



# Ecological Effects of Predator Harvesting and Environmental Noises on Oceanic Coral Reefs

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## Abstract

Coral reefs provide refuge for prey and are important for the preservation of an oceanic ecosystem. However, they have been experiencing severe destruction by environmental changes and human activities. In this paper, we propose and analyze a tri-trophic food chain model consisting of coral, Crown-of-thorns starfish (CoTS), and triton in deterministic and stochastic environments. We investigate the effects of harvesting in the deterministic system and environmental noises in the stochastic system, respectively. The existence of possible steady states along with their stability is rigorously discussed. From the economic perspective, we examine the existence of the bionomic equilibrium and establish the optimal harvesting policy. Subsequently, the deterministic system is extended to a stochastic system through nonlinear perturbation. The stochastic system admits a unique positive global solution initiating from the interior of the positive quadrant. The long-time behaviors of the stochastic system are explored. Numerical simulations are provided to validate and complement our theoretical results. We show that over-harvesting of triton is not beneficial to coral reefs and modest harvesting of CoTS may promote sustainable growth in coral reefs. In addition, the presence of strong noises can lead to population extinction.

**Keywords** Coral reefs · Harvesting · Stochastic · Extinction

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## 1 Introduction

Coral reefs, often known as “the rainforests of the sea”, are considered the most productive marine ecosystem in the world that are renowned for the staggering rich biodiversity and the various beneficial ecosystem services they provide. Coral reefs are the most diverse habitat supporting innumerable life above/below the water and sustaining the highest concentration of marine biodiversity (Speers et al 2016; Hughes et al 2017). The importance and the value of coral reefs extends far beyond the conservation of marine biodiversity. Coral reefs provide food for millions of humans worldwide, protect and create land, supply natural medicines as a source of medical advances, and are intrinsically full of beautiful natural wonder (Polidoro and Carpenter 2013). The condition of coral is a major indicator of the health of the global ecosystem.

However, in spite of the high levels of biomass, productivity, and species diversity, coral reefs are some of the world’s most fragile ecosystems and are vulnerable to changes in the external environment. Coral reefs can be damaged and degraded from human activity as well as environmental factors. Coral reefs are highly threatened and are declining worldwide at an alarming rate, primarily due to more frequent, larger, and more sustainable bleaching events observed over the past decades. Ecological pressures affecting the stability of coral reef ecosystems are usually divided into natural perturbation (e.g., hurricanes, disease outbreaks, coral bleaching, volcanic eruption) and anthropogenic pressures (e.g., global warming, environmental pollution, overfishing) (Cybulski et al 2020).

Recently, both natural and anthropogenic stressors on coral reefs have increased, resulting in large-scale loss of coral and potential shifts from coral-dominated to macroalgae-dominated community states (Holbrook et al 2022). The serious effects of coral mortality cascade through the ecosystem, which lead to decreased abundance or even extirpation of some species (Keith et al 2018). Therefore, the healthy development of coral reef ecosystems is a prerequisite for maintaining the biodiversity in coral reef areas. Currently, the reserves are being established for restoration, and the dynamic processes of coral reefs are being monitored. More effective measures should be carried out immediately to protect the marine environment and to reduce the harm caused by human activities (Hall et al 2023).

Crown-of-Thorns Starfish (CoTS *Acanthaster spp.*) is a carnivorous starfish that feeds on the living tissue of scleractinian (i.e., hard) coral, and is identified as the main natural enemy of coral (Ling et al 2020). CoTS is characterized by an exceptional reproductive capacity, such that several kilometers of coral be engulfed by CoTS aggregations during outbreaks, which is a major contributor to sustained declines in coral cover (Balu et al 2021). The “outbreak” state has been quantitatively defined when the rate of CoTS consuming coral is significantly greater than the coral growth rate (Birkeland and Lucas 1990; Plagányi et al 2020). Two primary hypotheses are put forward to explain the occurrence of outbreaks (Sweatman 2008). The first is the “terrestrial run-off hypothesis” (Birkeland 1982), including anthropogenic changes in environmental conditions that have eroded normal regulatory processes, which lead to largely unbounded population fluctuations (Asik et al 2019). The other is the “predator removal hypothesis” (Endean 1969), overfishing the key predators of CoTS results in an increase in the size of both juvenile and adult CoTS, which improves reproductive

performance. The origin and ultimate mechanisms underlying CoTS outbreaks are not yet fully understood, despite considerable research efforts (Pratchett et al 2017). At present, an advanced tool named Citizen Science has made it possible for scientists to detect, monitor, and document CoTS outbreaks, and to prioritize management responses at large scales. Citizen science is referred to as public participation in scientific research, which is advocated to overcome data limitations when large scales are considered and scientific resources are limited (Dumas et al 2020). Once an anomaly occurs, they will take effective measures to eliminate CoTS such as using injections of diluted bile salts into CoTS and artificial fishing (Rivera-Posada et al 2014). An early strain of research claimed that triton was thought to be the only known natural predator of adult CoTS (Kroon et al 2021). As one of the few active predators of adult CoTS, it is of great significance to coral reefs. From that perspective, the enemy of the enemy is a friend. However, triton is now considered naturally rare or endangered due to over-exploitation (Klein et al 2021). There is no doubt that controlling CoTS and protecting triton have an important sense in preserving coral reefs.

Declined reef health is characterized by increases in macroalgae. Many researchers studied coral-algal interactions and considered grazing by herbivorous reef fish. The pioneer work by Mumby et al (2007) showed that a coral reef ecosystem may lose resilience and shift to coral-depleted state through reductions in grazing intensity. Subsequently, Blackwood et al (2012) extended an analytic model to focus on the effects of over-harvesting of herbivorous reef fish and identified critical fishing effort levels to allow for coral recovery. Moreover, coral reefs are directly related to coral predators (Bhattacharyya and Pal 2011; Fattahpour et al 2019; Li et al 2014). Although the above mentioned papers considered predation in coral reef ecosystem, the investigation essentially focused on coral-macroalgal phase shift. Most studies suggested that overfishing reef fish may reduce the resilience of coral reefs by increasing coral-algal competition, such that the transition from the coral-dominated regime to the macroalgae-dominated regime. However, we predict that removing the top-down control of CoTS by overfishing triton would increase coral-CoTS interactions, because CoTS would dominate in the absence of triton. Therefore, one of our aims in this paper is to examine the effects of triton harvesting on the biomass of coral.

Coral reefs are dynamic systems influenced by both deterministic factors (e.g., coral-algal interactions and biological interactions) and stochastic factors (i.e., environmental noises). The large-scale stochastic disturbances (e.g., tropical storms, cold fronts, warming events, diseases, predator outbreaks) can be described by a continuous-time Markov chain model (Littler et al 2009; Kang and Lanchier 2011). The population is also inevitably disturbed by a variety of mild stochastic disturbances (e.g., sunlight, water level, temperature, acidity, wind) which are modeled by the approach of parameter perturbations (Liu et al 2011). It is well known that the environmental noises are unstable factor, increasing abundance fluctuations and extinction rates of populations. For example, noises can sometimes push the population size above the Allee threshold and promote population persistence, which indicates that noises can enhance the biodiversity of ecosystems (D'Odorico et al 2008). It was found that a population may die out due to random chance during periods when population size is extremely low, which illustrates how noises can be associated with negative consequences for population dynamics (Jnawali et al 2022). Mao et al (2002) revealed an important fact in

the Lotka-Volterra model that the environmental noises can suppress a potential population explosion. These results are valuable for further understanding the dynamics of populations in oceanic coral reefs. Moreover, ecosystem thresholds can be combined with stochastic noises to achieve targets for the restoration of ecosystem processes (Mumby et al 2007). Thus, another purpose in this paper is to reveal how the noises affect the population in coral reef ecosystems.

With an increased knowledge of coral reef ecosystem processes and a rise in computer power, dynamic models are useful tools in assessing the synergistic effects of local and global stressors on ecosystem functions.

The remaining paper is organized as follows. In Sect. 2, we propose a tri-trophic food chain model that simulates the biological interaction of predation among the three species: coral, CoTS and triton. The mathematical model also considers harvesting related to CoTS and triton. Then, stochastic environmental noises described by Brownian motion are introduced to establish the stochastic system. The equilibria dynamics of the deterministic system is studied in Sect. 3. The problem of the optimal harvest policy is solved by Pontryagin's maximal principle in Sect. 4. The dynamical behaviors of the stochastic system are investigated in Sect. 5. We provide a series of numerical simulations in Sect. 6. Finally, we conclude and discuss the paper in Sect. 7.

## 2 Model Formulation

In this section, we formulate our original model. Let  $x(t)$ ,  $y(t)$ , and  $z(t)$  be the population densities of coral, CoTS, and triton at time  $t$ , respectively. In order to characterize the interactions among coral, CoTS, and triton, we make the following assumptions:

- In the absence of CoTS, coral follows the logistic growth with intrinsic growth rate  $r_1$  and carrying capacity  $K_1$  (Sarkar et al 2021).
- As a carnivore, CoTS is a generalist predator. CoTS preys not only on coral, but also feeds on a variety of prey such as invertebrates. Thus, CoTS grows according to the logistic growth with intrinsic growth rate  $r_2$  and carrying capacity  $K_2$  (Wilmes et al 2016).
- Triton is a specialist predator and completely preys on CoTS for food.
- Experimental observations (Murray et al 2013) reveal that Holling type II functional response is quite accurate in predicting the observed functional response of invertebrates. Thus, the predation of CoTS and triton are assumed to follow the Holling type II functional response.
- There is a demand for CoTS and triton in the market; therefore, harvesting of both species is incorporated.

Based on the above assumptions, the interaction and population dynamics of coral, CoTS, and triton are governed by the following system of ordinary differential equations:

**Table 1** Parameters in (1)

Parameters	Description	Units
$r_1$	Intrinsic growth rate of $x$	/year
$r_2$	Intrinsic growth rate of $y$	/year
$K_1$	Carrying capacity of $x$	kg/km <sup>2</sup>
$K_2$	Carrying capacity of $y$	kg/km <sup>2</sup>
$m_1$	Predation rate of $y$ on $x$	km <sup>2</sup> kg <sup>-1</sup> year <sup>-1</sup>
$m_2$	Predation rate of $z$ on $y$	km <sup>2</sup> kg <sup>-1</sup> year <sup>-1</sup>
$e_1$	Conversion rate of $x$ by $y$	Dimensionless
$e_2$	Conversion rate of $y$ by $z$	Dimensionless
$a_1$	Half-saturation constant for $y$	kg/km <sup>2</sup>
$a_2$	Half-saturation constant for $z$	kg/km <sup>2</sup>
$h_1$	Harvesting rate of $y$	/year
$h_2$	Harvesting rate of $z$	/year
$d$	Natural mortality rate of $z$	/year

$$\begin{cases} \frac{dx}{dt} = r_1x \left(1 - \frac{x}{K_1}\right) - \frac{m_1xy}{a_1 + x}, \\ \frac{dy}{dt} = r_2y \left(1 - \frac{y}{K_2}\right) + \frac{e_1m_1xy}{a_1 + x} - \frac{m_2yz}{a_2 + y} - h_1y, \\ \frac{dz}{dt} = \frac{e_2m_2yz}{a_2 + y} - dz - h_2z. \end{cases} \tag{1}$$

The biological descriptions and units of parameters are listed in Table 1.

Next, we present the model parameterization to estimate the values of the key parameters. The South China Sea is taken as an example, which covers an area of about  $3.5 \times 10^6$  km<sup>2</sup>, where coral reefs occupy 38462 km<sup>2</sup> (Liao et al 2021). It was found that coral has a mass of 5 mg/cm<sup>2</sup> (Thornhill et al 2011), so the maximum weight of coral per square kilometer of the ocean is about 550 kg. In general, there are two CoTS per hectare under normal circumstances; however, it will increase dramatically (about 1000 CoTS per square kilometer) when CoTS outbreaks (Yao et al 2022). Typically, an adult CoTS weighs about 150 grams, so the average weight of CoTS per square kilometer of the ocean is 30 kg (about 150 kg during outbreaks). Therefore, it is estimated that  $K_1 \leq 550$  and  $30 \leq K_2 \leq 150$ . Moreover, an individual CoTS is estimated to consume about 10 m<sup>2</sup> of coral tissue in one year (Deaker and Byrne 2022). The loss of coral biomass yearly from each CoTS is about 0.5 kg. Thus,  $m_1 = 0.5$ . However, triton is either naturally rare or endangered due to unregulated harvesting, so we have limited knowledge of its life history. For simulation purposes, a biologically feasible parameter set is assumed:  $e_1 = 0.8$ ,  $m_2 = 0.4$ ,  $e_2 = 0.8$ ,  $d = 0.1$ .

System (1) is of deterministic type and neglects the effects of environmental noises. May (1973) pointed out that the birth rates, carrying capacity, competition coefficients or other parameters involved in the model exhibit random fluctuation to a greater or

lesser extent due to the environmental noises. Hence, system (1) has a few limitations in accurately characterizing the population dynamics. Since the physical and biological nature of the system cannot be predicted appropriately, the study of a stochastic system is more realistic than the deterministic one. There are several approaches to incorporate the stochastic fluctuations into population models (e.g., parametric perturbations (Liu 2022; Yuan et al 2020), stochastic perturbations around the positive equilibrium of the corresponding deterministic system (Beretta et al 1998), linear random perturbations (Caraballo et al 2020), nonlinear perturbations (Lv et al 2018)). In fact, the noises may be dependent on the intensity of each subpopulation. For example, prey will reduce intra-specific competition and spread for hiding in safe havens as the predator increases, which will reduce fluctuations in both prey and predator populations. Therefore, the nonlinear perturbations may provide an additional degree of realism in comparison with its linear counterpart. According to the technique by Zhang et al (2021), the intrinsic growth rate  $r_1$  of  $x$ , the intrinsic growth rate  $r_2$  of  $y$ , the intra-specific competition intensity  $r_1/K_1$  of  $x$ , the intra-specific competition intensity  $r_2/K_2$  of  $y$ , and the natural mortality rate  $d$  of  $z$  are estimated by an average value plus normally distributed errors. From the biological point of view, the sources of environmental noises affecting the three species are different. Here, we assume that the standard deviations (i.e., noise intensities) of the errors that occurred in the estimations of  $r_1$ ,  $r_1/K_1$  and  $r_2$ ,  $r_2/K_2$  are independent of the densities of  $x$  and  $y$ , respectively. Note that the triton is rare in the world, and then the environmental fluctuations are concerned with the number of triton. Therefore, for the death rate  $d$  of triton, its intensity only depends on the density of  $z$ . Specifically, the perturbations have the following form

$$\begin{aligned} r_1 &\rightarrow r_1 + \sigma_{11}\dot{B}_1(t), & -\frac{r_1}{K_1} &\rightarrow -\frac{r_1}{K_1} + \sigma_{12}\dot{B}_1(t), \\ r_2 &\rightarrow r_2 + \sigma_{21}\dot{B}_2(t), & -\frac{r_2}{K_2} &\rightarrow -\frac{r_2}{K_2} + \sigma_{22}\dot{B}_2(t), \\ -d &\rightarrow -d + (\sigma_{31} + \sigma_{32z})\dot{B}_3(t), \end{aligned}$$

where  $B_i(t)$  ( $i = 1, 2, 3$ ) are mutually independent standard Brownian motions defined on a complete probability space  $(\Omega, \mathcal{F}, \{\mathcal{F}_t\}_{t \geq 0}, \mathbb{P})$  with a filtration  $\{\mathcal{F}_t\}_{t \geq 0}$  satisfying the usual conditions (i.e., it is right continuous and increasing while  $\mathcal{F}_0$  contains all  $\mathbb{P}$ -null sets) and  $\sigma_{ij}^2$  ( $i = 1, 2, 3, j = 1, 2$ ) are the intensities of the white noise. It is easy to see that

$$r_i dt + \sigma_{ij} dB_i(t), \quad -\frac{r_i}{K_i} dt + \sigma_{ij} dB_i(t) \quad (i, j = 1, 2), \quad -d dt + (\sigma_{31} + \sigma_{32z}) dB_3(t)$$

are normally distributed and their variances tend to 0 as  $dt \rightarrow 0$  such that this way of introducing stochastic white noise into (1) is reasonable. Then, the stochastic system according to (1) writes as:

$$\begin{cases} dx = \left[ r_1x \left( 1 - \frac{x}{K_1} \right) - \frac{m_1xy}{a_1 + x} \right] dt + x(\sigma_{11} + \sigma_{12x})dB_1(t), \\ dy = \left[ r_2y \left( 1 - \frac{y}{K_2} \right) + \frac{e_1m_1xy}{a_1 + x} - \frac{m_2yz}{a_2 + y} - h_1y \right] dt + y(\sigma_{21} + \sigma_{22y})dB_2(t), \\ dz = \left[ \frac{e_2m_2yz}{a_2 + y} - dz - h_2z \right] dt + z(\sigma_{31} + \sigma_{32z})dB_3(t). \end{cases} \tag{2}$$

Denote by  $\mathbb{R}_+^n = \{x = (x_1, \dots, x_n) \in \mathbb{R}^n : x_i \geq 0, 1 \leq i \leq n\}$  and set  $\inf \emptyset = \infty$ . The transpose of a vector or matrix  $A$  is represented by  $A^T$ .

### 3 Dynamics of Deterministic System (1)

In what follows, we will discuss the positivity and boundedness of (1) to ensure the model is well-posed. The detailed proofs are presented in Appendix A.1 and Appendix A.2.

**Lemma 1**  $\mathbb{R}_+^3$  is a positive invariant set of (1).

**Theorem 1** The solutions of (1) are all bounded for any given initial values in  $\mathbb{R}_+^3$ .

Lemma 1 and Theorem 1 indicate that (1) is biologically meaningful and provide a foundation for the further study of the dynamics of (1). The following lemma is also very helpful for investigating (1). The proof can be found in Appendix A.3.

**Lemma 2** Consider a polynomial  $\alpha(x) = (-1)^n x^n + p_{n-1}x^{n-1} + \dots + p_1x + p_0$ , where  $p_0, p_1, \dots, p_{n-1}$  are real parameters and  $n$  is odd. If  $p_0 > 0$ , then  $\alpha(x)$  has at least one positive root.

