

Article

Global Stability and Bifurcation of a Three-Species Commensalism–Amensalism Model with Beddington–DeAngelis Functional Response

Xiaoran Li ^{1,2}, Qin Yue ^{1,*,†} and Fengde Chen ^{3,*,†} 

¹ School of Finance and Mathematics, West Anhui University, Lu'an 237000, China; 01000131@wxc.edu.cn

² Faculty of Economics and Business, Universiti Malaysia Sarawak, Kota Samarahan 94300, Sarawak, Malaysia

³ School of Mathematics and Statistics, Fuzhou University, Fuzhou 350108, China

* Correspondence: yueqin@wxc.edu.cn (Q.Y.); fdchen@fzu.edu.cn (F.C.); Tel.: +86-1361-505-6475 (F.C.)

† These authors contributed equally to this work.

Abstract

This paper investigates the dynamical behavior of a three-species commensalism–amensalism system with Beddington–DeAngelis functional response. The model describes a novel tripartite interaction: a neutral–commensal species (e.g., sea anemone) simultaneously engages in a commensal relationship with a commensal–amensal species (e.g., clownfish) and an indirect nutritional coupling with a neutral–amensal species (e.g., crustacean), while the commensal–amensal and neutral–amensal species interact amensalistically. This paper makes three principal contributions. First, by constructing a Volterra-type Lyapunov function, we rigorously prove the global asymptotic stability of the unique positive equilibrium of the (x, z) -subsystem in the positive quadrant, and further establish the global asymptotic stability of both the amensal-free equilibrium E_3 and the coexistence equilibrium E_4 in the positive octant. Second, selecting the commensal benefit coefficient c as the bifurcation parameter, we present a complete and rigorous proof of a transcritical bifurcation. Third, we provide systematic Maple-based numerical verification: the bifurcation diagram exhibits excellent agreement with the theoretical curve, and logarithmic-scale plots confirm exponential convergence rates. Ecologically, our results reveal a sharp threshold phenomenon: when the commensal benefit coefficient lies below a critical value c^* , the commensal species inevitably goes extinct and the system collapses to a two-species state; when c exceeds c^* , the commensal species can invade and achieve stable three-species coexistence. The explicit formula for this threshold provides a quantitative criterion for determining the minimum mutualistic strength required for persistence in conservation contexts. The results obtained in this paper substantially extend the existing theoretical understanding of three-species commensalism–amensalism systems.



Academic Editors: Quanxin Zhu, Alexander Zaslavski and Patricia J. Y. Wong

Received: 9 May 2026

Revised: 10 June 2026

Accepted: 29 June 2026

Published: 1 July 2026

Copyright: © 2026 by the authors.

Licensee MDPI, Basel, Switzerland.

This article is an open access article distributed under the terms and conditions of the [Creative Commons Attribution \(CC BY\)](https://creativecommons.org/licenses/by/4.0/) license.

Keywords: amensalism; Beddington–DeAngelis functional response; global stability; Lyapunov function; transcritical bifurcation; center manifold reduction

MSC: 34C23; 34D05; 34D20; 34D23; 37G10; 92D25

1. Introduction

While predation, competition, and mutualism have each spawned a vast mathematical literature, unilateral interactions—where one species affects another without being affected in return—remain comparatively understudied, despite their documented prevalence in

natural ecosystems [1]. The two canonical unilateral interactions are commensalism (one species benefits, the other is unaffected) and amensalism (one species is harmed, the other is unaffected).

Mathematical modelling of ecological interactions now constitutes a mature interdisciplinary enterprise, in which dynamical systems theory provides the principal framework for analyzing population persistence and species coexistence [2]. While bidirectional interactions—predation, competition, mutualism—have received sustained mathematical attention, the dynamical theory of unilateral interactions remains comparatively underdeveloped [3]. Recent field-informed modelling work has underscored the need for mechanistic treatments of mixed positive–negative interaction networks in spatially structured habitats [4].

Mougi [3] provided the first systematic evidence that unilateral interactions play critical roles in maintaining community stability. Through large-scale ecological network simulations, Mougi demonstrated that networks dominated by commensalistic and amensalistic interactions exhibit stability characteristics fundamentally different from those governed by bidirectional interactions. This landmark finding has stimulated a growing body of mathematical research, which we now review in a structured manner. One theme that will emerge is the contrast between models that permit oscillatory dynamics and those whose unilateral architecture precludes it.

1.1. Two-Species Unilateral Interaction Models

The mathematical study of unilateral interactions began with two-species systems. On the amensalism side, Sun [5] first proposed the basic Lotka–Volterra framework; subsequently, Guan and Chen [6] incorporated the Beddington–DeAngelis (BD) functional response with Allee effects, Luo and Wang [7] further analyzed the global dynamics under weak Allee effect, and Zhao et al. [8,9] extended it. More recent contributions include discrete-time models that uncover chaos and period-doubling [10], and systems incorporating strong Allee effects [11–14]. On the commensalism side, Chen et al. [15] studied a Holling type II model with stage structure, Fang et al. [16] considered Allee effects together with non-selective harvesting, Ditta et al. [17] explored periodic dynamics in a harvested discrete-time system, and Qu [18] introduced two time delays that induce Hopf bifurcations. Further developments, including seasonal commensalism and weak Allee effects, are surveyed in [19–21].

All of the above works, however, are confined to the two-species framework. In real ecosystems a single species often participates simultaneously in multiple unilateral interactions, making three-species models indispensable for capturing ecologically realistic scenarios.

1.2. Three-Species Models Involving Unilateral Interactions

We now present a systematic review of existing three-species models that incorporate unilateral interactions. These can be classified into four categories according to their interaction architecture.

1.2.1. Type I: Commensalism + Parasitism with a Shared Host

Puspitasari et al. [22] proposed a three-species model in which a commensal and a parasite share a common host: the commensal benefits from the host without cost, while the parasite benefits from (and harms) the host. Michaelis–Menten-type harvesting acts upon the commensal. Eight equilibria were identified and local stability was analyzed via eigenvalue methods; subsequent corrections and strengthened results were provided by Liu and Yue [23] and Chen, Zhou, and Lin [24]. Crucially, this model contains no amensalistic

interaction, and all interspecific coupling terms remain linear. Consequently, oscillatory dynamics are absent—a pattern shared by most pure unilateral-interaction models.

1.2.2. Type II: Predation + Competition + Commensalism (Food-Web Structure)

Gakkhar and Gupta [25] and Gupta, Jena, and Priyadarshi [26] investigated tri-trophic food-web models in which commensalism enters as a secondary interaction alongside predation and competition (with Holling type II or III functional responses). These systems exhibit rich oscillatory and even chaotic dynamics—Hopf bifurcations, stable limit cycles, period-2 solutions—that are driven primarily by the bidirectional antagonistic interactions rather than by unilateral interactions per se. This contrast suggests that models constructed exclusively from unilateral interactions may belong to a qualitatively distinct dynamical class from those incorporating bidirectional feedback—a distinction that the present paper will substantiate mathematically.

1.2.3. Type III: Amensalism + Parasitism

Abd Alhadi and Naji [27,28] proposed and analyzed three-species models that combine amensalism with parasitism. Global stability was established via Lyapunov functions, and transcritical bifurcations were identified through Sotomayor’s theorem. Commensalism, the positive counterpart of unilateral interactions, is conspicuously absent from these models, and all interaction terms retain the linear mass-action (Lotka–Volterra) form.

1.2.4. Type IV: Commensalism in a Food Chain with Harvesting

Jawad and Hassan [29] considered a four-species food chain in which commensalism appears as one among several interaction types; saddle-node, transcritical, and pitchfork bifurcations were reported. Amensalism is not present in this model.

1.2.5. Summary of the Literature Landscape

To crystallize how the present work differs from existing three-species formulations, we compare the key structural features of the four model categories in Table 1. The table highlights interaction types, functional response forms, coupling architecture, and the presence or absence of oscillatory dynamics—factors that collectively determine the mathematical behavior and ecological relevance of each model.

Table 1. Comparison of three-species models involving unilateral interactions.

Reference	Interaction Types	Functional Response	Coupling Structure	Oscillations?
Puspitasari et al. [22]	Commensalism + Parasitism	Michaelis–Menten (harvesting only)	Linear; shared host mediates both interactions	No
Gakkhar & Gupta [25]; Gupta et al. [26]	Predation + Competition + Commensalism	Holling II or III	Linear commensalism; predation-driven	Yes (Hopf, chaos)
Abd Alhadi & Naji [27,28]	Amensalism + Parasitism	Linear (mass action)	Two or three pairwise LV couplings	No
Jawad & Hassan [29]	Commensalism + Predation (4 species)	Linear	Food chain with linear commensalism	Not reported
Shofiyya et al. [30] [the present study]	Commensalism + Amensalism	BD (nonlinear)	Dual unilateral; (x, z) -subsystem autonomous	No proved

1.3. The Research Gap and the Present Contribution

Table 1 reveals a conspicuous gap in the literature: no existing three-species model simultaneously incorporates commensalism and amensalism as its two defining unilateral interactions. Type I models pair commensalism with parasitism rather than amensalism; Type II formulations embed commensalism within food webs governed primarily by predation and competition; Type III systems couple amensalism with parasitism and employ only linear interaction terms; and Type IV works involve four species without any amensalistic component.

In real ecosystems, however, a single species can simultaneously engage in both commensalistic and amensalistic relationships with different partners. A well-documented marine example illustrates precisely this configuration [31–33]. Specifically, sea anemones shelter clownfish without cost to themselves—a clear case of commensalism—while their toxins impair crustacean nervous systems (amensalism). Simultaneously, clownfish and crustaceans compete for resources, with clownfish being disadvantaged—a second amensalistic link. Meanwhile, crustacean movements generate water currents that indirectly enhance food delivery to the anemones, completing a three-species network in which commensalism and amensalism operate simultaneously. This ecologically motivated configuration had not been mathematically modeled until the recent work of Shofiyya et al. [30].

