On the dynamics of an intraguild predator–prey model

F. Capone\textsuperscript{a}, M.F. Carfora\textsuperscript{b}, R. De Luca\textsuperscript{a}, I. Torcicollo\textsuperscript{b,}\textsuperscript{*}

\textsuperscript{a}Department of Mathematics and Applications “R. Caccioppoli”, University of Naples Federico II, Via Cintia, Naples, Italy
\textsuperscript{b}Istituto per le Applicazioni del Calcolo “Mauro Picone”, Via P. Castellino 111, CNR, Naples, Italy

Received 20 April 2017; received in revised form 8 November 2017; accepted 18 January 2018

Available online xxxxx

Abstract

An intraguild predator–prey model with a carrying capacity proportional to the biotic resource, is generalized by introducing a Holling type II functional response. The longtime behavior of solutions is analyzed and, in particular, absorbing sets in the phase space are determined. The existence of biologically meaningful equilibria (boundary and internal equilibria) has been investigated. Linear and nonlinear stability conditions for biologically meaningful equilibria are performed. Finally, numerical simulations on different regimes of coexistence and extinction of the involved populations have been shown.

© 2018 International Association for Mathematics and Computers in Simulation (IMACS). Published by Elsevier B.V. All rights reserved.

Keywords: Intraguild predation; Stability; Longtime behavior; Holling type II functional response

1. Introduction

Studies of predator–prey models have been performed in theoretical ecology since the early days of this discipline after the pioneering works of Lotka and Volterra. Many researchers have paid great attention to the dynamics of populations (see for instance [3,4,21,23–25], and references therein) and a number of predator–prey models have been proposed and studied. Such a modeling provides challenges and ideas in many other fields of applied mathematics such as structural engineering, ecology, aerospace science and economics in which nonlinear mathematical models having a similar structure are considered (see for instance [1,2,20,21,26] and reference therein). In fact, many authors tried to make theory more realistic, by presenting various functional responses (see for instance [3,12,21,24,25]), different types of carrying capacity (see for instance [9,24,25]), non-autonomous systems [4], or heterogeneous mixed populations [3]. Generally, the idea of carrying capacity as the environment maximal load defines the limited growth of a population. Usually, in the classical predator–prey population growth models, the environmental carrying capacity is assumed to be a fixed quantity. This assumption is not realistic as the environment generally varies with time. To make this theory more realistic, functional forms of carrying capacities have been used. Just to give an idea, in order

\* Corresponding author.

E-mail addresses: fcapone@unina.it (F. Capone), f.carfora@iac.cnr.it (M.F. Carfora), roberta.deluca@unina.it (R. De Luca), i.torcicollo@iac.cnr.it (I. Torcicollo).

https://doi.org/10.1016/j.matcom.2018.01.004

0378-4754/© 2018 International Association for Mathematics and Computers in Simulation (IMACS). Published by Elsevier B.V. All rights reserved.
to capture the dynamical behavior between a population and its environment, carrying capacity as a state variable has been proposed (see for instance [9]). Recently, a modified predator–prey model, based on the ratio-dependent models, investigating the dynamics of a predator and a prey that share the same resource has been proposed in [23–25]. Distinct from other models, in [23–25], the authors formulate the carrying capacity proportional to a biotic resource and both predator and prey species can directly alter the amount of resource available by interacting with it. In addition, it is different from predation as traditionally defined, because a predator also competes with its prey for a common resource (intraguild predation (IGP)). In this way, a predator, not only directly gains energy and nutrients, but also reduces potential competition for food and it may have profound effects on community structure. Various studies suggest that direct effects of one species (predator) on another one (prey) can indirectly affect the biotic resource (other prey species) by releasing it, for example, from intense predation [8,13,14,17,22]. Several studies of IGP in natural communities have uncovered direct and indirect interactions involving spiders. In [10,15,16,27] the authors investigated a desert community of arachnids including spiders, solpugids and scorpions, all generalist predators on the same types of arthropod prey and preying on each other. In particular scorpions were continually removed from experimental plots (prey species) and the relative abundances of spiders and solpugids were tracked over time. Intraguild predation occurs also in systems (especially aquatic) with stage-or size-structured populations. Individual growth in size often induces ontogenetic diet shifts [6]. For example, during development, individuals of predatory species with large adult size tend to grow through size ranges that are comparable to their future prey species. Young (small) individuals of the predatory species thus utilize resources that are similar to those used by the prey species. As a result of an increase in individual size of the predatory species, this primary competitive interaction later shifts to a predator–prey interaction. An example is the interaction between Eurasian perch (predator), roach (prey species) and zooplankton (resource) [12].

To study the predator–prey dynamics, in [23–25], the authors propose a model based on a linear response function. The most well-known predator–prey response is a linear function, called mass action or also Holling type I. It is an adequate model if there is no handling time of the captured prey. This assumption is often regarded to be too crude since predators often experience satiation so that their consumption rate declines with abundant available food, a property that is clearly not shown by a linear function [7]. To better express the shape of consumption rate, the Holling type II functional response is introduced, which is the most widely used functional response. In the present paper, starting from [24], the above-mentioned model is thus formulated using a Holling type II functional response, as the latter better suited to model feeding, which is subject to satiation when too large amounts of prey are present [11].

In view of the large number of parameters of the model, a blind search in the parameter space for necessary and sufficient conditions that lead to stability of equilibrium is very difficult. However, we do provide an almost complete classification of all the cases that can arise. This mathematical effort specifically characterizes this investigation. It is instrumental to provide guidelines for the parameter choices, and its usefulness is shown by the fact that on this basis the latter better suited to model feeding, which is subject to satiation when too large amounts of prey are present [11].

The plan of the paper is the following. Section 2 is devoted to some preliminaries. Long-time behavior of solutions is investigated in Section 3, where the existence of absorbing sets is proved. The existence of biologically meaningful equilibria is analyzed in Section 4, while stability topics (linear and nonlinear stability) are performed in Sections 5–7. The paper ends with Section 8 concerning some numerical experiments and discussion of the obtained results.