Now, we explore the existence and stability of the equilibria of (1). (1) has the following possible equilibria or steady states:

$$E_0 = (0, 0, 0); \quad E_x = (K_1, 0, 0); \quad E_y = \left( 0, \frac{K_2(r_2 - h_1)}{r_2}, 0 \right);$$

$E_{xy} = (x_3, y_3, 0)$ , where  $x_3$  and  $y_3$  solve:

$$\begin{cases} r_1 \left( 1 - \frac{x}{K_1} \right) - \frac{m_1y}{a_1 + x} = 0, \\ r_2 \left( 1 - \frac{y}{K_2} \right) + \frac{e_1m_1x}{a_1 + x} - h_1 = 0; \end{cases} \tag{3}$$

$E_{yz} = (0, y_4, z_4)$ , where  $y_4$  and  $z_4$  solve:

$$\begin{cases} r_2 \left(1 - \frac{y}{K_2}\right) - \frac{m_2 z}{a_2 + y} - h_1 = 0, \\ \frac{e_2 m_2 y}{a_2 + y} - d - h_2 = 0; \end{cases} \tag{4}$$

$E_{xyz} = (x^*, y^*, z^*)$ , where  $x^*$ ,  $y^*$ , and  $z^*$  solve:

$$\begin{cases} r_1 \left(1 - \frac{x}{K_1}\right) - \frac{m_1 y}{a_1 + x} = 0, \\ r_2 \left(1 - \frac{y}{K_2}\right) + \frac{e_1 m_1 x}{a_1 + x} - \frac{m_2 z}{a_2 + y} - h_1 = 0, \\ \frac{e_2 m_2 y}{a_2 + y} - d - h_2 = 0. \end{cases} \tag{5}$$

The dynamical behavior of the equilibrium can be studied with the help of the Jacobian matrix at each equilibrium. The Jacobian matrix  $J(x, y, z)$  of (1) is:

$$J = \begin{pmatrix} r_1 - \frac{2r_1 x}{K_1} - \frac{m_1 a_1 y}{(a_1 + x)^2} & -\frac{m_1 x}{a_1 + x} & 0 \\ \frac{e_1 m_1 a_1 y}{(a_1 + x)^2} & r_2 - \frac{2r_2 y}{K_2} + \frac{e_1 m_1 x}{a_1 + x} - \frac{m_2 a_2 z}{(a_2 + y)^2} - h_1 & -\frac{m_2 y}{a_2 + y} \\ 0 & \frac{e_2 m_2 a_2 z}{(a_2 + y)^2} & \frac{e_2 m_2 y}{a_2 + y} - d - h_2 \end{pmatrix}.$$

The next step is to explore the local stability of the extinction equilibrium and the two single species equilibria. The proof of those results is presented in Appendix A.4-Appendix A.6.

**Theorem 2** (1) always has the extinction equilibrium  $E_0 = (0, 0, 0)$  which is unstable.

Theorem 2 implies that total extinction of the system is not possible.

**Theorem 3** The coral-dominated equilibrium  $E_x = (K_1, 0, 0)$  always exists. Moreover,  $E_x$  is locally asymptotically stable if

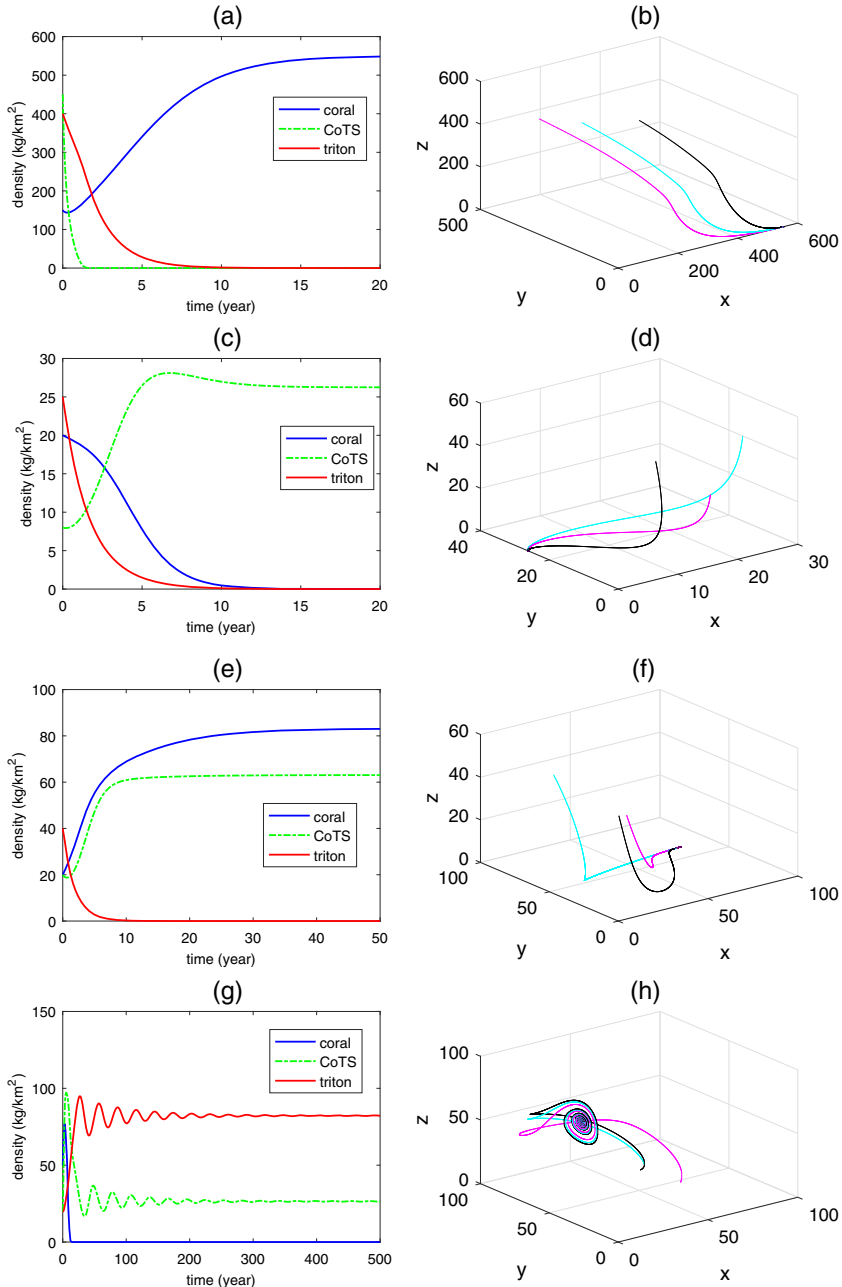
$$h_1 > r_2 + \frac{e_1 m_1 K_1}{a_1 + K_1}.$$

Theorem 3 indicates that CoTS goes extinct when the harvesting rate  $h_1$  is sufficiently high. Hence, triton also becomes extinct due to severe food shortages, but coral survives (see Fig. 1(a-b)).

**Theorem 4** The CoTS-dominated equilibrium  $E_y = (0, y_2, 0)$  exists if  $h_1 < r_2$ , where  $y_2 = K_2(r_2 - h_1)/r_2$ . Moreover,  $E_y$  is locally asymptotically stable if

$$r_1 < \frac{m_1 K_2 (r_2 - h_1)}{a_1 r_2}, \quad \mathcal{R}_1 := \frac{1}{d + h_2} \left( \frac{e_2 m_2 K_2 (r_2 - h_1)}{a_2 r_2 + K_2 (r_2 - h_1)} \right) < 1. \tag{6}$$





**Fig. 1** Time series dynamics (left column) and phase portraits (right column) for boundary equilibria scenario of (1): **a, b**  $E_x$  is the attractor and only coral survives; **c, d**  $E_y$  is the attractor and only CoTS survives; **e, f**  $E_{xy}$  is the attractor and indicates that both coral and CoTS coexist; **g, h**  $E_{yz}$  is the attractor and denotes that both CoTS and triton coexist. The values of the parameters are given in Table 2

In (6), by its definition,  $\mathcal{R}_1$  can be considered as the ecological reproduction number of triton (i.e., the average number of newborn triton in the lifespan of a triton), where  $e_2 m_2 K_2 (r_2 - h_1) / [a_2 r_2 + K_2 (r_2 - h_1)]$  is the birth rate of triton and  $1 / (d + h_2)$  is the average lifespan of triton. Theorem 4 shows that if coral has a low growth rate, CoTS has a high growth rate, and the ecological reproductive number of triton is small, then both coral and triton are completely eliminated while CoTS survives, that is, (6) guarantees that (1) is stabilized at  $E_y$  (see Fig. 1(c-d)).

The following two theorems provide sufficient conditions for the existence and stability of the two species coexistence equilibria. The detailed proofs can be found in Appendix A.7 and Appendix A.8.

**Theorem 5** *The triton-free equilibrium  $E_{xy} = (x_3, y_3, 0)$  exists if*

$$h_1 < r_2, \quad r_1 > \frac{m_1 K_2 (r_2 - h_1)}{a_1 r_2}. \tag{7}$$

$E_{xy}$  is locally asymptotically stable if

$$J_{11} + J_{22} < 0, \quad J_{11} J_{22} > J_{12} J_{21}, \quad \mathcal{R}_2 := \frac{1}{d + h_2} \frac{e_2 m_2 y_3}{a_2 + y_3} < 1,$$

where  $J_{ij}$  ( $i, j = 1, 2$ ) are located in the  $i$ th row and the  $j$ th column of  $J|_{E_{xy}}$ .

Theorem 5 reveals that under appropriate conditions, if the threshold parameter  $\mathcal{R}_2 < 1$ , both coral and CoTS have high growth rate, then coral and CoTS can coexist and triton is completely eliminated (see Fig. 1(e-f)).

**Theorem 6** *The coral-free equilibrium  $E_{yz} = (0, y_4, z_4)$  exists if*

$$h_1 < \frac{r_2 [e_2 m_2 K_2 - (d + h_2)(a_2 + K_2)]}{K_2 (e_2 m_2 - d - h_2)}, \quad d + h_2 < \frac{e_2 m_2 K_2}{a_2 + K_2}. \tag{8}$$

$E_{yz}$  is locally asymptotically stable if

$$r_1 < \frac{m_1 y_4}{a_1}, \quad r_2 > \frac{m_2 K_2 z_4}{(a_2 + y_4)^2}. \tag{9}$$

Theorem 6 implies that, if the growth rate  $r_1$  of coral, the harvesting rate  $h_1$  of CoTS, and the sum of natural mortality and harvesting rate  $d + h_2$  of triton are low, while the intrinsic growth rate  $r_2$  of CoTS is high, then CoTS and triton coexist while coral goes extinct (see Fig. 1(g-h)).

We next investigate the existence and stability of the interior equilibrium  $E_{xyz}(x^*, y^*, z^*)$ . It follows from the third equation of (5) that

$$y^* = \frac{a_2 (d + h_2)}{e_2 m_2 - d - h_2}.$$

Substituting  $y^*$  into the first equation of (5) gives:

$$x^2 + (a_1 - K_1)x + \frac{m_1 K_1 y^* - a_1 K_1 r_1}{r_1} = 0. \tag{10}$$

The existence of solution of (10) can be divided into two cases.

- If  $r_1 > \frac{m_1 y^*}{a_1}$  holds, then (10) has a unique positive root as follows

$$x^* = \frac{K_1 - a_1 + \sqrt{(a_1 - K_1)^2 + \frac{4K_1}{r_1}(a_1 r_1 - m_1 y^*)}}{2}.$$

- If  $\frac{4m_1 K_1 y^*}{(a_1 + K_1)^2} \leq r_1 < \frac{m_1 y^*}{a_1}$  and  $a_1 < K_1$  hold, then (10) can admit two positive roots  $x_1^*$  and  $x_2^*$ , where

$$x_1^* = \frac{K_1 - a_1 + \sqrt{(a_1 - K_1)^2 - \frac{4K_1}{r_1}(m_1 y^* - a_1 r_1)}}{2},$$

$$x_2^* = \frac{K_1 - a_1 - \sqrt{(a_1 - K_1)^2 - \frac{4K_1}{r_1}(m_1 y^* - a_1 r_1)}}{2}.$$

Then

$$z^* = \frac{a_2 + y^*}{m_2} \left( r_2 - h_1 - \frac{r_2}{K_2} y^* + \frac{e_1 m_1 x^*}{a_1 + x^*} \right)$$

can be expressed in terms of  $x^*$  and  $y^*$  rather than all the parameters involved in (1). The explicit expressions for  $x^*$  and  $y^*$  could be obtained by direct calculation when each parameter is provided. In the following, we consider the case that there exists only one positive equilibrium.

**Theorem 7** *The coexistence equilibrium  $E_{xyz}(x^*, y^*, z^*)$  exists if*

$$d + h_2 < e_2 m_2, \quad r_1 > \frac{m_1 a_2 (d + h_2)}{a_1 (e_2 m_2 - d - h_2)}, \quad r_2 > h_1 + \frac{r_2 a_2 (d + h_2)}{K_2 (e_2 m_2 - d - h_2)}. \tag{11}$$

$E_{xyz}$  is locally asymptotically stable if

$$r_1 > \frac{K_1 m_1 y^*}{(a_1 + x^*)^2}, \quad r_2 > \frac{K_2 m_2 z^*}{(a_2 + y^*)^2}, \quad A_1 A_2 > A_3,$$

where  $A_1, A_2, A_3$  are defined in (A1).  $E_{xyz}$  is globally asymptotically stable if

$$r_1 > \frac{K_1 m_1 y^*}{a_1 + x^*}, \quad r_2 > \frac{K_2 m_2 z^*}{a_2 + y^*}. \tag{12}$$

The proof of Theorem 7 is attached in Appendix A.9. It follows that, if the intrinsic growth rates of coral and CoTS are high and the harvesting rates of CoTS and triton are low, then the three species can coexist (see Fig. 2(a-b)).

In summary, (1) admits rich dynamics and possibly has different dynamic scenarios (see Fig. 1 for boundary dynamics and the parameters are given in Table 2). The simultaneous extinction of all three populations will never occur since  $E_0$  is unstable. Under suitable conditions, coral or CoTS can possibly dominate the system and tend to its carrying capacity in the absence of the other two populations, i.e.,  $E_x$  or  $E_y$  is attractive. The more interesting scenarios include the possible disappearance of triton only ( $E_{xy}$ ) or coral only ( $E_{yz}$ ). The coral, CoTS, and triton can coexist together at an interior equilibrium  $E_{xyz}$ . The sufficient criteria for the existence and asymptotic stability of some equilibria are presented by their components since the explicit expressions are too complex to be expounded in terms of the original parameters in (1) (e.g., one can derive them with the help of a Maple or Matlab program). In addition to the equilibrium dynamics, we can numerically observe the periodic dynamics of (1) (see Fig. 2(c-d) for cyclic oscillation). The global dynamics of (1) is very complex and is analytically challenging. The deterministic nature of (1) allows to carry out systematic numerical analyses to characterize the effects of key parameters on the dynamics of (1).

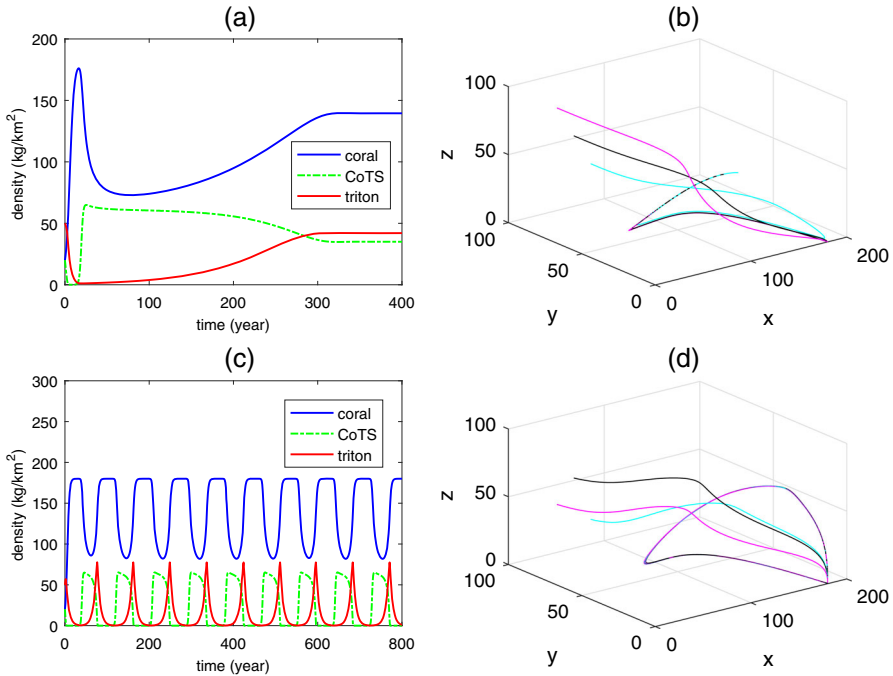
## 4 Optimal Harvesting

Artificial harvesting is an effective measure to control CoTS. The harvested CoTS can be processed into organic fertilizer for plant growth. Both the ecological effects and the economic benefits are fairly important (Fan and Wang 1998; Kang and Lanchier 2012; Liu and Bai 2016). The cost of CoTS harvesting cannot be ignored, such as rental boats, hiring divers, and diving equipments. In this section, we investigate the economic aspects of (1) by introducing harvesting efforts. The possibility of existence of a bionomic equilibrium is considered when the total revenue obtained by the harvested biomass equals the total cost for the harvesting effort. The optimal bioeconomic harvesting is studied by using Pontryagin's maximal principle.

In (1), both CoTS and triton are subject to a combined harvesting effort  $E$ . The combined harvesting effort is applied when a particular type of trawlers is used by the fishermen in a specific fishery area. But for a particular type of trawlers, the catchability may vary across different trophic levels (Kar et al 2019). According to the usual catch-per-unit-effort hypothesis (Rago and Van Dyne 1978), the harvesting rates take the form of  $h_1 = q_1 E$  and  $h_2 = q_2 E$ , where  $q_1$  and  $q_2$ , respectively, represent the catchability coefficients of CoTS and triton. It is assumed that the total cost is proportional to the harvesting effort and the total profit from the harvesting is proportional to the harvesting yield. The net economic rent or net revenue is given by

$$\Pi(y, z, E) = (p_1 q_1 y + p_2 q_2 z - c)E,$$

where  $p_1$  and  $p_2$  denote the price per unit biomass of population  $y$  and  $z$ , respectively,  $c$  represents the cost of per unit harvesting effort exerted. It is useful to find the



**Fig. 2** Time series dynamics (left column) and phase portraits (right column) for interior equilibrium scenario of (1): **a, b**  $\bar{E}_{xyz}$  is an attractor and all the three species survive, here  $h_2 = 0.18$ ; **c, d** all the three species coexist cyclically, here  $h_2 = 0.05$ . The values of the parameters except  $h_2$  are  $r_1 = 0.4$ ,  $r_2 = 0.8$ ,  $K_1 = 180$ ,  $K_2 = 60$ ,  $m_1 = 0.5$ ,  $a_1 = 55$ ,  $e_1 = 0.8$ ,  $m_2 = 0.4$ ,  $a_2 = 5$ ,  $e_2 = 0.8$ ,  $d = 0.1$ ,  $h_1 = 0.2$

bionomic equilibrium, which is a combination of the biological equilibrium and the economic equilibrium, defined as the interior equilibrium of (1) corresponding to zero net revenue (i.e.,  $\Pi = 0$ ).