Shofiyya et al. [30] proposed the following system, which is the object of study in the present paper:

$$\begin{cases} \frac{dx}{dt} = x(a_1 - b_1x) + \beta z, \\ \frac{dy}{dt} = y\left(a_2 - b_2y + \frac{cx}{mx + ny + 1} - \alpha z\right), \\ \frac{dz}{dt} = z\left(\frac{a_3}{x} - b_3z\right). \end{cases} \quad (1)$$

Here $x(t)$ denotes the neutral-commensal species (sea anemone), $y(t)$ the commensal-amensal species (clownfish), and $z(t)$ the neutral-amensal species (crustacean). Three interaction pathways define the network architecture. First, z supplies a nutritional subsidy to x through the linear term $+\beta z$, while x reciprocates via the per capita contribution a_3/x ; crucially, this (x, z) coupling is fully autonomous and independent of y . Second, x confers a commensal benefit upon y through the Beddington–DeAngelis functional response $\frac{cx}{mx+ny+1}$, whose saturation form accounts for handling time and mutual interference between the two populations. Third, z exerts an amensalistic suppression on y via the linear inhibition term $-\alpha z$. Thus the system embodies, within a single three-species framework, the two canonical forms of unilateral interaction.

Shofiyya et al. established positivity and boundedness of solutions, identified four equilibrium points (E_1, E_2, E_3, E_4), and derived local asymptotic stability conditions via the Routh–Hurwitz criterion (Theorems 4–7 in [30]). Their work laid the essential foundation, yet a closer reading reveals that several fundamental questions were left open.

The most significant of these concerns global stability. Theorems 6 and 7 of [30] provide only *local* asymptotic stability conditions— $c < c^*$ for the amensal-extinction equilibrium E_3 and $c < c^{**}$ for the coexistence equilibrium E_4 . Local stability guarantees attractivity solely within an infinitesimal neighborhood of the equilibrium; it cannot exclude the possibility that trajectories starting farther afield converge to a limit cycle or diverge altogether. For ecological models, where the central question is whether a population can recover from an arbitrarily large perturbation, *global* stability is the decisive criterion.

Closely related is the issue of bifurcation structure. The threshold values c^* and c^{**} mark the boundaries of the local stability regions for E_3 and E_4 , yet the dynamical mecha-

nism connecting these two equilibria—which, after all, represent the amensal-extinction and coexistence states of the very same ecological system—remains unidentified. One would naturally expect a transcritical bifurcation to mediate the transition, but neither the nature of the bifurcation at $c = c^*$ nor the direction of exchange of stability is established in the original work.

Finally, the numerical evidence presented in [30] is limited to a single set of initial conditions (see their Section 5); without a systematic exploration of the phase space or a bifurcation diagram, the analytical stability thresholds lack quantitative corroboration.

The present paper addresses each of these open problems through a systematic re-examination of the model proposed by Shofiyya et al. [30]. We first establish, in Section 3, the global asymptotic stability of both E_3 and E_4 : the proof proceeds by constructing a Volterra-type Lyapunov function that renders the autonomous (x, z) -subsystem globally stable in $\mathbb{R}_+^2$, and then leverages ω -limit set arguments together with the theory of asymptotically autonomous systems to lift this stability to the full three-dimensional dynamics. In Section 4 we turn to the bifurcation structure. All three conditions of Sotomayor’s theorem are verified rigorously, the normal form $\dot{y} = \mu(c)y - \gamma(c)y^2$ is derived on the center manifold, and we prove that the resulting transcritical bifurcation between E_3 and E_4 is global: over the entire range of the bifurcation parameter c , the system admits no limit cycles or other non-trivial attractors. We further explain this absence of oscillations as a structural consequence of the unilateral coupling architecture (Sections 4.3 and 6).

Section 5 complements the analysis with comprehensive numerical simulations—multiple initial conditions, a full bifurcation diagram, and quantitative validation of every theoretical prediction—together with the complete Maple code used to generate them.

The model formulation and necessary mathematical preliminaries are given in the next section.

The remainder of this paper is organized as follows. Section 2 recalls the model equations and summarizes the existing analytical results from [30]. Section 3 is devoted to the global stability analysis: we first establish the global asymptotic stability of the autonomous (x, z) -subsystem via a Volterra-type Lyapunov function, then leverage ω -limit set arguments and the theory of asymptotically autonomous systems to prove global stability of E_3 and E_4 . Section 4 presents a rigorous bifurcation analysis using Sotomayor’s theorem, deriving the normal form on the center manifold and demonstrating that the transcritical bifurcation between E_3 and E_4 is global—no limit cycles or other non-trivial attractors appear over the entire range of the bifurcation parameter c . Section 5 provides comprehensive numerical simulations, including a bifurcation diagram and multi-initial trajectories, that quantitatively validate all theoretical predictions. Section 6 concludes with a discussion that locates our findings within the wider landscape of ecological modelling, addresses the comparative absence of oscillatory dynamics in unilateral systems, and outlines directions for future extensions.

2. Model Description and Preliminaries

2.1. The Model Equations

We consider the following three-species system of ordinary differential equations due to Shofiyya et al. [30]:

$$\begin{cases} \frac{dx}{dt} = x(a_1 - b_1x) + \beta z := f_1(x, y, z), \\ \frac{dy}{dt} = y\left(a_2 - b_2y + \frac{cx}{mx + ny + 1} - \alpha z\right) := f_2(x, y, z), \\ \frac{dz}{dt} = z\left(\frac{a_3}{x} - b_3z\right) := f_3(x, y, z). \end{cases} \quad (2)$$

Here $x(t)$, $y(t)$, and $z(t)$ denote, respectively, the population densities at time t of the neutral–commensal species (sea anemone), the commensal–amensal species (clownfish), and the neutral–amensal species (crustacean). All parameters are positive real numbers: a_1, a_2, a_3 are intrinsic growth rates; b_1, b_2, b_3 are intraspecific competition coefficients; β is the coefficient of food subsidy provided by crustaceans to sea anemones; c is the commensal benefit coefficient of clownfish derived from sea anemones; m, n are the half-saturation constants of the Beddington–DeAngelis functional response; and α is the amensal inhibition coefficient of crustaceans on clownfish. Initial conditions satisfy $x(0), y(0), z(0) > 0$. The reader is referred to [30,34–37] for the detailed model derivation and additional ecological context.

Remark 1. A key structural feature of system (2) is that f_1 and f_3 do not depend explicitly on y ; hence the (x, z) -subsystem is fully autonomous and decoupled from y . This property serves as the cornerstone of our global stability analysis.

2.2. Existing Analytical Results

Shofiyya et al. [30] established the following foundational results, which we quote directly:

Theorem 1 (Positivity and Boundedness). *All solutions of system (2) with positive initial conditions remain positive for all $t \geq 0$ and are uniformly bounded in $\mathbb{R}_+^3$.*

Theorem 2 (Existence and Uniqueness of Solutions). *The right-hand side of system (2) is Lipschitz continuous on $\mathbb{R}_+^3$, and for any positive initial condition there exists a unique global solution.*

2.3. Equilibrium Points

System (2) possesses four nonnegative equilibrium points:

- E_1 : $E_1 = \left(\frac{a_1}{b_1}, 0, 0\right)$ —only the neutral–commensal species survives;
 E_2 : $E_2 = \left(\frac{a_1}{b_1}, y_2, 0\right)$ —the neutral–amensal species goes extinct, where

$$y_2 = \frac{-A_2 + \sqrt{(A_2)^2 - 4A_3}}{2},$$

where

$$A_1 = 1, \quad A_2 = \frac{a_1 m}{b_1 n} + \frac{1}{n} - \frac{a_2}{b_2}, \quad \text{and} \quad A_3 = -\left(\frac{a_1 a_2 m}{b_1 b_2 n} + \frac{a_2}{b_2 n} + \frac{a_1 c}{b_1 b_2 n}\right);$$

- E_3 : $E_3 = (x_3, 0, z_3)$ —the commensal–amensal species goes extinct;
 E_4 : $E_4 = (x^*, y^*, z^*)$ —three-species coexistence.

Here $x_3 = x^*$ is the unique positive real root of the cubic equation

$$x^3 - \frac{a_1}{b_1}x^2 - \frac{a_3\beta}{b_1 b_3} = 0, \quad (3)$$

and

$$z_3 = z^* = \frac{a_3}{b_3 x^*}. \quad (4)$$

E_1 and E_2 possess at least one positive eigenvalue and are therefore always unstable [30]. The local stability conditions for E_3 and E_4 are given in Theorems 6 and 7 of the original paper and are not repeated here. The central goal of the present paper is to elevate

these local results to global ones and to reveal the bifurcation structure connecting E_3 and E_4 .

3. Global Stability Analysis

3.1. Global Stability of the (x, z) -Subsystem

Consider the (x, z) -subsystem decoupled from y :

$$\begin{cases} \frac{dx}{dt} = x(a_1 - b_1x) + \beta z \equiv F_1(x, z), \\ \frac{dz}{dt} = z\left(\frac{a_3}{x} - b_3z\right) \equiv F_3(x, z). \end{cases} \quad (5)$$

This system possesses a unique positive equilibrium $(x^*, z^*) = (x_3, \frac{a_3}{b_3x_3})$ in $\mathbb{R}_+^2$.

Theorem 3. *The equilibrium (x^*, z^*) is globally asymptotically stable in $\mathbb{R}_+^2$ for system (5).*

Proof. Construct the following Volterra-type Lyapunov function:

$$V(x, z) = x - x^* - x^* \ln \frac{x}{x^*} + k\left(z - z^* - z^* \ln \frac{z}{z^*}\right), \quad (6)$$

where $k > 0$ is a positive parameter to be chosen. V is C^1 and positive definite on $\mathbb{R}_+^2$, and satisfies $\lim_{\|(x,z)\| \rightarrow \infty} V = +\infty$ (radial unboundedness).

