_+$, then we are done. Suppose that $\partial_\Gamma \mathcal{A} \cap \mathrm{Int}\mathbb{R}^3_+ \neq \emptyset$. Choose some $u \in \partial_\Gamma \mathcal{A} \cap \mathrm{Int}\mathbb{R}^3_+$. Since $\Gamma \cap \mathrm{Int}\mathbb{R}^3_+$ is positively invariant (see Proposition 2.1 with $M = 0$), the forward orbit of u still remains in $\partial_\Gamma \mathcal{A} \cap \mathrm{Int}\mathbb{R}^3_+$. So, the omega-limit set $\omega(u) \subset \partial_\Gamma \mathcal{A}$, which entails that $\tilde{E}_c \notin \omega(u)$. Furthermore, it follows from Remark 4 that $\omega(u)$ does not contain $\tilde{E}_0, \tilde{E}_B, \tilde{E}_A$. In other words, $\omega(u)$ contains no equilibrium. So, by virtue of the claim above, $\omega(u)$ itself is a locally asymptotically stable periodic orbit; and hence, we have $\omega(u) \subset \partial_\Gamma \mathcal{A} \cap \mathrm{Int}\mathbb{R}^3_+$, since the only non-wandering points on $\Gamma \setminus \mathrm{Int}\mathbb{R}^3_+$ are $\tilde{E}_0, \tilde{E}_B, \tilde{E}_A$. Now, one can choose some point $p \in \mathcal{A} \cap \mathrm{Int}\mathbb{R}^3_+$ sufficiently close to $\omega(u)$. On the one hand, p is attracted to $\tilde{E}_c$. On the other hand, p will be asymptotic to the stable periodic orbit $\omega(u)$, a contradiction. Thus, we have proved $\tilde{E}_c$ is globally asymptotically stable in $\Gamma \cap \mathrm{Int}\mathbb{R}^3_+$. ■

3.2.3. Proof of Theorem 2.2.

Theorem 2.2 is directly from Lemmas 3.1-3.2 and Proposition 3.6. □

3.3. Uniform Persistence of the system (BAM).

In this subsection, we focus on the uniform persistence of the 4-dimensional Barnacle-Algae-Mussel system (BAM). We will prove Theorem 2.3, which provides an amenable sufficient and necessary condition for the uniform persistence of (BAM) on Σ.

For this purpose, we denote the boundary equilibria for system (BAM) on Σ by

$$E_0 = (0, 0, 0, 0),\ E_B = (B_0^*, 0, 0, 0),\ E_A = (0, 0, A^*, 0),\ \bar{E}_c = (\bar{B}_0, \bar{B}_A, \bar{A}, 0), \tag{3.20}$$

and

$$E_1 = (B_0^{**}, 0, 0, M^*), \;\; E_2 = (0, 0, \hat{A}, \hat{M}). \tag{3.21}$$

Here, $B_0^* = 1 - \frac{m_B}{c_{BR}}$, $A^* = 1 - \frac{m_A}{c_{AR}}$ and $(\bar{B}_0, \bar{B}_A, \bar{A})$ satisfies(2.5)-(2.7); and moreover, $B_0^{**} = \hat{A} = m_M/c_M$ and

$$M^* = \frac{c_{BR}(c_M - m_M) - c_M m_B}{c_M(c_M + c_{BR})} \quad \text{and} \quad \hat{M} = \frac{c_{AR}(c_M - m_M) - c_M m_A}{c_M(c_M + c_{AR})}. \tag{3.22}$$

Remark 5. (i). $E_0, E_B, E_A, \bar{E}_c$ in (3.20) correspond to the equilibria $\tilde{E}_0, \tilde{E}_B, \tilde{E}_A, \tilde{E}_c$ of system (BA) in Section 3.2. For brevity, we may also write

$$E_0 = (\tilde{E}_0, 0), \;\; E_B = (\tilde{E}_B, 0), \;\; E_A = (\tilde{E}_A, 0), \;\; \bar{E}_c = (\tilde{E}_c, 0),$$

in the context without any confusion.

(ii). For clarity, we may also rewrite $M^* = \frac{1 - \frac{m_M}{c_M} - \frac{m_B}{c_{BR}}}{1 + \frac{c_M}{c_{BR}}}$ and $\hat{M} = \frac{1 - \frac{m_M}{c_M} - \frac{m_A}{c_{AR}}}{1 + \frac{c_M}{c_{AR}}}$, respectively.

In order to study the existence of E_1, E_2 (see (3.21)), as well as the existence of the positive equilibrium for (BAM), we introduce the conditions

(A1): $\dfrac{m_B}{c_{BR}} + \dfrac{m_M}{c_M} < 1$;

(A2): $\dfrac{m_A}{c_{AR}} + \dfrac{m_M}{c_M} < 1$.