**Theorem 8** *The bionomic equilibrium  $(\bar{x}, \bar{y}, \bar{z}, \bar{E})$  exists if the following inequalities hold*

$$r_1 < \frac{m_1 K_2}{a_1}, \quad \frac{p_1}{p_2} > e_2 + \frac{m_1 c}{a_1 r_1 q_1 p_2}. \tag{13}$$

The proof of Theorem 8 is given in Appendix B.1. It is obvious that  $\bar{E}$  is the critical threshold effort that determines the profitability of the harvesting. When  $E > \bar{E}$ , the total cost will exceed the total revenue, the harvesting causes a major loss for fisherman, and then  $E > \bar{E}$  cannot be maintained indefinitely due to the fact that the fisherman would withdraw from the fishery. When  $E < \bar{E}$ , the investment is profitable such that more and more fishermen will be attracted in an open access fishery, and  $E < \bar{E}$  also cannot be maintained indefinitely due to the increasing harvesting intensity. When the revenue is equal to the total cost of harvesting,  $E = \bar{E}$  can be established.

**Table 2** Parameter values for attractors of (1) depicted in Fig. 1

Figures	Parameters	Attractors
(a) and (b)	$r_1 = 0.35, r_2 = 0.7, K_1 = 550, K_2 = 84, m_1 = 0.5, a_1 = 200, e_1 = 0.8, m_2 = 0.4, a_2 = 10, e_2 = 0.8, d = 0.1, h_1 = 1.2, h_2 = 0.5$	$E_x$ is an attractor, coral can survive, but CoTS and triton cannot
(c) and (d)	$r_1 = 0.05, r_2 = 0.8, K_1 = 550, K_2 = 30, m_1 = 0.5, a_1 = 20, e_1 = 0.8, m_2 = 0.4, a_2 = 5, e_2 = 0.8, d = 0.1, h_1 = 0.1, h_2 = 0.7$	$E_y$ is an attractor, CoTS can survive, but coral and triton cannot
(e) and (f)	$r_1 = 0.46, r_2 = 0.8, K_1 = 165, K_2 = 60, m_1 = 0.5, a_1 = 55, e_1 = 0.8, m_2 = 0.4, a_2 = 5, e_2 = 0.8, d = 0.1, h_1 = 0.2, h_2 = 0.7$	$E_{xy}$ is an attractor, only triton cannot survive
(g) and (h)	$r_1 = 0.5, r_2 = 0.9, K_1 = 550, K_2 = 80, m_1 = 0.5, a_1 = 20, e_1 = 0.8, m_2 = 0.4, a_2 = 30, e_2 = 0.8, d = 0.1, h_1 = 0.02, h_2 = 0.05$	$E_{yz}$ is an attractor, only coral cannot survive

In what follows, we will study the optimal harvesting strategy with the fuzzy net discount rate of inflation. The objective is to maximize the expected present discounted value of future profit flows from harvesting in both CoTS and triton.

Let  $\tilde{q}$  and  $\tilde{\zeta}$  be the inflation and discount rates, and they are considered as fuzzy numbers, essentially. The net present value  $\mathcal{J}$  of continuous stream of revenue is now considered to evaluate an optimal harvesting policy defined by

$$\mathcal{J}(y, z, E) = \int_0^{\infty} e^{-\tilde{\delta}t} (p_1 q_1 y + p_2 q_2 z - c) E dt, \quad (14)$$

where  $\tilde{\delta} = \tilde{\zeta} - \tilde{q}$  represents the net discount rate of inflation. Our objective is to maximize  $\mathcal{J}$  by solving this fuzzy optimization problem. The harvesting strategies not only guarantee profit maximization, but also maintain an optimal level for species. That is to say,  $y(t)$  and  $z(t)$  tend to a non-zero number as  $t$  tends to  $\infty$  such that  $\mathcal{J}$  reaches the maximum. The control variable  $E$  is subjected to the constraints  $0 \leq E \leq E_{\max}$  and the fuzzy number  $\tilde{\delta}$  is expressed as an interval number  $[\delta_u, \delta_v]$  (Dawed et al 2020; Maity and Maiti 2008). Maximizing  $\mathcal{J}$  is equivalent to maximizing  $[\mathcal{J}_u, \mathcal{J}_v]$ , where:

$$\begin{aligned}
 \text{Max}[\mathcal{J}_u, \mathcal{J}_v] &= \int_0^\infty e^{-[\delta_u, \delta_v]t} (p_1q_1y + p_2q_2z - c)Edt, \\
 \mathcal{J}_u &= \int_0^\infty e^{-\delta_v t} (p_1q_1y + p_2q_2z - c)Edt, \\
 \mathcal{J}_v &= \int_0^\infty e^{-\delta_u t} (p_1q_1y + p_2q_2z - c)Edt, \\
 \delta_u &= \varsigma_u - \varrho_v, \quad \delta_v = \varsigma_v - \varrho_u, \quad \tilde{\zeta} = [\varsigma_u, \varsigma_v], \quad \tilde{\varrho} = [\varrho_u, \varrho_v].
 \end{aligned} \tag{15}$$

By the method of weighted sum, it yields that

$$\text{Max}\mathcal{J} = \text{Max}[\mathcal{J}_u, \mathcal{J}_v] = \xi_1\mathcal{J}_u + \xi_2\mathcal{J}_v,$$

where  $\xi_1 \geq 0$  and  $\xi_2 \geq 0$  are two weights, such that  $\xi_1 + \xi_2 = 1$ . The Hamiltonian function can be written as

$$\begin{aligned}
 \mathcal{F} &= (\xi_1e^{-\delta_v t} + \xi_2e^{-\delta_u t}) (p_1q_1y + p_2q_2z - c)E + \chi_1 \left( r_1x - \frac{r_1}{K_1}x^2 - \frac{m_1xy}{a_1 + x} \right) \\
 &+ \chi_2 \left( r_2y - \frac{r_2}{K_2}y^2 + \frac{e_1m_1xy}{a_1 + x} - \frac{m_2yz}{a_2 + y} - q_1Ey \right) \\
 &+ \chi_3 \left( \frac{e_2m_2yz}{a_2 + y} - dz - q_2Ez \right),
 \end{aligned} \tag{16}$$

where  $\chi_1, \chi_2,$  and  $\chi_3$  are the adjoint variables.

The optimal control  $E$  must satisfy the conditions:

$$E = \begin{cases} E_{\max}, & \text{if } \frac{\partial \mathcal{F}}{\partial E} > 0, \\ 0, & \text{if } \frac{\partial \mathcal{F}}{\partial E} < 0. \end{cases}$$

Since  $\frac{\partial \mathcal{F}}{\partial E}$  causes  $E$  to switch between level 0 and  $E_{\max}$ ,  $\frac{\partial \mathcal{F}}{\partial E}$  is called switching function. The optimal control is the so-called ‘‘bang-bang control’’ from one extreme point to another one depending on the sign of the switching function. When the switching function is zero on nontrivial time intervals, the Hamiltonian function is independent of the control variable  $E$ , then it is called a singular control (Lenhart and Workman 2007; Djomegni et al 2019). Hence, the optimal effort level to be applied now follows:

$$E = \begin{cases} E_{\max}, & \text{if } \frac{\partial \mathcal{F}}{\partial E} > 0, \\ E^{**}, & \text{if } \frac{\partial \mathcal{F}}{\partial E} = 0, \\ 0, & \text{if } \frac{\partial \mathcal{F}}{\partial E} < 0. \end{cases}$$

When  $\frac{\partial \mathcal{F}}{\partial E} = 0$ , it follows that

$$(\xi_1e^{-\delta_v t} + \xi_2e^{-\delta_u t}) (p_1q_1y + p_2q_2z - c) - \chi_2q_1y - \chi_3q_2z = 0, \tag{17}$$

which implies that the cost of harvest per unit of effort equals the discounted value of the future marginal profit of the effort at the steady state level. The following theorem gives the sum up of the above analyses. The detailed proof is attached in Appendix B.2.

**Theorem 9** *The optimal equilibrium solution  $(x^{**}, y^{**}, z^{**}, E^{**})$  of the control problem can be obtained by solving the steady state equations (B4) together with (B12). Moreover, the maximum net present revenue is:*

$$\mathcal{J}(y^{**}, z^{**}, E^{**}) = \frac{(p_1q_1y^{**} + p_2q_2z^{**} - c)E^{**}}{\tilde{\delta}}.$$

Theorem 9 demonstrates that, in the case of profit from harvesting, the policy makers should recommend the optimal effort  $E^{**}$ . The maximum profit will be achieved while all the species in the ecosystem are sustainable. This finding provides analytical support for the safe harvesting in bio-economical management.

### 5 Dynamics of Stochastic System (2)

In this section, we investigate the dynamics of (2) in the biologically reasonable region  $\mathbb{R}_+^3$ . Since (2) satisfies the local Lipschitz condition, for any initial value  $(x_0, y_0, z_0) \in \mathbb{R}_+^3$ , (2) has a unique local solution  $(x(t), y(t), z(t)) \in \mathbb{R}_+^3$ . That is to say, this solution may possibly explode in finite time almost surely. Theorem 10 below shows that (2) has a unique positive global solution with positive initial value by applying Lyapunov’s direct method. One can find the detailed proof in Appendix C.1. In order to facilitate the discussion, the following lemma is introduced.

**Lemma 3** *The function*

$$f(x) = -p_1x^{\theta+2} + p_2x^2 + p_3x^{\theta+1} + p_4x + p_5x^\theta, \quad x \geq 0$$

*has a maximum value, where  $p_i > 0$  ( $i = 1, 2, 3, 4, 5$ ) and  $0 < \theta < 1$ .*

**Theorem 10** *For any given initial value  $(x_0, y_0, z_0) \in \mathbb{R}_+^3$ , there is a unique solution  $(x(t), y(t), z(t))$  of (2) for  $t \geq 0$  and the solution remains in  $\mathbb{R}_+^3$  with probability 1.*

We next explore the long-term dynamical behaviors of (2). The following theorem shows that the  $\tilde{\theta}$ -th moment of the solution of (2) is bounded, whose proof is presented in Appendix C.2.

**Theorem 11** *Assume that  $\tilde{X}(t)$  is the solution of (2) with any initial value  $(x_0, y_0, z_0) \in \mathbb{R}_+^3$ , then, for any  $0 < \tilde{\theta} \leq 1$ , there exists a positive constant  $\mathcal{G}(\tilde{\theta})$  such that*

$$\limsup_{t \rightarrow \infty} \mathbb{E}x^{\tilde{\theta}} \leq \mathcal{G}(\tilde{\theta}), \quad \limsup_{t \rightarrow \infty} \mathbb{E}y^{\tilde{\theta}} \leq \mathcal{G}(\tilde{\theta}), \quad \limsup_{t \rightarrow \infty} \mathbb{E}z^{\tilde{\theta}} \leq \mathcal{G}(\tilde{\theta}).$$



Asymptotic moment estimate, an important property of stochastic population systems, guarantees that (2) is biologically well-defined. Theorem 11 shows that no matter how the environmental stochasticity varies,  $\tilde{\theta}$ -th moment of the solution of (2) is always bounded.

From a biological point of view, the coming two theorems characterize the extinction scenario of (2). The proofs can be found in Appendix C.3 and Appendix C.4.

**Theorem 12** *Let  $(x(t), y(t), z(t))$  be the solution of (2) with initial value  $(x_0, y_0, z_0) \in \mathbb{R}_+^3$ . Assume that*

$$r_1 > \frac{\sigma_{11}^2}{2}, \quad \mu := r_2 - h_1 - \frac{\sigma_{21}^2}{2} + e_1 m_1 \int_0^\infty \frac{x\varphi(x)}{a_1 + x} dx < 0,$$

*then both  $y(t)$  and  $z(t)$  die out with probability one, i.e.,  $\lim_{t \rightarrow \infty} y(t) = 0$ ,  $\lim_{t \rightarrow \infty} z(t) = 0$ . Moreover, the distribution of  $x(t)$  converges weakly to the measure which has the following density*

$$\varphi(x) = Q x^{2r_1/\sigma_{11}^2 - 2} (\sigma_{11} + \sigma_{12}x)^{-2r_1/\sigma_{11}^2 - 2} \exp \left\{ \frac{2r_1(\sigma_{11} + K_1\sigma_{12})}{K_1\sigma_{11}\sigma_{12}(\sigma_{11} + \sigma_{12}x)} \right\},$$

*where  $Q$  is a constant such that  $\int_0^\infty \varphi(x) dx = 1$ .*

**Theorem 13** *Let  $(x(t), y(t), z(t))$  be the solution of (2) with initial value  $(x_0, y_0, z_0) \in \mathbb{R}_+^3$ . If  $r_1 < \sigma_{11}^2/2$ , then  $x(t)$  dies out, i.e.,  $\lim_{t \rightarrow \infty} x(t) = 0$ . If  $r_2 - h_1 < \sigma_{21}^2/2$ , then both  $y(t)$  and  $z(t)$  die out, i.e.,  $\lim_{t \rightarrow \infty} y(t) = 0$ ,  $\lim_{t \rightarrow \infty} z(t) = 0$ .*

Theorem 12 and Theorem 13 provide sufficient conditions for the survival and extinction of coral, which are completely determined by the intensity of environmental noise  $\sigma_{11}^2$ . When the intensity of environmental noise is small enough, coral will be stochastically persistent; otherwise, coral will become extinct. From the expression of the threshold  $\mu$ , it is observed that both the harvesting rate  $h_1$  and the noise intensity  $\sigma_{21}^2$  together determine whether or not CoTS will become extinct. When the harvesting intensity and the noise are large enough, it will lead to the extinction of CoTS in the ecosystem and consequently the triton population goes extinct. That is to say, the extinction of triton has nothing to do with the environmental disturbances, but because of insufficient food sources. It indicates that large noises are devastating to both coral and CoTS; in other words, the ability of either coral or CoTS to adapt to external environmental fluctuations is limited. Moreover, we note that the higher-order perturbation of CoTS does not influence the persistence criterion in terms of the threshold  $\mu$ .

From the ecological viewpoint, the detailed comparison between the deterministic system (1) and the stochastic system (2) leads to the following conclusions:

- (1) In Theorem 2, total extinction is impossible for the deterministic system (1), whereas, it may happen in the stochastic system (2) due to the existence of environmental noises.

- (2) In Theorem 3, if the harvesting rate  $h_1$  is smaller than the growth rate  $r_2$ , then  $E_x = (K_1, 0, 0)$  is unstable in the deterministic system (1). However, as long as the noise intensity is sufficiently large, CoTS in the stochastic system (2) will become extinct even if the harvesting rate  $h_1$  is small enough.
- (3) Theorem 4 exhibits CoTS-dominated scenario in the deterministic system (1), while it cannot happen in the stochastic system (2). Since the environmental noises are taken into account, CoTS and triton always exist or become extinct at the same time. The situation in which CoTS persists but triton goes extinct in the stochastic system is hard to achieve from the aspects of theoretical deduction and numerical analysis.

Our results provide more evidence that environmental noises are critical and cannot be neglected when the harvesting strategies are considered. The large environmental noises are detrimental to the persistence of the species and may lead to extinction. In real-world applications, this may happen when a serious epidemic or severe weather occurs. The results are important for resource exploitation because they clearly illustrate how noises can alter the dynamics of the species.

## 6 Numerical Simulations

In this section, some numerical simulations are performed to further expound the effects of harvesting on the dynamics of (1) and the effects of environment noises on the dynamics of (2).

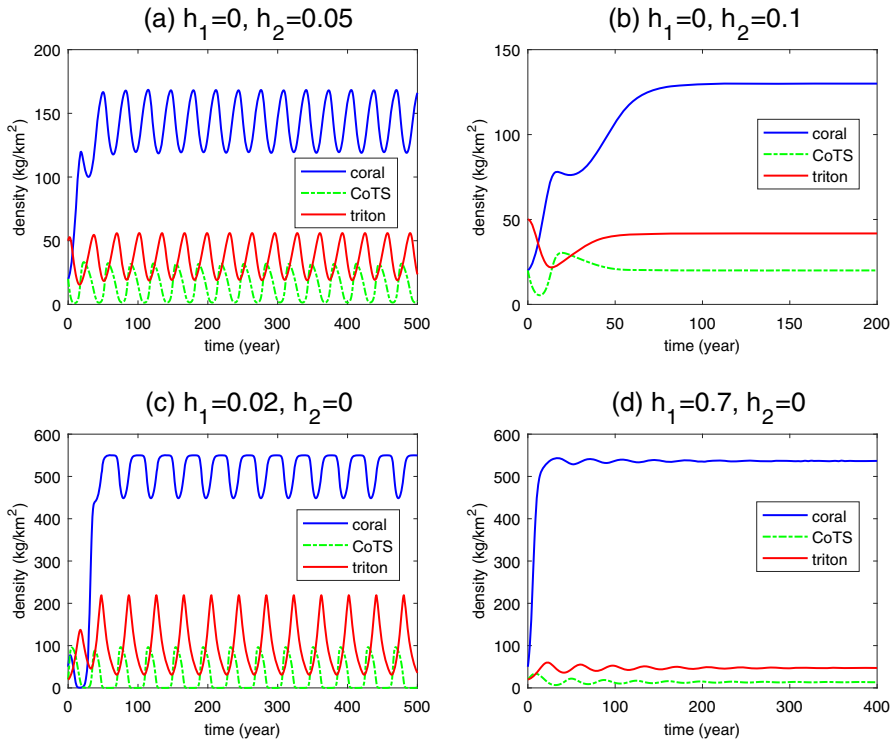
### 6.1 Effects of Harvesting

In what follows, we study the effects of harvesting rates  $h_1$  and  $h_2$  on the population dynamics of the whole system. The exploration is divided into three cases.

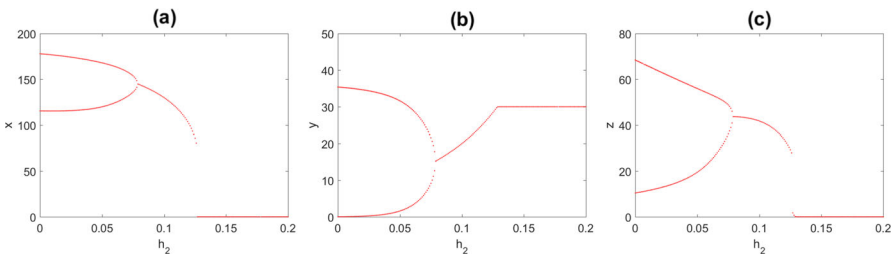
When  $h_1 = 0$ ,  $h_2 \neq 0$ , (1) exhibits cyclic oscillation when  $h_2$  is small. As  $h_2$  is increased from  $h_2 = 0.05$  to  $h_2 = 0.1$ , the three species coexist at an equilibrium (see Fig. 3(a-b)). The effects of  $h_2$  in the form of bifurcation diagram are shown in Fig. 4. When  $h_2$  is further increased, coral and triton will go to extinction while only CoTS can survive. This example explains that, if the harvesting intensity of triton is slight, then coral can survive periodically even if no measures are taken to harvest CoTS. However, the harvesting of triton is not beneficial to control the biomass of CoTS such that coral becomes extinct suddenly.