2. Preliminaries

In this paper we analyze an extension of the model proposed in [25], by considering a Holling type II functional response \( F(X) = \frac{X}{a + X} \). Denoting by \( X, Y, Z \) respectively the prey, predator and biotic resource populations, the dynamics is governed by the following equations

\[
\frac{dX}{dt} = r_1X \left(1 - \frac{X}{pZ}\right) - \frac{aXY}{\alpha_1 + X} \tag{1a}
\]

\[
\frac{dY}{dt} = r_2Y \left(1 - \frac{Y}{qZ}\right) + \frac{bXY}{\alpha_1 + X} \tag{1b}
\]

\[
\frac{dZ}{dt} = cZ - dZ^2 - eXZ - fYZ \tag{1c}
\]
being $\alpha_1$ the half saturation constant; $r_i$ ($i = 1, 2$), growth rates of prey and predator; $pZ$ and $qZ$ set the environmental carrying capacity for each population $X$ and $Y$, respectively. It is assumed that $0 < p < 1$ and $0 < q < 1$ with $p + q = 1$ so that $pZ + qZ = Z$ is the total carrying capacity. The constants $a$ and $b$ stand for the capturing rate and the conversion rate of the consumed prey to predator respectively. In Eq. (1c), the biotic resource grows logistically with developmental rate $c$ and carrying capacity $r_1$. Furthermore, the biotic resource is consumed by $X$ and $Y$ with the uptake constants $e$ and $f$ respectively. All the constants appearing in (1a)–(1c) are assumed to be positive. By introducing the nondimensional variables

$$u = \frac{b}{r_1}X, \quad v = \frac{a}{r_1}Y, \quad w = \frac{bp}{r_1}Z, \quad \tau = r_1t$$

and

$$\eta = \frac{b}{r_1}, \quad k = \frac{bab_1}{r_1}, \quad \alpha = \frac{r_2}{r_1}, \quad \beta = \frac{bp}{qa}, \quad \gamma = \frac{c}{r_1}, \quad \epsilon = \frac{d}{b}, \quad \phi = \frac{e}{a}, \quad \delta = \frac{f}{bp}.$$ 

model (1a)–(1c) becomes

$$\dot{u} = u \left(1 - \frac{u}{w}\right) - \eta \frac{uv}{k + u}$$

(4a)

$$\dot{v} = \alpha v \left(1 - \frac{\beta v}{w}\right) + \eta \frac{uv}{k + u}$$

(4b)

$$\dot{w} = w \left(\gamma - \epsilon u - \phi v - \delta w\right)$$

(4c)

where we have denoted by $\dot{u}, \dot{v}, \dot{w}$ the derivatives with respect to $\tau$. In view of (4a)–(4c), one easily obtains that

$$u(\tau) = u_0 \exp \int_0^\tau \left(1 - \frac{u}{w} - \frac{\eta v}{k + u}\right) d\tau,$$

(5a)

$$v(\tau) = v_0 \exp \int_0^\tau \left[\alpha \left(1 - \frac{\beta v}{w}\right) + \frac{\eta u}{k + u}\right] d\tau,$$

(5b)

$$w(\tau) = w_0 \exp \int_0^\tau \left(\gamma - \epsilon u - \phi v - \delta w\right) d\tau.$$ 

Hence

$$\{u_0 > 0, v_0 > 0, w_0 > 0\} \Rightarrow \{u(\tau) > 0, v(\tau) > 0, w(\tau) > 0\}, \forall \tau > 0,$$

(6)

i.e. the positive octant is invariant.

3. Absorbing sets

In this section we investigate the asymptotic behavior of solutions of (4a)–(4c) showing that solutions are ultimately bounded. To this aim we recall the following

**Definition 1.** A set $\mathcal{A}$ of the phase space is said to be an absorbing set if:

1. $\mathcal{A}$ is positively invariant, i.e.

   $$x_0 \in \mathcal{A} \Rightarrow x(t) \in \mathcal{A}, \forall t \geq 0.$$

2. $\mathcal{A}$ is attractive, i.e. there exists an open set $\mathcal{H} \supset \mathcal{A}$ such that

   $$\lim_{t \to \infty} d(x_0, \mathcal{A}) = 0,$$

   (7)

   for any initial data $x_0 \in \mathcal{H}$, and where $d$ is the distance of $x_0$ from $\mathcal{A}$, i.e.

   $$d(t) = \inf_{\mathcal{A}} |x - x_0|.$$

**Theorem 1.** \(\forall \bar{\epsilon}\) the set

$$\mathcal{S}_\bar{\epsilon} = \left\{(u, v, w) \in \mathbb{R}^3_+ : 0 < u < \frac{\gamma}{\delta} + \bar{\epsilon}, 0 < v < \frac{\gamma(\alpha k_2 + \eta \gamma)}{\alpha \beta k \delta^2} + \bar{\epsilon}, 0 < w < \frac{\gamma}{\delta} + \bar{\epsilon}\right\}$$

(8)

is an absorbing set of the phase space.
Proof. From (4c) it turns out that
\[ \dot{w} \leq w(\gamma - \delta w), \tag{9} \]
which leads to
\[ w(\tau) \leq \frac{\gamma}{\delta} + \bar{\epsilon}, \quad \forall \tau \geq \tau_1. \tag{10} \]
Analogously, since in view of (4a) one has
\[ \dot{u} \leq u \left( 1 - \frac{\delta}{\gamma} u \right), \tag{11} \]
it follows that
\[ u(\tau) \leq \frac{\gamma}{\delta} + \bar{\epsilon}, \quad \forall \tau \geq \tau_2. \tag{12} \]
In view of (4b), from (10) and (12), on taking \( \tau \geq \tau_3 = \max\{\tau_1, \tau_2\} \), one has
\[ \dot{v} \leq v \left( \frac{\alpha k \delta + \eta \gamma}{k \delta} - \frac{\alpha \beta \delta}{\gamma} v \right). \tag{13} \]
Hence there exists \( \tau_4 > \tau_3 \) such that
\[ v(\tau) \leq \frac{\gamma (\alpha k \delta + \eta \gamma)}{\alpha \beta \delta^2} + \bar{\epsilon}, \quad \forall \tau \geq \tau_4. \tag{14} \]
In view of (10), (12) and (14), it follows that \( \forall \bar{\epsilon} > 0 \), \( S_{\bar{\epsilon}} \) is attractive. Simple calculation shows that \( \forall \bar{\epsilon} > 0 \), \( S_{\bar{\epsilon}} \) is also positively invariant and the thesis is proved.