We also define the quantity

$$\sigma \triangleq \frac{c_M}{m_M} \frac{c_{AR} + c_M}{c_{AB}} (M^* - \hat{M}). \tag{3.23}$$

Remark 6.According to the supporting data in [1], $c_{AB} = 0.049, c_{BR} = 0.018, c_{AR} = 0.021, c_M = 0.078, m_B = 0.003, m_A = 0.013, m_M = 0.017$. Then one can directly obtain that $M^* \approx 0.115394, \hat{M} \approx 0.0547889, \sigma \approx 0.561388$ and $0 < \sigma < 1$.

In the following sections, we discuss the dynamics of system (BAM) according to the quantity σ and the conditions (A1)-(A2).

Lemma 3.7. *For system* (BAM)*, we have*

(a) E_1 *exists if and only if* (A1) *holds, and* E_B *exists if* E_1 *exists ;*

(b) E_2 *exists if and only if* (A2) *holds, and* E_A *exists if* E_2 *exists;*

(c) *The positive equilibrium* E_c *exists if and only if* (A1) *and* $0 < \sigma < 1$. *Moreover, if* E_c *exists, then it is unique and* $E_c = (\tilde{B}_0, \tilde{B}_A, \tilde{A}, \tilde{M}) \in \Sigma \cap \mathrm{Int}\mathbb{R}_+^4$*, satisfies*

$$\tilde{B}_0[c_{AB}\tilde{A} + c_M\tilde{M} + m_B - c_{BR}(1 - \tilde{B}_0 - \tilde{A} - \tilde{M})] = \tilde{B}_A[c_{BR}(1 - \tilde{B}_0 - \tilde{A} - \tilde{M}) + m_A], \tag{3.24}$$

$$\tilde{B}_A(c_M\tilde{M} + m_B + m_A) = c_{AB}\tilde{B}_0\tilde{A}, \tag{3.25}$$

$$c_{AR}(1 - \tilde{B}_0 - \tilde{A}) + c_{AB}\tilde{B}_0 - (c_{AR} + c_M)\tilde{M} = m_A, \tag{3.26}$$

$$\tilde{B}_0 + \tilde{A} = \frac{m_M}{c_M}. \tag{3.27}$$

Proof. (a) Clearly, for system (BAM), the equilibrium $E_1 = (B_0^{**}, 0, 0, M^*)$ exists if and only if $B_0^{**} = \frac{m_M}{c_M}$ and $M^* = \frac{1 - \frac{m_M}{c_M} - \frac{m_B}{c_{BR}}}{1 + \frac{c_M}{c_{BR}}}$, which implies that E_1 exists if and only if (A1) holds. Moreover, one can easily verify that E_B exists whenever E_1 exists.

(b) Similarly, the equilibrium $E_2 = (0, 0, \hat{A}, \hat{M})$ exists if and only if $\hat{A} = \frac{m_M}{c_M}$ and $\hat{M} = \frac{1 - \frac{m_M}{c_M} - \frac{m_A}{c_{AR}}}{1 + \frac{c_M}{c_{AR}}}$, which entails that E_2 exists if and only if (A2) holds. Moreover, one can easily verify that E_A exists whenever E_2 exists.

(c) The positive equilibrium $E_c = (\tilde{B}_0, \tilde{B}_A, \tilde{A}, \tilde{M})$, if exists, should satisfy (3.24)-(3.27). By (3.24), we have

$$\tilde{B}_0[m_B - \triangle_* + c_{AB}\tilde{A} + c_M\tilde{M}] = \tilde{B}_A(\triangle_* + m_A), \tag{3.28}$$

where $\triangle_* = c_{BR}(1 - \frac{m_M}{c_M}) - c_{BR}\tilde{M}$. Since $\tilde{B}_0\tilde{B}_A \neq 0$, together with (3.25), one can deduce from (3.28) that

$$[m_B - \triangle_* + c_{AB}\tilde{A} + c_M\tilde{M}][c_M\tilde{M} + m_B + m_A] = c_{AB}\tilde{A}[\triangle_* + m_A]. \tag{3.29}$$

Rewrite (3.29) as $[c_M\tilde{M} - (\triangle_* - m_B)](c_M\tilde{M} + m_A + m_B) = c_{AB}\tilde{A}[(\triangle_* - m_B) - c_M\tilde{M}]$. Then, we obtain either $c_M\tilde{M} = \triangle_* - m_B$ or $c_M\tilde{M} = -(m_B + m_A + c_{AB}\tilde{A})$. Noting that $\tilde{M} > 0$, it follows that $\tilde{M} = (\triangle_* - m_B)/c_M$. Hence,

$$\tilde{M} = M^* = \frac{c_{BR}(1 - \frac{m_M}{c_M}) - m_B}{c_{BR} + c_M} > 0, \tag{3.30}$$

if (A1) holds. Moreover, by plugging (3.27) into (3.26), we obtain that

$$c_{AB}\tilde{A} + (c_{AR} + c_M)\tilde{M} = (c_{AR} - m_A) + \frac{m_M}{c_M}(c_{AB} - c_{AR}).$$