When  $h_2 = 0$ ,  $h_1 \neq 0$ , the three species will coexist cyclically with  $h_1$  being small. As  $h_1$  increases from  $h_1 = 0.02$  to  $h_1 = 0.7$ , the coexistence of the three species is stable (see Fig. 3(c-d)). The effects of  $h_1$  in the form of bifurcation diagram are shown in Fig. 5. Compared with the scenario in Fig. 1(g), we find that, if the harvesting of triton is fully cut down, then coral can survive periodically under the same harvesting intensity of CoTS. The protection of triton is beneficial to coral, and the over-exploitation of CoTS will lead coral survive solely.

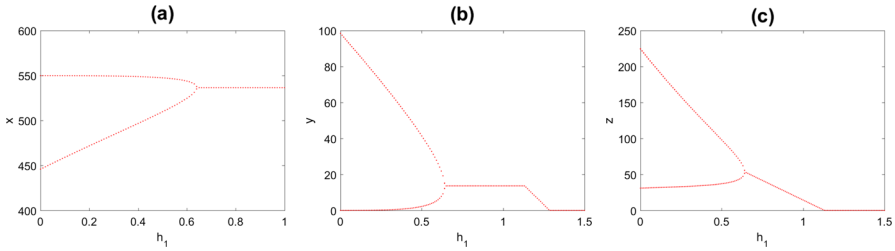
When  $h_1 \neq 0$ ,  $h_2 \neq 0$ , the three species can coexist cyclically if  $h_1 = 0.2$ ,  $h_2 = 0.02$ . As  $h_2$  increases to  $h_2 = 0.4$ , coral and CoTS coexist at an equilibrium but triton



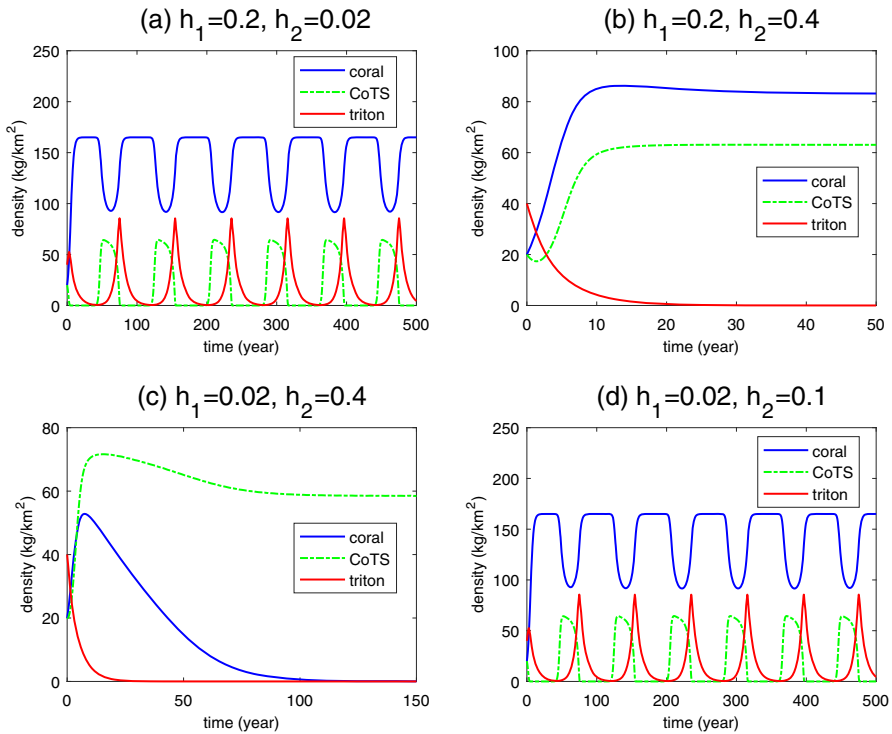
**Fig. 3** Time series dynamics of (1) under different harvesting scenarios: **a**, **b** only triton is harvested and all the three species change from cyclic coexistence to stable coexistence equilibrium as  $h_2$  increases, here  $r_1 = 0.2$ ,  $r_2 = 0.7$ ,  $K_1 = 180$ ,  $K_2 = 30$ ,  $m_1 = 0.5$ ,  $a_1 = 50$ ,  $e_1 = 0.8$ ,  $m_2 = 0.4$ ,  $a_2 = 12$ ,  $e_2 = 0.8$ ,  $d = 0.1$ ; **c**, **d** only CoTS is harvested and all the three species change from cyclic coexistence to stable coexistence equilibrium as  $h_1$  increases, here  $r_1 = 0.5$ ,  $r_2 = 0.9$ ,  $K_1 = 550$ ,  $K_2 = 80$ ,  $m_1 = 0.5$ ,  $a_1 = 20$ ,  $e_1 = 0.8$ ,  $m_2 = 0.4$ ,  $a_2 = 30$ ,  $e_2 = 0.8$ ,  $d = 0.1$



**Fig. 4** Bifurcation diagram of (1) with respect to  $h_2$  ( $h_1 = 0$ ). As  $h_2$  increases, coral and triton will go to extinction but CoTS can survive. The values of the parameters except  $h_1$  and  $h_2$  are the same as those in Fig. 3a, b



**Fig. 5** Bifurcation diagram of (1) with respect to  $h_1$  ( $h_2 = 0$ ). As  $h_1$  increases, only coral can survive. The values of the parameters except  $h_1$  and  $h_2$  are the same as those in Fig. 3c, d



**Fig. 6** Time series dynamics of (1) when both CoTS and triton are harvested. The parameters except  $h_1$ ,  $h_2$  and the initial value are the same as those in Fig. 1e, f

tends to extinction (see Fig. 6(a-b)). However, the above situation is easily upset once  $h_1$  is decreased. Figure 6(c) reveals that, when  $h_2 = 0.4$  is fixed but  $h_1$  is reduced to  $h_1 = 0.02$ , coral will tend to extinct. Under this circumstance, only by decreasing the harvesting intensity of triton to  $h_2 = 0.1$  can lead the three species coexist cyclically (see Fig. 6(d)). This example illustrates that the appropriate harvesting can encourage the three species to coexist. In order to keep the coexistence, the harvesting rate  $h_1$  should be controlled strictly and  $h_2$  cannot be too large. We also give the dynamic evolution of coral, CoTS, and triton with varying  $h_1$  and  $h_2$  (see Fig. 7).

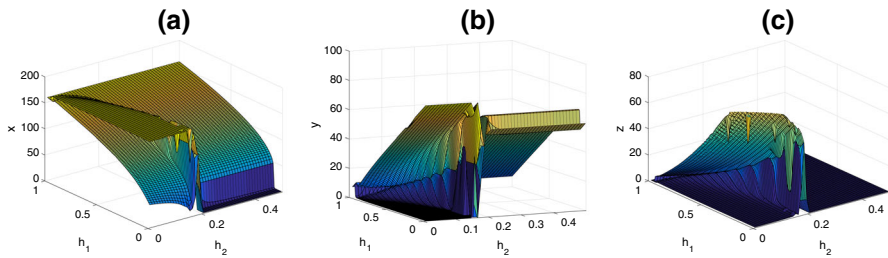


Fig. 7 Bifurcation surface of (1) with  $h_1$  and  $h_2$  being the bifurcation parameters

### 6.2 Effects of Environmental Noises

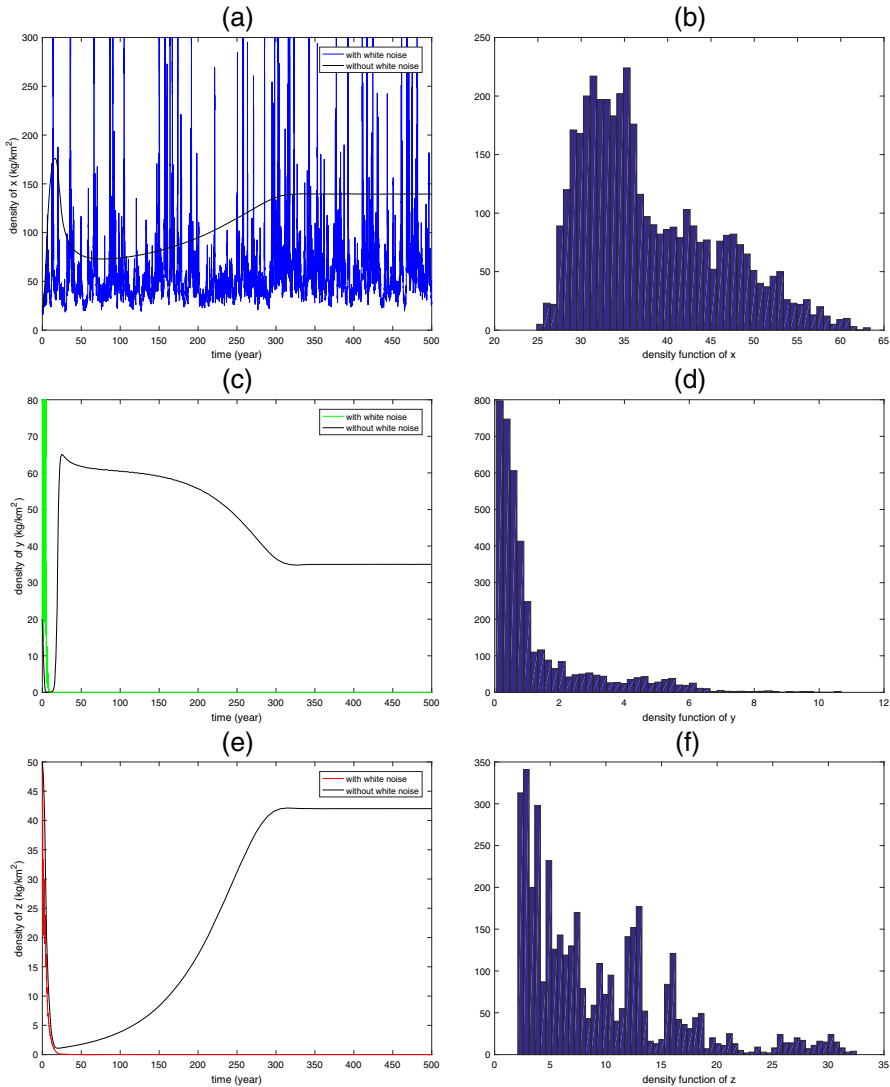
Numerical simulations are presented for (2) to verify the theoretical findings and to investigate the effects of stochastic noises. By employing Milstein’s higher-order method (Higham 2001), (2) is transformed into the following discretized system:

$$\begin{cases}
 \tilde{u}_{k+1} = \tilde{u}_k + \left[ r_1 \tilde{u}_k \left( 1 - \frac{\tilde{u}_k}{K_1} \right) - \frac{m_1 \tilde{u}_k \tilde{v}_k}{a_1 + \tilde{u}_k} \right] \Delta t + \tilde{u}_k (\sigma_{11} + \sigma_{12} \tilde{u}_k) \sqrt{\Delta t} \tilde{\xi}_k \\
 \quad + \frac{\tilde{u}_k}{2} (\sigma_{11}^2 + 3\sigma_{11}\sigma_{12}\tilde{u}_k + 2\sigma_{12}^2\tilde{u}_k^2) (\tilde{\xi}_k^2 - 1) \Delta t, \\
 \tilde{v}_{k+1} = \tilde{v}_k + \left[ r_2 \tilde{v}_k \left( 1 - \frac{\tilde{v}_k}{K_2} \right) + \frac{e_1 m_1 \tilde{u}_k \tilde{v}_k}{a_1 + \tilde{u}_k} - \frac{m_2 \tilde{v}_k \tilde{w}_k}{a_2 + \tilde{v}_k} - h_1 \tilde{v}_k \right] \Delta t \\
 \quad + \tilde{v}_k (\sigma_{21} + \sigma_{22} \tilde{v}_k) \sqrt{\Delta t} \tilde{\eta}_k + \frac{\tilde{v}_k}{2} (\sigma_{21}^2 + 3\sigma_{21}\sigma_{22}\tilde{v}_k + 2\sigma_{22}^2\tilde{v}_k^2) (\tilde{\eta}_k^2 - 1) \Delta t, \\
 \tilde{w}_{k+1} = \tilde{w}_k + \left[ \frac{e_2 m_2 \tilde{v}_k \tilde{w}_k}{a_2 + \tilde{v}_k} - d \tilde{w}_k - h_2 \tilde{w}_k \right] \Delta t + \tilde{w}_k (\sigma_{31} + \sigma_{32} \tilde{w}_k) \sqrt{\Delta t} \tilde{\vartheta}_k \\
 \quad + \frac{\tilde{w}_k}{2} (\sigma_{31}^2 + 3\sigma_{31}\sigma_{32}\tilde{w}_k + 2\sigma_{32}^2\tilde{w}_k^2) (\tilde{\vartheta}_k^2 - 1) \Delta t,
 \end{cases} \tag{18}$$

where  $\tilde{\xi}_k$ ,  $\tilde{\eta}_k$ , and  $\tilde{\vartheta}_k$  ( $k = 1, 2, \dots$ ) are independent Gaussian random variables  $\sim N(0, 1)$ . The numerical results are achieved with the help of MATLAB.

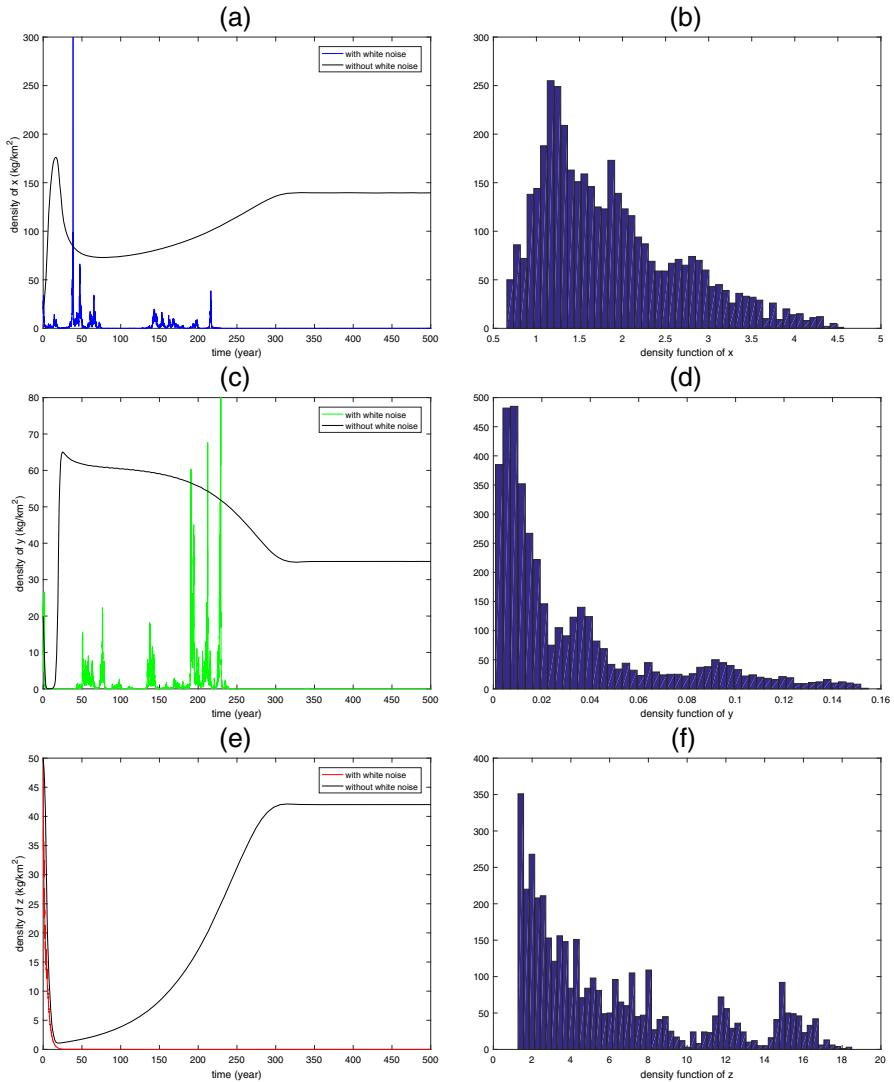
We present two examples to verify the extinction scenario of (2). Taking the same parameter values and initial values as those in Fig. 2(a-b). Figure 8 shows that coral will persist in a long term. Both CoTS and triton will tend to zero eventually, which strongly supports Theorem 12. As the noise intensity continues to increase, the population will be completely extinct which is shown in Theorem 13. Figure 9 demonstrates that all the species become extinct due to high intensity of noises even they coexist in the deterministic environment. Therefore, the large environmental noises are not conducive to the survival of population system.

It is worth mentioning that external perturbation may destroy the stability of an equilibrium in a deterministic system, which will lead to a weak stability phenomenon called stationary distribution, representing an ecological balance. Paying attention to the existence of stationary distribution is an important research field of stochastic



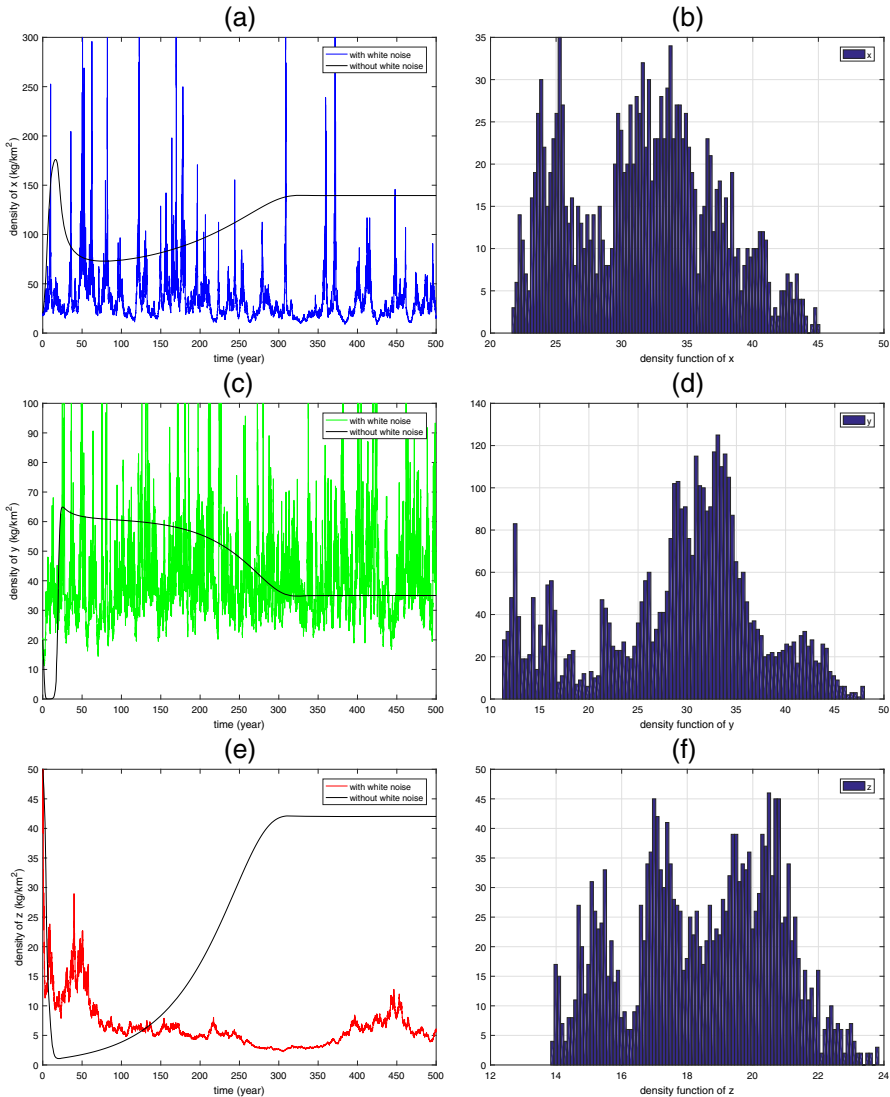
**Fig. 8** Only coral persist: **a**, **c**, and **e** show time series of  $x$ ,  $y$ , and  $z$  for (2); **b**, **d**, and **f** exhibit the histogram of the probability density function of  $x$ ,  $y$  and  $z$  for (2). Here  $\sigma_{11} = 0.01$ ,  $\sigma_{12} = 0.01$ ,  $\sigma_{21} = 1.5$ ,  $\sigma_{22} = 0.01$ ,  $\sigma_{31} = 0.01$ ,  $\sigma_{32} = 0.01$

differential equations (Khas'minskii 2011; Qi et al 2022; Zhao et al 2022). We keep the same parameter values and initial values as those in Fig. 2(a-b) and choose the following noise intensities:  $\sigma_{11} = 0.01$ ,  $\sigma_{12} = 0.01$ ,  $\sigma_{21} = 0.01$ ,  $\sigma_{22} = 0.01$ ,  $\sigma_{31} = 0.01$ ,  $\sigma_{32} = 0.01$ . Clearly, we can obtain  $r_1 > \sigma_{11}^2/2$  and  $\mu > 0$ . Figure 10 (a), (c), and (e) indicate a stationary distribution of all the species. When this is true, the histograms shown in Fig. 10 (b), (d), and (f) can be regarded as approximate probability distribution



**Fig. 9** All species go extinct: **a**, **c**, and **e** show time series of  $x$ ,  $y$ , and  $z$  for (2); **b**, **d**, and **f** exhibit the histogram of the probability density function of  $x$ ,  $y$ , and  $z$  for (2). Here  $\sigma_{11} = 0.9$ ,  $\sigma_{12} = 0.01$ ,  $\sigma_{21} = 1.1$ ,  $\sigma_{22} = 0.01$ ,  $\sigma_{31} = 0.01$ ,  $\sigma_{32} = 0.01$

for the stationary distribution. Furthermore,  $\mu$  is a threshold which determines whether the stochastic system will ecologically persist or not.