The Lie derivative along system (5) is

$$\dot{V} = \left(1 - \frac{x^*}{x}\right)F_1 + k\left(1 - \frac{z^*}{z}\right)F_3.$$

Using the equilibrium conditions $a_1 = b_1x^* - \frac{\beta z^*}{x^*}$ and $a_3 = b_3x^*z^*$, we expand term by term:

$$\begin{aligned} \left(1 - \frac{x^*}{x}\right)F_1 &= -b_1(x - x^*)^2 + \beta(x - x^*)\left(\frac{z}{x} - \frac{z^*}{x^*}\right), \\ k\left(1 - \frac{z^*}{z}\right)F_3 &= -\frac{kb_3z^*}{x}(x - x^*)(z - z^*) - kb_3(z - z^*)^2. \end{aligned}$$

Using the identity $\frac{z}{x} - \frac{z^*}{x^*} = \frac{x^*(z - z^*) - z^*(x - x^*)}{xx^*}$ and combining, we obtain:

$$\begin{aligned} \dot{V} &= -\left(b_1 + \frac{\beta z^*}{xx^*}\right)(x - x^*)^2 + \left(\frac{\beta}{x} - \frac{kb_3z^*}{x}\right)(x - x^*)(z - z^*) \\ &\quad - kb_3(z - z^*)^2. \end{aligned}$$

Choosing $k = \frac{\beta}{b_3z^*}$ to eliminate the cross term, we obtain:

$$\dot{V} = -b_1(x - x^*)^2 - \frac{\beta z^*}{xx^*}(x - x^*)^2 - \frac{\beta}{z^*}(z - z^*)^2 \leq 0. \quad (7)$$

Since $x, x^* > 0$, we have $\dot{V} < 0$ for all $(x, z) \neq (x^*, z^*)$. The equality $\dot{V} = 0$ holds if and only if $x = x^*$ and $z = z^*$, and the maximal invariant set contained in $\{\dot{V} = 0\}$ is the singleton $\{(x^*, z^*)\}$. By Lyapunov's direct method and LaSalle's invariance principle [38], (x^*, z^*) is globally asymptotically stable. $\square$

Remark 2. *The key to the construction (6) lies in exploiting the natural structure of the Volterra-type function $\int_{x^*}^x \frac{\xi - x^*}{\xi} d\xi$ in ecological models, which enables the cross term to be eliminated exactly*

by a suitable choice of k . This method is superior to conventional quadratic Lyapunov functions because it simultaneously guarantees global positive definiteness and radial unboundedness on $\mathbb{R}_+^2$.

3.2. Global Stability of E_3

Define the bifurcation function

$$\mu(c) = a_2 + \frac{cx^*}{mx^* + 1} - \frac{\alpha a_3}{b_3 x^*}. \quad (8)$$

Theorem 4. If $\mu(c) < 0$, i.e.,

$$c < c^* \equiv \frac{mx^* + 1}{x^*} \left(\frac{\alpha a_3}{b_3 x^*} - a_2 \right), \quad (9)$$

then the equilibrium $E_3 = (x^*, 0, z^*)$ is globally asymptotically stable in $\mathbb{R}_+^3$.

Proof. By Theorem 3, for any initial condition $(x(0), z(0)) \in \mathbb{R}_+^2$, we have $x(t) \rightarrow x^*$ and $z(t) \rightarrow z^*$.

Consider the dynamics of y :

$$\frac{dy}{dt} = y \left(a_2 - b_2 y + \frac{cx}{mx + ny + 1} - \alpha z \right) \leq y \left(a_2 - b_2 y + \frac{cx}{mx + 1} - \alpha z \right).$$

Since $x(t) \rightarrow x^*$ and $z(t) \rightarrow z^*$, for any $\varepsilon > 0$ there exists $T > 0$ such that for all $t \geq T$:

$$\frac{dy}{dt} \leq y(\mu(c) - b_2 y + \varepsilon).$$

Because $\mu(c) < 0$, we choose $\varepsilon = |\mu(c)|/2$. Then for $t \geq T$:

$$\frac{dy}{dt} \leq y \left(\frac{\mu(c)}{2} - b_2 y \right) \leq \frac{\mu(c)}{2} y < 0 \quad (y > 0).$$

Hence $y(t)$ decreases monotonically with zero as a lower bound, so $\lim_{t \rightarrow \infty} y(t) = 0$.

More rigorously, let $p \in \mathbb{R}_+^3$ be an arbitrary initial point. Its ω -limit set $\omega(p)$ is nonempty, compact, connected, and invariant. By the convergence of x and z :

$$\omega(p) \subseteq \Sigma_3 := \{(x^*, y, z^*) : y \geq 0\}.$$

On Σ_3 , the limit equation is

$$\frac{dy}{dt} = y \left(a_2 - b_2 y + \frac{cx^*}{mx^* + ny + 1} - \alpha z^* \right) \equiv yF(y). \quad (10)$$

Noting that $F'(y) = -b_2 - \frac{cnx^*}{(mx^* + ny + 1)^2} < 0$. As $y \rightarrow \infty$, the dominant term $-b_2 y \rightarrow -\infty$. Hence, F is a strictly decreasing function, since $F(0) = \mu(c) < 0$, it follows that $F(y) < 0$ for all $y > 0$, which means that the compact invariant sets are only $\{0\}$. Thus E_3 is globally asymptotically stable. $\square$

3.3. Global Stability of E_4

Theorem 5. If $\mu(c) > 0$, i.e.,

$$c > c^* \equiv \frac{mx^* + 1}{x^*} \left(\frac{\alpha a_3}{b_3 x^*} - a_2 \right), \quad (11)$$

then the coexistence equilibrium $E_4 = (x^*, y^*, z^*)$ is globally asymptotically stable in $\mathbb{R}_+^3$.

Proof. If $\mu(c) > 0$, then for $F(y)$ defined in (10), $F(0) = \mu(c) > 0$, $F(y)$ is strictly decreasing on $[0, \infty)$, the equation $F(y) = 0$ has a unique positive root $y = y^*$ in $(0, \infty)$, and $F(y) > 0$ for $0 \leq y < y^*$, $F(y) < 0$ for $y > y^*$. Hence y^* is globally asymptotically stable for (10) on $(0, \infty)$.

By Theorem 3, $(x(t), z(t)) \rightarrow (x^*, z^*)$. Take any $p \in \mathbb{R}_+^3$; its ω -limit set satisfies

$$\omega(p) \subseteq \Sigma := \{(x^*, y, z^*) : y \geq 0\}.$$

Σ is invariant under the flow of (2), so $\omega(p)$ is also an ω -limit set of (10). Equation (10) is a one-dimensional autonomous ODE; its compact ω -limit sets must be fixed points, and hence

$$\omega(p) \subseteq \{(x^*, 0, z^*), (x^*, y^*, z^*)\} = \{E_3, E_4\}.$$

Since $\mu(c) > 0$, $y = 0$ is a repeller for (10) (for $0 < y < \delta$, $\dot{y} > 0$). The initial condition $y(0) > 0$ ensures $y(t) \not\rightarrow 0$, so $\omega(p) = \{E_4\}$. Thus E_4 is globally asymptotically stable. $\square$

4. Transcritical Bifurcation

4.1. Equilibrium Coincidence and Spectral Analysis

From (8), $\mu(c)$ is strictly increasing in c ; hence there exists a unique c^* such that $\mu(c^*) = 0$. At $c = c^*$, we have $E_3(c^*) = E_4(c^*) = (x^*, 0, z^*)$ —the two equilibria coincide.

To perform the bifurcation analysis, we translate the system at $E_3(c^*)$. Let $u = x - x^*$, $v = y$, $w = z - z^*$, and denote $\mathbf{u} = (u, v, w)^T$. The system becomes

$$\begin{cases} \dot{u} = f_1(x^* + u, z^* + w), \\ \dot{v} = v \left[a_2 - b_2 v + \frac{c(x^* + u)}{m(x^* + u) + nv + 1} - \alpha(z^* + w) \right] = f_2(x^* + u, z^* + w), \\ \dot{w} = f_3(x^* + u, z^* + w). \end{cases} \quad (12)$$

For simplicity, we denote

$$\dot{\mathbf{u}} = \mathbf{F}(\mathbf{u}; c), \quad (13)$$

and $\mathbf{F}(\mathbf{0}; c^*) = \mathbf{0}$.

The Jacobian matrix at this equilibrium reveals the spectral structure that underpins the bifurcation analysis. Evaluating at $(\mathbf{0}, c^*)$ yields

$$\begin{aligned} \left. \frac{\partial f_1}{\partial x} \right|_{E_3} &= a_1 - 2b_1 x^*, & \left. \frac{\partial f_1}{\partial y} \right|_{E_3} &= 0, \\ \left. \frac{\partial f_1}{\partial z} \right|_{E_3} &= \beta, & \left. \frac{\partial f_2}{\partial x} \right|_{E_3} &= 0, \\ \left. \frac{\partial f_2}{\partial y} \right|_{E_3} &= a_2 + \frac{cx^*}{mx^* + 1} - \alpha z^* = \mu(c), & \left. \frac{\partial f_2}{\partial z} \right|_{E_3} &= 0, \\ \left. \frac{\partial f_3}{\partial x} \right|_{E_3} &= -\frac{a_3 z^*}{(x^*)^2}, & \left. \frac{\partial f_3}{\partial y} \right|_{E_3} &= 0, \\ \left. \frac{\partial f_3}{\partial z} \right|_{E_3} &= \frac{a_3}{x^*} - 2b_3 z^* = -b_3 z^*. \end{aligned}$$

Note that $a_1 = b_1 x^* - \frac{\beta z^*}{x^*}$, and hence

$$\left. \frac{\partial f_1}{\partial x} \right|_{E_3} = a_1 - 2b_1 x^* = -b_1 x^* - \frac{\beta z^*}{x^*}.$$

Hence,

$$A(c^*) = D_{\mathbf{u}}\mathbf{F}(\mathbf{0}; c^*) = \begin{pmatrix} A_{11} & 0 & \beta \\ 0 & 0 & 0 \\ A_{31} & 0 & A_{33} \end{pmatrix}, \quad (14)$$

where

$$A_{11} = -b_1 x^* - \frac{\beta z^*}{x^*} < 0, \quad A_{31} = -\frac{a_3 z^*}{(x^*)^2} < 0, \quad A_{33} = -b_3 z^* < 0.$$

Proposition 1. $A(c^*)$ possesses a simple zero eigenvalue; the remaining two eigenvalues have negative real parts.

Proof. The characteristic polynomial is

$$\det(\lambda I - A(c^*)) = \lambda \cdot \det \begin{pmatrix} \lambda - A_{11} & -\beta \\ -A_{31} & \lambda - A_{33} \end{pmatrix}.$$

The 2×2 block is precisely the Jacobian of the (x, z) -subsystem at (x^*, z^*) . From the negative definiteness of $\tilde{V}$ in Theorem 3, this block has negative trace and positive determinant; hence both eigenvalues have negative real parts. The full spectrum is therefore $\{0, \lambda_2, \lambda_3\}$ with $\text{Re}(\lambda_{2,3}) < 0$. $\square$

4.2. Sotomayor Verification and Center Manifold Reduction

Theorem 6 (Transcritical Bifurcation). Let c^* be defined by (9). System (2) undergoes a transcritical bifurcation at $(E_3(c^*), c^*)$. Specifically:

- (i) There exist $\delta > 0$ and C^1 families of equilibria $\{E_3(c), E_4(c)\}_{|c-c^*|<\delta}$ passing through $(E_3(c^*), c^*)$;
- (ii) For $c < c^*$, $E_3(c)$ is locally asymptotically stable, while $E_4(c)$ does not lie in $\mathbb{R}_+^3$ ($y^*(c) < 0$);
- (iii) For $c > c^*$, $E_3(c)$ is unstable, while $E_4(c)$ lies in $\mathbb{R}_+^3$ and is locally asymptotically stable;
- (iv) On the center manifold, the reduced dynamics are governed by the transcritical normal form

$$\dot{v} = \mu(c) v - \gamma(c) v^2 + O(v^3, \mu v^2, \mu^2 v), \quad (15)$$

$$\text{where } \gamma(c) = b_2 + \frac{c n x^*}{(m x^* + 1)^2} > 0.$$

Proof. We apply Sotomayor's theorem [39] and verify its three conditions.