So, together with (3.30), we have $\tilde{A} = \frac{1}{c_{AB}}[c_{AR}(1 - \frac{m_M}{c_M}) - m_A - (c_{AR} + c_M)M^*] + \frac{m_M}{c_M} = \frac{m_M}{c_M}(1 - \sigma)$. Hence, $\tilde{B}_0$ and $\tilde{B}_A$ are determined by (3.27)and (3.25) as $\tilde{B}_0 = \frac{m_M}{c_M}\sigma$ and $\tilde{B}_A = \frac{m_M^2 c_{AB}\sigma(1-\sigma)}{c_M^2(c_M M^* + m_A + m_B)}$, respectively. In other words, we obtain

$$E_c = (\frac{m_M}{c_M}\sigma, \frac{m_M^2 c_{AB}\sigma(1 - \sigma)}{c_M^2(c_M M^* + m_A + m_B)}, \frac{m_M}{c_M}(1 - \sigma), M^*). \tag{3.31}$$

Consequently, E_c is unique if it exists.

Next, we will show that E_c exists if and only if (A1) and $0 < \sigma < 1$. Indeed, if $E_c = (\tilde{B}_0, \tilde{B}_A, \tilde{A}, \tilde{M})$ exists, then (3.31) and Remark 5(ii) imply that $0 < \sigma < 1$ and (A1) must hold. On the other hand, it is clear that (A1) implies $\tilde{M} > 0$. Moreover, together with $\tilde{A} = \frac{m_M}{c_M}\sigma$ and $\tilde{B}_0 = \frac{m_M}{c_M}\sigma$, it follows from $0 < \sigma < 1$ that $\tilde{A} > 0$ and $\tilde{B}_0 > 0$. Therefore, E_c exists. ■

Before going further, we note that the Jacobian of system (BAM) is

$$\begin{pmatrix} L_3 & c_{BR}(1 - B_0 - A - M) + m_A & -(c_{BR} + c_{AB})B_0 - c_{BR}B_A & -(c_{BR} + c_M)B_0 - c_{BR}B_A \\ c_{AB}A & -(m_A + m_B + c_M M) & c_{AB}B_0 & -c_M B_A \\ (c_{AB} - c_{AR})A & 0 & L_4 & -(c_{AR} + c_M)A \\ c_M M & 0 & c_M M & c_M(B_0 + A) - m_M) \end{pmatrix}, \tag{3.32}$$

where $L_3 = -2c_{BR}B_0 - c_{BR}B_A - (c_{BR}+c_{AB})A - (c_{BR}+c_M)M + c_{BR} - m_B$ and $L_4 = (c_{AR}-m_A) + (c_{AB}-c_{AR})B_0 - 2c_{AR}A - (c_{AR}+c_M)M$.

Lemma 3.8. (i) *E_1 is unstable if $\sigma < 1$; and E_1 is locally asymptotically stable if $\sigma > 1$.*

(ii) *E_2 is unstable if $\sigma > 0$; and E_2 is locally asymptotically stable if $\sigma < 0$.*

(iii) *$\bar{E}_c$ is unstable if* (A1) *holds; $\bar{E}_c$ is locally asymptotically stable if $\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} > 1$.*

Proof. (i). A direct calculation yields that the Jacobian (3.32) at $E_1 = (B_0^{**}, 0, 0, M^*)$ is

$$\begin{pmatrix} L_3\,|_{E_1} & c_{BR}(1-B_0^{**}-M^*)+m_A & -(c_{BR}+c_{AB})B_0^{**} & -(c_{BR}+c_M)B_0^{**} \\ 0 & -(m_A+m_B+c_MM^*) & c_{AB}B_0^{**} & 0 \\ 0 & 0 & L_4\,|_{E_1} & 0 \\ c_MM^* & 0 & c_MM^* & 0 \end{pmatrix}.$$

The eigenvalues of E_1 is determined by

$$(\lambda - L_4|_{E_1}) \cdot (\lambda + m_A + m_B + c_MM^*) \cdot [\lambda^2 - L_3|_{E_1}\lambda + c_M(c_M + c_{BR}B_0^{**}M^*] = 0.$$

Here $L_3|_{E_1} = -2c_{BR}B_0^{**} - (c_{BR}+c_M)M^* + c_{BR} - m_B = -2c_{BR}B_0^{**} < 0$, and

$$\begin{aligned} L_4|_{E_1} &= c_{AR} - m_A + (c_{AB}-c_{AR})B_0^{**} - (c_{AR}+c_M)M^* \\ &= (\hat{M} - M^*)(c_{AR}+c_M) + \tfrac{m_M}{c_M}c_{AB} = c_{AB}\tfrac{m_M}{c_M}(1-\sigma). \end{aligned}$$

Consequently, the only possible positive eigenvalue is $L_4|_{E_1}$. In other words, E_1 is L.A.S. if $\sigma > 1$; and E_1 is unstable if $\sigma < 1$.

