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Analysis of Kramer's coral-reef food web model

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The model of a coral reef ecosystem, proposed by D.B. Kramer and published in Ecology and Society in 2008, explored the implications of changes in biological parameters and changes in economic and social interaction variables governing the fishing behaviour of anglers targeting the two fish species included in the model, herbivore and piscivore fish. This model is parametrized based on evidence provided in the literature. The recognition of multiple species in the model as well as the inclusion of adaptive harvesting behaviour may supposedly allow to explore policy or management options. This paper reviews, extends and sharpens the analysis undertaken in original article, and reveals both mathematical and interpretational mistakes in it. We use analytical and numerical methods to show that, contrary to the assertion in discussed article, some of the equilibrium outcomes are independent of the parameter values that were identified as important in this paper. At the same time the model is highly sensitive to the setting of some parameter values as well as to the structures representing interactions in the model. We suggest ways in which the model can be modified so that it would become interpretable.

Keywords: coral reef ecosystems, dynamical system, ecosystem simulation, equilibria, fisheries management, socio-economic values.

The management of fisheries continues to be a challenging problem [1–5]. Although fisheries have been a major area of research in resource economics for more than half a century, most studies employ simplified or single-species models when in fact the focus is increasingly on the management of trade-offs between different biological outcomes and socio-economic values. Fisheries management can benefit greatly from models that are rich enough to allow a sound analysis of the trade-offs involved in the fisheries management. This requires the use of ecosystem models that recognize multiple species or species categories [6], together with behavioural or economic models [7] that capture the main drivers of fishing choices among anglers.

D.B. Kramer proposed in [8] a four species ecosystem model of a coral reef food web along with a model of adaptive fish harvesting behaviour, where fisheries choose among herbivore and piscivore fishing activities depending of the relative profitability of the two fishing alternatives. He uses numerical simulation and evaluates the effects of changes in model parameters and the economic and social drivers of fishing behaviour. This paper analyses the model proposed in [8] and highlights the weaknesses in the model including equilibrium values for components that are independent of model setup. The purpose of this analysis is to identify the essential changes required to obtain an interpretable baseline model in future attempts aimed at developing models that would allow the effects of recreational fishing on coral reefs ecosystems to be evaluated.

The paper is organized as follows. In the next section, we summarize the key features of the model and its parameterization. In section "Analysis", we present results from mathematical and numerical analysis of the model and compare our finding to those in [8]. We highlight the results where the key variables of interest are independent of parameter values. Also we will show that the outcomes or the stability of these variables are highly sensitive to changes in parameter values.

A key observation is that the equilibrium herbivore biomass outcome (in the absence of fishing) is independent of algal levels, highlighting the inadequacy of some of the specifications in the model. Further, the analysis shows that algal growth rates are far more important than coral growth rates. The results suggest that some components of the model could benefit from alternative specifications. We summarize and conclude the paper in section "Conclusions".

Kramer's coral reef ecosystem model

Kramer's model is a trophic-dynamic model based on a modified Lotka-Volterra model of predator-prey interactions [9, 10] and interspecies competition (some versions of such models are discussed in [10, 11, 12]). The model incorporates algal growth, coral growth and the growth of two fish categories, herbivore and piscivore biomass. The relationships governing the dynamics of these model components are shown in equations (1)–(4) below.

Algal cover:

$$\frac{dA}{dt} = r_A A(t)\left(\frac{K_A - A(t) - a_{AC}C(t)}{K_A}\right) - a_{AH}\cdot H(t)A(t) \quad (1)$$

where: $A(t)$ is algal cover as proportion of sea floor at time t ; r_A is intrinsic rate of growth for algae; K_A is the carrying capacity of algae as proportion of sea floor; a_{AC} is a competition coefficient of coral on algae; and a_{AH} is an interaction coefficient between herbivores and algae. The interaction between herbivores and algae is modelled as a simple linear relationship because of the absence of evidence of more complex relationship between the two [8]. The competition for light and space between algae and coral is modelled using the a_{AC} coefficient which measures the strength of interspecific competition relative to intraspecific competition.

Coral cover:

$$\frac{dC}{dt} = r_C C(t)\left(\frac{K_C - C(t) - a_{CA}\left(\frac{A(t)^{Slope}}{A(t)^{Slope} + HA^{Slope}}\right)}{K_C}\right), \quad (2)$$

where: $C(t)$ is coral cover as proportion of sea floor at time t; r_C is intrinsic rate of growth for coral; K_C is the carrying capacity of coral as proportion of sea floor; a_{CA} is the competition coefficient of algae on coral; and *Slope* and *HA* are, according to [8], the slope and a half saturation constant of the sigmoidal Hill function in (2). (We shall discuss the validity of these notations in the next section). The effect of algae on coral is modelled in [8] as a nonlinear relationship because, as the algal biomass increases, the composition of the algal biomass shifts from turf algae to macro-algae, with a dramatic detrimental effect on coral cover.