Right and left eigenvectors. Right eigenvector $\mathbf{v}$ satisfies $A(c^*)\mathbf{v} = \mathbf{0}$. Since the second column of $A(c^*)$ is entirely zero:

$$\mathbf{v} = (0, 1, 0)^T. \quad (16)$$

Left eigenvector $\mathbf{w}$ satisfies $\mathbf{w}^T A(c^*) = \mathbf{0}^T$:

$$(w_1, w_2, w_3) \begin{pmatrix} A_{11} & 0 & \beta \\ 0 & 0 & 0 \\ A_{31} & 0 & A_{33} \end{pmatrix} = (0, 0, 0).$$

Writing component-wise:

$$\begin{cases} w_1 A_{11} + w_3 A_{31} = 0, \\ w_1 \beta + w_3 A_{33} = 0. \end{cases}$$

The coefficient determinant of this homogeneous linear system is

$$\Delta = A_{11}A_{33} - \beta A_{31} = \det \begin{pmatrix} A_{11} & \beta \\ A_{31} & A_{33} \end{pmatrix}.$$

This is precisely the Jacobian determinant of the (x, z) -subsystem. Since this subsystem is asymptotically stable at (x^*, z^*) , we have $\Delta > 0$. Hence the homogeneous system admits only the trivial solution $w_1 = w_3 = 0$. The component w_2 is free; we take

$$\mathbf{w} = (0, 1, 0)^T. \quad (17)$$

The normalization condition $\mathbf{w}^T \mathbf{v} = 1$ is automatically satisfied.

Verification of (S1): $\mathbf{w}^T \mathbf{F}_c(\mathbf{0}, c^*) = 0$.

Computing $\mathbf{F}_c = \frac{\partial}{\partial c} \mathbf{F}$:

$$\mathbf{F}_c(\mathbf{u}; c) = \frac{\partial}{\partial c} \begin{pmatrix} x(a_1 - b_1 x) + \beta z \\ y \left(a_2 - b_2 y + \frac{cx}{mx + ny + 1} - \alpha z \right) \\ z(a_3/x - b_3 z) \end{pmatrix} = \begin{pmatrix} 0 \\ \frac{xy}{mx + ny + 1} \\ 0 \end{pmatrix}.$$

At $(\mathbf{0}, c^*)$, we have $x = x^*, y = 0, z = z^*$, and hence

$$\mathbf{F}_c(\mathbf{0}; c^*) = (0, 0, 0)^T.$$

and $\mathbf{w}^T \mathbf{F}_c = 0$. Hence (S1) holds.

Verification of (S2): $\mathbf{w}^T [D_{\mathbf{u}} \mathbf{F}_c \mathbf{v}] \neq 0$.

First compute $D_{\mathbf{u}} \mathbf{F}_c$:

$$D_{\mathbf{u}} \mathbf{F}_c = \begin{pmatrix} 0 & 0 & 0 \\ \frac{\partial}{\partial x} \left(\frac{xy}{mx + ny + 1} \right) & \frac{\partial}{\partial y} \left(\frac{xy}{mx + ny + 1} \right) & \frac{\partial}{\partial z} \left(\frac{xy}{mx + ny + 1} \right) \\ 0 & 0 & 0 \end{pmatrix}.$$

Computing term by term:

$$\frac{\partial}{\partial x} \left(\frac{xy}{mx + ny + 1} \right) = y \cdot \frac{mx + ny + 1 - mx}{(mx + ny + 1)^2} = \frac{y(ny + 1)}{(mx + ny + 1)^2},$$

$$\frac{\partial}{\partial y} \left(\frac{xy}{mx + ny + 1} \right) = \frac{x}{mx + ny + 1} - \frac{nxy}{(mx + ny + 1)^2} = \frac{x(mx + 1)}{(mx + ny + 1)^2}.$$

At $(\mathbf{0}, c^*)$ (where $y = 0$):

$$D_{\mathbf{u}} \mathbf{F}_c(\mathbf{0}; c^*) = \begin{pmatrix} 0 & 0 & 0 \\ 0 & \frac{x^*}{mx^* + 1} & 0 \\ 0 & 0 & 0 \end{pmatrix}.$$

Thus

$$D_{\mathbf{u}}\mathbf{F}_c(\mathbf{0}; c^*) \mathbf{v} = \begin{pmatrix} 0 & 0 & 0 \\ 0 & \frac{x^*}{mx^*+1} & 0 \\ 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} 0 \\ 1 \\ 0 \end{pmatrix} = \begin{pmatrix} 0 \\ \frac{x^*}{mx^*+1} \\ 0 \end{pmatrix}.$$

$$\mathbf{w}^T[D_{\mathbf{u}}\mathbf{F}_c \mathbf{v}] = (0, 1, 0) \begin{pmatrix} 0 \\ \frac{x^*}{mx^*+1} \\ 0 \end{pmatrix}^T = \frac{x^*}{mx^*+1} > 0.$$

Hence (S2) holds.

Verification of (S3): $\mathbf{w}^T[D_{\mathbf{u}}^2\mathbf{F}(\mathbf{v}, \mathbf{v})] \neq 0$.

The second derivative $D_{\mathbf{u}}^2\mathbf{F}(\mathbf{v}, \mathbf{v})$:

$$D_{\mathbf{u}}^2\mathbf{F}(\mathbf{v}, \mathbf{v}) = \sum_{i,j \in \{u,v,w\}} \frac{\partial^2 \mathbf{F}}{\partial u_i \partial u_j} v_i v_j = \frac{\partial^2 \mathbf{F}}{\partial v^2},$$

since only $v_2 = v_y = 1 \neq 0$, while all other $v_i = 0$. We compute $\frac{\partial^2 f_2}{\partial y^2}$:

$$f_2 = y \left(a_2 - b_2 y + \frac{cx}{mx + ny + 1} - \alpha z \right).$$

$$\frac{\partial f_2}{\partial y} = a_2 - 2b_2 y + \frac{cx}{mx + ny + 1} - \alpha z - \frac{cnxy}{(mx + ny + 1)^2},$$

$$\begin{aligned} \frac{\partial^2 f_2}{\partial y^2} &= -2b_2 - \frac{cnx}{(mx + ny + 1)^2} - \frac{cnx}{(mx + ny + 1)^2} + \frac{2cn^2xy}{(mx + ny + 1)^3} \\ &= -2b_2 - \frac{2cnx}{(mx + ny + 1)^2} + \frac{2cn^2xy}{(mx + ny + 1)^3}. \end{aligned}$$

At $(\mathbf{0}, c^*)$ (where $y = 0$):

$$\frac{\partial^2 f_2}{\partial y^2} \Big|_{(\mathbf{0}, c^*)} = -2b_2 - \frac{2c^*nx^*}{(mx^* + 1)^2}.$$

The remaining components satisfy $\frac{\partial^2 f_1}{\partial y^2} = \frac{\partial^2 f_3}{\partial y^2} = 0$. Hence

$$D_{\mathbf{u}}^2\mathbf{F}(\mathbf{v}, \mathbf{v}) \Big|_{(\mathbf{0}, c^*)} = \begin{pmatrix} 0 \\ -2b_2 - \frac{2c^*nx^*}{(mx^* + 1)^2} \\ 0 \end{pmatrix}.$$

$$\mathbf{w}^T[D_{\mathbf{u}}^2\mathbf{F}(\mathbf{v}, \mathbf{v})] = -2b_2 - \frac{2c^*nx^*}{(mx^* + 1)^2} < 0 \neq 0.$$

Therefore, (S3) holds. By Sotomayor's theorem, the system undergoes a transcritical bifurcation at $(\mathbf{0}, c^*)$. Conclusion (i) is proved.

Center manifold reduction. By Proposition 1, the center direction is $\mathbf{v}$ and the stable directions span the (u, w) -plane. The center manifold theorem [40] guarantees the existence of a local C^1 center manifold:

$$W_{\text{loc}}^c = \{(u, v, w) : u = h_1(v, c), w = h_2(v, c), |v| < \delta, |c - c^*| < \delta\},$$

where $h_i(0, c^*) = 0$ and $Dh_i(0, c^*) = 0$.

On W_{loc}^c , the v -dynamics become

$$\dot{v} = v \left[a_2 - b_2 v + \frac{c(x^* + h_1)}{m(x^* + h_1) + nv + 1} - \alpha(z^* + h_2) \right].$$

Expanding the BD term in a Taylor series and using $h_i = O(v^2, \mu v, \mu^2)$ (the center manifold is quadratically tangent to the center direction):

$$\frac{c(x^* + h_1)}{m(x^* + h_1) + nv + 1} = \frac{cx^*}{mx^* + 1} - \frac{cnx^*}{(mx^* + 1)^2} v + O(v^2, \mu v, \mu^2).$$

Substituting:

$$\begin{aligned} \dot{v} &= v \left[\mu(c) - \left(b_2 + \frac{cnx^*}{(mx^* + 1)^2} \right) v + O(v^2, \mu v, \mu^2) \right] \\ &= \mu(c) v - \gamma(c) v^2 + O(v^3, \mu v^2, \mu^2 v). \end{aligned}$$

Conclusion (iv) is proved. The inequality $\gamma(c) > 0$ confirms that the normal form is indeed of transcritical type (rather than pitchfork).