(ii). Similarly, the Jacobian of Jacobian (3.32) at $E_2 = (0, 0, \hat{A}, \hat{M})$ is

$$\begin{pmatrix} L_3\,|_{(0,0,\hat{A},\hat{M})} & c_{BR}(1-\hat{A}-\hat{M})+m_A & 0 & 0 \\ c_{AB}\hat{A} & -(m_A+m_B+c_M\hat{M}) & 0 & 0 \\ (c_{AB}-c_{AR})\hat{A} & 0 & L_4\,|_{(0,0,\hat{A},\hat{M})} & -(c_{AR}+c_M)\hat{A} \\ c_M\hat{M} & 0 & c_M\hat{M} & 0 \end{pmatrix}.$$

Again, one can calculate the eigenvalues of E_2 as $\mu_1 = -c_{AB}\hat{A} - m_A - m_B - c_M\hat{M} < 0$, $\mu_2 = c_{BR}(1-\hat{A}-\hat{M}) - m_B - c_M\hat{M} = (c_{BR}+c_M)(M^\star - \hat{M})$, and μ_3, μ_4 are the roots of the equation $\lambda^2 + c_{AB}\hat{A}\lambda + c_M(c_{AR}+c_M)\hat{A}\hat{M} = 0$. Clearly, $\mathrm{Re}\mu_3 < 0$ and $\mathrm{Re}\mu_4 < 0$. Moreover, $\mu_2 > 0$ if and only if $\sigma > 0$. So, E_2 is unstable if $\sigma > 0$ and E_2 is L. A. S. if $\sigma < 0$.

(iii). The Jacobian (3.32) at $\bar{E}_c$ is as

$$\begin{pmatrix} -c_{BR}\bar{B} - c_{AB}\bar{A} & m_A+m_B & -(c_{BR}+c_{AB})\bar{B}_0 - c_{BR}\bar{B}_A & -(c_{BR}+c_M)\bar{B}_0 - c_{BR}\bar{B}_A \\ c_{AB}\bar{A} & -(m_A+m_B) & c_{AB}\bar{B}_0 & -c_M\bar{B}_A \\ (c_{AB}-c_{AR})\bar{A} & 0 & -c_{AR}\bar{A} & -(c_{AR}+c_M)\bar{A} \\ 0 & 0 & 0 & c_M(\bar{B}_0+\bar{A}) - m_M \end{pmatrix}.$$

So, by Lemma 3.3(i), the eigenvalue $c_M(\bar{B}_0+\bar{A}) - m_M$ determines the stability of $\bar{E}_c$. Recall that $\bar{B}_0 + \bar{A} = 1 - \frac{m_B}{c_{BR}}$. Then $c_M(\bar{B}_0+\bar{A}) - m_M > 0$ if and only if (A1) holds. Thus, we have obtained that $\bar{E}_c$ is unstable if (A1) holds, and $\bar{E}_c$ is L.A.S. if $\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} > 1$. ■

As a summary, Table 1 illustrates the the existence and stability of the equilibria for system (BAM).

Based on all the above analysis, we are ready to prove Theorem 2.3:

Proof of Theorem 2.3: (i). This follows directly from Lemma 3.7(c).

(ii) We only show that (BAM) is uniformly persistent if and only if E_c exists. The necessity is a standard theory of uniform persistence (see, e.g. [4, 33]). So, we need to prove the sufficiency part.

For this purpose, we assume that E_c exists, i.e., (A1) and $0 < \sigma < 1$. By (H1) and Lemma 3.7(a), E_0, E_B, E_1 always exist. Then, one of the following four alternatives must occur:

(Alt$_1$): (A2) holds and $\frac{m_B}{c_{BR}} < \frac{m_A}{c_{AR}}$, by which $E_A, E_2, \bar{E}_c$ exist.

(**Alt**$_2$): (A2) holds and $\frac{m_B}{c_{BR}} \geq \frac{m_A}{c_{AR}}$, by which E_A, E_2 exist and $\bar{E}_c$ does not exist.