Herbivorous fish biomass:

$$\begin{aligned}\frac{dH}{dt} &= a_{HA}\cdot H(t)\cdot A(t) - a_{HH}\cdot H(t) - \\ &-a_{HP}\cdot H(t)\cdot P(t) - popS_H a_{HM} E_H H(t)\end{aligned} \quad (3)$$

where $H(t)$ is herbivorous fish density at time t, a_{HH} is a density-dependent coefficient of herbivorous fish, a_{HA} is an interaction coefficient of algae on herbivorous fish, a_{HP} is an interaction coefficient of piscivores on herbivores, and the last addend represents the fisher's contribution, with the parameters *pop* for the total population of fishers per square kilometre, S_H for the proportion of fishers who harvest herbivores, a_{HM} for the catch efficiency of fishers, and E_H for the fishing effort in hours fished per day.

Piscivorous fish biomass:

$$\begin{aligned}\frac{dP}{dt} &= a_{PH}\cdot P(t)\cdot H(t) - a_{PP}\cdot P(t) - \\ &- popS_P a_{PM} E_P P(t)\end{aligned}, \quad (4)$$

where $P(n)$ is the piscivorous fish density at time t, a_{PP} is the density-dependent coefficient of piscivorous fish, a_{PH} is an interaction coefficient of herbivores on piscivores, and the meanings of the parameters in the term representing the fishers' contribution $popS_P a_{PM} E_P P(t)$ is analogous to the respective ones in the equation for the herbivorous biomass (3).

Kramer in [8] presents further details on the parameterization of the biophysical components of the trophic model and sensitivity analysis done on the model parameters. Table 1 presents the parameter values used in [8] along with reasonable ranges for these values. The focus of his sensitivity analysis is on the growth rates (r_A, r_C), carrying capacity levels (K_A, K_C), and the fishing effort including the number of fishers (*pop*).

Analysis

Below, we present results from the analysis of the model. Analytical methods are first used to describe the interior equilibria and their interpretability as well as the sensitivity of model outcomes to some of the parameter values. This is followed by a discussion of the results from numerical analysis focusing on grow rates and carrying capacity levels for corals and algae.

Analytical results

Interior equilibria and the problem with the interpretability of the model

The interior equilibria are the ones for which none of the variables vanishes at the stationary points. In a way these are the most interesting equilibria, since they correspond to a sustainable system. The values of the variables at these equilibria will be denoted $\hat{A}$, $\hat{C}$, $\hat{H}$, $\hat{P}$. They are determined by the system of equations

$$\frac{dA}{dt} = \frac{dC}{dt} = \frac{dH}{dt} = \frac{dP}{dt} = 0 \quad (5)$$

combined with the requirement that none of the values of the variables is zero, which means (for non-negative quantities) that they are strictly positive at the stationary points:

Table

Parameters used in Kramer’s model

Parameter	Description	Value	Reasonable Value/Range	Ref.
$A(0)$	Initial algae cover as proportion of sea floor	0.3	0.1–0.5	Own guess
r_A	Algal intrinsic rate of growth	0.3	0.05–0.40	[13]
K_A	Algal carrying capacity as cover	0.8	Prey carrying capacity in absence of predators (given a value)	[8]
a_{AC}	Competition coefficient of coral on algae	0.8	Leave as is for now	[17]
a_{AH}	Interaction coefficient of herbivorous fish on algae	3.3e-5	7.33e-05	[14]
$C(0)$	Initial coral cover as proportion of sea floor	0.3	0–0.5	Own guess
r_C	Coral intrinsic rate of growth	0.2	0.04–0.2	[15, 16]
K_{AC}	Coral carrying capacity as cover	0.7	Prey carrying capacity in absence of predators (given a value)	[17, 18]
a_{CA}	Competition coefficient of algae on coral	0.6	Leave as is	
Slope	Slope of the Hill function	7.0	Leave as is	
HA	Half saturation constant of Hill function	0.3	Leave as is	
$H(0)$	Initial herbivorous fish density	2100	Take 50% below and above 2100 as range	[14]
a_{HH}	Density-dependent coefficient of herbivorous fish	7.0e-03 or 0	4.00e-03	[14]
a_{HA}	Interaction coefficient of algae on herbivorous fish	0.1	1.33e-06	[14]
a_{HP}	Interaction coefficient of piscivorous fish on herbivorous fish	1.0e-5	1.14e-04	[14]
E_H	Effort level of fishers harvesting herbivorous fish	2.0	1–5	
a_{HM}	Harvest catchability coefficient of herbivorous fish	1.9e-5	Leave as is	
$P(0)$	Initial piscivorous fish density	1400	Range: ±50% of this	[14, 19]
a_{PP}	Density-dependent coefficient of piscivorous fish	7.0e-3	4.00e-03	[14]
a_{PH}	Interaction coefficient of herbivorous fish on piscivorous fish	6.8e-6	1.14e-05	[14]
E_P	Effort level of fishers harvesting piscivorous fish	2.0	1–5	[20]
Pop	Total population of fishers	50	10–100	
a_{PM}	Harvest catchability coefficient of piscivorous fish	4.3e-5	Leave as is	