4. Biologically meaningful equilibria

Steady states are the non-negative solutions of the system
\[ u \left[ 1 - \frac{u}{w} - \eta \frac{v}{k + u} \right] = 0 \tag{15a} \]
\[ v \left[ \alpha - \alpha \beta \frac{v}{w} + \eta \frac{u}{k + u} \right] = 0 \tag{15b} \]
\[ w \left[ \gamma - \epsilon u - \phi v - \delta w \right] = 0. \tag{15c} \]
Avoiding the solution \( E_0 = (0, 0, 0) \) which is not biologically meaningful, the boundary equilibria are given by
\[ E_1 = \left( 0, 0, \frac{\gamma}{\delta} \right), \quad E_2 = \left( 0, \frac{\gamma}{\beta \delta + \phi}, \frac{\beta \gamma}{\beta \delta + \phi} \right), \quad E_3 = \left( \frac{\gamma}{\delta + \epsilon}, 0, \frac{\gamma}{\delta + \epsilon} \right). \tag{16} \]
Ecologically, \( E_1 \) represents a steady-state that is free from predator and prey (resource only), \( E_2 \) is free from prey (predator and resource only), while \( E_3 \) is free from predator (prey and resource only). The interior equilibrium \( \bar{E} = (\bar{u}, \bar{v}, \bar{w}) \) with non-null components, which represents the coexistence of predator and prey, is given by
\[ \bar{v} = \frac{[\alpha k + (\alpha + \eta)\bar{u}] (\gamma - \epsilon \bar{u})}{\alpha k (\beta + \phi) + [\alpha \beta \delta + \phi (\alpha + \eta)] \bar{u}}, \tag{17a} \]
\[ \bar{w} = \frac{[\alpha \beta \delta + \phi] [\alpha \beta \delta + \phi (\alpha + \eta)] \bar{u}}{\alpha \beta (k + \bar{u}) (\gamma - \epsilon \bar{u})}, \tag{17b} \]
being \( 0 < \bar{u} < \frac{\gamma}{\delta + \epsilon} \) a positive root of the equation
\[ Au^3 + Bu^2 + Cu + D = 0 \tag{18} \]
where
\[ A = \alpha^2 \beta \delta^2 + \alpha^2 \beta^2 \delta \epsilon + \alpha^2 \beta \epsilon^2 \eta + \alpha \beta \epsilon^2 \eta^2 + 2 \alpha^2 \beta \delta \phi + \alpha^2 \beta \epsilon \phi + 2 \alpha \beta \delta \eta \phi + \alpha \beta \epsilon \eta \phi + \alpha^2 \phi^2 + 2 \alpha \eta \phi^2 + \eta^2 \phi^2 > 0 \tag{19} \]
\[
B = \alpha^2 \beta^2 \gamma \delta + 2k \alpha^2 \beta^2 \delta^2 + 2k \alpha^2 \beta^2 \delta \varepsilon - 2 \alpha^2 \beta \gamma \varepsilon \eta + k \alpha^2 \beta \varepsilon^2 \eta + 2k \alpha \beta \delta \eta \phi + k \alpha \beta \varepsilon \eta \phi + k \alpha^2 \beta^2 \phi^2 + 2k \alpha \eta \phi^2
\]

(20)

\[
C = -2k \alpha^2 \beta^2 \gamma \delta + k^2 \alpha^2 \beta^2 \delta^2 + k^2 \alpha^2 \beta^2 \delta \varepsilon + \alpha^2 \beta \gamma^2 \eta
- 2k \alpha^2 \beta \gamma \varepsilon \eta + \alpha \beta \gamma^2 \eta^2 - 2k \alpha^2 \beta \gamma \phi + 2k^2 \alpha^2 \beta \delta \phi + k^2 \alpha^2 \beta \varepsilon \phi
- k \alpha \beta \gamma \eta \phi + k^2 \alpha^2 \phi^2
\]

(21)

\[
D = k \alpha^2 \beta \gamma [-k \beta \delta + \gamma \eta - \phi].
\]

(22)

On setting
\[
u = \xi - \frac{B}{3A}, \quad P = \frac{C}{A} - \frac{B^2}{3A^2}, \quad Q = \frac{D}{A} - \frac{BC}{3A^2} + \frac{2B^3}{27A^3}.
\]

(23)

(18) becomes
\[
\xi^3 + P \xi + Q = 0.
\]

(24)

The solutions to (24) are
\[
\xi_1 = \xi_+ + \xi_-, \quad \xi_{2,3} = -\frac{\xi_+ + \xi_-}{2} \pm \frac{i}{2} \sqrt{3}
\]

where
\[
\xi_+ = \sqrt[3]{-\frac{Q}{2} + \sqrt{\frac{Q^2}{4} + \frac{P^3}{27}}} , \quad \xi_- = \sqrt[3]{-\frac{Q}{2} - \sqrt{\frac{Q^2}{4} + \frac{P^3}{27}}}.
\]

(25)

hence, for \(i = 1, 2, 3\)
\[
(\tilde{u}, \tilde{v}, \tilde{w}) \equiv \left(\xi_i - \frac{B}{3A}, \gamma - \frac{\varepsilon}{\phi} \tilde{u} - \delta \tilde{w}, \frac{\alpha \beta (k + \tilde{u})(\gamma - \varepsilon \tilde{u}) + \alpha k (\beta \delta \phi + \phi (\alpha + \eta) \tilde{u})}{\alpha k (\beta \delta + \phi) + [\alpha \beta \delta + \phi (\alpha + \eta) \tilde{u}]}ight).
\]

Precisely, if \(\tilde{A} = \frac{Q^2}{4} + \frac{P^3}{27}\) is non positive (positive), then three (only one) real solutions are created.

**Theorem 2.** If
\[
k > \frac{\gamma \eta}{\beta \delta + \phi},
\]

(26)

then (18) admits at least one solution such that \(0 < \tilde{u} < \frac{\gamma}{\delta}\).

**Proof.** Setting \(g(u) = Au^3 + Bu^2 + Cu + D\) it turns out that
\[
\lim_{u \to \infty} g(u) = \infty, \quad g\left(\frac{\gamma}{\delta}\right) > 0.
\]

(27)

Hence if \(g(0) = D < 0\), then (18) admits at least one solution such that \(0 < \tilde{u} < \frac{\gamma}{\delta}\). The proof is immediately reached since \(D < 0\) if and only if (26) holds.

From now on, we will denote by \((u^*, v^*, w^*)\) the generic equilibrium.