(**Alt**$_3$): (A2) does not hold and $\frac{m_A}{c_{AR}} < 1$, by which $E_A, \bar{E}_c$ exist and E_2 does not exist.

(**Alt**$_4$): (A2) does not hold and $\frac{m_A}{c_{AR}} \geq 1$, by which $\bar{E}_c$ may exist and E_A, E_2 do not exist.

In the following, we will focus on (**Alt**$_1$) and prove the uniform persistence of (3.25) for this alternative. The other alternatives can be treated by the similar arguments.

To this end, under the assumptions (A1), $0 < \sigma < 1$ and (**Alt**$_1$), we will prove in the following three claims which are crucial to our proof of the uniform persistence.

Claim 1: $\exists\, \varepsilon_1 > 0$ such that $\liminf_{t\to\infty} A(t) \geq \varepsilon_1$, whenever $A(0) > 0$ in Σ. In order to prove Claim 1, we define the persistence function on Σ as $\rho_1(B_0, B_A, A, M) \triangleq A$ and let $\Sigma_A = \rho_1^{-1}(0)$. Then, we will show $\bigcup_{y\in\Sigma_A} \omega(y) = \{E_0, E_B, E_1\}$. In fact, since $B_A \leq A$ on Σ, one has $B_A = A = 0$ on Σ_A. So, the dynamics on Σ_A is governed by the two-dimensional system

$$\begin{cases} \dot{B}_0 = B_0[c_{BR}(1 - B_0 - M) - c_M M - m_B] \triangleq f_1, \\ \dot{M} = M(c_M B_0 - m_M) \triangleq f_2. \end{cases} \tag{3.33}$$

Clearly, (B_0^{**}, M^*) is a locally stable equilibrium for system (3.33). Moreover, along any

Equilibria	Conditions on Existence	Conditions on Asymptotic Stability
$E_0 = (\tilde{E}_0, 0)$	always exists	always unstable
$E_B = (\tilde{E}_B, 0)$	always exists	$\lambda_* < 0$ & $\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} > 1$
$E_A = (\tilde{E}_A, 0)$	$c_{AR} > m_A$	$\lambda_* > 0$, $\frac{m_B}{c_{BR}} > \frac{m_A}{c_{AR}}$ & $\frac{m_A}{c_{AR}} + \frac{m_M}{c_M} > 1$
$\bar{E}_c = (\tilde{E}_c, 0)$	$\lambda_* > 0$ and $\frac{m_B}{c_{BR}} < \frac{m_A}{c_{AR}}$.	$\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} > 1$
$E_1 = (B_0^{**}, 0, 0, M^*)$	$\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} < 1$	$\sigma > 1$
$E_2 = (0, 0, \hat{A}, \hat{M})$	$\frac{m_A}{c_{AR}} + \frac{m_M}{c_M} < 1$	$\sigma < 0$
$E_c = (\tilde{B}_0, \tilde{B}_A, \tilde{A}, \tilde{M})$	$\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} < 1$ and $0 < \sigma < 1$	Unknown

Table 3.1

Existence and Stability of Equilibria for system (BAM) on Σ, under the Standing Assumption (H1): Here, λ_* is defined in Theorem 2.2 or in (3.3); σ is defined in Theorem 2.3 or in (3.23). Note that $\frac{m_B}{c_{BR}} < \frac{m_A}{c_{AR}}$ iff $\Delta_1 < 0$ (see Remark 3); while $\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} < 1$ iff (A1) holds; and $\frac{m_A}{c_{AR}} + \frac{m_M}{c_M} < 1$ iff (A2) holds.

ω-periodic solution,

$$\begin{aligned}\oint_0^\omega \left(\frac{\partial f_1}{\partial B_0}+\frac{\partial f_2}{\partial M}\right)dt &= \oint_0^\omega [c_{BR}(1-B_0-M)-c_M M-m_B+(c_M B_0-m_M)-c_{BR}B_0]dt\\ &= \oint_0^\omega \left(\frac{\dot B_0}{B_0}+\frac{\dot M}{M}-c_{BR}B_0\right)dt<0.\end{aligned}$$

It then follows from the so-called Weak Negative Bendixson Criteria (c.f. [5,16]) that (B_0^{**}, M^*) is globally asymptotically stable for any positive initial values for (3.33). Thus, we have obtained $\bigcup_{y\in\Sigma_A}\omega(y)=\{E_0,E_B,E_1\}$ and it is an isolated and acyclic covering of the limit sets on Σ_A.

