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A dynamical model of the coral-algae competition in a coral reef ecosystem

© 2020. I. Bica ORCID: 0000-0003-0791-3016, M. Solomonovich ORCID: 0000-0002-3210-2904,
MacEwan University,
Building 7, 10700 – 104, Ave NW, Edmonton, Alberta, Canada, T5J 4S2,
e-mail: bicai@macewan.ca, solomonovichm@macewan.ca

A coral reef system is a biodiverse ecosystem in which coral is in mutual competitive partnership with algae. The survival of coral in this competition with algae is vital for the well-being of any coral reef ecosystem. In ideal conditions, the coral mass concentration and algae mass concentration are in a stable equilibrium. However, in practice, it is not always the case due to numerous factors of natural and anthropogenic origin. It is not easy to take into account all these factors when studying the question of survival of the reef ecosystem. We propose a dynamical system that describes the competition between coral and algae and contains terms that describe two major features inherent in this competition. The first one is the accelerated growth of algae when the amount of the turf algae exceeds a certain threshold, and it transforms into macroalgae, which grows much faster and has a detrimental effect on the corals. The second feature is associated with the grazing of the herbivory and other marine life on corals and algae. We apply both analytical and numerical techniques to study the system to find out what kind of equilibria such a system may exhibit. The results of our analysis show that although the boost in the growth of algae may devastate the corals, the latter may still survive if the algae are also subject to sufficiently intense grazing.

Keywords: coral reef ecosystems, coral-algae interaction, equilibrium, dynamical systems, nullclines, competitive ecosystem.

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Динамическая модель конкуренции кораллов и водорослей в экосистеме коралловых рифов

© 2020. И. Бика, доктор философии, доцент,
М. Соломонович, доктор философии, доцент,
Университет Макьюэна,
здание 7, 10700 – 104, Авеню Северо-Запад,
Эдмонтон, Альберта, Канада, T5J 4S2,
e-mail: bicai@macewan.ca, solomonovichm@macewan.ca

Система коралловых рифов – это многокомпонентная экосистема, в которой кораллы находятся во взаимном конкурентном партнёрстве с водорослями. Выживание кораллов в конкуренции с водорослями жизненно важно для благополучия любой экосистемы коралловых рифов. В идеальных условиях биомасса кораллов и биомасса водорослей находятся в устойчивом равновесии. Однако на практике это не всегда так из-за множества факторов природного и антропогенного характера. Учесть все эти факторы при изучении вопроса о выживании рифовой экосистемы непросто. Мы предлагаем динамическую модель экосистемы, которая описывает конкуренцию между кораллами и водорослями и включает факторы, описывающие две основные особенности, присущие этой конкуренции. Первая – это ускоренный рост бентосных водорослей, когда их количество превышает определённый порог, и начинается интенсивное размножение макроводорослей, которые растут намного быстрее и губительно действуют на кораллы. Вторая особенность связана с питанием растительноядных и других обитателей коралловых рифов. Мы применяем как аналитические, так и численные методы для изучения системы, чтобы выявить характеристики равновесного состояния такой экосистемы. Результаты анализа показывают, что, хотя ускорение роста водорослей может разрушить кораллы, последние могут выжить, если водоросли также будут подвергаться достаточно интенсивному поглощению растительноядными видами морских животных, входящих в экосистему коралловых рифов.

Ключевые слова: экосистемы коралловых рифов, взаимодействие кораллов и водорослей, равновесие, динамические системы, нулевые линии, конкурентная экосистема.

The world-wide endeavor to protect and support coral reefs as an essential part of the ocean's ecosystem is becoming more and more predominant and challenging tasks every year while humankind has been facing new challenges such as climate change and increased pollution [1–6].

Corals provide homes for many sorts of creatures under the sea. Many species, both plant and animal origin are associated with coral reef ecosystems. This biodiversity, with all kinds of interactions between the species, results in the extreme complexity of coral reef ecosystems [7–11].

The dynamics of growth and deterioration of the corals are also affected by the climate disturbances and various anthropogenic factors [1, 2, 4, 6, 12] such as pollution, recreational fishing [4, 12–14, 16], and even seemingly innocent ones such as snorkeling [17].

In the present work, we want to bring awareness of the importance of modeling the dynamics of the coral reefs from a mathematical perspective. Based on our evaluations, we identify the factors that play a decisive role in coral reef survival. At the same time, we address the parameters that influence the dynamics and how to manage them to support coral reef survival. Since the number of the variables of such a system is enormous, the model must suggest which ones are the most decisive, and concentrate on those, while adding the others as higher-order effects to the basic model.

Currently, despite some diversity of opinions [18], the majority of researchers consider coral-algae competition for light and oxygen as the primary factor influencing the coral reef survival.