**Fig. 10** Coral, CoTS, and triton present coexistence for a long time: **a**, **c**, and **e** show time series of  $x$ ,  $y$ , and  $z$  for (2); **b**, **d**, and **f** exhibit density function of  $x$ ,  $y$ , and  $z$  for (2). Here  $\sigma_{11} = 0.01$ ,  $\sigma_{12} = 0.01$ ,  $\sigma_{21} = 0.01$ ,  $\sigma_{22} = 0.01$ ,  $\sigma_{31} = 0.01$ ,  $\sigma_{32} = 0.01$

### 7 Discussion

Overfishing is regarded as a major stressor of coral reefs and can shift areas from a coral-dominated to a macroalgae-dominated state. Most of the modeling focuses on the effects of overfishing the predators of macroalgae, without considering another principal cause of coral reefs degradation, which is the consumption of coral by CoTS resulting in mass coral mortality during CoTS outbreaks. Due to CoTS densities



increasing with the removal of its predator triton, it is significant to turn attention to coral-CoTS dynamics through the abundance of triton. This perspective motivates us to design a tri-trophic food chain model to describe coral-CoTS-triton interactions based on the “predator removal hypothesis” (Eudean 1969) in an oceanic coral reef ecosystem. We aim to systematically explore the effects of harvesting on the deterministic system (1) and environmental noises on the persistence or extinction of populations in stochastic system (2). Both theoretical analysis and numerical simulations have positive effects on understanding the dynamics of coral reef system. We show that the harvesting of triton is not beneficial to coral, once triton vanishes or faces extinction due to overfishing, it is high time to take measures to harvest CoTS such that coral can survive. Additionally, large white noises are negative for the survival of populations and accelerate population extinction, while small white noises can guarantee the existence of stationary distribution standing for weak stability and the persistence of (2).

Our work provides an extension of the following research results. Zikkah et al (2020) considered biological interactions between coral-CoTS and macroalgae grazers on coral reefs based on the pioneer work by Mumby et al (2007). However, they overlooked the harvesting of CoTS, and the predation of CoTS was simplified as Holling type I functional response. Quintero et al (2016) explored the predator-prey relationship between coral-CoTS and the top predator wrasse. They showed how overfishing wrasse indirectly leads to a more rapid depletion of coral by CoTS predation, which coincides with one of our main conclusions. In their established model, the top predator grows logistically and the carrying capacity is based on the current density of coral. Different from their biological background, the top predator triton in our study is a specialist predator and completely preys on CoTS. We also consider the influence of environmental noises such that our system is more realistic to reflect coral reef dynamics.

The effects of harvesting and environmental noises have been investigated in Sects. 6.1 and 6.2, respectively. We can safely draw the following conclusions:

- (1) If no harvesting strategy is taken to control CoTS, then extinction is the fate of coral with the increased harvesting intensity of triton (Fig. 4). This is consistent with the results by Dulvy et al (2004), which suggests that predator removal by exploitation may allow outbreaks of CoTS indirectly resulting in cascading changes in ecosystem structure and function.
- (2) If no harvesting strategy is taken to control triton, then the three species can coexist cyclically (Fig. 3(c)) or reach an equilibrium (Fig. 3(d)). Only coral can survive with an increased harvesting of CoTS.
- (3) If both CoTS and triton are harvested, then multiple scenarios can happen: three species coexist cyclically, coexist stably over a long period of time, coral and CoTS coexist with the disappearance of triton, or only CoTS can survive (Fig. 7).
- (4) The three species of (2) will die out ultimately if  $r_1 < \sigma_{11}^2/2$  and  $r_2 - h_1 < \sigma_{21}^2/2$ . In the real world, this may happen when a serious disease or sudden weather change occurs. However, this is in sharp contrast to the dynamics of (1), which suggests that the stochastic system is more realistic than the deterministic system.

- (5) Coral will survive while CoTS and triton go extinct if  $r_1 > \sigma_{11}^2/2$  and  $\mu < 0$ . In this case, we notice that  $h_1$  can be smaller than  $r_2 + e_1 m_1 K_1 / (a_1 + K_1)$ . However, coral remains persistent while CoTS and triton become extinct ultimately in (1) provided that  $h_1$  is sufficiently large (Theorem 3). Therefore, the presence of environmental noises brings a difference to the population dynamics and significantly affects the dynamics of the system, especially it can lead to the extinction of species.
- (6) System (2) admits a unique stationary distribution if  $r_1 > \sigma_{11}^2/2$  and  $\mu > 0$ , where the sign of threshold  $\mu$  specifies whether or not CoTS and triton go extinct or persist in the long term, which implies that a weak white noise can guarantee the existence of stationary distribution (Fig. 10).

Moreover, the optimal solution of the control problem is either a bang-bang or a singular control, but cannot be a combination of them. The investment should not be above a maximal effort  $\bar{E}$ ; otherwise, it will result in economic loss. Considering the case of profit from harvesting, policymakers should recommend the optimal effort  $E^{**}$  such that it will guarantee the maximum profit and also ensure the sustainability of all species. According to Law of the People's Republic of China on the Protection of Wildlife, the state's key protected wild animals are classified into the first-grade and the second-grade protected wild animals. Triton has been a second-grade animal under state protection in China and illegal acquisition of national protected animal will be punished by law accordingly. The local government should forbid illegal fishing activities. Other countries having triton resources also should reduce the harvesting of triton to protect coral reefs.

The results in this paper are not exhaustive but rather a starting point of further investigation. An oceanic coral reef system based on the "predator removal hypothesis" (Endean 1969) is established to assess the synergistic effects of several key stressors. However, the mechanisms underlying CoTS outbreaks are so complicated that more trophic levels, more environmental factors, and other management strategies should be taken into account. According to the "terrestrial run-off hypothesis" (Birkeland 1982), the increase in certain nutrients in the ocean leads to the abundance of phytoplankton (Yan et al 2021). Therefore, the survival rate of CoTS larvae becomes higher. In particular, the mortality rates of CoTS at immature and mature stage are dramatically different. If CoTS population can be monitored as juveniles, then human interventions can be carried out once the density of juveniles approaches the critical value. From this point of view, it is reasonable to consider the system with stage structure of CoTS in coral-CoTS interaction. In addition, the environmental noise is assumed to be described by Gaussian white noises in this study, while in real-world application, the coral reef ecosystem is threatened by both coral diseases and ocean acidification but these natural disasters cannot be well described by white noises. It is significant to consider stochastic models driven by random fluctuations (e.g., Lévy noise and Markovian switching) except white noise and to investigate the effect of other type noises on the coral reef ecosystems.

In mathematics, the proof of the existence of a stationary distribution under  $r_1 > \sigma_{11}^2/2$  and  $\mu > 0$  still remains an open problem, though Fig. 10 indicates a stationary distribution of all the species. To our knowledge, there is a limitation of the

available mathematical technique. The methods of constructing a series of appropriate Lyapunov functions based on the positive equilibrium of (1) and utilizing the explicit density function of the solution to the corresponding one-dimensional stochastic differential equation are invalid to obtain the existence of a stationary distribution from the theoretical perspective. Future work includes developing new methods to obtain sufficient conditions for the existence of a unique ergodic stationary distribution. For stochastic dynamic model, a more important but challenging problem is to estimate the parameters in the model. If the key parameters can be determined or estimated from some collected data, especially  $\sigma$  being rarely estimated, it will be more convenient and more effective to well forecast and early warn the outbreaks of CoTS. All these issues are left as potential avenues for future research.

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**Data Availability** All data generated or analyzed during this study are included in this published article.

## Declarations

**Statements and Declarations** The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Appendix A: Proofs for Deterministic System

### A.1 Proof of Lemma 1

**Proof** According to the first equation of (1), we have

$$x(t) = x(0)\exp\left(\int_0^t \left[r_1 \left(1 - \frac{s}{K_1}\right) - \frac{m_1 y}{a_1 + s}\right] ds\right).$$

Similarly, we obtain

$$y(t) = y(0)\exp\left(\int_0^t \left[r_2 \left(1 - \frac{s}{K_2}\right) + \frac{e_1 m_1 x}{a_1 + x} - \frac{m_2 z}{a_2 + s} - h_1\right] ds\right)$$

and

$$z(t) = z(0)\exp\left(\int_0^t \left(\frac{e_2 m_2 y}{a_2 + y} - d - h_2\right) ds\right).$$

It is clear that  $x(t) > 0$ ,  $y(t) > 0$ , and  $z(t) > 0$  whenever  $x(0) > 0$ ,  $y(0) > 0$ , and  $z(0) > 0$ . Then any solution from the first quadrant of  $xyz$ -plane gives a positive solution. This completes the proof.  $\square$

### A.2 Proof of Theorem 1

**Proof** Define  $W = e_1e_2x + e_2y + z$ . Taking time derivative of  $W$  leads to

$$\begin{aligned} \frac{dW}{dt} + (d + h_2)W &= e_1e_2r_1x \left(1 - \frac{x}{K_1}\right) + e_2r_2y \left(1 - \frac{y}{K_2}\right) - e_2h_1y - dz - h_2z \\ &\quad + (d + h_2)(e_1e_2x + e_2y + z) \\ &\leq -\frac{e_1e_2r_1}{K_1} \left(x - \frac{K_1(r_1 + d + h_2)}{2r_1}\right)^2 + \frac{e_1e_2K_1(r_1 + d + h_2)^2}{4r_1} \\ &\quad - \frac{e_2r_2}{K_2} \left(y - \frac{K_2(r_2 + d + h_2)}{2r_2}\right)^2 + \frac{e_2K_2(r_2 + d + h_2)^2}{4r_2} \\ &\leq \frac{e_1e_2K_1(r_1 + d + h_2)^2}{4r_1} + \frac{e_2K_2(r_2 + d + h_2)^2}{4r_2} \\ &:= \mu. \end{aligned}$$

Due to the positivity of parameters and the nonnegativity of solutions, we obtain

$$0 \leq W(x, y, z) \leq \frac{\mu}{d + h_2}(1 - e^{-(d+h_2)t}) + W(x(0), y(0), z(0))e^{-(d+h_2)t}.$$

Taking the limit of the above inequality as  $t$  tends to  $\infty$ , we obtain

$$\limsup_{t \rightarrow \infty} W(x, y, z) \leq \frac{\mu}{d + h_2}.$$

Therefore, all solutions of (1) with initial values  $(x(0), y(0), z(0)) \in \mathbb{R}_+^3 Z$  are eventually confined to the region

$$\Omega = \left\{ (x, y, z) \in \mathbb{R}_+^3 : 0 \leq e_1e_2x + e_2y + z \leq \frac{\mu}{d + h_2} + 1 \right\}.$$

□

### A.3 Proof of Lemma 2

**Proof** When  $n = 1$ , it is obvious that the claim is valid. Assume that the claim holds for  $n = 2k - 1$ . Then, when  $n = 2k + 1$ , one has

$$\alpha(x) = (-1)^{2k+1}x^{2k+1} + p_{2k}x^{2k} + \dots + p_1x + p_0.$$

If  $\alpha(x) = 0$  has one positive root, then the claim is valid. If all the roots are negative, then there is a contradiction with  $p_0 > 0$ . Thus,  $\alpha(x) = 0$  has at least a pair of conjugate complex roots denoted by  $x_0 = a + bi$ ,  $\bar{x}_0 = a - bi$  with  $a \neq 0$ . Then,

$$\alpha(x) = (x - a - bi)(x - a + bi)\tilde{\alpha}(x) = (x^2 - 2ax + a^2 + b^2)\tilde{\alpha}(x),$$

where  $\tilde{\alpha}(x) = (-1)^{2k-1}x^{2k-1} + q_{2k-2}x^{2k-2} + \dots + q_1x + q_0$  and  $q_0(a^2 + b^2) = p_0 > 0$ . By the method of mathematical induction,  $\alpha(x)$  has at least one positive root if  $p_0 > 0$ . The proof is complete.  $\square$

### A.4 Proof of Theorem 2

**Proof** The local stability of equilibria is determined by computing the eigenvalues of the Jacobian matrix about each equilibrium. The Jacobian matrix of (1) at  $E_0$  is

$$J|_{E_0} = \begin{pmatrix} r_1 & 0 & 0 \\ 0 & r_2 - h_1 & 0 \\ 0 & 0 & -d - h_2 \end{pmatrix}.$$

The three eigenvalues of this matrix are

$$\lambda_1 = r_1, \quad \lambda_2 = r_2 - h_1, \quad \lambda_3 = -d - h_2.$$

Obviously,  $E_0 = (0, 0, 0)$  is unstable. The proof is complete.  $\square$

### A.5 Proof of Theorem 3

**Proof** The Jacobian matrix of (1) at  $E_x$  reads

$$J|_{E_x} = \begin{pmatrix} -r_1 & -\frac{m_1K_1}{a_1+K_1} & 0 \\ 0 & r_2 + \frac{e_1m_1K_1}{a_1+K_1} - h_1 & 0 \\ 0 & 0 & -d - h_2 \end{pmatrix}.$$

The three eigenvalues of this matrix are

$$\lambda_1 = -r_1, \quad \lambda_2 = r_2 + \frac{e_1m_1K_1}{a_1 + K_1} - h_1, \quad \lambda_3 = -d - h_2.$$

The equilibrium  $E_x = (K_1, 0, 0)$  is locally asymptotically stable if  $h_1 > r_2 + e_1m_1K_1/(a_1 + K_1)$ , otherwise it is a saddle point with stable manifold in  $x - z$  plane and unstable manifold in  $y$  direction. The proof is complete.  $\square$

### A.6 Proof of Theorem 4

**Proof** The Jacobian matrix of (1) at  $E_y$  takes the form

$$J|_{E_y} = \begin{pmatrix} r_1 - \frac{m_1y_2}{a_1} & 0 & 0 \\ \frac{e_1m_1y_2}{a_1} & -r_2 + h_1 & -\frac{m_2y_2}{a_2+y_2} \\ 0 & 0 & \frac{e_2m_2y_2}{a_2+y_2} - d - h_2 \end{pmatrix}.$$

Its eigenvalues are

$$\lambda_1 = r_1 - \frac{m_1 K_2 (r_2 - h_1)}{a_1 r_2}, \quad \lambda_2 = -(r_2 - h_1),$$

$$\lambda_3 = \frac{e_2 m_2 K_2 (r_2 - h_1) - [a_2 r_2 + K_2 (r_2 - h_1)](d + h_2)}{a_2 r_2 + K_2 (r_2 - h_1)}.$$

Then it is not difficult to show that all the eigenvalues of  $J|_{E_y}$  have negative real parts when (6) is satisfied, then  $E_y$  is locally asymptotically stable. The proof is complete.  $\square$

### A.7 Proof of Theorem 5

**Proof** By (3), one has

$$y_3 = \frac{(a_1 + x_3)(r_1 K_1 - r_1 x_3)}{m_1 K_1}.$$

Substituting the above equation into the second equation of (3) shows that  $x_3$  is a positive solution of the following equation:

$$-x^3 + (K_1 - 2a_1)x^2 + \hat{v}x + a_1^2 K_1 - \frac{a_1 m_1 K_1 K_2 (r_2 - h_1)}{r_1 r_2} = 0,$$

where  $\hat{v} = [m_1 K_1 K_2 (h_1 - r_2 - e_1 m_1) + a_1 r_1 r_2 (2K_1 - a_1)] / (r_1 r_2)$ . From Lemma 2, it follows that  $x_3$  is positive if (7) is satisfied.

The Jacobian matrix of (1) at  $E_{xy}$  writes

$$J|_{E_{xy}} = \begin{pmatrix} \frac{m_1 x_3 y_3}{(a_1 + x_3)^2} - \frac{r_1}{K_1} x_3 & -\frac{m_1 x_3}{a_1 + x_3} & 0 & 0 \\ \frac{e_1 m_1 a_1 y_3}{(a_1 + x_3)^2} & -\frac{r_2}{K_2} y_3 & -\frac{m_2 y_3}{a_2 + y_3} & 0 \\ 0 & 0 & \frac{e_2 m_2 y_3}{a_2 + y_3} & -d - h_2 \end{pmatrix}.$$

The characteristic equation of  $J|_{E_{xy}}$  of (1) is

$$\left[ \lambda^2 - (J_{11} + J_{22})\lambda + J_{11}J_{22} - J_{12}J_{21} \right] \left[ \lambda - \left( \frac{e_2 m_2 y_3}{a_2 + y_3} - d - h_2 \right) \right] = 0.$$

Then  $\lambda_1 < 0$ ,  $\lambda_2 < 0$ , and  $\lambda_3 < 0$  under the conditions of Theorem 5. Thus,  $E_{xy} = (x_3, y_3, 0)$  is locally asymptotically stable. The proof is complete.  $\square$

### A.8 Proof of Theorem 6

**Proof** By (4), one has

$$y_4 = \frac{a_2(d + h_2)}{e_2 m_2 - d - h_2}, \quad z_4 = \frac{(a_2 + y_4)[K_2(r_2 - h_1) - r_2 y_4]}{m_2 K_2}.$$

It is trivial to show that  $E_{yz} = (0, y_4, z_4)$  exists when (8) is satisfied.