$$\hat{A}>0; \hat{C}>0; \hat{H}>0; \hat{P}>0. \quad (6)$$

After performing elementary algebraic operations, the above system (5) under conditions (6) can be reduced to the following system of equations:

$$\hat{C} = K_C - a_{CA}\frac{\hat{A}^m}{\hat{A}^m+\alpha} \quad (7)$$

$$\hat{H} = \frac{a_{PP}+c_1 a_{PM}}{} \quad (8)$$

$$\hat{P} = \frac{a_{HA}}{a_{HP}}\hat{A} - \frac{a_{HH}+a_{HM}c_2}{a_{HP}} \quad (9)$$

$$\frac{\hat{A}^m}{\hat{A}^m+\alpha}=\gamma+\beta\hat{A}. \qquad (10)$$

In this system we have replaced the notations *Slope* and $(HA)^{Slope}$ in Hill's function with more succinct m and α respectively, and introduced for brevity a few constants:

$$c_1=popS_PE_P;\ c_2=popS_HE_H, \qquad (11)$$

$$\beta=\frac{1}{a_{CA}a_{AC}}, \qquad (12)$$

$$\gamma=\frac{r_Aa_{AC}K_C-r_AK_A+K_Aa_{AH}\hat{H}}{r_Aa_{CA}a_{AC}}. \qquad (13)$$

For all the other parameters we assume the same notations and values as in the paper [8] by Kramer (Table).

Let us note that in the absence of fishing we have

$$c_1=c_2=0. \qquad (14)$$

This will be the case of our interest in the current paper, since before studying the impact of human activities on the ecosystem we would like to establish a reliable model for describing the dynamics of interaction between its components, which in this case are algae, corals, herbivores, and piscivores.

It follows immediately from equation (9) that the equilibrium value for the H-variable is completely determined by the parameters of the P-equation (4). In particular, in the absence of fishing

$$\hat{H}=\frac{a_{PP}}{a_{PH}}\approx 1029.4. \qquad (15)$$

Therefore, according to the model [1], the equilibrium value for the herbivorous fish biomass is completely independent from any other parameters and variables; in particular it does not depend on the equilibrium value of the A-variable. The latter is unacceptable, since algae, according to the model, is the only source of nutrition for herbivorous fish.

For this reason the model proposed in [8] is not interpretable. In order to fix the problem inherent in the model, one should include in equations (3) and (4) nonlinear terms that would adequately describe the predator-prey interaction in the system.

Another feature that makes the model proposed in [8] unacceptable as a baseline model of a coral ecosystem is the absence of parameter r_C from the equations (7–10) that determine the location and existence of the interior equilibria of the dynamical system which is expected to describe the ecosystem. It is impossible to interpret the fact that the growth rate of corals does not influence the existence and location of an equilibrium state of a coral ecosystem.

Interior equilibria and high sensitivity of the model with respect to the values of some parameters

As we have shown above, the model proposed in [8] is not interpretable, at least in the component describing the dynamics of the fish biomass. Still it is worth studying some other features of the model. In particular, we can assume that the amount of the biomass of herbivorous fish is stable (at the $\hat{H}$-level determined by (15)), and concentrate on the dynamics of the A-C interactions inherent in the model. In particular, we shall study the sensitivity of the results concerning the interior equilibria of the system with respect to the two parameters that determine the behavior of the Hill function present in equation (2), which allegedly describes the dynamics of the corals biomass.

Let us concentrate on equations (7) and (10) that describe the A- and C- coordinates of the interior equilibria. Since the H-coordinate is fixed as mentioned above, the P-coordinate can be found from (9) as soon as the A-coordinate has been determined.

When introducing Hill function [21] in the model, [1] argues that "the shape of this function is controlled by two parameters" and that "*Slope* is the steepness of the curve at the inflection point".