**Remark 1.** From (15c) it follows that (since \(w^* \neq 0\))
\[
\gamma - \varepsilon u^* - \phi v^* - \delta w^* = 0.
\]

(28)

Then it follows that
\[
u^* < \frac{\gamma}{\varepsilon}, \quad v^* < \frac{\gamma}{\phi}, \quad w^* < \frac{\gamma}{\delta}
\]

(29)
5. Preliminaries to stability

Introducing the perturbation fields

\[ X_1 = u - u^*, \quad X_2 = v - v^*, \quad X_3 = w - w^*, \]

system (4a)–(4c) becomes

\[
\frac{d}{d\tau} \begin{pmatrix} X_1 \\ X_2 \\ X_3 \end{pmatrix} = J \begin{pmatrix} X_1 \\ X_2 \\ X_3 \end{pmatrix} + \begin{pmatrix} F_1 \\ F_2 \\ F_3 \end{pmatrix},
\]

being \( J \) the Jacobian matrix

\[
J = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix},
\]

with

\[
a_{11} = 1 - 2 \frac{u^*}{w^*} - \eta \frac{k v^*}{(k + u^*)^2}, \quad a_{12} = - \frac{\eta u^*}{k + u^*}, \quad a_{13} = \left( \frac{u^*}{w^*} \right)^2,
\]

\[
a_{21} = \frac{\eta k v^*}{(k + u^*)^2}, \quad a_{22} = \alpha + \frac{\eta u^*}{k + u^*} - \frac{2 \alpha \beta v^*}{w^*}, \quad a_{23} = \alpha \beta \left( \frac{v^*}{w^*} \right)^2,
\]

\[
a_{31} = - \varepsilon w^*, \quad a_{32} = - \phi w^*, \quad a_{33} = - \delta w^*
\]

and \((F_1(X_1, X_2, X_3), F_2(X_1, X_2, X_3), F_3(X_1, X_2, X_3))\) being the non-linear terms

\[
F_1 = - \left[ \frac{1}{\theta_3 X_3 + w^*} - \frac{\eta k (\theta_2 X_2 + v^*)}{(k + \theta_1 X_1 + u^*)^3} \right] X_1^2 \frac{(\theta_1 X_1 + u^*)^2}{(\theta_3 X_3 + w^*)^3} X_3^2
\]

\[
- \frac{\eta k}{(k + \theta_1 X_1 + u^*)^2} X_1 X_2 + 2 \frac{(\theta_1 X_1 + u^*)}{(\theta_1 X_1 + w^*)^3} X_1 X_3,
\]

\[
F_2 = - \frac{\eta k (\theta_2 X_2 + v^*)}{(k + \theta_1 X_1 + u^*)^3} X_1^2 \frac{\alpha \beta}{(\theta_3 X_3 + w^*)^3} X_3^2
\]

\[
- \frac{\eta k}{(k + \theta_1 X_1 + u^*)^2} X_1 X_2 + \frac{2 \alpha \beta (\theta_2 X_2 + v^*)}{(\theta_3 X_3 + w^*)^3} X_2 X_3,
\]

\[
F_3 = - \varepsilon X_1 X_3 - \phi X_2 X_3 - \delta X_3^2,
\]

with \( \theta_i \in (0, 1), (i = 1, 2, 3) \).

6. Linear stability

To investigate the linear stability of the biologically meaningful equilibria \( E_i \) \((i = 1, 2, 3)\) and \( \bar{E} \), in this section we will analyze the roots of the characteristic equation linked to the Jacobian matrix \( J \), i.e.

\[
\lambda^3 - I_1 \lambda^2 + I_2 \lambda - I_3 = 0
\]

where \( I_i \) \((i = 1, 2, 3)\) are the principal invariants of \( J \). As it is well known in literature, the necessary and sufficient conditions guaranteeing that all the roots of (37) have negative real part (and hence that the equilibria are linearly stable) are the Routh–Hurwitz conditions:

\[
I_1 < 0, \quad I_3 < 0, \quad I_1 I_2 - I_3 < 0.
\]

Remark 2. Let us remark that the instability of the biologically meaningful equilibria \( E_i \) \((i = 1, 2, 3)\) and \( \bar{E} \) is guaranteed when at least one of (38) is reversed. For instance, the instability of the equilibria can occur via an
oscillatory state when (37), besides a real root, admits pure imaginary roots. In particular, \( \lambda = \pm i \omega \), with \( \omega \in \mathbb{R} - \{0\} \), is a root of (37) if and only if

\[
\begin{align*}
\omega^2 &= I_2, \\
\omega^2 &= \frac{I_3}{I_1}, \\
I_1 &\in \mathbb{R} - \{0\}.
\end{align*}
\]

(39a) 

(39b)

Let us start to investigate the linear stability of \( E_1, E_2, E_3 \). The Jacobian matrix in \( E_1 = (0, 0, \frac{\gamma}{\delta}) \) is given by

\[
J_{|E_1} = \begin{pmatrix}
1 & 0 & 0 \\
0 & \alpha & 0 \\
-\epsilon \gamma \delta & -\phi \gamma \delta & -\gamma
\end{pmatrix}.
\]

(40)

Since \( J_{|E_1} \) admits two real positive eigenvalues \( \lambda_1 = 1, \lambda_2 = \alpha \), \( E_1 \) is linearly unstable.

The Jacobian matrix in \( E_3 = (\frac{\gamma}{\delta + \epsilon}, 0, \frac{\gamma}{\delta + \epsilon}) \) is given by

\[
J_{|E_3} = \begin{pmatrix}
-1 & -\frac{\eta \gamma}{k(\delta + \epsilon) + \gamma} & 1 \\
0 & \alpha + \frac{\eta \gamma}{k(\delta + \epsilon) + \gamma} & 0 \\
-\epsilon \gamma \delta + \epsilon & -\phi \gamma \delta + \epsilon & -\delta \gamma \delta + \epsilon
\end{pmatrix}.
\]

(41)

Since \( J_{|E_3} \) admits a real positive eigenvalue \( \lambda_1 = \alpha + \frac{\eta \gamma}{k(\delta + \epsilon) + \gamma} \), \( E_3 \) is linearly unstable.

Let us pass now to investigate the linear stability of \( E_2 = \left(0, \frac{\gamma}{\beta \delta + \phi}, \frac{\beta \gamma}{\beta \delta + \phi}\right) \). Since

\[
J_{|E_2} = \begin{pmatrix}
1 - \frac{\eta \gamma}{k(\beta \delta + \phi)} & 0 & 0 \\
-\alpha & -\frac{\beta \gamma}{\beta \delta + \phi} \\
-\frac{\phi \beta \gamma}{\beta \delta + \phi} & \delta \beta \gamma & \frac{\phi \beta \gamma}{\beta \delta + \phi}
\end{pmatrix}
\]

(42)

the principal invariants \( I_i \), \( i = 1, 2, 3 \) of (42) are given by

\[
\begin{align*}
I_1 &= 1 - \frac{\eta \gamma}{k(\beta \delta + \phi)} - \alpha - \frac{\beta \delta \gamma}{\beta \delta + \phi} \\
I_2 &= -\left(\alpha + \frac{\beta \delta \gamma}{\beta \delta + \phi}\right) \left(1 - \frac{\eta \gamma}{k(\beta \delta + \phi)}\right) + \alpha \gamma \\
I_3 &= \alpha \gamma \left[1 - \frac{\gamma \eta}{k(\beta \delta + \phi)}\right].
\end{align*}
\]

(43a) 

(43b) 

(43c)

The following theorem holds.