The Jacobian matrix of (1) evaluated at  $E_{yz}$  reads

$$J |_{E_{yz}} = \begin{pmatrix} r_1 - \frac{m_1 y_4}{a_1} & 0 & 0 \\ \frac{e_1 m_1 y_4}{a_1} & \frac{m_2 y_4 z_4}{(a_2 + y_4)^2} - \frac{r_2}{K_2} y_4 - \frac{m_2 y_4}{a_2 + y_4} & 0 \\ 0 & \frac{e_2 m_2 a_2 z_4}{(a_2 + y_4)^2} & 0 \end{pmatrix}.$$

The characteristic equation of  $J |_{E_{yz}}$  is

$$\left[ \lambda^2 - \left( \frac{m_2 y_4 z_4}{(a_2 + y_4)^2} - \frac{r_2}{K_2} y_4 \right) \lambda + \frac{e_2 a_2 m_2^2 y_4 z_4}{(a_2 + y_4)^3} \right] \left[ \lambda - \left( r_1 - \frac{m_1 y_4}{a_1} \right) \right] = 0.$$

Then,  $\lambda_1 < 0$ ,  $\lambda_2 < 0$ , and  $\lambda_3 < 0$  when (9) holds. Therefore,  $E_{yz} = (0, y_4, z_4)$  is locally asymptotically stable. The proof is complete.  $\square$

### A.9 Proof of Theorem 7

**Proof** It is not difficult to show that  $y^* > 0$  and  $z^* > 0$  when (11) is satisfied. The existence of  $E_{xyz}(x^*, y^*, z^*)$  follows from direct calculation. The Jacobian matrix of (1) evaluated at  $E_{xyz}$  is

$$J |_{E_{xyz}} = \begin{pmatrix} \frac{m_1 x^* y^*}{(a_1 + x^*)^2} - \frac{r_1}{K_1} x^* & -\frac{m_1 x^*}{a_1 + x^*} & 0 \\ \frac{e_1 m_1 a_1 y^*}{(a_1 + x^*)^2} & \frac{m_2 y^* z^*}{(a_2 + y^*)^2} - \frac{r_2}{K_2} y^* - \frac{m_2 y^*}{a_2 + y^*} & 0 \\ 0 & \frac{e_2 m_2 a_2 z^*}{(a_2 + y^*)^2} & 0 \end{pmatrix}.$$

The characteristic equation of  $J |_{E_{xyz}}$  of (1) is

$$\lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3 = 0,$$

where

$$A_1 = -(J_{11} + J_{22}), \quad A_2 = J_{11} J_{22} - J_{23} J_{32} - J_{12} J_{21}, \quad A_3 = J_{11} J_{23} J_{32}. \quad (A1)$$

It is obvious that  $A_1 > 0$  and  $A_3 > 0$  when the conditions in Theorem 7 are satisfied. By the Routh-Hurwitz criterion, it follows that  $E_{xyz}$  is locally asymptotically stable if  $A_1 A_2 > A_3$ .

For the global asymptotic stability of  $E_{xyz}$ , consider the positive definite Lyapunov function

$$V(x, y, z) = l_1 \left( x - x^* - x^* \ln \frac{x}{x^*} \right) + \left( y - y^* - y^* \ln \frac{y}{y^*} \right) + l_2 \left( z - z^* - z^* \ln \frac{z}{z^*} \right),$$

where  $l_1$  and  $l_2$  are positive constants to be determined later.

By calculating the derivative of  $V(x, y, z)$  along the solutions of (1), we obtain

$$\begin{aligned} \frac{dV}{dt} = & l_1(x - x^*) \left[ r_1 \left( 1 - \frac{x}{K_1} \right) - \frac{m_1 y}{a_1 + x} - r_1 \left( 1 - \frac{x^*}{K_1} \right) + \frac{m_1 y^*}{a_1 + x^*} \right] \\ & + (y - y^*) \left[ r_2 \left( 1 - \frac{y}{K_2} \right) + \frac{e_1 m_1 x}{a_1 + x} \right. \\ & \left. - \frac{m_2 z}{a_2 + y} - r_2 \left( 1 - \frac{y^*}{K_2} \right) - \frac{e_1 m_1 x^*}{a_1 + x^*} + \frac{m_2 z^*}{a_2 + y^*} \right] \\ & + l_2(z - z^*) \left( \frac{e_2 m_2 y}{a_2 + y} - \frac{e_2 m_2 y^*}{a_2 + y^*} \right). \end{aligned}$$

After simplification,

$$\begin{aligned} \frac{dV}{dt} = & -l_1 \left[ \frac{r_1}{K_1} - \frac{m_1 y^*}{(a_1 + x)(a_1 + x^*)} \right] (x - x^*)^2 \\ & - \left[ \frac{r_2}{K_2} - \frac{m_2 z^*}{(a_2 + y)(a_2 + y^*)} \right] (y - y^*)^2 \\ & + \left[ \frac{e_1 m_1 a_1}{(a_1 + x)(a_1 + x^*)} - \frac{l_1 m_1 a_1}{(a_1 + x)(a_1 + x^*)} \right. \\ & \left. - \frac{l_1 m_1 x^*}{(a_1 + x)(a_1 + x^*)} \right] (x - x^*)(y - y^*) \\ & + \left[ \frac{l_2 e_2 m_2 a_2}{(a_2 + y)(a_2 + y^*)} \right. \\ & \left. - \frac{m_2 a_2}{(a_2 + y)(a_2 + y^*)} - \frac{m_2 y^*}{(a_2 + y)(a_2 + y^*)} \right] (y - y^*)(z - z^*). \tag{A2} \end{aligned}$$

Set

$$l_1 = \frac{e_1 a_1}{a_1 + x^*}, \quad l_2 = \frac{a_2 + y^*}{e_2 a_2} \tag{A3}$$

such that the right hand side of (A2) can be written as  $-X^T D X$ , where  $X^T = (x - x^*, y - y^*, z - z^*)$  and the symmetric matrix  $D$  is given by

$$D = \begin{pmatrix} \frac{l_1 r_1}{K_1} - \frac{l_1 m_1 y^*}{(a_1 + x)(a_1 + x^*)} & 0 & 0 \\ 0 & \frac{r_2}{K_2} - \frac{m_2 z^*}{(a_2 + y)(a_2 + y^*)} & 0 \\ 0 & 0 & 0 \end{pmatrix}.$$

Then  $dV/dt < 0$  if and only if the symmetric matrix  $D$  is positive definite, which is equivalent to (12). Therefore,  $E_{xyz}$  is globally asymptotically stable. The proof is complete. □



## Appendix B: Proofs for Optimal Harvesting

### B.1 Proof of Theorem 8

**Proof** The bionomic equilibrium solves the system of algebraic equations

$$\begin{cases} r_1x \left(1 - \frac{x}{K_1}\right) - \frac{m_1xy}{a_1 + x} = 0, \\ r_2y \left(1 - \frac{y}{K_2}\right) + \frac{e_1m_1xy}{a_1 + x} - \frac{m_2yz}{a_2 + y} - q_1Ey = 0, \\ \frac{e_2m_2yz}{a_2 + y} - dz - q_2Ez = 0, \\ (p_1q_1y + p_2q_2z - c)E = 0. \end{cases} \tag{B4}$$

Define

$$\bar{\Omega} = \left\{ (x, y, z, E) \mid 0 \leq x \leq K_1, \frac{a_2d}{e_2m_2 - d} \leq y \leq \frac{c}{p_1q_1}, \right. \\ \left. 0 \leq z \leq \frac{c}{p_2q_2}, 0 \leq E \leq \frac{e_2m_2c}{q_2(c + a_2p_1q_1)} \right\}.$$

Obviously,  $\bar{\Omega}$  is a positive invariant set of (B4). From the first equation, one has

$$\bar{y} = \frac{r_1}{m_1} \left(1 - \frac{\bar{x}}{K_1}\right) (a_1 + \bar{x}).$$

Substituting  $\bar{y}$  into the third equation produces

$$\bar{E} = \frac{1}{q_2} \frac{e_2m_2 \frac{r_1}{m_1} \left(1 - \frac{\bar{x}}{K_1}\right) (a_1 + \bar{x})}{a_2 + \frac{r_1}{m_1} \left(1 - \frac{\bar{x}}{K_1}\right) (a_1 + \bar{x})} - \frac{d}{q_2},$$

where  $\bar{E} > 0$  since  $d < \frac{e_2m_2\bar{y}}{a_2 + \bar{y}}$ . Similarly, we have

$$\bar{z} = \frac{c}{p_2q_2} - \frac{p_1q_1r_1}{p_2q_2m_1} \left(1 - \frac{\bar{x}}{K_1}\right) (a_1 + \bar{x}),$$

where  $\bar{z} > 0$  since  $c > p_1q_1\bar{y}$ . According to the second equation of (B4), we can see  $\bar{x}$  is a positive root of the following equation

$$r_2 \left[ 1 - \frac{r_1}{m_1K_2} \left(1 - \frac{x}{K_1}\right) (a_1 + x) \right] + \frac{e_1m_1x}{a_1 + x} \\ - \frac{m_2 \left[ \frac{c}{p_2q_2} - \frac{p_1q_1r_1}{p_2q_2m_1} \left(1 - \frac{x}{K_1}\right) (a_1 + x) \right]}{a_2 + \frac{r_1}{m_1} \left(1 - \frac{x}{K_1}\right) (a_1 + x)} = 0$$

$$-\frac{q_1}{q_2} \frac{e_2 m_2 \frac{r_1}{m_1} \left(1 - \frac{x}{K_1}\right) (a_1 + x)}{a_2 + \frac{r_1}{m_1} \left(1 - \frac{x}{K_1}\right) (a_1 + x)} + \frac{dq_1}{q_2} = 0,$$

which can be simplified by

$$-\frac{r_1^2 r_2}{m_1^2 K_1^2 K_2} x^5 + \Theta_1 x^4 + \Theta_2 x^3 + \Theta_3 x^2 + \Theta_4 x + \Theta_0 = 0, \tag{B5}$$

where

$$\Theta_0 = a_1 \left( a_2 + \frac{a_1 r_1}{m_1} \right) \left( r_2 - \frac{a_1 r_1 r_2}{m_1 K_2} + \frac{dq_1}{q_2} \right) + \frac{a_1 r_1 m_2 q_1}{m_1 q_2} \left( \frac{p_1}{p_2} - e_2 - \frac{m_1 c}{a_1 r_1 q_1 p_2} \right)$$

must be a positive constant under the condition  $r_1 < \frac{m_1 K_2}{a_1}$  and  $\frac{p_1}{p_2} > e_2 + \frac{m_1 c}{a_1 r_1 q_1 p_2}$ . From Lemma 2, it follows that there exists at least one positive root  $\bar{x}$ . Therefore, the positive bionomic equilibrium exists if (13) is satisfied. The proof is complete.  $\square$

### B.2 Proof of Theorem 9

**Proof** By Pontryagin’s maximum principle (1987), the adjoint equations read

$$\frac{d\chi_1}{dt} = -\frac{\partial \mathcal{F}}{\partial x}, \quad \frac{d\chi_2}{dt} = -\frac{\partial \mathcal{F}}{\partial y}, \quad \frac{d\chi_3}{dt} = -\frac{\partial \mathcal{F}}{\partial z}.$$

Consider the equilibrium of (B4), then the adjoint equations reduce to

$$\frac{d\chi_1}{dt} = \left( \frac{r_1}{K_1} x - \frac{m_1 x y}{(a_1 + x)^2} \right) \chi_1 - \frac{e_1 m_1 a_1 y}{(a_1 + x)^2} \chi_2, \tag{B6}$$

$$\begin{aligned} \frac{d\chi_2}{dt} &= \frac{m_1 x}{a_1 + x} \chi_1 \\ &+ \left( \frac{r_2}{K_2} y - \frac{m_2 y z}{(a_2 + y)^2} \right) \chi_2 - \frac{e_2 m_2 a_2 z}{(a_2 + y)^2} \chi_3 \\ &- (\xi_1 e^{-\delta_v t} + \xi_2 e^{-\delta_u t}) p_1 q_1 E, \end{aligned} \tag{B7}$$

$$\frac{d\chi_3}{dt} = \frac{m_2 y}{a_2 + y} \chi_2 - (\xi_1 e^{-\delta_v t} + \xi_2 e^{-\delta_u t}) p_2 q_2 E. \tag{B8}$$

Then

$$\begin{aligned} &\chi_2'' - \left( \frac{r_1}{K_1} x - \frac{m_1 x y}{(a_1 + x)^2} \right)' \chi_2 \\ &= - \left( \frac{r_1}{K_1} x - \frac{m_1 x y}{(a_1 + x)^2} \right) \left( \frac{r_2}{K_2} y - \frac{m_2 y z}{(a_2 + y)^2} \right) \chi_2 \end{aligned}$$

$$\begin{aligned}
 &+ \left( \frac{r_1}{K_1}x - \frac{m_1xy}{(a_1+x)^2} \right) \frac{e_2m_2a_2z}{(a_2+y)^2} \chi_3 \\
 &+ \left( \frac{r_1}{K_1}x - \frac{m_1xy}{(a_1+x)^2} \right) (\xi_1e^{-\delta_v t} + \xi_2e^{-\delta_u t}) p_1q_1E - \frac{m_1x}{a_1+x} \frac{e_1m_1a_1y}{(a_1+x)^2} \chi_2 \\
 &+ \left( \frac{r_2}{K_2}y - \frac{m_2yz}{(a_2+y)^2} \right) \chi_2' - \frac{e_2m_2a_2z}{(a_2+y)^2} \left( \frac{m_2y}{a_2+y} \chi_2 - (\xi_1e^{-\delta_v t} + \xi_2e^{-\delta_u t}) p_2q_2E \right).
 \end{aligned}
 \tag{B9}$$

Combining (17) with (B9), one has

$$\chi_2'' + Q_1\chi_2' + Q_2\chi_2 = \mathcal{M}e^{-\delta_v t} + \mathcal{N}e^{-\delta_u t},
 \tag{B10}$$

where

$$\begin{aligned}
 Q_1 &= - \left( \frac{r_1}{K_1}x - \frac{m_1xy}{(a_1+x)^2} \right) - \left( \frac{r_2}{K_2}y - \frac{m_2yz}{(a_2+y)^2} \right), \\
 Q_2 &= \left( \frac{r_1}{K_1}x - \frac{m_1xy}{(a_1+x)^2} \right) \left( \frac{r_2}{K_2}y - \frac{m_2yz}{(a_2+y)^2} \right) \\
 &\quad + \left( \frac{r_1}{K_1}x - \frac{m_1xy}{(a_1+x)^2} \right) \frac{e_2m_2a_2z}{(a_2+y)^2} \frac{q_1y}{q_2z} \\
 &\quad + \frac{m_1x}{a_1+x} \frac{e_1m_1a_1y}{(a_1+x)^2} + \frac{e_2m_2a_2z}{(a_2+y)^2} \frac{m_2y}{a_2+y} \\
 \mathcal{M} &= \left( \frac{r_1}{K_1}x - \frac{m_1xy}{(a_1+x)^2} \right) \frac{e_2m_2a_2z}{(a_2+y)^2} \frac{\xi_1(p_1q_1y + p_2q_2z - c)}{q_2z} \\
 &\quad + \left( \frac{r_1}{K_1}x - \frac{m_1xy}{(a_1+x)^2} \right) \xi_1 p_1q_1E + \frac{e_2m_2a_2z}{(a_2+y)^2} \xi_1 p_2q_2E, \\
 \mathcal{N} &= \left( \frac{r_1}{K_1}x - \frac{m_1xy}{(a_1+x)^2} \right) \frac{e_2m_2a_2z}{(a_2+y)^2} \frac{\xi_2(p_1q_1y + p_2q_2z - c)}{q_2z} \\
 &\quad + \left( \frac{r_1}{K_1}x - \frac{m_1xy}{(a_1+x)^2} \right) \xi_2 p_1q_1E + \frac{e_2m_2a_2z}{(a_2+y)^2} \xi_2 p_2q_2E.
 \end{aligned}$$

This leads to the solution

$$\chi_2 = \Xi_1 e^{\Delta_1 t} + \Xi_2 e^{\Delta_2 t} + \frac{\mathcal{M}}{\delta_v^2 - Q_1\delta_v + Q_2} e^{-\delta_v t} + \frac{\mathcal{N}}{\delta_u^2 - Q_1\delta_u + Q_2} e^{-\delta_u t},$$

where  $\Xi_1$  and  $\Xi_2$  are constants of integration,  $\Delta_1$  and  $\Delta_2$  are the roots of the auxiliary equation  $\Delta^2 + Q_1\Delta + Q_2 = 0$ . Imposing the transverse condition  $\chi_2(t) \rightarrow 0$  as  $t \rightarrow \infty$  leads to  $\Xi_1 = \Xi_2 = 0$ . Then,

$$\chi_2 = \frac{\mathcal{M}}{\delta_v^2 - Q_1\delta_v + Q_2} e^{-\delta_v t} + \frac{\mathcal{N}}{\delta_u^2 - Q_1\delta_u + Q_2} e^{-\delta_u t}.$$

Substituting  $\chi_2$  into (17) reaches

$$\chi_3 = \left( \frac{p_1q_1y + p_2q_2z - c}{q_2z} \xi_1 - \frac{q_1y}{q_2z} \frac{\mathcal{M}}{\delta_v^2 - Q_1\delta_v + Q_2} \right) e^{-\delta_v t} + \left( \frac{p_1q_1y + p_2q_2z - c}{q_2z} \xi_2 - \frac{q_1y}{q_2z} \frac{\mathcal{N}}{\delta_u^2 - Q_1\delta_u + Q_2} \right) e^{-\delta_u t}.$$

Similarly,

$$\chi_1'' + \tilde{Q}_1\chi_1' + \tilde{Q}_2\chi_1 = \tilde{\mathcal{M}}e^{-\delta_v t} + \tilde{\mathcal{N}}e^{-\delta_u t}, \tag{B11}$$

where

$$\begin{aligned} \tilde{Q}_1 &= \frac{m_1xy}{(a_1+x)^2} - \frac{r_1}{K_1}x, & \tilde{Q}_2 &= \frac{e_1m_1^2a_1xy}{(a_1+x)^3}, \\ \tilde{\mathcal{M}} &= -\frac{e_1m_1a_1y}{(a_1+x)^2} \left( \frac{r_2}{K_2}y - \frac{m_2yz}{(a_2+y)^2} \right) \frac{\mathcal{M}}{\delta_v^2 - Q_1\delta_v + Q_2} + \frac{e_1m_1a_1y}{(a_1+x)^2} p_1q_1E\xi_1 \\ &\quad + \frac{e_1m_1a_1y}{(a_1+x)^2} \frac{e_2m_2a_2z}{(a_2+y)^2} \left( \frac{p_1q_1y + p_2q_2z - c}{q_2z} \xi_1 - \frac{q_1y}{q_2z} \frac{\mathcal{M}}{\delta_v^2 - Q_1\delta_v + Q_2} \right), \\ \tilde{\mathcal{N}} &= -\frac{e_1m_1a_1y}{(a_1+x)^2} \left( \frac{r_2}{K_2}y - \frac{m_2yz}{(a_2+y)^2} \right) \frac{\mathcal{N}}{\delta_u^2 - Q_1\delta_u + Q_2} + \frac{e_1m_1a_1y}{(a_1+x)^2} p_1q_1E\xi_2 \\ &\quad + \frac{e_1m_1a_1y}{(a_1+x)^2} \frac{e_2m_2a_2z}{(a_2+y)^2} \left( \frac{p_1q_1y + p_2q_2z - c}{q_2z} \xi_2 - \frac{q_1y}{q_2z} \frac{\mathcal{N}}{\delta_u^2 - Q_1\delta_u + Q_2} \right). \end{aligned}$$

$\chi_1$  can be simplified as

$$\chi_1 = \frac{\tilde{\mathcal{M}}}{\delta_v^2 - \tilde{Q}_1\delta_v + \tilde{Q}_2} e^{-\delta_v t} + \frac{\tilde{\mathcal{N}}}{\delta_u^2 - \tilde{Q}_1\delta_u + \tilde{Q}_2} e^{-\delta_u t}.$$

It is not difficult to find that the shadow prices  $\chi_1(t)e^{\delta_u t}$ ,  $\chi_2(t)e^{\delta_u t}$ , and  $\chi_3(t)e^{\delta_u t}$  are bounded and constant over time in optimal equilibrium when they satisfy the transversality condition at  $\infty$  (Sadhukhan et al 2010).