It is easy to show that this statement is false. Using the following notations to save space,

$$m = Slope, \qquad (16)$$

$$\alpha = (HA)^m, \qquad (17)$$

the Hill function from [8] can be rewritten as

$$G(x)=\frac{x^m}{x^m+\alpha}, \qquad (18)$$

and its first two derivatives are

$$G'(x)=\frac{\alpha m x^{m-1}}{(x^m+\alpha)^2}; \qquad (19)$$

$$G''(x)=\frac{\alpha m(m+1)x^{m-2}\left(\alpha\dfrac{m-1}{m+1}-x^m\right)}{\left(\alpha+x^m\right)^3}. \qquad (20)$$

From the latter formula one can easily find the inflection point

$$x_{in} = \sqrt[m]{\frac{m-1}{m+1}\alpha}, \qquad (21)$$

and the slope of the curve (tangent to the curve at this point)

$$G'(x_{in}) = \frac{m^2-1}{4m} \cdot \frac{1}{\sqrt[m]{\frac{m-1}{m+1}\alpha}}, \qquad (22)$$

which is clearly not equal to *m*, or the *Slope*, contrary to the claim in [8].

For the following particular choice of parameter values

$$HA = 0.3;\ Slope = 7, \qquad (23)$$

used in [1] for "baseline model", the slope at the inflection point will be

$$G'(x_{in}) = \frac{12}{7} \cdot \left(\frac{4}{3}\right)^{\frac{1}{7}} \cdot \frac{1}{HA} \approx 5.94. \qquad (24)$$

This problem in the model would not have been important or worthy of a detailed discussion if the model had not been very sensitive to the parameters involved in Hill function. This sensitivity is evident when analyzing equation (10), which determines the *A*-coordinate of the interior equilibria.

On the diagram below[1] (Figure 1) the points of equilibria can be seen as the points of intersection of the graphs of a sigmoidal Hill function $G(A) = \frac{A^m}{A^m + \alpha}$, and a straight line $F(A) = \gamma + \beta A$, representing respectively the left hand side and the right hand side of the equation (10).

The graphs (1–4) of the Hill function correspond to four different values of the parameter $HA = \sqrt[7]{\alpha}$:

(1): *HA* = 0.3 (baseline model value, used in [1];

(2): *HA* = 0.26;

(3): *HA* = 0.4;

(4): *HA* = 0.44.

As we see from the diagram, sigmoid (1), which corresponds to the choice of the parameter *HA*=0.3, assumed in [8], has three points of intersection with the straight line, which deliver three *A*-coordinates of possible interior equilibria:

$$\hat{A}_1 \approx 0.15;\ \hat{A}_2 \approx 0.25;\ \hat{A}_3 \approx 0.63. \qquad (25)$$

When the value of *HA* decreases to 0.26, the two lower-level equilibria merge into one as sigmoid curve (2) just touches the line at the lower end. If the value of *HA* decreases further, beyond 0.26, the lower-level equilibria disap-

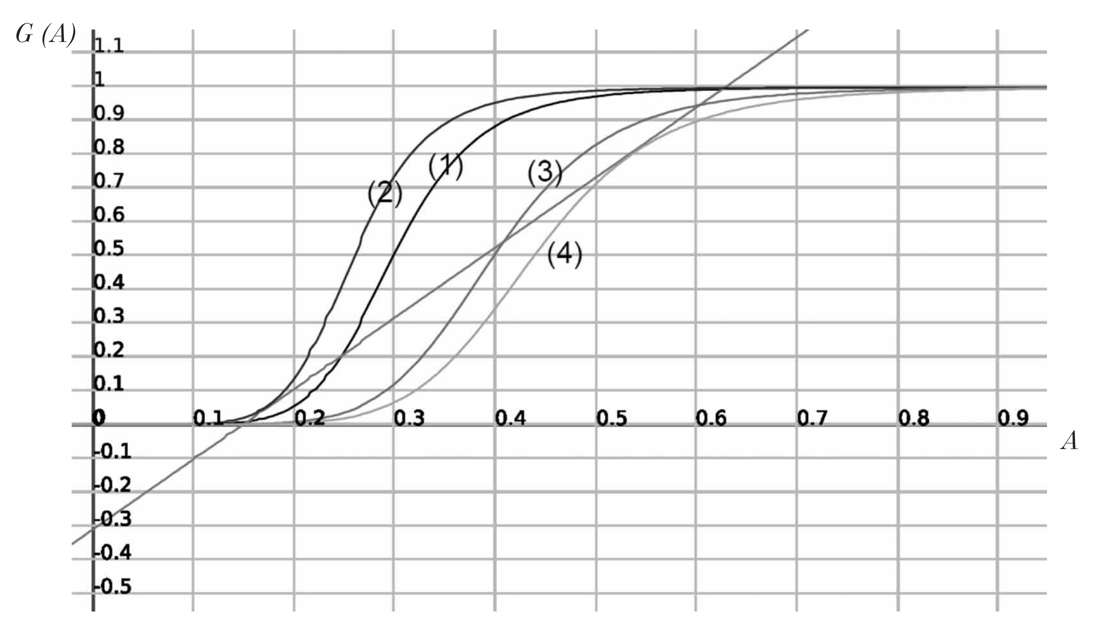

Fig. 1. The *A*-coordinates of the interior equilibria are the horizontal coordinates of the points of intersection of a sigmoid with the straight line

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[1] The software *fooplot* (http:// fooplot.com) is used for sketching the graphs in Figures 1 and 3 below.

pear in a saddle-node bifurcation, leaving only one equilibrium point, located at almost the saturation level, close to the value of $G(\hat{A}_3) \approx 0.99$ from (25).