**Theorem 3.** The boundary equilibrium \( E_2 \) is linearly stable if and only if

\[
\frac{\gamma \eta}{k(\beta \delta + \phi)} > 1.
\]

(44)

**Proof.** In view of (43c),

\[
I_3 < 0 \iff \frac{\gamma \eta}{k(\beta \delta + \phi)} > 1,
\]

(45)

i.e. (44) is necessary for the (linear) stability. In order to prove sufficiency, if (44) holds, from (43a), it easily follows that \( I_1 < 0 \). In view of
Theorem 4. If

\[ I_1 I_2 - I_3 = \left[ 1 - \frac{\eta y}{k(\beta \delta + \phi)} - \alpha - \frac{\beta \delta y}{\beta \delta + \phi} \right] \left[ -\left( \alpha + \frac{\beta \delta y}{\beta \delta + \phi} \right) \left( 1 - \frac{\eta y}{k(\beta \delta + \phi)} \right) + \alpha y \right] \]

\[ - \alpha y \left[ 1 - \frac{y \eta}{k(\beta \delta + \phi)} \right] = - \left( 1 - \frac{\eta y}{k(\beta \delta + \phi)} \right)^2 \left( \alpha + \frac{\beta \delta y}{\beta \delta + \phi} \right) \]

\[ + \left( \alpha + \frac{\beta \delta y}{\beta \delta + \phi} \right)^2 \left( 1 - \frac{\eta y}{k(\beta \delta + \phi)} \right) - \alpha y \left( \alpha + \frac{\beta \delta y}{\beta \delta + \phi} \right). \]

Hence, when (44) holds, then \( I_1 I_2 - I_3 < 0 \) and (38) are satisfied.

The Jacobian matrix evaluated in \( \bar{E} = (\bar{u}, \bar{v}, \bar{w}) \) reduces to (32) where, in particular, in view of (15b) one has that

\[ \alpha + \eta \bar{u} \bar{v} = \alpha \beta \bar{v} \]

and hence \( a_{22} \) reduces to

\[ a_{22} = - \frac{\alpha \beta \bar{v}}{\bar{w}} < 0. \]

The principal \( J |_{\bar{E}} \) invariants are given by

\[ I_1 = 1 - 2 \frac{\bar{u}}{\bar{w}} - \frac{\alpha \beta \bar{v}}{\bar{w}} - \delta \bar{w} - \frac{k \eta \bar{v}}{(k + \bar{u})^2} \]

\[ I_2 = -\delta \bar{w} + \frac{\varepsilon \bar{u}^2}{\bar{w}} + \bar{v} \left( -\frac{\alpha \beta}{\bar{w}} + \alpha \beta \delta + \frac{k \delta \eta \bar{w}}{(k + \bar{u})^2} \right) \]

\[ + \bar{u} \left( \frac{2 \alpha \beta \bar{v}}{\bar{w}^2} + 2 \delta + \frac{k \eta^2 \bar{v}}{(k + \bar{u})^3} \right) + \alpha \beta \bar{v}^2 \left( \frac{k \eta}{(k + \bar{u})^2} + \phi \right) \]

\[ I_3 = -\frac{k \bar{u} \bar{v} \eta (\bar{w}^2 \delta \eta + \phi \bar{u}(k + \bar{u}))}{\bar{w}(k + \bar{u})^3} + \alpha \beta \bar{v} \left\{ \delta \left[ 1 - \frac{2 \bar{u}}{\bar{w}} - \frac{k \eta \bar{v}}{(k + \bar{u})^2} \right] \right\} \]

\[ - \frac{\bar{u}^2 \varepsilon}{\bar{w}^2} + \bar{u} \bar{v} \left\{ \frac{\bar{w} \varepsilon \eta}{k + \bar{u}} - 2 \phi \right\} + \frac{\phi \bar{v}}{\bar{w}} \left( 1 - \frac{k \eta \bar{v}}{(k + \bar{u})^2} \right). \]

Finding necessary and sufficient conditions guaranteeing that (38) (with \( I_j = \bar{I}_j, j = 1, 2, 3 \)) are verified is almost complicated due to the presence of a lot of parameters. Hence, in order to obtain at least sufficient conditions ensuring linear stability of the coexistence equilibrium \( \bar{E} \), we perform the Lyapunov stability analysis. To this end, let us consider the Lyapunov functional \( \mathcal{E} \) (see [18,19]) given by

\[ \mathcal{E} = \frac{1}{2} \mu_1 X_1^2 + \frac{1}{2} \mu_2 X_2^2 + \frac{1}{2} \mu_3 X_3^2, \]

with \( \mu_i \) positive constants \( i = 1, 2, 3 \).

Theorem 4. If

\[ 1 - 2 \frac{\bar{u}}{\bar{w}} - \eta \left( \frac{k \bar{v}}{(k + \bar{u})^2} \right) < 0 \]

\[ \left[ \frac{\alpha \beta \varepsilon \bar{v}(k + \bar{u})}{k \bar{u}} - \phi \right]^2 < \frac{\alpha \beta \varepsilon \bar{v}(k + \bar{u})}{k \bar{u}} \]

then \( \bar{E} \) (when exists) is linearly stable in the \( \mathcal{E} \)-norm.

Proof. Choosing

\[ \frac{\mu_1}{\mu_2} = - \frac{a_{21}}{a_{12}}, \quad \frac{\mu_1}{\mu_3} = - \frac{a_{31}}{a_{13}}, \]

the time derivative of \( \mathcal{E} \), along the solutions of the linearized version of system (31) is

\[ \dot{\mathcal{E}} = \mu_1 a_{11} X_1^2 + \frac{\mu_3}{\mu_5} \left[ \frac{\mu_2}{\mu_3} a_{22} X_2^2 + 2 \left( \frac{\mu_2}{\mu_3} a_{23} + a_{32} \right) X_2 X_3 + a_{33} X_3^2 \right]. \]
Since \( a_{ii} < 0, \ (i = 2, 3) \) and (53a) guarantees that \( a_{11} < 0 \), from (55) if easily follows that
\[
\left(\frac{\mu_2}{\mu_3} a_{23} + a_{12}\right)^2 < \frac{\mu_2}{\mu_3} a_{22} a_{33},
\]
implies that \( \dot{E} \) is negative definite. Substituting \( \mu_1, \mu_2, \mu_3 \) as in (54), on taking into account (33a)–(33c), the thesis is proved.