Substituting the values of  $\chi_2, \chi_3$  into (B8), one obtains

$$\begin{aligned} E &= \left\{ \left[ \delta_v \left( \frac{p_1q_1y + p_2q_2z - c}{q_2z} \xi_1 - \frac{q_1y}{q_2z} \frac{\mathcal{M}}{\delta_v^2 - Q_1\delta_v + Q_2} \right) + \frac{m_2y}{a_2+y} \frac{\mathcal{M}}{\delta_v^2 - Q_1\delta_v + Q_2} \right] e^{-\delta_v t} \right. \\ &\quad \left. + \left[ \delta_u \left( \frac{p_1q_1y + p_2q_2z - c}{q_2z} \xi_2 - \frac{q_1y}{q_2z} \frac{\mathcal{N}}{\delta_u^2 - Q_1\delta_u + Q_2} \right) + \frac{m_2y}{a_2+y} \frac{\mathcal{N}}{\delta_u^2 - Q_1\delta_u + Q_2} \right] e^{-\delta_u t} \right\} \\ &\quad 1/\left[ (\xi_1 e^{-\delta_v t} + \xi_2 e^{-\delta_u t}) p_2q_2 \right]. \tag{B12} \end{aligned}$$

The optimal equilibrium solution  $(x^{**}, y^{**}, z^{**}, E^{**})$  of the control problem can be obtained by solving steady state equations together with (B12). Moreover, the maximum net present revenue is

$$\begin{aligned} \mathcal{J}(y^{**}, z^{**}, E^{**}) &= \int_0^\infty e^{-\tilde{\delta}t} (p_1q_1y^{**} + p_2q_2z^{**} - c)E^{**} dt \\ &= \frac{(p_1q_1y^{**} + p_2q_2z^{**} - c)E^{**}}{\tilde{\delta}}. \end{aligned}$$

The proof is complete. □

## Appendix C: Proofs for Stochastic System

### C.1 Proof of Theorem 10

**Proof** Since (2) has a unique local solution  $(x(t), y(t), z(t)) \in \mathbb{R}_+^3$  on  $[0, \tau_e)$  a.s., where  $\tau_e$  is the explosion time. In order to show that this solution is global, i.e.,  $\tau_e = \infty$  a.s., let  $n_0 \geq 0$  be sufficiently large such that  $x_0, y_0,$  and  $z_0$  are lying within the interval  $[1/n_0, n_0]$ . For each integer  $n \geq n_0$ , define the stopping time as

$$\tau_n = \inf \left\{ t \in [0, \tau_e) : \min\{x(t), y(t), z(t)\} \leq \frac{1}{n} \text{ or } \max\{x(t), y(t), z(t)\} \geq n \right\}.$$

Obviously,  $\tau_n$  is increasing as  $n \rightarrow \infty$ . Set  $\tau_\infty = \lim_{n \rightarrow \infty} \tau_n$ , whence  $\tau_\infty \leq \tau_e$  a.s. Hence, it only needs to prove that  $\tau_\infty = \infty$  a.s. It can be proved by contradiction arguments. Assume that the statement is not true, then there exist a pair of constants  $T > 0$  and  $\kappa \in (0, 1)$  such that  $\mathbb{P}\{\tau_\infty \leq T\} > \kappa$ . Whence there exists an integer  $n_1 \geq n_0$  such that  $\mathbb{P}\{\tau_n \leq T\} \geq \kappa, n \geq n_1$ . Define a  $C^2$ -function  $V: \mathbb{R}_+^3 \rightarrow \mathbb{R}_+$  by

$$\begin{aligned} V(x, y, z) &= x^\theta - \ln x - \frac{1}{\theta} \left( 1 - \ln \frac{1}{\theta} \right) + y^\theta - \ln y - \frac{1}{\theta} \left( 1 - \ln \frac{1}{\theta} \right) \\ &\quad + z^\theta - \ln z - \frac{1}{\theta} \left( 1 - \ln \frac{1}{\theta} \right) \end{aligned}$$

with  $0 < \theta < 1$ . The nonnegativity of  $V$  follows from  $u^\theta - \ln u - (1 - \ln(1/\theta))/\theta \geq 0, u \geq 0$ . By applying Itô's formula, one has

$$\begin{aligned} \mathcal{L}(x^\theta) &= \theta r_1 x^\theta \left( 1 - \frac{x}{K_1} \right) - \frac{m_1 \theta x^\theta y}{a_1 + x} + \frac{1}{2} \theta (\theta - 1) x^\theta (\sigma_{11} + \sigma_{12} x)^2, \\ \mathcal{L}(y^\theta) &= \theta r_2 y^\theta \left( 1 - \frac{y}{K_2} \right) + \frac{\theta e_1 m_1 x y^\theta}{a_1 + x} - \frac{\theta m_2 y^\theta z}{a_2 + y} \\ &\quad - \theta h_1 y^\theta + \frac{1}{2} \theta (\theta - 1) y^\theta (\sigma_{21} + \sigma_{22} y)^2, \\ \mathcal{L}(z^\theta) &= \frac{\theta e_2 m_2 z^\theta y}{a_2 + y} - \theta d z^\theta - \theta h_2 z^\theta + \frac{1}{2} \theta (\theta - 1) z^\theta (\sigma_{31} + \sigma_{32} z)^2, \\ \mathcal{L}(\ln x) &= r_1 \left( 1 - \frac{x}{K_1} \right) - \frac{m_1 y}{a_1 + x} - \frac{1}{2} (\sigma_{11} + \sigma_{12} x)^2, \\ \mathcal{L}(\ln y) &= r_2 \left( 1 - \frac{y}{K_2} \right) + \frac{e_1 m_1 x}{a_1 + x} - \frac{m_2 z}{a_2 + y} - h_1 - \frac{1}{2} (\sigma_{21} + \sigma_{22} y)^2, \\ \mathcal{L}(\ln z) &= \frac{e_2 m_2 y}{a_2 + y} - d - h_2 - \frac{1}{2} (\sigma_{31} + \sigma_{32} z)^2. \end{aligned}$$

Then, by Lemma 3,

$$\begin{aligned}
 \mathcal{L}V &= \theta r_1 x^\theta \left(1 - \frac{x}{K_1}\right) - \frac{m_1 \theta x^\theta y}{a_1 + x} + \frac{\theta(\theta - 1)}{2} x^\theta (\sigma_{11} + \sigma_{12}x)^2 - r_1 \left(1 - \frac{x}{K_1}\right) \\
 &\quad + \frac{m_1 y}{a_1 + x} + \frac{1}{2} (\sigma_{11} + \sigma_{12}x)^2 + \theta r_2 y^\theta \left(1 - \frac{y}{K_2}\right) + \frac{\theta e_1 m_1 x y^\theta}{a_1 + x} - \frac{\theta m_2 y^\theta z}{a_2 + y} \\
 &\quad - \theta h_1 y^\theta + \frac{\theta(\theta - 1)}{2} y^\theta (\sigma_{21} + \sigma_{22}y)^2 - r_2 \left(1 - \frac{y}{K_2}\right) - \frac{e_1 m_1 x}{a_1 + x} + \frac{m_2 z}{a_2 + y} \\
 &\quad + h_1 + \frac{1}{2} (\sigma_{21} + \sigma_{22}y)^2 + \frac{\theta e_2 m_2 z^\theta y}{a_2 + y} - \theta d z^\theta - \theta h_2 z^\theta \\
 &\quad + \frac{\theta(\theta - 1)}{2} z^\theta (\sigma_{31} + \sigma_{32}z)^2 - \frac{e_2 m_2 y}{a_2 + y} + d + h_2 + \frac{1}{2} (\sigma_{31} + \sigma_{32}z)^2 \\
 &\leq -\frac{\theta(1 - \theta)}{2} \sigma_{12}^2 x^{\theta+2} + \frac{1}{2} \sigma_{12}^2 x^2 + \left(\frac{r_1}{K_1} + \sigma_{11}\sigma_{12}\right) x + \theta r_1 x^\theta \\
 &\quad - \frac{\theta(1 - \theta)}{2} \sigma_{22}^2 y^{\theta+2} + \frac{1}{2} \sigma_{22}^2 y^2 + \left(\frac{r_2}{K_2} + \frac{m_1}{a_1} + \sigma_{21}\sigma_{22}\right) y + (\theta r_2 + \theta e_1 m_1) y^\theta \\
 &\quad - \frac{\theta(1 - \theta)}{2} \sigma_{32}^2 z^{\theta+2} + \frac{1}{2} \sigma_{32}^2 z^2 + \left(\frac{m_2}{a_2} + \sigma_{31}\sigma_{32}\right) z + \theta e_2 m_2 z^\theta \\
 &\quad + d + h_1 + h_2 + \frac{1}{2} \sigma_{11}^2 + \frac{1}{2} \sigma_{21}^2 + \frac{1}{2} \sigma_{31}^2 \\
 &\leq \rho_1 + \rho_2 + \rho_3 + d + h_1 + h_2 + \frac{1}{2} \sigma_{11}^2 + \frac{1}{2} \sigma_{21}^2 + \frac{1}{2} \sigma_{31}^2 := \rho,
 \end{aligned}$$

where

$$\begin{aligned}
 \rho_1 &= \sup_{(x,y,z) \in \mathbb{R}_+^3} \left\{ -\frac{\theta(1-\theta)}{2} \sigma_{12}^2 x^{\theta+2} + \frac{\sigma_{12}^2}{2} x^2 + \left(\frac{r_1}{K_1} + \sigma_{11}\sigma_{12}\right) x + \theta r_1 x^\theta \right\}, \\
 \rho_2 &= \sup_{(x,y,z) \in \mathbb{R}_+^3} \left\{ -\frac{\theta(1-\theta)}{2} \sigma_{22}^2 y^{\theta+2} + \frac{\sigma_{22}^2}{2} y^2 + \left(\frac{r_2}{K_2} + \frac{m_1}{a_1} + \sigma_{21}\sigma_{22}\right) y + (\theta r_2 + \theta e_1 m_1) y^\theta \right\}, \\
 \rho_3 &= \sup_{(x,y,z) \in \mathbb{R}_+^3} \left\{ -\frac{\theta(1-\theta)}{2} \sigma_{32}^2 z^{\theta+2} + \frac{\sigma_{32}^2}{2} z^2 + \left(\frac{m_2}{a_2} + \sigma_{31}\sigma_{32}\right) z + \theta e_2 m_2 z^\theta \right\},
 \end{aligned}$$

and  $\rho$  is a positive constant being independent of  $x, y, z$ , and  $t$ . Consequently,

$$\begin{aligned}
 dV &\leq \rho dt + (\theta x^\theta - 1)(\sigma_{11} + \sigma_{12}x)dB_1(t) \\
 &\quad + (\theta y^\theta - 1)(\sigma_{21} + \sigma_{22}y)dB_2(t) + (\theta z^\theta - 1)(\sigma_{31} + \sigma_{32}z)dB_3(t).
 \end{aligned}$$

Integrating it from 0 to  $\tau_n \wedge T$  and taking expectation produces

$$\mathbb{E}(V(x(\tau_n \wedge T), y(\tau_n \wedge T), z(\tau_n \wedge T))) \leq V(x_0, y_0, z_0) + \rho T.$$

Set  $\Omega_n = \{\omega \in \Omega : \tau_n = \tau_n(\omega) \leq T\}$ , then  $\mathbb{P}(\Omega_n) \geq \kappa$ , and, for any  $\omega \in \Omega_n, x(\tau_n, \omega), y(\tau_n, \omega)$  or  $z(\tau_n, \omega)$ , equals either  $n$  or  $1/n$ . Hence,

$$V(x_0, y_0, z_0) + \rho T \geq \mathbb{E}(I_{\Omega_n} V(x(\tau_n), y(\tau_n), z(\tau_n))) \geq \rho \min \left\{ n^\theta - \ln n - \frac{1}{\theta} \left( 1 - \ln \frac{1}{\theta} \right), n^{-\theta} + \ln n - \frac{1}{\theta} \left( 1 - \ln \frac{1}{\theta} \right) \right\},$$

where  $I_{\Omega_n}$  denotes the indicator function of  $\Omega_n$ . Let  $n \rightarrow \infty$ , then there is a contradiction

$$\infty > V(x_0, y_0, z_0) + \rho T = \infty.$$

Therefore,  $\tau_\infty = \infty$ . The proof is complete. □

**C.2 Proof of Theorem 11**

**Proof** Define

$$\tilde{V}(x, y, z) = (e_1 e_2 x + e_2 y + z)^{\tilde{\theta}}.$$

By the generalized Itô’s formula, one has

$$\begin{aligned} d\tilde{V} &= \mathcal{L}\tilde{V}dt + e_1 e_2 \tilde{\theta} (e_1 e_2 x + e_2 y + z)^{\tilde{\theta}-1} x (\sigma_{11} + \sigma_{12} x) dB_1(t) \\ &\quad + e_2 \tilde{\theta} (e_1 e_2 x + e_2 y + z)^{\tilde{\theta}-1} y (\sigma_{21} + \sigma_{22} y) dB_2(t) \\ &\quad + \tilde{\theta} (e_1 e_2 x + e_2 y + z)^{\tilde{\theta}-1} z (\sigma_{31} + \sigma_{32} z) dB_3(t), \end{aligned}$$

where

$$\begin{aligned} \mathcal{L}\tilde{V} &= \tilde{\theta} (e_1 e_2 x + e_2 y + z)^{\tilde{\theta}-1} \left( e_1 e_2 r_1 x \left( 1 - \frac{x}{K_1} \right) + e_2 r_2 y \left( 1 - \frac{y}{K_2} \right) \right. \\ &\quad \left. - e_2 h_1 y - (d + h_2) z \right) \\ &\quad - \frac{\tilde{\theta} (1 - \tilde{\theta})}{2} (e_1 e_2 x + e_2 y + z)^{\tilde{\theta}-2} \\ &\quad \times \left( [e_1 e_2 x (\sigma_{11} + \sigma_{12} x)]^2 + [e_2 y (\sigma_{21} + \sigma_{22} y)]^2 + [z (\sigma_{31} + \sigma_{32} z)]^2 \right). \end{aligned}$$

For any  $0 < \beta < d + h_2$ , applying Itô’s formula to  $e^{\beta t} \tilde{V}$  leads to

$$\begin{aligned} &e^{\beta t} (e_1 e_2 x(t) + e_2 y(t) + z(t))^{\tilde{\theta}} \\ &= (e_1 e_2 x_0 + e_2 y_0 + z_0)^{\tilde{\theta}} + \int_0^t e^{\beta s} G(\tilde{X}(s)) ds \\ &\quad + e_1 e_2 \tilde{\theta} \int_0^t e^{\beta s} ((e_1 e_2 x(s) + e_2 y(s) + z(s))^{\tilde{\theta}-1} x(s) (\sigma_{11} + \sigma_{12} x(s))) dB_1(s) \end{aligned}$$

$$\begin{aligned}
& + e_2 \tilde{\theta} \int_0^t e^{\beta s} ((e_1 e_2 x(s) + e_2 y(s) + z(s))^{\tilde{\theta}-1} y(s) (\sigma_{21} + \sigma_{22} y(s))) dB_2(s) \\
& + \tilde{\theta} \int_0^t e^{\beta s} ((e_1 e_2 x(s) + e_2 y(s) + z(s))^{\tilde{\theta}-1} z(s) (\sigma_{31} + \sigma_{32} z(s))) dB_3(s),
\end{aligned}$$

where

$$\begin{aligned}
G(\tilde{X}) &= \beta (e_1 e_2 x + e_2 y + z)^{\tilde{\theta}} + \tilde{\theta} (e_1 e_2 x + e_2 y + z)^{\tilde{\theta}-1} \\
&\quad \times \left( e_1 e_2 r_1 x \left( 1 - \frac{x}{K_1} \right) + e_2 r_2 y \left( 1 - \frac{y}{K_2} \right) - e_2 h_1 y - (d + h_2) z \right) \\
&\quad - \frac{\tilde{\theta}(1-\tilde{\theta})}{2} (e_1 e_2 x + e_2 y + z)^{\tilde{\theta}-2} \\
&\quad \times ([e_1 e_2 x (\sigma_{11} + \sigma_{12} x)]^2 + [e_2 y (\sigma_{21} + \sigma_{22} y)]^2 + [z (\sigma_{31} + \sigma_{32} z)]^2).
\end{aligned}$$