Similarly, the two base-case equilibria at the higher *A*- values merge, and then disappear when the value of *HA* increases beyond 0.44: curve (4) is tangent to the straight line, and for any value of *HA* above 0.44 the curves will intersect only at one point, which corresponds to the lower level equilibrium.

This analysis shows that the outcomes of the model are highly sensitive to the choice of *HA* value, and a similar analysis can be conducted to show that the results are also sensitive to the choice of the value of the *Slope* parameter. However, the article [8] has not provided any arguments for the baseline choices of the values of these parameters.

Equilibria in the A-C plane

Another issue in paper [8] concerns the location and the number of equilibria located in the interior of the *A-C* plane ($A \neq 0$, $C \neq 0$, $H \neq 0$, $P \neq 0$). The paper claims: “The coral and algal nullclines based on baseline parameters values cross three times and represent three interior equilibria (Fig.1).”, whereas a simple calculation shows that these nullclines intersect only ones.

In order to see that, one can just use equation (2) for the nullcline obtained from the *C*-equation in [8]:

$$C(t) = \left(\frac{K_A - A(t)}{a_{AC}}\right),$$

which is equivalent to

$$C = \frac{K_A}{a_{AC}} - \frac{1}{a_{AC}} A,$$

and substitute the baseline values from that paper: $K_A = 0.8; \quad a_{AC} = 0.8$, which results in the following equation:

$$C = 1 - \frac{5}{4} A. \tag{26}$$

Thus the *C*-intercept of the null-cline is 1, not 0.9 as presented in Figure 1 of article [8]. The corrected straight null-cline is shown in dotted-dashed line in the diagram below, which reproduces Figure 1 from [8]. This line will have only one intersection with the sigmoid-shaped null-cline, and the equilibrium occurs close to the saturation level of the *A*-coordinate. From the interpretational viewpoint that means that the nonlinear term represented by the Hill function could be replaced by a constant without any substantial changes in the configuration and stability of equilibria.

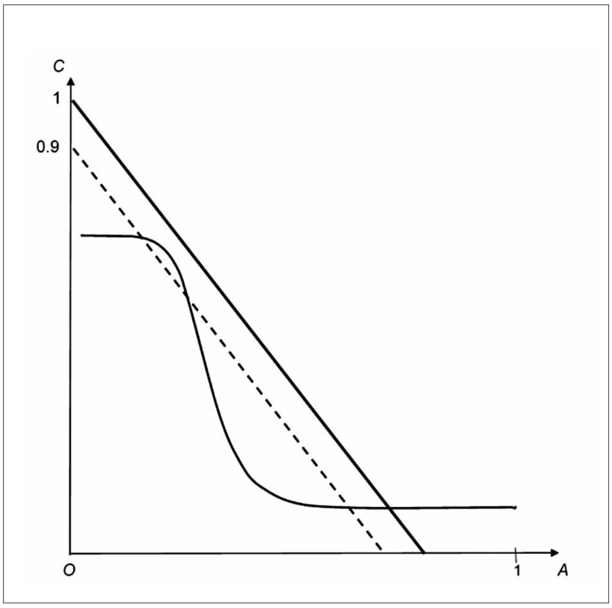

Fig. 2. The diagram shows the corrected depiction of the null-clines in the *A-C* plane. The location of the equilibrium is determined by the point of intersection of the sigmoid and the continuous straight line. The dashed straight line shows the erroneous null-cline from Figure 1 in article [8]; it had three points of intersection with the sigmoid, and thus led the author to the erroneous conclusion of the existence of three equilibria in the *A-C* phase plane

Thus it has been established that for the baseline set of parameters the system has only one interior equilibrium in the *A-C* plane. It can be shown, however, that by varying the parameters, one can obtain up to three interior equilibria in that plane. In particular, this can be achieved by changing the value of the parameter *HA*.