7. Nonlinear stability

In this section we perform the nonlinear stability analysis of \( E_2 \) and \( \tilde{E} \). Setting
\[
\tilde{\Phi} = \alpha_1 X_1 F_1 + \alpha_2 X_2 F_2 + \alpha_3 X_3 F_3,
\]
with \( F_i, \ (i = 1, 2, 3) \) given by (34)–(36) and \( \alpha_i, \ (i = 1, 2, 3) \), positive constants, the following lemma holds.

**Lemma 1.** There exists a positive constant \( \delta_1 \) such that
\[
\tilde{\Phi} \leq \delta_1 (X_1^2 + X_2^2 + X_3^2)^{\frac{3}{2}}.
\]

**Proof.** From (8) and (29), it turns out that
\[
\theta_1 X_1 + u^* = \theta_1 u + (1 - \theta_1) u^* \leq \theta_1 \frac{\gamma}{\delta} + (1 - \theta_1) \frac{\gamma}{\epsilon} := M_1
\]
\[
\theta_2 X_2 + v^* = \theta_2 v + (1 - \theta_2) v^* \leq \theta_2 \frac{\gamma (\alpha k \delta + \eta \gamma)}{\alpha \beta k \delta^2} + (1 - \theta_2) \frac{\gamma}{\phi} := M_2.
\]
Furthermore
\[
\theta_3 X_3 + w^* = \theta_3 w + (1 - \theta_3) w^* > (1 - \theta_3) w^* \]
\[
k + \theta_1 X_1 + u^* = k + \theta_1 u + (1 - \theta_1) u^* > k.
\]
Therefore
\[
\tilde{\Phi} \leq c_1 |X_1|^3 + c_2 |X_2|^3 + c_3 |X_3|^3 + c_4 |X_1| |X_2|^2
\]
\[
+ c_5 |X_2| |X_1|^2 + c_6 |X_3| |X_2|^2 + c_7 |X_2| |X_3|^2 + c_8 |X_1| |X_2|^2 + c_9 |X_3| |X_2|^2
\]
(61)

being
\[
c_1 = \left( \frac{\alpha_1}{(1 - \theta_3) w^*} + \frac{\alpha_1 \eta k M_2}{k^3} \right), \quad c_2 = \frac{\alpha_2 \alpha k}{(1 - \theta_3) w^*},
\]
\[
c_3 = \alpha_3 \delta, \quad c_4 = \frac{M_2 \alpha_1}{(1 - \theta_3)^3 (w^*)^3} + \alpha_3 \epsilon, \quad c_5 = \frac{\alpha_1 \eta}{k} + \frac{\alpha_2 \eta M_2}{k^2},
\]
\[
c_6 = \frac{2 M_1 \alpha_1}{(1 - \theta_3)^2 (w^*)^2}, \quad c_7 = \frac{\alpha_2 \alpha k M_2^2}{(1 - \theta_3)^3 (w^*)^3} + \alpha_3 \phi,
\]
\[
c_8 = \frac{\alpha_2 \eta}{k}, \quad c_9 = \frac{2 \alpha_2 \alpha_3 k M_2}{(1 - \theta_3)^3 (w^*)^2}.
\]

Setting
\[
d_1 = \max \{c_1, c_5, c_6\}, \quad d_2 = \max \{c_2, c_8, c_9\}, \quad d_3 = \max \{c_3, c_4, c_7\},
\]
from (61) one obtains that
\[
\tilde{\Phi} \leq (|X_1| + |X_2| + |X_3|)(d_1 X_1^2 + d_2 X_2^2 + d_3 X_3^2),(64)
\]

Since
\[
|X_1| + |X_2| + |X_3| \leq 2 \sqrt{2} [X_1^2 + X_2^2 + X_3^2],
\]
(65)

Please cite this article in press as: F. Capone et al., On the dynamics of an intraguild predator-prey model, Mathematics and Computers in Simulation (2018).
https://doi.org/10.1016/j.matcom.2018.01.004.
setting
\[ \delta_1 = 2\sqrt{2} \max\{d_1, d_2, d_3\}. \]  
(66)
it follows that (58) is proved.

Let us first investigate the nonlinear stability of \( E_2 \). Setting
\[ X_1 = \beta_1 Y_1, \quad X_2 = \beta_2 Y_2, \quad X_3 = \beta_3 Y_3 \]  
(67)
with \( \beta_i, \ (i = 1, 2, 3) \) positive constants to be suitably chosen later, system (31) becomes
\[ \frac{d}{d\tau} \begin{pmatrix} Y_1 \\ Y_2 \\ Y_3 \end{pmatrix} = \begin{pmatrix} a_{11} & 0 & 0 \\ b_{21} & a_{22} & b_{23} \\ b_{31} & b_{32} & a_{33} \end{pmatrix} \begin{pmatrix} \bar{F}_1 \\ \bar{F}_2 \\ \bar{F}_3 \end{pmatrix}, \]  
(68)
with
\[ b_{ij} = \frac{\beta_j}{\beta_i}, \ (i, j = 1, 2, 3), \]  
(69)
and \( a_{ij}, \ F_i, \ (i, j = 1, 2, 3) \) are given by (33a)–(33c) and (34)–(36) with \( u^* = 0, v^* = \gamma/(\beta\delta + \phi), w^* = \beta\gamma/(\beta\delta + \phi) \). Let us introduce the functional (see [18, 19])
\[ W = \frac{1}{2} Y_1^2 + V \]  
(70a)
\[ V = \frac{1}{2} \left[ A^*(Y_2^2 + Y_3^2) + (a_{22}Y_3 - b_{32}Y_2)^2 + (b_{23}Y_3 - a_{33}Y_2)^2 \right] \]  
(70b)
with
\[ A^* = a_{22}a_{33} - a_{23}a_{32} > 0. \]  
(71)
Setting
\[ A_1 = A^* + b_{32}^2 + a_{33}^2, \quad A_2 = A^* + b_{23}^2 + a_{22}^2 \]  
(72a)
\[ A_3 = a_{22}b_{32} + b_{23}a_{33}, \quad \Gamma^* = a_{22} + a_{33} \]  
(72b)
the time derivative of \( W \) along the solutions of (68) is
\[ \dot{W} = a_{11}Y_1^2 + A^*\Gamma^*(Y_2^2 + Y_3^2) + \bar{\phi} + \phi^*, \]  
(73)
with
\[ \bar{\phi} = \frac{1}{\beta_3} Y_1 F_1 + \frac{A_1}{\beta_2} Y_2 F_2 + \frac{A_2}{\beta_3} Y_3 F_3 \]  
(74a)
\[ \phi^* = (A_1b_{21} - A_3b_{31})Y_1 Y_2 + (A_2b_{31} - A_3b_{21})Y_1 Y_3 \]  
(74b)
and \( F_i = F_i(\beta_1 X_1, \beta_2 X_2, \beta_3 X_3) \) given by (34)–(36). The following theorem holds.