Next, we still need to show that the stable manifold $W^s(E_l)\subset\Sigma_A$, for $l=0,B_0,1$. Due to the element L_4 in the Jacobian form (3.32) for (BAM), this is automatically satisfied for $l=0$ (since $c_{AR}>m_A$), $l=B_0$ (since $L_4|_{(B_0^{**},0,0,M^*)}=(c_{AR}-m_A)+B_0^*(c_{AB}-c_{AR})=\lambda_*>0$) and $l=1$ (since $L_4|_{E_1}=(1-\sigma)\cdot c_{AB}m_M/c_M>0$). Therefore, by using the celebrated persistence Theorems (see [33, Theorem 5.2 and Theorem 8.17]) for the function ρ_1 on Σ, we have obtained Claim 1.

Claim 2: $\exists\varepsilon_2>0$ *such that* $\liminf_{t\to\infty}B(t)\geq\varepsilon_2$, *whenever* $B(0)>0$ *in* Σ. To prove this claim, we define another persistence function on Σ as $\rho_2(B_0,B_A,A,M)\triangleq B$ and let $\Sigma_B=\rho_2^{-1}(0)$. Clearly, $B_0=B_A=B=0$ on Σ_B. So, the dynamics on Σ_B is governed by the two-dimensional system

$$\begin{cases}\dot A=A[c_{AR}(1-A-M)-c_M M-m_A],\\ \dot M=M(c_M A-m_M).\end{cases}\tag{3.34}$$

Similarly as the proof of Claim 1, one can deduce from the local stability analysis of $(\hat A,\hat M)$ and the Weak Negative Bendixson Criteria to obtain that $\bigcup_{y\in\Sigma_B}\omega(y)=\{E_0,E_A,E_2\}$ is an isolated and acyclic covering of the limit sets on Σ_B.

In order to show $W^s(E_l)\subset\Sigma_B$, for $l=0,A,2$, we need to recall equation (2.1), that is,

$$\dot B=B[c_{BR}(1-B_0-A)-(c_{BR}+c_M)M-m_B].\tag{3.35}$$

So, it is clear that $W^s(E_0)\subset\Sigma_B$. Since $\frac{m_B}{c_{BR}}<\frac{m_A}{c_{AR}}$ and $c_{AR}(1-A^*)=m_A$, one has $c_{BR}(1-A^*)-m_B<0$; and hence, $W^s(E_A)\subset\Sigma_B$. As for E_2, we note that $\sigma>0$ (hence $M^*>\hat M$). This implies that $c_{BR}-m_B-c_{BR}m_M/c_M-c_{BR}\hat M-c_M\hat M>0$, that is, $c_{BR}-c_{BR}\hat A-(c_{BR}+c_M)\hat M-m_B>0$. Together with (3.35), this yields that $W^s(E_2)\subset\Sigma_B$. Again, by using the persistence Theorems ([33, Theorem 5.2 and Theorem 8.17]) for the function ρ_2 on Σ, we have obtained Claim 2.

Claim 3: $\exists\varepsilon_3>0$ *such that* $\liminf_{t\to\infty}M(t)\geq\varepsilon_3$, *whenever* $B(0)>0, A(0)>0$ *and* $M(0)>0$ *in* Σ. For this claim, we introduce the persistence function $\rho_3(B_0,B_A,A,M)\triangleq\min\{A,B,M\}$ on Σ, and let $\Sigma_\star=\rho_3^{-1}(0)$. So, $y\in\Sigma_\star$ if and only if at least one of A,B,M vanishes at y.

Combining with $\bigcup_{y\in\Sigma_A\cup\Sigma_B}\omega(y)=\{E_0,E_B,E_A,E_1,E_2\}$ (by Claims 1&2) and Theorem 2.2(ii-b), one obtains that $\bigcup_{y\in\Sigma_*}\omega(y)=\{E_0,E_B,E_1,E_A,E_2,\bar{E}_c\}$. Among these equilibria, we have the following typical chains in $\Sigma_\star$:

$$E_0\mapsto E_B\mapsto\bar{E}_c\,(\text{or }E_1),\;\; E_0\mapsto E_A\mapsto\bar{E}_c\,(\text{or }E_2)\quad\text{ in }\Sigma_\star.$$

We further assert that there is no chain starting from E_1 (or E_2 or $\bar{E}_c$) in $\Sigma_\star$. Suppose that there is a chain $(B(t),A(t),M(t))_{t\in\mathbb{R}}$ in $\Sigma_\star$ starting from E_1, for instance. Then, Claim 2 entails that $\inf_{t\in\mathbb{R}}B(t)>0$. Hence, this chain orbit $(B(t),A(t),M(t))$ can only be asymptotic (in $\Sigma_\star$) to either E_B or $\bar{E}_c$ as $t\to+\infty$, which is impossible due to the property of $\Sigma_\star$ mentioned above. Similarly, one can utilize Claim 1 (or 2) to exclude the existence of a chain in $\Sigma_\star$ emerging from E_2 (or $\bar{E}_c$). Thus, we have proved the assertion. Therefore, $\bigcup_{y\in\Sigma_*}\omega(y)$ is an acyclic covering of the limit sets on $\Sigma_\star$.