The diagram below (Fig. 2) shows the graphs of the functions $y = G(A)$, and $y = F_1(A)$, whose points of intersection determine the location of the interior equilibria in the *A-C* plane ($A \neq 0$, $C \neq 0$, $H = 0$, $P = 0$) according to the dynamical system from [1]. *G(A)* represents the sigmoidal Hill function, and $F_1(A)$ represents the straight line:

$$G(A) = \frac{A^7}{A^7 + (HA)^7}; \; F(A) = \frac{1}{a_{CA}}(\gamma + \beta A), \quad \text{where}$$

$$\gamma = K_C - \frac{K_A}{a_{AC}}; \; \beta = \frac{1}{a_{AC}}. \tag{27}$$

If we assume the set of parameters from Kramer [8], the Hill function is represented by the leftmost sigmoid (1). For this curve we assume *HA*=0.3. As we can see, this curve will have exactly one intersection point with the straight line, hence there must be a unique equilibrium,

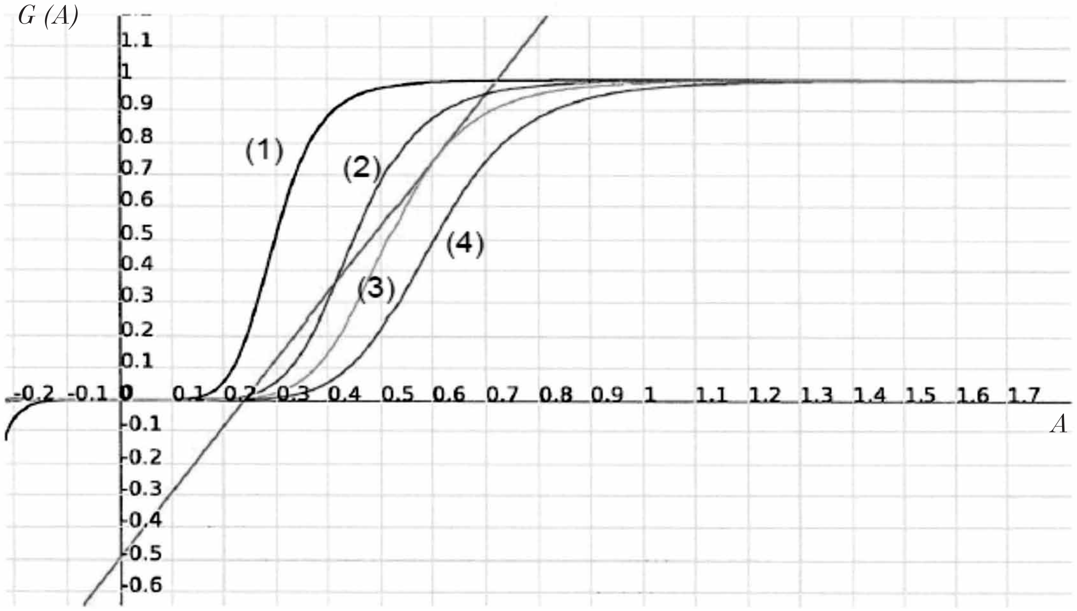

Fig. 3. The number and locations of the interior equilibria in the *A-C* plane depending on the values of *HA*

which occurs close to the saturation level for *A* (see Figure 2 above and our comment to Figure 1 from [8]).

We observe that the system may have up to three equilibria, if some parameters of the model are changed. In particular, by choosing a higher value for the parameter *HA*, we shall make the sigmoid *less steep*, and the curves may intersect more than once. In Figure 3, the three sigmoids following the first one to the right, are obtained by choosing the values of *(HA)* to be 0.450 (curve (2)), 0.515 (curve (3)), and 0.600 (curve (4)) respectively.

The second curve has three points of intersection with the straight line, hence the system will have three equilibria in this case. By increasing the value of the parameter *HA* from 0.4 to 0.515, we move two higher level equlibria towards each other; they merge into one at the value of *HA* close to 0.515: one can see that the line touches the corresponding sigmoid at one point. With the further increase of *(HA)*, the pair of equilibria disappears. Usually such a process is a result of saddle-node bifurcation, occurring at the value of the parameter close to the critical value, 0.515 in this case. It is obvious from the behaviour of the sigmoids that a similar bifurcation must have taken place earlier for the value of *HA* somewhere between 0.30 and 0.45.

As we have already noted above, the system is highly sensitive to the values of the parameters included in the Hill function. Therefore, the choice of values for the model parameters should be done carefully and needs to be substantiated.

Results from numerical experiments

As we have shown in the previous section, the model proposed in [1] is not interpretable due to inconsistencies in the dynamical equations representing the fish populations (*H* and *P* – variables). The other two equations in Kramer's model describe the competition between the algae and corals. Although these equations contain some terms and parameters whose values are not sufficiently explained, it is interesting to evaluate whether these equations can be candidates for inclusion in a baseline model. In this section we describe the results of some numerical experiments testing the sensitivity of the results obtained the growth rates (r_A, r_C) and the carrying capacities (K_A, *KC*) of the algae and coral variables, respectively.