**Theorem 5.** Condition (44) guarantees the nonlinear (local) stability of \( E_2 \) in the \( W \)-norm.

**Proof.** Choosing
\[ \beta_2 = \beta_3 = 1, \]  
(75)
it turns out that
\[ \phi^* \leq \beta_1 m|Y_1|(|Y_2| + |Y_3|), \]  
(76)
with
\[ m = \sup \{|A_1b_{21} - A_3b_{31}|, |A_2b_{31} - A_3b_{21}|\}. \]  
(77)
Cauchy inequality leads to
\[
\Phi^* \leq \frac{m^2 \beta_1^2}{2|A^* I^*|} Y_1^2 + \frac{1}{2} |A^* I^*|(Y_2^2 + Y_3^2).
\] (78)

Choosing
\[
\beta_1^2 = \frac{|a_{11}| |A^* I^*|}{m^2},
\] (79)

it follows that
\[
\Phi^* \leq \frac{1}{2} |a_{11}| Y_1^2 + \frac{1}{2} |A^* I^*|(Y_2^2 + Y_3^2).
\] (80)

Passing now to evaluate \(\tilde{\Phi}\), by virtue of Lemma 1, there exists a positive constant \(\delta_1\) such that
\[
\tilde{\Phi} \leq \delta_1(Y_1^2 + Y_2^2 + Y_3^2)^{\frac{1}{2}}.
\] (81)

In view of (80) and (81), it turns out that
\[
\dot{W} \leq -\frac{1}{2} |a_{11}| Y_1^2 - \frac{1}{2} |A^* I^*|(Y_2^2 + Y_3^2) + \delta_1(Y_1^2 + Y_2^2 + Y_3^2)^{\frac{1}{2}}.
\] (82)

Since
\[
p_1(Y_1^2 + Y_2^2 + Y_3^2) \leq W \leq q_1(Y_1^2 + Y_2^2 + Y_3^2)
\]
\[
p_1 = \min \left\{ \frac{1}{2}, \frac{A^*}{2} \right\}, \quad q_1 = \max \left\{ \frac{A^*}{2} + a_{22}^2 + b_{23}^2 + b_{32}^2 + a_{33}^2, \frac{1}{2} \right\}
\] (83a)
\[
(83b)
\]

from (82) it follows that
\[
\dot{W} \leq -\left( \frac{\delta_2}{p_1} - \frac{\delta_1}{q_1 \sqrt{q_1}} \right) W^\frac{3}{2},
\] (84)

with \(\delta_2 = \min\{|a_{11}|, |A^* I^*|\}. Then
\[
W(0) \leq \frac{\delta_2 q_1 \sqrt{q_1}}{p_1 \delta_1},
\] (85)

by recursive arguments implies that \(\dot{W} < 0\) and hence there is coincidence between linear and non linear (local) stability in the \(W\)-norm for \(E_2\).

Let us pass now to investigate the nonlinear stability of the coexistence equilibrium.

**Theorem 6.** If (53a)–(53b) hold, the coexistence equilibrium is nonlineraely (locally) stable in the \(E\)-norm.

**Proof.** The time derivative of \(E\) along the solutions of (31) is given by
\[
\dot{E} = \mu_1 a_{11} X_1^2 + \frac{\mu_2}{2} \left[ \frac{\mu_2}{\mu_3} a_{22} X_2^2 + \frac{\mu_2}{\mu_3} a_{33} X_3^2 \right] + \tilde{\Phi}
\] (86)

where \(\tilde{\Phi}\) is given by (57) with \(\alpha_i = \mu_i, (i = 1, 2, 3)\) and \(F_i, (i = 1, 2, 3)\) are given by (34)–(36) with \((\bar{u}, \bar{v}, \bar{w})\) at the place of \((u^*, v^*, w^*)\). In view of (53a)–(53b) and (58), (86) leads to
\[
\dot{E} \leq -\delta_2 (X_1^2 + X_2^2 + X_3^2) + \delta_1 (X_1^2 + X_2^2 + X_3^2)^{\frac{3}{2}},
\] (87)

with
\[
\delta_2 = \min\{\mu_1 |a_{11}|, \mu_2 |a_{22}|, \mu_3 |a_{33}|\}.
\] (88)

From (87), it turns out that
\[
\dot{E} \leq \left( -\frac{\delta_2}{k_2} + \frac{\delta_1}{k_1 \sqrt{k_1}} \right) E,
\] (89)
being $k_1 = \frac{1}{2} \min_{1 \leq i \leq 3} \mu_i$ and $k_2 = \frac{1}{2} \max_{1 \leq i \leq 3} \mu_i$. Hence

$$E(0)^\frac{1}{2} < \frac{\delta_2 k_1 \sqrt{E_1}}{\delta_1 k_2},$$

by recursive arguments, implies that $\dot{E} < 0$.

8. Numerical experiments and discussion

In this section we explore some specific configurations in the parameters space that lead to different dynamic behaviors of the system (4a)–(4c). Specifically, we are interested in showing, by means of some examples, the conditions ensuring durable coexistence of both predator and prey populations. Confirming the analysis in [24], and with a similar approach as in [12] the most significant indicator in this context is the equilibrium value of the biotic resource $\gamma/\delta$, whose level can determine the survival of the prey population. In fact, by analyzing Eqs. (4a)–(4c) either in the absence of the predator or in the absence of the prey and, finally, in the presence of the prey, the density of both populations is conditioned by the resource equilibrium $\gamma/\delta$. Following this remark, we note that, by tuning $\gamma$ we are able to control the number of positive roots of (18) and then the number of internal equilibria $\bar{E}$. To show some specific examples, we reduce the dimensionality of the parameter space by fixing $\alpha = 1.5$, $\beta = \delta = \eta = \phi = 1$, $\epsilon = 3$, $k = 0.7$. It is now possible to plot the internal equilibrium $\bar{E}$ against $\gamma$: Fig. 1 shows the solution $\bar{u}$ of (18) (Fig. 1(a)) as a function of the enrichment parameter $\gamma$, and the corresponding functions $\bar{v}$ (Fig. 1(b)) and $\bar{w}$ (Fig. 1(c)). Referring to Fig. 1(a), the solid line represents stable solutions, while the dotted line corresponds to a second internal equilibrium (unstable) only in the small $\gamma$ interval $[1.4,1.6]$. The stability/instability of these equilibria has been verified, for $\gamma < 1.6$, by observing the behavior of $I_1$, $I_1I_2 - I_3$, $I_3$ with $I_i$ ($i = 1, 2, 3$) given by (49)–(51).