The reduced one-dimensional system has two equilibria: $v = 0$ (corresponding to E_3) and $v = \mu/\gamma$ (the y -component of E_4). Their stability follows directly: when $\mu < 0$, $v = 0$ is stable and $v = \mu/\gamma < 0$ lies outside the nonnegative half-line; when $\mu > 0$, $v = 0$ is unstable and $v = \mu/\gamma > 0$ is stable. By the reduction principle [40], the local stability of the full system is completely determined by the reduced dynamics. Conclusions (ii) and (iii) are proved. $\square$

4.3. Global Nature of the Bifurcation and Structural Absence of Oscillations

Combining the results of Sections 3 and 4, we obtain the following global conclusion:

Corollary 1 (Global Transcritical Bifurcation). *Under the conditions of Theorem 6:*

- For $c < c^*$, E_3 is the unique global attractor of system (2) in $\mathbb{R}_+^3$;
- For $c > c^*$, E_4 is the unique global attractor of system (2) in $\mathbb{R}_+^3$;
- The system possesses no limit cycles, invariant tori, or other non-trivial compact invariant sets.

This elevates what is usually a merely local transcritical bifurcation to a global transcritical bifurcation: over the entire range of the bifurcation parameter, the system converges to a unique equilibrium, and the dynamics are globally devoid of complexity.

Remark 3 (Structural reasons for the absence of oscillatory dynamics). *The conclusion that system (2) admits no Hopf bifurcation, no limit cycles, and no quasiperiodic solutions is not an artifact of the particular parameter values chosen; it has a clear structural origin rooted in the unilateral coupling architecture. Three independent mathematical arguments support this result.*

- (i) **Jacobian sign structure precludes Hopf bifurcation.** At the bifurcation point $E_3(c^*)$, the Jacobian (14) has its second column identically zero—a direct consequence of the fact that y does not appear in $\dot{x}$ or $\dot{z}$. The characteristic polynomial therefore factorizes as $\lambda \cdot \det(\lambda I - J_{xz})$, where J_{xz} is the Jacobian of the (x, z) -subsystem. Since J_{xz} is a 2×2 matrix whose eigenvalues have strictly negative real parts for all admissible parameters (Proposition 1), the full 3×3 Jacobian can never possess a pair of purely imaginary eigenvalues. Hence Hopf bifurcation is ruled out a priori by the sign pattern of the interaction matrix—no additional genericity conditions need to be checked.

- (ii) **Asymptotic reduction to one-dimensional monotone dynamics.** As established in Sections 3.2 and 3.3, the ω -limit set of every trajectory lies in the invariant fiber $\Sigma_3 = \{(x^*, y, z^*) : y \geq 0\}$, on which the y -dynamics reduce to the scalar ODE $\dot{y} = yF(y)$ with $F'(y) < 0$ for all $y \geq 0$. A one-dimensional autonomous system cannot support periodic orbits, and the strict monotonicity of F further guarantees that convergence is monotone rather than oscillatory. The transcritical normal form $\dot{v} = \mu v - \gamma v^2$ derived in Theorem 6 is precisely the universal unfolding of this one-dimensional dynamics on the center manifold.
- (iii) **Absence of bidirectional feedback loops.** In classical ecological models, oscillations arise from closed negative-feedback cycles: prey stimulates predator growth, which in turn suppresses prey, creating alternating phases of expansion and decline. In system (2), all inter-specific interactions are strictly unilateral—the commensal benefit $\frac{cx}{mx+ny+1}$ flows from sea anemones to clownfish without reciprocation, and the amensal inhibition $-\alpha z$ acts on clownfish without clownfish affecting crustaceans. No species both influences and is influenced by another. The dynamical consequence is that the interaction graph contains no directed cycles, and the system is effectively open-loop with respect to interspecific couplings.

These structural features are not peculiar to the present model; they characterize the entire class of continuous-time ODE systems in which the (x, z) -subsystem is autonomous and the third species y is a passive responder. Within this class, the transcritical bifurcation proved in Theorem 6 is the only codimension-one bifurcation that can occur in the positive orthant.

5. Numerical Verification

5.1. Simulation Setup and Case Studies

We adopt the following parameter set (ecologically plausible and satisfying $c^* > 0$):

Parameter	Value	Biological Meaning
a_1	2.0	Intrinsic growth rate of sea anemone
b_1	1.0	Intraspecific competition of sea anemone
β	1.0	Food subsidy from crustaceans to sea anemone
a_2	0.5	Intrinsic growth rate of clownfish
b_2	1.0	Intraspecific competition of clownfish
α	1.0	Amensal inhibition coefficient
a_3	2.0	Growth parameter of crustacean
b_3	1.0	Intraspecific competition of crustacean
m	1.0	BD half-saturation constant (with respect to x)
n	1.0	BD half-saturation constant (with respect to y)
c	Variable	Commensal benefit coefficient (bifurcation parameter)

Computation yields: $x^* \approx 2.3593$, $z^* \approx 0.8477$, $c^* \approx 0.4951$.

Case A: $c = 0.3 < c^*$ (Extinction of the commensal species).

Five distinct initial conditions are chosen to verify global convergence:

IC	$x(0)$	$y(0)$	$z(0)$
IC1	1.0	0.5	0.3
IC2	3.0	1.0	1.5
IC3	0.5	0.2	0.1
IC4	4.0	1.5	2.0
IC5	2.0	0.05	0.5

Numerical simulations ($T = 80$, fourth-order Runge–Kutta with adaptive step size) reveal: $x(t) \rightarrow 2.3593$ and $z(t) \rightarrow 0.8477$ for all initial conditions; and $y(t)$ decreases monotonically to 0 ($y(80) < 10^{-8}$ for all ICs). In the 3D phase portrait, all trajectories

converge to $E_3 = (2.3593, 0, 0.8477)$ on the (x, z) -plane. Figures 1–3 are the time series solution of $x(t)$, $y(t)$ and $z(t)$, respectively. Figure 4 is the 3D phase portrait of the system. Figure 5 is the projection of solutions onto the xz -plane. One could see that $(x(t), z(t)) \rightarrow (x^*, z^*)$ as $t \rightarrow +\infty$.

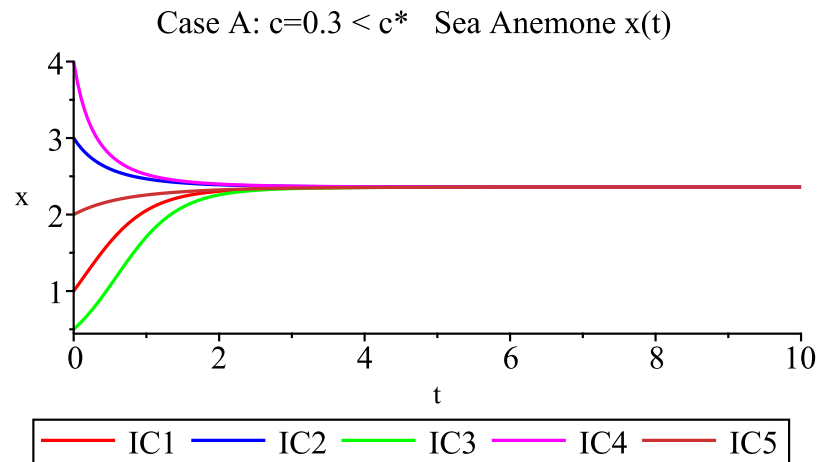


Figure 1. Time series solutions of sea anemone $x(t)$ for case $c = 0.3$.

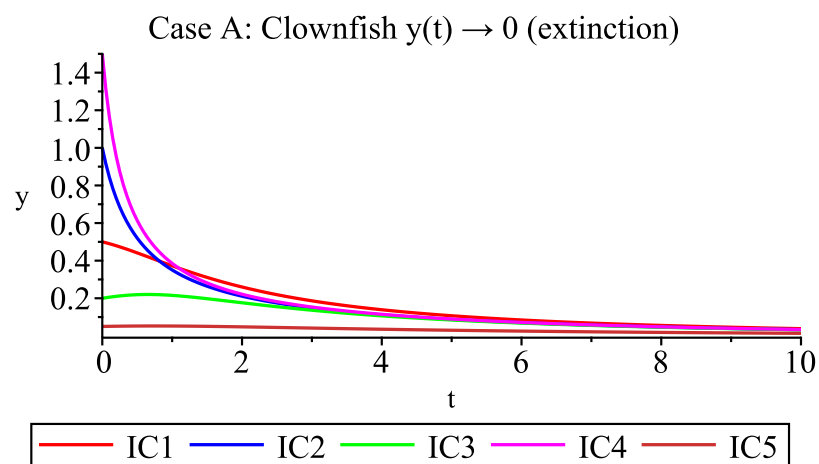


Figure 2. Time series solutions of clownfish $y(t)$ for case $c = 0.3$.

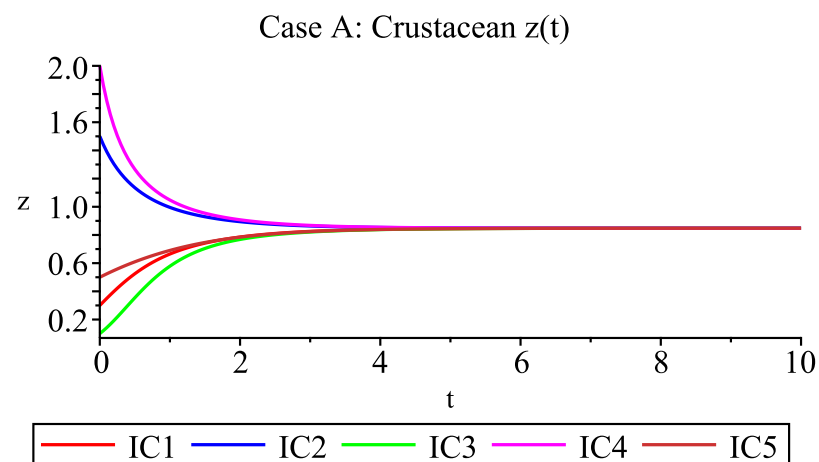


Figure 3. Time series solutions of crustacean $z(t)$ for case $c = 0.3$.

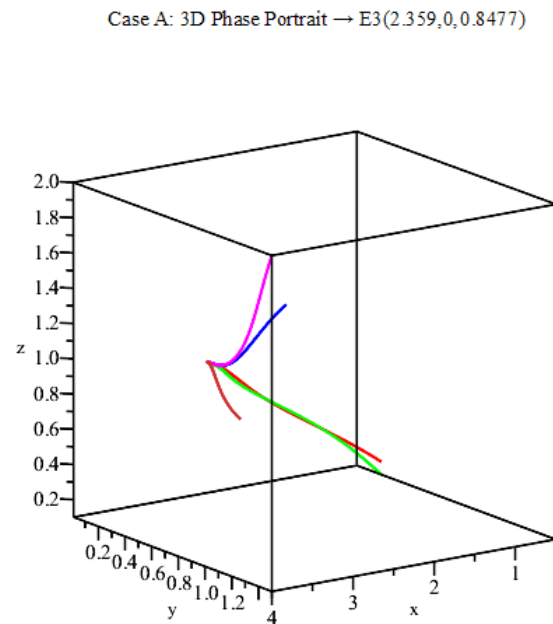


Figure 4. 3D phase portrait of the system for the case $c = 0.3$.