Our discussion is based on the numerical local analysis of the system proposed in [1] near interior equilibria, in the absence of fishing (i.e. the population of fishers are set to zeroes, or $popS_H = popS_P = 0$ in the system (1–4)).

The interior equilibria of the system are found by solving numerically the system (7–10) in the assumption that none of the variables is 0. The stability of an equilibrium is determined by the eigenvalues of the Jacobi matrix that determines the linearization of the dynamical system (1–4) at the equilibrium point. All the numerical experiments described below have been performed by means of MAPLE software (http://www.maplesoft.com/products/maple/).

Sensitivity of the model with respect to the intrinsic growth rates (r_A, r_C):

The following observations can be made based on the analysis.

The analytical and numerical analysis of the system (1–4) show that the value of r_A does influence the existence and locations of equilibrium points for the system governed by equations (1–4). At the same time, the coral reef growth rate parameter r_C is not present in the equations (7–10), hence its value has no effect on the existence and locations of the equilibria.

The latter is another feature that makes the model offered in [8] non-interpretable.

Although the parameter r_C does not affect the existence of equilibria, it is present in the expression for the Jacobi matrix, linearization of the system (1–4); thus variations in the value of r_C, except in a certain range to be described later, do affect the eigenvalues of the Jacobi matrix, and hence the stability of the system at the equilibrium points. (Still, as we shall see below, the variations of the parameter within the given range [0.04, 0.2] do not change the type of the equilibrium observed: it is a stable focus for any value of r_C within the aforementioned range).

The system has no interior equilibria for the following growth rate parameter values: $0.05 \leq r_A < 0.1029279759$ and $0.04 < r_C < 0.2$, the system has no interior equilibria. For $r_A \geq 0.1029279759$ and an arbitrary r_C from within the given range, the system has one stable equilibrium point (a stable focus).

The following examples show the location of the equilibrium, and the eigenvalues for the lower boundary value (we shall call it *critical value*) of r_A, and the minimum and maximum possible values of r_C.

Hereafter, when listing the coordinates of the equilibria, and the corresponding eigenvalues, we shall write them in the order in which we have listed the dynamical variables in the system (1–4), namely: *A*, *C*, *H*, *P*.

Example: For the critical value of r_A = 0.029279759 and the maximum value of r_C = 0.2, we consider the following set of parameters:

r_A:= 0.1029279759
k_A:= 0.8
a_{AC}:= 0.8
a_{AH}:= 0.000033
r_C:= 0.2
K_C:= 0.7
a_{CA}:= 0.6
Slope:= 7
H_A:= 0.3
a_{HH}:= 0.007
a_{HA}:= 0.1
a_{HP}:= 0.00001

For the above set of parameters we obtain the following equilibrium point values for algae (*A*), corals (*C*), herbivorous (*H*) and piscivorous (*P*) fish:

[0.391364709313790,
0.180751790672836,
1029.41176470588,
3213.64709313790].

The eigenvalues corresponding to this equilibrium point are:

[-0.0957523410904594]
-0.00312186944856979 +
0.0307721473670114·*I*
-0.00312186944856979 –
0.0307721473670114·*I*
$-0.260486516142944 \cdot 10^{-6}$

This equilibrium point is a stable focus. For an illustration of the behaviour of the system near the equilibrium, one can see below three-dimensional projections of the phase portraits onto the subspaces (*A*,*C*,*H*), (*A*,*C*,*P*), (*A*,*P*,*H*) and (*C*,*H*,*P*):

Conclusions

The authors of this paper started studying the model proposed in [1] with the purpose of applying it to discuss the effects of recreational fishing on the ecosystem of a coral reef. After studying the model we have come to the conclusion that it requires substantial modifications.

The original model is not acceptable as a model describing the ecosystem of coral reefs, and therefore not suitable for studying the effects of fishing on a coral reef ecosphere.

The major problems with the model are the following:

1. The equilibrium value for the herbivorous fish biomass variable *H* depends only on the parameters included in the piscivorous fish biomass equation, and does not depend on any other parameters or the equilibrium values of any other variables, including the algae biomass, which is the only source of food for herbivorous fish.
2. The existence and location of interior equilibria do not depend upon the intrinsic growth rate of corals r_C. This feature is difficult to interpret or justify.

The above problems could be fixed by adding plausible nonlinear terms in the dynamical equations for the *C*, *H*, and *P* variables.