The subsequent values, along with all the points lying on the dashed line, represent negative solutions of (18), not leading to biologically meaningful equilibria. As a consequence, also in Fig. 1(b) and (c) only the solid line and the first part of the dotted line represent significant internal equilibria.

It is worth noting that our analysis confirms the so-called enrichment paradox, thoroughly discussed in [5]: while the resource always increases with high levels of the enrichment parameter, the prey decreases and eventually even dies out. Accordingly to this analysis, by choosing $\gamma = 2$, as expected we obtain the dynamics shown in Fig. 2. In this case (18) does not admit any real positive root, so that there is not any internal equilibrium: we start the simulation from non-zero initial data ($u_0 = v_0 = 0.1$, $w_0 = 0.2$), but the prey population (black solid line) dies out, while both the predator population (gray line) and the resource (light gray line) stabilize reaching the boundary equilibrium $E_2$, as can be seen in Fig. 2(a). Choosing an even higher initial value for the prey population ($u_0 = 0.5$), as shown in Fig. 2(b), the same boundary equilibrium is reached. We remark that, for such a value of $\gamma$ the boundary equilibrium $E_2$ is stable according to (44).

With a smaller value for the enrichment, $\gamma = 1.1$, (18) admits a single positive root $\bar{u} \approx 0.175$, and then there is a single internal equilibrium $\bar{E} \approx (0.175, 0.305, 0.270)$: as shown in Fig. 3, starting the simulation from any non-zero initial data the system reaches a state of coexistence of both prey and predator populations. We recall that, for such values of $\gamma$, $\bar{E}$ is stable.

Finally, in the intermediate enrichment regime, for example for $\gamma = 1.5$, (18) admits two different positive roots, $\bar{u}_1 \approx 0.046$ and $\bar{u}_2 \approx 0.193$ and then there are two internal equilibria, $\bar{E}_1 \approx (0.046, 0.695, 0.667)$ and $\bar{E}_2 \approx (0.193, \ldots)$.
0.491, 0.429). Nevertheless, as shown in Fig. 4, when the simulation starts from an initial datum $u_0$ greater than 0.01, the system always reaches the internal equilibrium $E_2$. On the contrary, lower values of $u_0$ lead to extinction of the prey population and the system reaches the boundary equilibrium $E_2$. Let us now consider a different parameters configuration: as already observed, higher values of the enrichment $\gamma$ can lead to prey extinction. But if at the same time we limit the growth of the predator population, by acting on its growth parameter $\alpha$, the system is destabilized: oscillations in the trajectories appear and they eventually decay to equilibrium after a very long time. As an example, Fig. 5(a) shows the trajectories of the system for the parameters choice $\alpha = 0.015$, $\beta = 0.5$, $\gamma = 1.85$, $\delta = 0.025$, $\epsilon = 2$, $\eta = 1$, $k = 0.9$, $\phi = 2.5$. The trajectories show some damped oscillations before reaching the equilibrium $\bar{E} \approx (0.03, 0.68, 0.11)$, as can be clearly seen in the related phase space plot (Fig. 5(b)).

For an even smaller predator growth parameter ($\alpha = 0.003$), the oscillations are persistent around the equilibrium $\bar{E} \approx (0.01, 0.73, 0.06)$ as shown in Fig. 6(a) and the trajectories approach a limit cycle (Fig. 6(b)). Indeed, numerical solutions have been evaluated for a much longer time span, $t_{\text{max}} = 3000$ (not shown here to preserve clarity of the figure), without any damping. This numerical experiment highlights the results reported in Remark 2, when all of the others parameters have been fixed as above and $\gamma = \bar{\gamma}$ solution of $\bar{I}_2 = \bar{I}_3/\bar{I}_1$ ($\gamma \approx 1.85$). Biologically, all the three species coexist and have densities that vary periodically over time with a common period $T = 2\pi/\omega \approx 27$, where $\omega \approx 0.23$ is the approximate angular frequency (pulsation). Note the relative positions of the three abundance peaks, with the biotic resource peaking first, followed by a peak in the prey population (the mid-level species), with the maximum in the top predator population coming last, as one would expect from biological considerations. From the analysis above we can conclude that the predator growth rate $\alpha$ is an important factor for the system and can affect its stability. However, it is worth noting that, when stability fails and the trajectories move away from the equilibrium, in any case, they remain confined within the absorbing set whose existence has been proved (Theorem 1).

Acknowledgments

The study in this paper has been performed under the auspices of the G.N.F.M. of INdAM. R. De Luca and I. Torcicollo acknowledge Progetto Giovani GNFM 2017 “Analisi dei sistemi biologici complessi”. The authors thank anonymous referee for suggestions which have led to improvements in the manuscript.
Fig. 4. Trajectories of the system (4a)–(4c) when all parameters are set as in Fig. 1 and $\gamma = 1.5$. In this case, even if there are two internal equilibria, depending on the initial datum $u_0$, the system reaches the greatest one of them or the boundary equilibrium $E_2$. In part (a) it is $u_0 = 0.015$, while in (b) it is $u_0 = 0.01$; in both plots it is $v_0 = 0.1$, $w_0 = 0.2$. Black, gray and light gray lines represent $u$, $v$, $w$, respectively.

Fig. 5. Trajectories of the system (4a)–(4c) with the parameters set as $\alpha = 0.015$, $\beta = 0.5$, $\gamma = 1.85$, $\delta = 0.025$, $\epsilon = 2$, $\eta = 1$, $k = 0.9$, $\phi = 2.5$ (a). Black, gray and light gray lines represent $u$, $v$, $w$, respectively and initial conditions are $u_0 = 0.2$, $v_0 = w_0 = 0.4$. In this case, with small values of the parameter $\alpha$ the system shows damped oscillations while approaching the steady state, as can be seen in the related phase space plot (b).

Fig. 6. Trajectories of the system (4a)–(4c) with the parameters set as $\alpha = 0.003$, $\beta = 0.5$, $\gamma = 1.85$, $\delta = 0.025$, $\epsilon = 2$, $\eta = 1$, $k = 0.9$, $\phi = 2.5$ (a). Black, gray and light gray lines represent $u$, $v$, $w$, respectively and initial conditions are $u_0 = 0.2$, $v_0 = w_0 = 0.4$. Here the system shows persistent oscillations; in the corresponding phase space plot (b) the limit cycle is clearly seen.

References