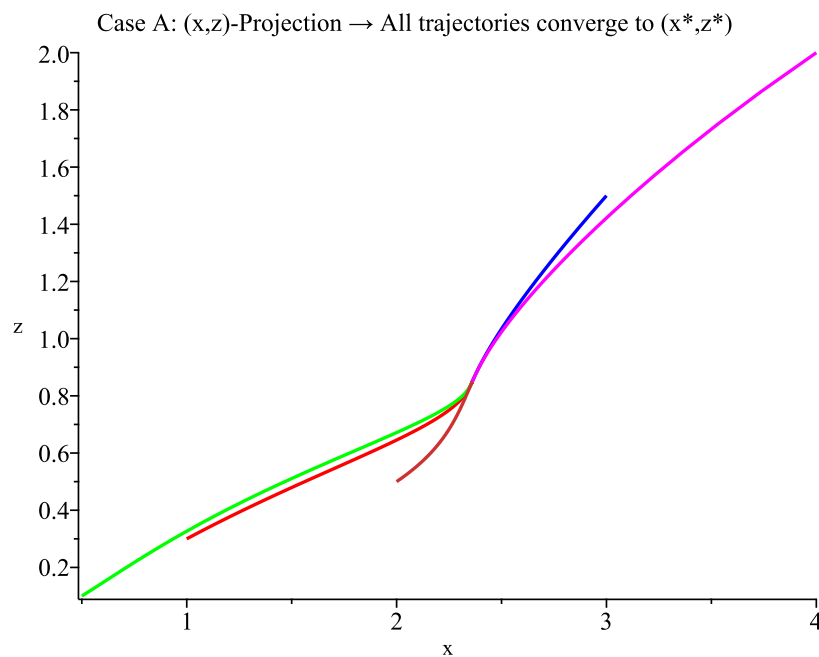


Figure 5. Projection of solutions onto the xz -plane.

Case B: $c = 0.7 > c^*$ (Three-species coexistence).

With $c = 0.7$, we obtain $y^* \approx 0.12613$. Using five distinct initial conditions distributed across the phase space (with $y(0)$ values 0.3, 0.8, 0.05, 1.5, 0.01), all trajectories converge to $E_4 = (2.3593, 0.1263, 0.8477)$. Figures 6–8 are the time series solution of $x(t)$, $y(t)$ and $z(t)$, respectively. Figure 9 is the 3D phase portrait of the system.

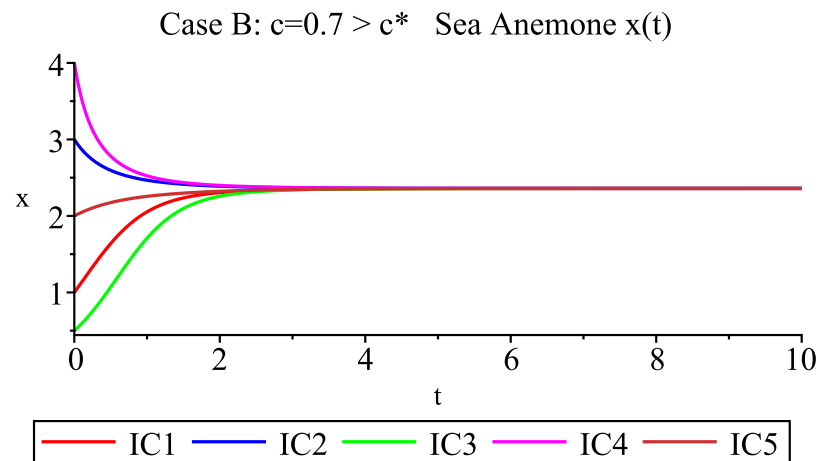


Figure 6. Time series solutions of sea anemone $x(t)$ for case $c = 0.7$.

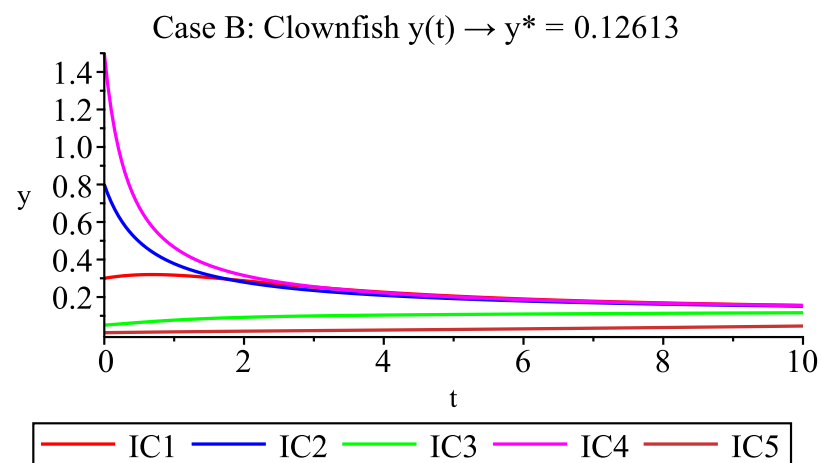


Figure 7. Time series solutions of clownfish $y(t)$ for case $c = 0.7$.

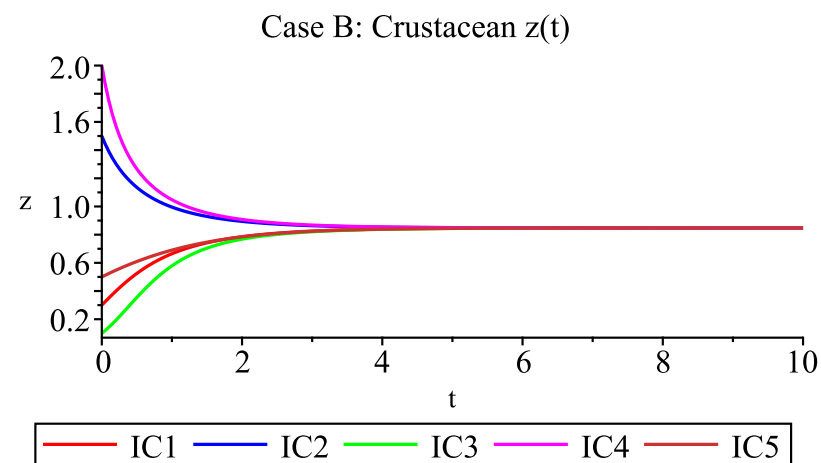
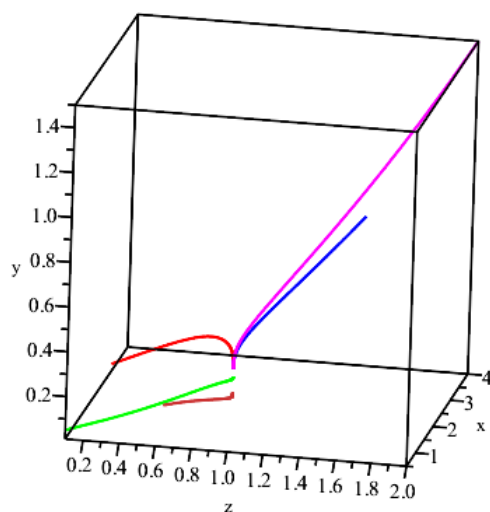
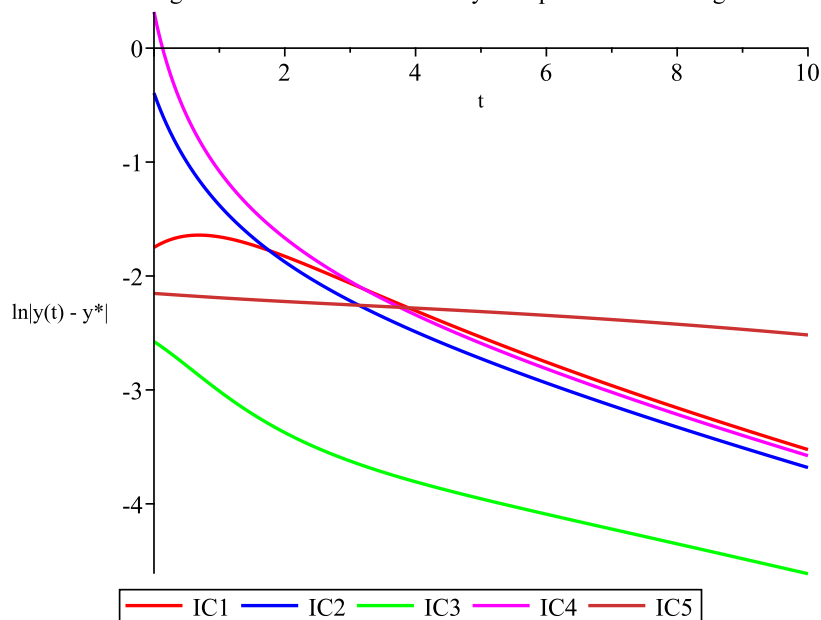


Figure 8. Time series solutions of crustacean $z(t)$ for case $c = 0.7$.

Case B: 3D Phase Portrait $\rightarrow E_4(2.359, 0.1261, 0.8477)$

Figure 9. 3D phase portrait of the system for the case $c = 0.7$.

The $\ln |y(t) - y^*|$ plot (Figure 10) exhibits a clear linear decay trend, confirming the exponential convergence rate. Theoretically, the exponential decay rate is governed by $\gamma(0.7) \approx 1.02$, corresponding to a half-life of approximately 0.68 time units.

Case B: Logarithmic Scale - Linear Decay = Exponential Convergence


Figure 10. Graph of the function $\ln |y(t) - y^*|$.

5.2. Bifurcation Diagram and Numerical Validation

Scanning $c \in [0.05, 1.0]$ (step size 0.025, 40 values in total), for each c we integrate from $(x, y, z) = (2, 0.3, 0.5)$ to $T = 200$ and record $y(200)$ as the steady-state value $y(\infty)$. Comparison of the numerical scatter plot (blue filled circles) with the theoretical bifurcation curve $y^*(c)$ (red solid line) (Figure 11) demonstrates:

- For $c < c^* \approx 0.495$, $y(\infty) = 0$ (the zero branch), in exact agreement with the theory;

- For $c > c^*$, $y(\infty) > 0$ (the nonzero branch), and the numerical points lie almost perfectly on the theoretical curve;
- At $c = c^*$, the zero and nonzero branches intersect, exhibiting the classical transcritical bifurcation morphology.