Moreover, again by Claims 1-2, one has $W^s(E_j)\subset\Sigma_A(\subset\Sigma_\star)$ for $j=0,B_0,1$ and $W^s(E_l)\subset\Sigma_B(\subset\Sigma_\star)$ for $l=0,A,2$. So, in order to show that $W^s(E_l)\subset\Sigma_\star$ for any $E_l\in\bigcup_{y\in\Sigma_*}\omega(y)$, it suffices to prove that $W^s(\bar{E}_c)\subset\Sigma_\star$. This can be easily done by checking the Jacobian form (3.32) at $\bar{E}_c$ with $c_M(\bar{B}_0+\bar{A})-m_A>0$ (because (A1) holds).

By utilizing the persistence Theorems ([33, Theorem 5.2 and Theorem 8.17]) again for the function ρ_3 on Σ, we have obtained Claim 3.

Now, based on Claims 1-3, let $\varepsilon_0=\min\{\varepsilon_1,\varepsilon_2,\varepsilon_3\}>0$. Then we have that $\liminf_{t\to\infty}B(t)\geq\varepsilon_0$, $\liminf_{t\to\infty}A(t)\geq\varepsilon_0$, $\liminf_{t\to\infty}M(t)\geq\varepsilon_0$, whenever $B(0)>0,A(0)>0$ and $M(0)>0$ in Σ. If, in addition, $B_0(0)>0$ and $B_A(0)>0$, then we will show that $B_0(t)$ and $B_A(t)$ are all uniformly persistent. To this end, we may assume that $B(t),A(t),M(t)\geq\varepsilon_0$ for t sufficiently large. Fix any $\varepsilon\in(0,\varepsilon_0)$. Due to the B_A-equation in system (BAM) on Σ, we have

$$\begin{aligned}\dot{B}_A(t)&=c_{AB}AB_0-(c_MM+m_B+m_A)B_A\\&\geq c_{AB}\varepsilon_0B_0-(c_M+m_B+m_A)B_A\geq c_{AB}\varepsilon_0(\varepsilon_0-\varepsilon)-(c_M+m_B+m_A)\varepsilon,\end{aligned}$$

whenever $B_A(t)\leq\varepsilon$ for t sufficiently large. So, one can choose ε sufficiently small so that $\dot{B}_A(t)>0$ whenever $B_A(t)\leq\varepsilon$ for t sufficiently large. Consequently, we have $B_A(t)\geq\varepsilon$ for t sufficiently large; and hence,

$$\begin{aligned}\dot{B}_0(t)\;&=B_0[c_{BR}(1-B_0-A-M)-c_{AB}A-c_MM-m_B]+B_A[c_{BR}(1-B_0-A-M)+m_A]\\&\geq-B_0[c_{AB}A+c_MM+m_B]+B_Am_A\geq-B_0[c_{AB}+c_M+m_B]+\varepsilon m_A,\end{aligned}$$

for t sufficiently large. Then, one can choose some small $\delta\in(0,\varepsilon)$ such that $\dot{B}_0(t)>0$ whenever $B_0(t)\leq\delta$ for t sufficiently large. This implies that $B_0(t)\geq\delta$ for t sufficiently large. Thus, $B_0(t)$ and $B_A(t)$ are uniformly persistent. We have completed the proof. ☐

4. Discussion.

There are many mathematical models in ecology showing that chaos can be produced, for examples, the well known discretized logistic equation in [25,26], a three-level food chain with Holling type II functional responses [10] and a resources-consumers model of n phytoplankton species competing for k complementary resources, with $k\geq3,n>4$ in [15]. In [2,7], the authors did experiments in laboratory and constructed mathematical models to give the evidences that chaos can be generated in insect population and plankton community respectively. However, for the real-world ecological community, Benincà et al. [1] is perhaps the first article to present evidences that the erratic fluctuations in an intertidal rock-pool ecosystem are caused by competitive interactions that cause chaotic dynamics. Furthermore, they constructed the patch occupancy model (1.1) based on species interaction in a seasonal cycle environment. They also did extensive numerical simulations to show chaos is possible for the model (1.1) under some parameters ranges. In this article we study this model of barnacle-algae-mussel interactions without external seasonal forcing. Our work turns out to be the first attempt to initiate the research on rigorously analyzing this new model from both mathematical and biological points of view.