The model proposed in [8] has some other, smaller deficiencies: the choice of the parameters

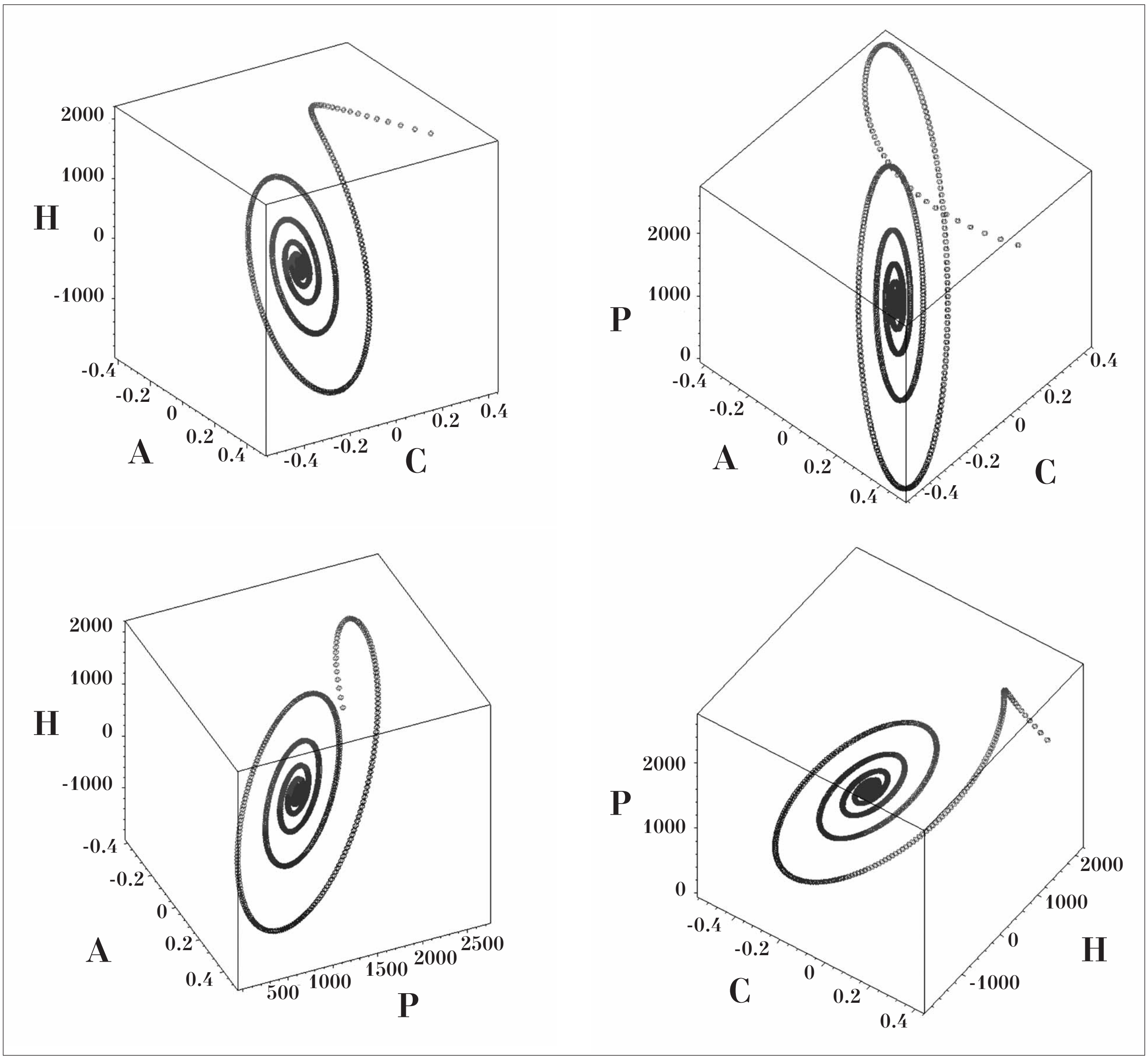

Fig. 4. 3D presentation of the phase trajectory of coral-reef model ecosystem in ACPH space

determining the behaviour of the Hill function is not substantiated in any way, although, as we have shown clearly, small variations (about 10%) in the value of the *HA* parameter in the function may change the entire behaviour of the dynamical system described by the model. It can also be shown that the other parameter in the function, *Slope*, has a great influence on the location of interior equilibria of the system.

The variations in the values of these parameters may lead to interesting bifurcations, changing the qualitative behaviour of the system, and therefore the parameters should be chosen carefully from a range that can be justified based on what is known about the system.

This paper has also identified errors in calculations used to describe the interior equilibria in the algae-coral subsystem (section "Equilibria in the A-C plane"). The recognition of these errors may lead to a different interpretation, and even to the exclusion of the Hill function from the *C*-equation.

However, as some of our numerical experiments have shown (see section "Results from numerical experiments"), the model proposed in [8] does have some interpretable components, such as the behaviour of the equilibria with respect to the variations in the values of carrying capacities. These features could be retained for possible inclusion in a corrected and suitable model of a coral-reef ecosystem.

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