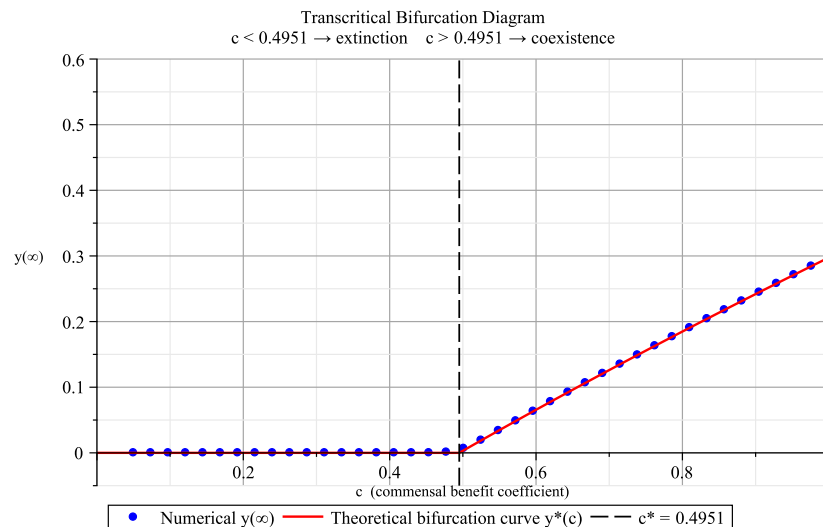


Figure 11. Transcritical bifurcation diagram.

Verification of the limit function $F(y)$.

For $c = 0.7$, plotting $F(y) = a_2 - b_2y + \frac{cx^*}{mx^* + ny + 1} - \alpha z^*$ confirms that $F(y)$ is strictly decreasing ($F'(y^*) \approx -1.02$) and that $F(y) = 0$ has a unique root y^* in $(0, 0.5)$, ruling out the possibility of multiple coexisting equilibria in the one-dimensional limit equation (Figure 12).

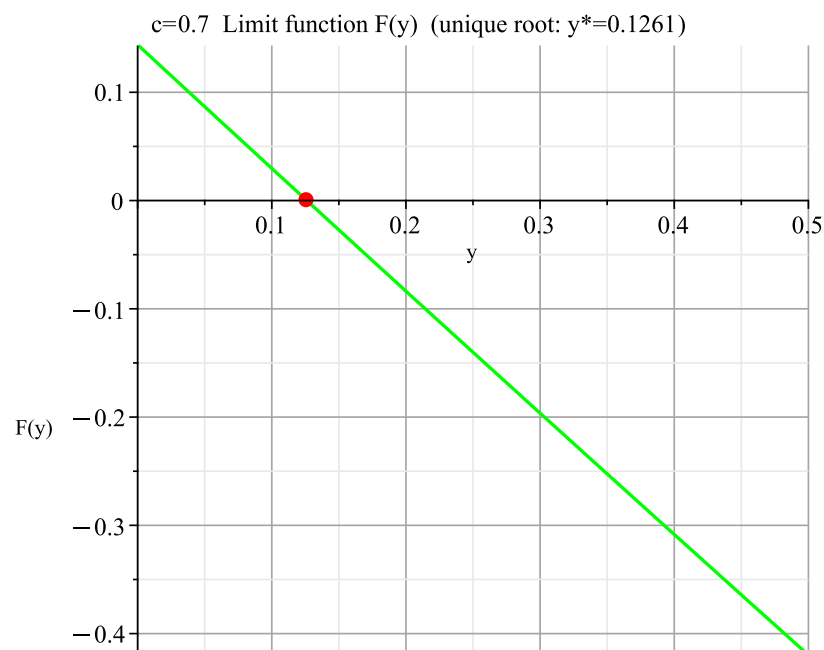


Figure 12. Strictly decreasing of function $F(y)$, $y \in (0, +\infty)$.

6. Discussion

6.1. Comparison with Existing Results

Shofiyya et al. [30] obtained, via local linearization, the stability condition $c < c^*$ for E_3 and $c < c^{**}$ for E_4 , but did not reveal the bifurcation relationship between the two equilibria. The present paper has proved that:

- As c approaches c^* from below, E_3 and E_4 coincide at $(x^*, 0, z^*)$;
- A transcritical bifurcation occurs at $c = c^*$, with stability exchanged between E_3 and E_4 ;
- The bifurcation is **global**; i.e., there exist no attractors other than the locally stable equilibrium.

In other words, the stability condition $c < c^*$ for E_3 in the original paper is algebraically equivalent to the existence condition $B_3 < 0$ for E_4 —indeed, $B_3 < 0 \iff c > c^*$, which we have rigorously proved. The condition $c < c^{**}$ in the original paper is thus essentially a more conservative subset of $c > c^*$.

6.2. Superiority of the Lyapunov Approach

Global stability analysis of systems with three or more species has traditionally been avoided due to the difficulty of constructing Lyapunov functions. The success of the present paper stems from two structural features of the model: the decoupling of the (x, z) -subsystem, and the algebraic form of the BD functional response, which allows the cross term to be eliminated by tuning a single parameter. The applicability of the Volterra-type function $\int_{x^*}^x \frac{\xi - x^*}{\xi} d\xi$ in commensalism–amensalism systems suggests that similar constructions may be systematically feasible for a broad class of ecological models with unilateral interactions.

6.3. Ecological Implications

The central ecological findings of this paper can be summarized in three points:

- (1) A threshold dictates invasion success. The persistence of the commensal species (clownfish) is determined by a precise threshold c^* . This threshold represents a delicate balance between the commensal benefit term $\frac{cx^*}{mx^*+1}$ and the amensal loss term $\frac{\alpha a_3}{b_3 x^*}$ —the former must exceed the latter minus the intrinsic growth rate for the commensal species to invade.
- (2) The foundational role of neutral species. Regardless of the presence of the commensal species, the neutral species (sea anemone and crustacean) maintain stable positive densities. This is consistent with conclusions from two-species commensalism [15] and amensalism [9] models: neutral species constitute the cornerstone of community persistence.
- (3) Convergent dynamics without oscillations. Global convergence to a fixed point implies the absence of the oscillatory behavior commonly observed in predator–prey systems. This feature stems from the very nature of unilateral interactions—the lack of bidirectional negative feedback loops predisposes the dynamics toward monotone convergence. A detailed mathematical and ecological discussion is provided in Section 6.4.

6.4. Structural Absence of Oscillatory Dynamics

The global convergence result established in Sections 3 and 4 and Corollary 1 implies that system (2) exhibits no oscillatory behavior whatsoever—no Hopf bifurcations, no limit cycles, no periodic or quasiperiodic solutions. This finding naturally raises three questions, which we address below.

6.4.1. Is the Absence of Oscillations an Intrinsic Structural Property of Unilateral Interactions?

The evidence presented in this paper, together with the pattern observed across the literature surveyed in Section 1 (see Table 1), strongly supports an affirmative answer. As detailed in Remark 3, the absence of oscillations stems from three structural features shared by pure unilateral-interaction models: (i) the Jacobian possesses a zero column, factorizing the characteristic polynomial and precluding purely imaginary eigenvalues; (ii) the asymptotic dynamics reduce to a one-dimensional gradient-like system on an invariant fiber; and (iii) no species both affects and is affected by another—bidirectional feedback loops, the engines of oscillation in predator–prey and food-web models, are absent.

These features are not parameter-dependent; they follow directly from the interaction architecture. Table 1 reveals a striking dichotomy: models incorporating at least one bidirectional antagonistic interaction (Type II: predation + competition + commensalism) exhibit Hopf bifurcations and chaos [25,26], while all pure unilateral-interaction models (Types I, III, IV) display only equilibrium convergence. This suggests that the dynamical simplicity observed here is a *signature* of pure unilateral interaction networks, not a limitation of the specific model.

6.4.2. Could Modifications of the Model Produce Hopf or Hopf-like Bifurcations?

While the present model is structurally incapable of supporting oscillatory dynamics, several biologically plausible modifications could alter this conclusion. First, introducing a time delay in the commensal benefit term (e.g., $\frac{cx(t-\tau)}{mx(t-\tau)+ny(t)+1}$) would increase the effective dimensionality of the system and could destabilize the equilibrium via a delay-induced Hopf bifurcation—a mechanism already documented in two-species commensalism models [18]. Second, allowing the amensal toxicity parameter α to depend on the population density of the neutral species (reflecting metabolic costs of toxin production by sea anemones) would introduce a density-dependent feedback that breaks the autonomous nature of the (x, z) -subsystem. Third, replacing the singular term a_3/x with a Holling-type or Michaelis–Menten functional response would modify the Jacobian sign pattern and could, in conjunction with other modifications, produce a pair of purely imaginary eigenvalues. Investigating these enriched model variants constitutes a natural direction for future work.

6.4.3. How Does This Behavior Compare with Related Ecological Models Exhibiting Cyclic Dynamics?

The contrast with classical ecological models is instructive. In the Lotka–Volterra predator–prey system and its derivatives, the bidirectional antagonistic interaction creates a closed feedback loop that generates neutrally stable cycles or, with nonlinear functional responses, stable limit cycles via Hopf bifurcation [2,39]. Even in models where commensalism or amensalism is present, oscillatory dynamics persist as long as at least one bidirectional interaction remains in the network—as exemplified by the Type II models in Table 1 and by broader food-web modelling studies [4].

What distinguishes system (2) is that it is, to the best of our knowledge, the first three-species model in which *all* interspecific interactions are strictly unilateral (commensalism + amensalism) *and* a nonlinear functional response (Beddington–DeAngelis) is employed. The resulting dynamical picture—global convergence to a unique equilibrium, with a single transcritical bifurcation as the only qualitative transition—may therefore be viewed not as a shortcoming but as a characteristic dynamical signature of pure unilateral interaction networks. From an ecological standpoint, this suggests that communities structured predominantly by commensalistic and amensalistic interactions may exhibit

greater long-term predictability and be less prone to boom–bust population cycles than those governed by predation and competition.