We rigorously prove a biological observation: the cover (i.e., the fraction of patches occupied) by barnacles overgrown with crustose algae is smaller than the cover by crustose algae, i.e., $B_A \leq A$. The mathematical statement is that the region $\Sigma = \{(B_0, B_A, A, M) \in \mathbb{R}^4_+ : B_0 + A + M \leq 1, B_A \leq A\}$ is positively invariant, where $\mathbb{R}^4_+$ is the nonnegative orthant in $\mathbb{R}^4$. In order to study the dynamical behavior of (BAM), we propose the basic assumption (H1): $c_{AB} > c_{AR}$ and $c_{BR} > m_B$; which means that the crustose algae settle more firmly on barnacles than on the bare rock and the colonization rate of barnacles over the bare rock is greater than the mortality rate of barnacles. According to the data reported in Benincà et al. [1], $c_{AB} = 0.049$ day^{-1}, $c_{AR} = 0.021$ day^{-1}, $c_{BR} = 0.018$ day^{-1} and $m_B = 0.003$ day^{-1}. Consequently, assumption (H1) clearly makes biological sense.

In the first part of this paper, we give in Theorem 2.2 a complete description of the global dynamics of system (BAM) without mussel, i.e., $M = 0$ (see system (BA) or (1.3)). We not only prove the local stability of all equilibria, but also their global stability. For the system (BA) (or equilalently, (1.3)), the most important result is proving the global stability of positive equilibrium $\tilde{E}_c$. In fact, we transform system (BA) to a type-K competitive system (SAT) by changing variables $(B_0, B_A, A) \to (S, A, T)$, where $T := A - B_A, S := A + B_0$. Then we construct a Lyapunov function and utilize the stability criterion in term of the second compound equations (e.g., [21, 28]) to prove the nonexistence of periodic orbits for system (SAT), which help us show the global stability of $\tilde{E}_c$.

After understanding the 3-dimensional dynamics of (BA), we study in the second part of this paper the 4-dimensional dynamics (BAM) (or equivalently, (1.2)) with the presence of mussel, i.e., $M \neq 0$. In an ecological system, uniform persistence is well-known as the coexistence of all the species. We present in Theorem 2.3 an amenable sufficient and necessary condition (i.e., $\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} < 1$ and $0 < \sigma < 1$) for the uniform persistence of system (BAM). Here we emphasize that, for the proof of uniform persistence of (BAM), it is a nontrivial task to verify the isolated acyclic-covering property of the limit sets on the boundary of our working 4-dimensional region Σ. We accomplish it by repeatedly utilizing the persistence Theory in [33] to guarantee the uniformly positive lower bounds of A, B and M, gradually. We further point out that the condition "$\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} < 1$ and $0 < \sigma < 1$" is equivalent to the existence of positive equilibrium E_c (see Theorem 2.3 and Remark 2). Therefore, (BAM) is uniformly persistent if and only if E_c exists. For the extinction of species, it is still a challenge problem and we leave it for future study.

To interpret the biological meaning of the condition $0 < \sigma < 1$ and $\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} < 1$, we note from the proof of Lemma 3.8(i)-(ii) that the quantity "σ" essentially describes the biological invasion from E_1 and E_2, which are extinction steady states with crustose algae and barnacle vanishing, respectively. From the proof of Lemma 3.8(iii), the quantity "$\frac{m_B}{c_{BR}} + \frac{m_M}{c_M}$" characterizes the biological invasion from $\bar{E}_c$, which is extinction steady state with mussel vanishing. More precisely, $\sigma < 1$ means that crustose algae is able to invade the extinction state E_1; while $\sigma > 0$ means that barnacle is able to invade the extinction state E_2; and moreover, $\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} < 1$ means that mussel is able to invade the extinction state $\bar{E}_c$.

Again from the data used in Benincà et al. [1], we obtain that $\frac{m_B}{c_{BR}} + \frac{m_M}{c_M} \approx 0.384615$ and $\sigma \approx 0.561388$, which entails that E_c exists and (BAM) is uniformly persistent.

The close relationship between our study of the autonomous system (1.2) and the periodically forced system (1.1) relies on the parameter α in (F_*), which represents the strength of seasonal forcing; and on the unique positive steady state E_c for (1.2). When $\alpha = 0$ (i.e., the strength of seasonal forcing is vanishing), system (1.1) is reduced to the autonomous system (1.2). We conjecture that E_c is globally asymptotically stable in $\Sigma \cap \text{Int}\mathbb{R}^4_+$ for system (1.2). For the system (1.1) with periodic perturbation, in their numerical simulation in [1] (Fig. S15 supplemental material), Benincà et al. have shown that, as the parameter α varies, there is a route of periodic-doubling to chaos and the Lyapunov exponent becomes positive for $\alpha \geq 0.28$. It is a difficult open problem to theoretically prove that the chaos occurs for $\alpha \geq 0.28$. Our analysis provide useful information for the necessary conditions for chaotic dynamics of the periodically forced system (1.1).

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