On the one hand,

$$\begin{aligned}
& [e_1 e_2 x (\sigma_{11} + \sigma_{12} x)]^2 + [e_2 y (\sigma_{21} + \sigma_{22} y)]^2 + [z (\sigma_{31} + \sigma_{32} z)]^2 \\
& \geq (e_1 e_2 \sigma_{12})^2 x^4 + (e_2 \sigma_{22})^2 y^4 + \sigma_{32}^2 z^4 \\
& \geq \min\{(e_1 e_2 \sigma_{12})^2, (e_2 \sigma_{22})^2, \sigma_{32}^2\} (x^4 + y^4 + z^4);
\end{aligned}$$

on the other side,

$$\begin{aligned}
(e_1 e_2 x + e_2 y + z)^4 &\leq 3^3 [(e_1 e_2 x)^4 + (e_2 y)^4 + z^4] \\
&\leq 3^3 \max\{(e_1 e_2)^4, e_2^4, 1\} (x^4 + y^4 + z^4) \\
&\leq 3^3 (x^4 + y^4 + z^4),
\end{aligned}$$

where the following Hölder inequality has been used

$$\left| \sum_{i=1}^k p_i \right|^n \leq k^{n-1} \sum_{i=1}^k |p_i|^n.$$

Hence,

$$\begin{aligned}
G(\tilde{X}) &\leq \beta (e_1 e_2 x + e_2 y + z)^{\tilde{\theta}} + \tilde{\theta} (e_1 e_2 x + e_2 y + z)^{\tilde{\theta}-1} \\
&\quad \times \left( e_1 e_2 r_1 x \left( 1 - \frac{x}{K_1} \right) + e_2 r_2 y \left( 1 - \frac{y}{K_2} \right) - e_2 h_1 y - (d + h_2) z \right) \\
&\quad - \frac{\tilde{\theta}(1-\tilde{\theta})}{54} (e_1 e_2 x + e_2 y + z)^{\tilde{\theta}+2} \min\{(e_1 e_2 \sigma_{12})^2, (e_2 \sigma_{22})^2, \sigma_{32}^2\},
\end{aligned}$$



which is bounded, say by  $\mathcal{G}^*(\tilde{\theta})$ . Then

$$\begin{aligned} &\mathbb{E} \left[ e^{\beta(t \wedge \tau_n)} (e_1 e_2 x((t \wedge \tau_n)) + e_2 y((t \wedge \tau_n)) + z((t \wedge \tau_n)))^{\tilde{\theta}} \right] \\ &\leq (e_1 e_2 x_0 + e_2 y_0 + z_0)^{\tilde{\theta}} + \mathcal{G}^*(\tilde{\theta}) \int_0^{t \wedge \tau_n} e^{\beta s} ds. \end{aligned}$$

Letting  $n \rightarrow \infty$  and then  $t \rightarrow \infty$  yields

$$\begin{aligned} &\limsup_{t \rightarrow \infty} \mathbb{E} \left[ (e_1 e_2 x(t) + e_2 y(t) + z(t))^{\tilde{\theta}} \right] \\ &\leq \lim_{t \rightarrow \infty} e^{-\beta t} \left( (e_1 e_2 x_0 + e_2 y_0 + z_0)^{\tilde{\theta}} + \frac{\mathcal{G}^*(\tilde{\theta})(e^{\beta t} - 1)}{\beta} \right) \\ &= \frac{\mathcal{G}^*(\tilde{\theta})}{\beta}. \end{aligned}$$

It follows that

$$\limsup_{t \rightarrow \infty} \mathbb{E} x^{\tilde{\theta}} \leq \frac{\mathcal{G}^*(\tilde{\theta})}{\beta(e_1 e_2)^{\tilde{\theta}}}, \quad \limsup_{t \rightarrow \infty} \mathbb{E} y^{\tilde{\theta}} \leq \frac{\mathcal{G}^*(\tilde{\theta})}{\beta e_2^{\tilde{\theta}}}, \quad \limsup_{t \rightarrow \infty} \mathbb{E} z^{\tilde{\theta}} \leq \frac{\mathcal{G}^*(\tilde{\theta})}{\beta}.$$

Set

$$\mathcal{G}(\tilde{\theta}) = \frac{\mathcal{G}^*(\tilde{\theta})}{\beta} \max \left\{ (e_1 e_2)^{-\tilde{\theta}}, e_2^{-\tilde{\theta}}, 1 \right\},$$

then

$$\limsup_{t \rightarrow \infty} \mathbb{E} x^{\tilde{\theta}} \leq \mathcal{G}(\tilde{\theta}), \quad \limsup_{t \rightarrow \infty} \mathbb{E} y^{\tilde{\theta}} \leq \mathcal{G}(\tilde{\theta}), \quad \limsup_{t \rightarrow \infty} \mathbb{E} z^{\tilde{\theta}} \leq \mathcal{G}(\tilde{\theta}).$$

The proof is complete. □

### C.3 Proof of Theorem 12

**Proof** Note that, for any  $(x_0, y_0, z_0) \in \mathbb{R}_+^3$ , the solution of (2) is positive, then

$$dx \leq r_1 x \left( 1 - \frac{x}{K_1} \right) dt + x(\sigma_{11} + \sigma_{12}x)dB_1(t).$$

Consider the following auxiliary one-dimensional stochastic differential equation

$$dX(t) = r_1 X \left( 1 - \frac{X}{K_1} \right) dt + X(\sigma_{11} + \sigma_{12}X)dB_1(t) \tag{C13}$$

with an initial value  $X(0) = x_0 > 0$ . Set

$$f(x) = r_1 x \left( 1 - \frac{x}{K_1} \right), \quad \sigma(x) = x(\sigma_{11} + \sigma_{12}x), \quad x \in (0, \infty).$$

Direct calculation shows that

$$\int \frac{f(v)}{\sigma^2(v)} dv = \frac{r_1}{\sigma_{11}^2} \ln \frac{v}{\sigma_{11} + \sigma_{12}v} + \frac{r_1(\sigma_{11} + K_1\sigma_{12})}{K_1\sigma_{11}\sigma_{12}(\sigma_{11} + \sigma_{12}v)} + Q.$$

Then

$$\begin{aligned} & \int_0^\infty \frac{1}{\sigma^2(x)} \exp \left\{ \int_1^x \frac{2f(v)}{\sigma^2(v)} dv \right\} dx \\ &= C \int_0^\infty x^{\frac{2r_1}{\sigma_{11}^2}-2} (\sigma_{11} + \sigma_{12}x)^{-\frac{2r_1}{\sigma_{11}^2}-2} \exp \left\{ \frac{2r_1(\sigma_{11} + K_1\sigma_{12})}{K_1\sigma_{11}\sigma_{12}(\sigma_{11} + \sigma_{12}x)} \right\} dx, \end{aligned}$$

where

$$C = (\sigma_{11} + \sigma_{12})^{\frac{2r_1}{\sigma_{11}^2}} \exp \left\{ -\frac{2r_1(\sigma_{11} + K_1\sigma_{12})}{K_1\sigma_{11}\sigma_{12}(\sigma_{11} + \sigma_{12})} \right\}.$$

Letting

$$\begin{aligned} \tilde{\phi}(x) &= x^{2(r_1/\sigma_{11}^2-1)} (\sigma_{11} + \sigma_{12}x)^{-2(r_1/\sigma_{11}^2+1)} \exp \left\{ \frac{2r_1(\sigma_{11} + K_1\sigma_{12})}{K_1\sigma_{11}\sigma_{12}(\sigma_{11} + \sigma_{12}x)} \right\}, \\ \tilde{\phi}_1(x) &= x^{2(r_1/\sigma_{11}^2-1)} \exp \left\{ \frac{2r_1(\sigma_{11} + K_1\sigma_{12})}{K_1\sigma_{11}\sigma_{12}(\sigma_{11} + \sigma_{12}x)} \right\}, \end{aligned}$$

then

$$\lim_{x \rightarrow 0^+} \frac{\tilde{\phi}(x)}{\tilde{\phi}_1(x)} = \sigma_{11}^{-2(r_1/\sigma_{11}^2+1)} > 0,$$

which implies that  $\int_0^1 \tilde{\phi}(x) dx$  has the same convergence as  $\int_0^1 \tilde{\phi}_1(x) dx$ . Since

$$\int_0^1 \tilde{\phi}_1(x) dx \leq \exp \left\{ \frac{2r_1(\sigma_{11} + K_1\sigma_{12})}{K_1\sigma_{11}^2\sigma_{12}} \right\} \int_0^1 x^{2(r_1/\sigma_{11}^2-1)} dx$$

and  $r_1 > \sigma_{11}^2/2$ , one has  $\int_0^1 x^{2(r_1/\sigma_{11}^2-1)} dx < +\infty$ . On th

$$\tilde{\phi}_2(x) = x^{-2} \exp \left\{ \frac{2r_1(\sigma_{11} + K_1\sigma_{12})}{K_1\sigma_{11}\sigma_{12}(\sigma_{11} + \sigma_{12}x)} \right\},$$

then

$$\lim_{x \rightarrow +\infty} \frac{\tilde{\phi}(x)}{\tilde{\phi}_2(x)} = \sigma_{12}^{-2(r_1/\sigma_{11}^2+1)} > 0,$$

which implies that  $\int_1^\infty \tilde{\phi}(x) dx$  has the same convergence as  $\int_1^\infty \tilde{\phi}_2(x) dx$ . Then

$$\int_1^\infty \tilde{\phi}_2(x) dx \leq \exp \left\{ \frac{2r_1(\sigma_{11} + K_1\sigma_{12})}{K_1\sigma_{11}\sigma_{12}(\sigma_{11} + \sigma_{12})} \right\} \int_1^\infty \frac{1}{x^2} dx < +\infty.$$

Whence

$$\int_0^\infty \frac{1}{\sigma^2(x)} \exp \left\{ \int_1^x \frac{2f(v)}{\sigma^2(v)} dv \right\} dx < \infty.$$

Due to the ergodic property (Kutoyants and Kutojanc 2004), the invariant density of (C13) is

$$\varphi(x) = Qx^{2r_1/\sigma_{11}^2-2}(\sigma_{11} + \sigma_{12}x)^{-2r_1/\sigma_{11}^2-2} \exp \left\{ \frac{2r_1(\sigma_{11} + K_1\sigma_{12})}{K_1\sigma_{11}\sigma_{12}(\sigma_{11} + \sigma_{12}x)} \right\},$$

where  $Q$  is a constant such that  $\int_0^\infty \varphi(x) dx = 1$ . From the ergodic theorem, it follows that

$$\lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t X(s) ds = \int_0^\infty x\varphi(x) dx \quad a.s.$$

Let  $X(t)$  be the solution of (C13) with  $X(0) = x_0$ , then, by the comparison theorem of one-dimensional stochastic differential equation (Peng and Zhu 2006), one has  $x(t) \leq X(t)$  for  $t \geq 0$  a.s.

Applying the Itô's formula yields

$$d(\ln y) = \left[ r_2 - \frac{r_2}{K_2} + \frac{e_1 m_1 x}{a_1 + x} - \frac{m_2 z}{a_2 + y} - h_1 - \frac{\sigma_{21}^2}{2} - \sigma_{21} \sigma_{22} y - \frac{\sigma_{22}^2}{2} y^2 \right] dt + (\sigma_{21} + \sigma_{22} y) dB_2(t). \tag{C14}$$

Integrating both sides of (C14) from 0 to  $t$  and then dividing it by  $t$  leads to

$$\frac{\ln y(t) - \ln y_0}{t} \leq r_2 - h_1 - \frac{\sigma_{21}^2}{2} + \frac{e_1 m_1}{t} \int_0^t \frac{x(s)}{a_1 + x(s)} ds - \frac{\sigma_{22}^2}{2t} \int_0^t y^2(s) ds + \frac{\sigma_{21} B_2(t)}{t} + \frac{\sigma_{22}}{t} \int_0^t y(s) dB_2(s). \tag{C15}$$

Let  $\tilde{M}(t) = \sigma_{22} \int_0^t y(s) dB_2(s)$ , then  $\tilde{M}(t)$  is a local martingale whose quadratic variations is  $\langle \tilde{M}, \tilde{M} \rangle_t = \sigma_{22}^2 \int_0^t y^2(s) ds$ . By employing the exponential martingales inequality (Mao 2007), for any positive constant  $\delta$ , one obtains

$$\mathbb{P} \left\{ \sup_{0 \leq t \leq \delta} \left[ \tilde{M}(t) - \frac{1}{2} \langle \tilde{M}, \tilde{M} \rangle_t \right] > 2 \ln \delta \right\} \leq \frac{1}{\delta^2}.$$

From Borel-Cantelli Lemma (Mao 2007), it follows that, for almost all  $\omega \in \Omega$ , there exists a  $\delta_0 = \delta_0(\omega)$  such that

$$\sup_{0 \leq t \leq \delta} \left[ \tilde{M}(t) - \frac{1}{2} \langle \tilde{M}, \tilde{M} \rangle_t \right] \leq 2 \ln \delta.$$

Then

$$\tilde{M}(t) \leq 2 \ln \delta + \frac{1}{2} \langle \tilde{M}, \tilde{M} \rangle_t = 2 \ln \delta + \frac{\sigma_{22}^2}{2} \int_0^t y^2(s) ds, \quad 0 \leq t \leq \delta, \quad \delta \geq \delta_0, \quad a.s.$$

Hence, for  $0 \leq \delta - 1 \leq t < \delta$ , the following inequality holds:

$$\frac{\ln y(t) - \ln y_0}{t} \leq r_2 - h_1 - \frac{\sigma_{21}^2}{2} + \frac{e_1 m_1}{t} \int_0^t \frac{X(s)}{a_1 + X(s)} ds + \frac{\sigma_{21} B_2(t)}{t} + \frac{2 \ln \delta}{\delta - 1}. \tag{C16}$$

Taking the superior limit on both sides of (C16) and using  $\lim_{t \rightarrow \infty} B_2(t)/t = 0$  a.s., by the strong law of large numbers for local martingale (Mao 2007), one gets

$$\limsup_{t \rightarrow \infty} \frac{\ln y(t)}{t} \leq r_2 - h_1 - \frac{\sigma_{21}^2}{2} + e_1 m_1 \int_0^\infty \frac{x \varphi(x)}{a_1 + x} dx < 0,$$

that is,  $\lim_{t \rightarrow \infty} y(t) = 0$ , and then  $\lim_{t \rightarrow \infty} z(t) = 0$  a.s. As a result, for any  $\epsilon > 0$ , there exists an  $\Omega_\epsilon \subset \Omega$  such that

$$\mathbb{P}(\Omega_\epsilon) > 1 - \epsilon, \quad \frac{m_1xy}{a_1 + x} \leq \frac{m_1\epsilon x}{a_1 + x}.$$

Note that

$$dx(t) \geq \left[ r_1x \left( 1 - \frac{x}{K_1} \right) - \frac{m_1\epsilon x}{a_1 + x} \right] dt + x(\sigma_{11} + \sigma_{12}x)dB_1(t)$$

and

$$dx(t) \leq r_1x \left( 1 - \frac{x}{K_1} \right) dt + x(\sigma_{11} + \sigma_{12}x)dB_1(t),$$

the distribution of the process  $x(t)$  converges to the measure with the density  $\varphi$ . The proof is complete. □

### C.4 Proof of Theorem 13

**Proof** Applying the Itô’s formula to  $\ln x$  produces

$$d(\ln x) = \left[ r_1 - \frac{r_1}{K_1}x - \frac{m_1y}{a_1 + x} - \frac{\sigma_{11}^2}{2} - \sigma_{11}\sigma_{12}x - \frac{\sigma_{12}^2}{2}x^2 \right] dt + (\sigma_{11} + \sigma_{12}x)dB_1(t). \tag{C17}$$

Integrating (C17) from 0 to  $t$  and dividing it by  $t$  on both sides leads to

$$\frac{\ln x(t) - \ln x_0}{t} \leq r_1 - \frac{\sigma_{11}^2}{2} - \frac{\sigma_{12}^2}{2t} \int_0^t x^2(s)ds + \frac{\sigma_{11}B_1(t)}{t} + \frac{\sigma_{12}}{t} \int_0^t x(s)dB_1(s). \tag{C18}$$

Let  $M(t) = \sigma_{12} \int_0^t x(s)dB_1(s)$ , then  $M(t)$  is a local martingale whose quadratic variations is  $\langle M, M \rangle_t = \sigma_{12}^2 \int_0^t x^2(s)ds$ . By employing the exponential martingales inequality (Mao 2007), for any positive constant  $\delta$ , one obtains the following inequality

$$\mathbb{P} \left\{ \sup_{0 \leq t \leq \delta} \left[ M(t) - \frac{1}{2} \langle M, M \rangle_t \right] > 2 \ln \delta \right\} \leq \frac{1}{\delta^2}.$$

From Borel-Cantelli Lemma (Mao 2007), it follows that, for almost all  $\omega \in \Omega$ , there exists  $\delta_0 = \delta_0(\omega)$  such that

$$\sup_{0 \leq t \leq \delta} \left[ M(t) - \frac{1}{2} \langle M, M \rangle_t \right] \leq 2 \ln \delta.$$

It is trivial to show that

$$M(t) \leq 2 \ln \delta + \frac{1}{2} \langle M, M \rangle_t = 2 \ln \delta + \frac{\sigma_{12}^2}{2} \int_0^t x^2(s) ds, \quad 0 \leq t \leq \delta, \quad \delta \geq \delta_0, \quad a.s.$$

Hence, for  $0 \leq \delta - 1 \leq t < \delta$ , the following inequality holds

$$\frac{\ln x(t) - \ln x_0}{t} \leq r_1 - \frac{\sigma_{11}^2}{2} + \frac{\sigma_{11} B_1(t)}{t} + \frac{2 \ln \delta}{\delta - 1}. \tag{C19}$$

Taking the superior limit on the both sides of (C19) and noting that  $\lim_{t \rightarrow \infty} B_1(t)/t = 0$  a.s. the strong law of large numbers for local martingale (Mao 2007) implies that

$$\limsup_{t \rightarrow \infty} \frac{\ln x(t)}{t} \leq r_1 - \frac{\sigma_{11}^2}{2} < 0,$$

then  $\lim_{t \rightarrow \infty} x(t) = 0$  a.s. Therefore, there exists a set  $\Omega_\epsilon \subset \Omega$  such that

$$\mathbb{P}(\Omega_\epsilon) > 1 - \epsilon, \quad \frac{e_1 m_1 x y}{a_1 + x} \leq \frac{e_1 m_1 \epsilon y}{a_1 + \epsilon} < \frac{e_1 m_1 \epsilon}{a_1} y.$$

Applying the Itô’s formula to  $\ln y$ , integrating it from 0 to  $t$ , and dividing it by  $t$  on both sides, one has

$$\begin{aligned} \frac{\ln y(t) - \ln y_0}{t} &\leq r_2 \\ &+ \frac{e_1 m_1 \epsilon}{a_1} - h_1 - \frac{\sigma_{21}^2}{2} - \frac{\sigma_{22}^2}{2t} \int_0^t y^2(s) ds + \frac{\sigma_{21} B_2(t)}{t} \\ &+ \frac{\sigma_{22}}{t} \int_0^t y(s) dB_2(s). \end{aligned} \tag{C20}$$

Taking the superior limit on both sides of (C20) and using the arbitrariness of  $\epsilon$  yield

$$\limsup_{t \rightarrow \infty} \frac{\ln y(t)}{t} \leq r_2 - h_1 - \frac{\sigma_{21}^2}{2} < 0,$$

which implies that  $\lim_{t \rightarrow \infty} y(t) = 0$  and  $\lim_{t \rightarrow \infty} z(t) = 0$  a.s. The proof is complete. □

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