7. Conclusions

This paper has provided a systematic and in-depth study of the three-species commensalism–amensalism model proposed by Shofiyya et al. [30]. The main conclusions are as follows:

- (1) By constructing a Volterra-type Lyapunov function, we proved that the unique positive equilibrium of the (x, z) -subsystem is globally asymptotically stable in $\mathbb{R}_{+}^2$, and subsequently established, via ω -limit set analysis, the global asymptotic stability of E_3 (amensal extinction) and E_4 (three-species coexistence). These results elevate the local stability conclusions of the original paper to the global level.
- (2) We rigorously proved that the system undergoes a transcritical bifurcation at $c = c^*$. Through verification of all three conditions of Sotomayor’s theorem and center manifold reduction, we derived the classical normal form $\dot{y} = \mu(c)y - \gamma(c)y^2$. The bifurcation is global: over the entire range of c , the system converges precisely to a unique equilibrium.
- (3) We provided complete Maple-based numerical verification: time series and 3D phase portraits for multiple initial conditions, together with a bifurcation diagram, were all in excellent agreement with the theoretical conclusions. Logarithmic-scale plots confirmed the exponential convergence rate.

From a methodological perspective, this paper demonstrates how the organic combination of Lyapunov’s direct method, Sotomayor’s bifurcation theorem, and center manifold reduction can achieve a complete qualitative analysis for a class of ecological models with unilateral interactions. From an ecological perspective, this paper reveals a precise invasion threshold in commensalism–amensalism systems, providing quantitative insight into how unilateral interactions shape community structure.

Author Contributions: Writing—original draft preparation, X.L., Q.Y. and F.C.; writing—review and editing, X.L., Q.Y. and F.C. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Social Science Project of Anhui Provincial Department of Education (2025AHGXSK30179), Anhui Provincial Research Center for Eco-agriculture of Chinese Medicinal Herbs Research Platform Project, the Social Science Project of Anhui Provincial Department of Education (2022AH051657) and the Natural Science Foundation of Fujian Province (2024J01273).

Data Availability Statement: Data are contained within the article.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Veiga, J.P. Commensalism, amensalism, and synnecrosis. In *Encyclopedia of Evolutionary Biology*; Kliman, R.M., Ed.; Academic Press: Oxford, UK, 2016; pp. 322–328.
2. Murray, J.D. *Mathematical Biology: I. An Introduction*, 3rd ed.; Interdisciplinary Applied Mathematics; Springer: Berlin/Heidelberg, Germany, 2002; Volume 17.
3. Mougi, A. The roles of amensalistic and commensalistic interactions in large ecological network stability. *Sci. Rep.* **2016**, *6*, 29929.
4. Savoca, M.S.; Giuffrida, A.; Morabito, S.; De Marco, A.; Giacobbe, S. Modelling prey–predator interactions in Messina beachrock pools. *Ecol. Model.* **2020**, *434*, 109206.
5. Sun, G.C. Qualitative analysis of a two-species amensalism model. *J. Jiamusi Univ. (Nat. Sci. Ed.)* **2003**, *21*, 283–286.
6. Guan, X.; Chen, F. Dynamical analysis of a two species amensalism model with Beddington–DeAngelis functional response and Allee effect on the second species. *Nonlinear Anal. Real World Appl.* **2019**, *48*, 71–93.

7. Luo, D.; Wang, Q. Global dynamics of a Beddington–DeAngelis amensalism system with weak Allee effect on the first species. *Appl. Math. Comput.* **2021**, *408*, 126368.
8. Zhao, M.; Du, Y. Stability and bifurcation analysis of an amensalism system with Allee effect. *Adv. Differ. Equ.* **2020**, *2020*, 341.
9. Zhao, M.; Ma, Y.; Du, Y. Global dynamics of an amensalism system with Michaelis–Menten type harvesting. *Electron. Res. Arch.* **2023**, *31*, 549.
10. Chong, Y.; Chen, F. Global stability, bifurcations and chaos control in a discrete amensalism model with cover and saturation effect. *J. Appl. Anal. Comput.* **2025**, *15*, 2977–3003.
11. Guo, X.; Ding, L.; Hui, Y.; Song, X. Dynamics of an amensalism system with strong Allee effect and nonlinear growth rate in deterministic and fluctuating environment. *Nonlinear Dyn.* **2024**, *112*, 21389–21408.
12. Luo, D.; Qiu, Y. Global dynamics of a Holling-II amensalism system with a strong Allee effect on the harmful species. *Int. J. Bifurc. Chaos* **2024**, *34*, 2450115.
13. Bugalia, S.; Kumar, S.; Triapthi, J.P.; Martcheva, M. Dynamic interplay of Allee effect and harvesting in a diseased amensalism model: Unraveling ecological complexity. *Math. Comput. Simul.* **2026**, *245*, 295–324.
14. Singh, M.K.; Sharma, A. Analysis of qualitative behaviour of two-species amensalism model under constant-yield harvesting. In *AIP Conference Proceedings*; AIP Publishing LLC: Melville, NY, USA, 2025; Volume 3283, p. 040017.
15. Chen, F.; Li, Z.; Chen, L. Dynamic behaviors of a stage structure commensalism system with Holling type II commensalistic benefits. *Wseas Trans. Math.* **2022**, *21*, 810–824.
16. Fang, K.; Wang, Y.; Chen, F.; Chen, X. Dynamics of a modified Lotka–Volterra commensalism system incorporating Allee effect and symmetric non-selective harvest. *Symmetry* **2025**, *17*, 852.
17. Ditta, A.; Naik, P.A.; Ahmed, R.; Huang, Z. Exploring periodic behavior and dynamical analysis in a harvested discrete-time commensalism system. *Int. J. Dyn. Control* **2025**, *13*, 63.
18. Qu, M. Dynamical analysis of a Beddington–DeAngelis commensalism system with two time delays. *J. Appl. Math. Comput.* **2023**, *69*, 4111–4134.
19. Tassaddiq, A.; Ahmed, R.; Ditta, A. Exploring stability and bifurcation in a discretized commensalism model. *Nonlinear Dyn.* **2025**, *113*, 28463–28475.
20. Sari, T. Commensalism and syntrophy in the chemostat: A unifying graphical approach. *AIMS Math.* **2024**, *9*, 18625–18669.
21. Osuna, O.; Villavicencio-Pulido, G. A seasonal commensalism model with a weak Allee effect to describe climate-mediated shifts. *Sel. Mat.* **2024**, *11*, 212–221.
22. Puspitasari, N.; Kusumawinahyu, W.M.; Trisilowati. Dynamic analysis of the symbiotic model of commensalism and parasitism with harvesting in commensal populations. *JTAM (J. Teor. Dan Apl. Mat.)* **2021**, *5*, 193–204.
23. Liu, X.; Yue, Q. Stability property of the boundary equilibria of a symbiotic model of commensalism and parasitism with harvesting in commensal populations. *AIMS Math.* **2022**, *7*, 18793–18808.
24. Chen, F.; Zhou, Q.; Lin, S. Global stability of symbiotic model of commensalism and parasitism with harvesting in commensal populations. *WSEAS Trans. Math.* **2022**, *21*, 424–428.
25. Gakkhar, S.; Gupta, K. A three species dynamical system involving prey–predation, competition and commensalism. *Appl. Math. Comput.* **2016**, *273*, 54–67.
26. Gupta, P.; Jena, I.; Priyadarshi, A. Complex dynamics of a tri-trophic food web model under commensalism, refuse and competition. *J. Sci. Res. (Banaras Hindu Univ.)* **2023**, *67*, 57–72.
27. Abd Alhadi, A.R.S.; Naji, R.K. The contribution of amensalism and parasitism in the three-species ecological system’s dynamic. *Commun. Math. Biol. Neurosci.* **2024**, *2024*, 33.
28. Abd Alhadi, A.R.S.; Naji, R.K. The role of amensalism and parasitism on the dynamics of three species ecological system. *Results Control Optim.* **2025**, *19*, 100571.
29. Jawad, S.; Hassan, S.K. Bifurcation analysis of commensalism interaction and harvesting on food chain model. *Braz. J. Biom.* **2023**, *41*, 218–233.
30. Shofiyya, N.; Kusumawinahyu, W.M.; Habibah, U. Model of three species commensalism-amensalism symbiosis with Beddington–DeAngelis functional responses. *CAUCHY—J. Mat. Murni Dan Apl.* **2025**, *10*, 1054–1068.
31. Cariello, L.; De Santis, A.; Fiore, F.; Piccoli, R.; Spagnuolo, A.; Zanetti, L.; Parente, A. Calitoxin, a neurotoxic peptide from the sea anemone *Calliactis parasitica*: Amino-acid sequence and electrophysiological properties. *Biochemistry* **1989**, *28*, 2484–2489.
32. Alwi, C.; Muzammil, W.; Susiana, S. Makanan dan kebiasaan makan kepiting merah (*Thalamita spinimana*, Dana 1852) di perairan Dompok, Tanjungpinang, Kepulauan Riau. *J. Mar. Res.* **2022**, *11*, 729–737.
33. Fish, J.; Fish, S. *A Student’s Guide to the Seashore*; Cambridge University Press: Cambridge, UK, 2011.
34. Camp, E.F.; Hobbs, J.-P.A.; De Brauwer, M.; Dumbrell, A.J.; Smith, D.J. Cohabitation promotes high diversity of clownfishes in the coral triangle. *Proc. R. Soc. B Biol. Sci.* **2016**, *283*, 20160277.
35. Xia, Y.; Zhao, N. New results on global exponential convergence of discontinuous HCNNs with time-varying leakage delays. *Complex Syst. Stab. Control* **2026**, *2*, 8.

36. Florko, K.R.N.; Davidson, E.R.; Lees, K.J.; Hammer, L.J.; Lavoie, M.F.; Lennox, R.J.; Simard, E.; Archambault, P.; Auger-Méthé, M.; McKindsey, C.W.; et al. Tracking movements of decapod crustaceans: A review of a half-century of telemetry-based studies. *Mar. Ecol. Prog. Ser.* **2021**, *679*, 219–239.
37. Clarke, J.L.; Davey, P.A.; Aldred, N. Sea anemones (*Exaiptasia pallida*) use a secreted adhesive and complex pedal disc morphology for surface attachment. *BMC Zool.* **2020**, *5*, 5.
38. Chen, L.S. *Mathematical Models and Methods in Ecology*; Science Press: Beijing, China, 1988. (In Chinese)
39. Perko, L. *Differential Equations and Dynamical Systems*, 3rd ed.; Springer Science & Business Media: Berlin/Heidelberg, Germany, 2013.
40. Carr, J. *Applications of Centre Manifold Theory*; Springer Science & Business Media: Berlin/Heidelberg, Germany, 2012.

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.