The primary producer in the trophic structure of a coral reef is algae. The algae produce their energy, and they consist of the following types: zooxanthellae, coralline, and calcareous algae, and turf algae (known as well as "algal turfs"). The algal turfs are dense benthic algae, composed of filamentous algae and phytoplankton. Algae provide nutrients and oxygen, and they are essential in the growth and maintenance of coral reef ecosystems. Among algal functional groups, the turf algae are integral to the healthy function of a coral reef ecosystem. Turf algae [19], have a high growth rate, and due to their physical location within a reef system, they are less susceptible to water turbulence and grazing. The overgrow of algal turfs will force the coral to react in defense, and depending on the nature of the coral, fast or slow- growing, the turf algae will be either a competitor or a predator within the coral reef ecosystem [20]. The balance between algae and coral is essential for both to sustain a healthy ecosystem; too little algae will not offer the coral enough food and oxygen, while too many algae will suffocate the coral. The suffocation of the coral will result in the decay of the living coral mass, and eventually, the coral dies out.

For example, decaying living coral mass can manifest through coral bleaching, coral dying from the base, or coral polyps expelling their population of zooxanthella. Once the coral dies out, the proliferation of algae will turn into itself, and eventually, it will reach a saturation point.

The present work focuses on the interaction between coral and algae as competing species, and it addresses the model proposed in [21] by developing some ideas presented in our recent paper [22]. We consider the presence of herbivory as well feeding on algae and other marine life feeding on corals as well as algae. Depending on the model parameters, the dynamical model proposed may generate various outcomes: the coral and the algae may become "partners" that sustain a well-balanced reef ecosystem, or they may turn against each other, i. e., one of the species contributes to the extinction of the other.

Coral-algae model

The model proposed below is a modification of the classical Lotka-Volterra model of two competing species. The changes reflect the intrinsic features of the coral-algae competition in the ecosphere of a coral reef.

The first modification includes the presence of the so-called shift leading to non- linearity in the competition, i. e., when the density of the biomass of algae exceeds a certain threshold, the composition of the algal community shifts from turf algae to macro-algae [21, 23]. The latter grows faster than the turf algae; also, it is less amenable to the herbivory grazing, and it creates a higher shading effect. This shift gives algae an advantage in the competition with corals.

The second modification includes contributions from the herbivorous fish and other plant and coral-eating marine life. These are modeled by linear functions, which, of course, is a simplification we assume in this basic version of the model.

Thus, we propose the following autonomous system of differential equations:

$$\dot{x}=r_1x\left(1-\frac{x}{K_1}\right)-\frac{c_{12}r_1xy}{K_1}-\beta_1x \quad (1)$$

$$\dot{y}=r_2x\left(1-\frac{y}{K_2}\right)-\frac{c_{21}r_2xy}{K_2}+\alpha yH\left(y-\eta\right)-\beta_2y \quad (2)$$

x and y represent the proportions of the population densities of coral and algae, respectively. r_1 and r_2 represent the intrinsic growth rates of coral and algae, respectively. K_1 and K_2 represent the carrying capacities of coral and algae, respectively. c_{12} is the effect of algae onto coral, and c_{21} is the effect of coral onto algae. The term associated with the Heaviside function [24]:

$$H(y-\eta)=\begin{cases}0, y<\eta\\ 1, y\geq\eta\end{cases} \quad (3)$$

will play an "activation" role in the model; when the density of the algae biomass exceeds a certain threshold value η, the shift occurs: macroalgae starts dominating the composition of the algal community, which increases the rate of the algal growth. $\eta\in(0,1)$ is an a priori set up monitoring threshold for the algae, y. If $y<\eta$ and $\beta_1=\beta_2=0$, the model is simply a competitive Lotka-Volterra model [25, 26]. Otherwise, the model is a modified competitive Lotka-Volterra model, where the behavior of the dynamical system depends on the values of the parameters. The parameter $\alpha\in(0,1)$ is a "boosting" parameter for coral; when $y\geq\eta$, the term αy will contribute to the faster proliferation of algae. The small and positive parameters β_1 and β_2 reflect the effect of the herbivorous fish [27], and coral-eating marine life [28], on coral and algae, respectively. In the present study, we consider the effect of the herbivorous fish as a linear function. In reality, these functions are more sophisticated, and the parameters β_1 and β_2 may depend upon many factors, including even the coral reef's topography, which affects how herbivorous fish, parrotfishes and surgeonfishes, graze [29]. Thus, the dynamical system (1–2) takes into account specific features of the coral-algae competition, namely the more intrusive nature of macroalgae as compared to the turf algae, and the effect the herbivorous fish and coral-eating animals have on the coral and algae populations.

We start by considering the dynamical system (1–2) in the area $y<\eta$, where, as we show below, it has an interior equilibrium point with:

$$x=\frac{K_2\beta_2c_{12}r_1-K_2c_{12}r_1r_2-K_1\beta_1r_2+K_1r_1r_2}{r_1r_2(1-c_{12}c_{21})}$$
$$y=\frac{K_1\beta_1c_{21}r_2-K_1c_{21}r_1r_2-K_2\beta_2r_1+K_2r_1r_2}{r_1r_2(1-c_{12}c_{21})}, \quad (4)$$

where:

$$K_2\beta_2c_{12}r_1-K_2c_{12}r_1r_2-K_1\beta_1r_2+K_1r_1r_2>0$$
$$K_1\beta_1c_{21}r_2-K_1c_{21}r_1r_2-K_2\beta_2r_1+K_2r_1r_2>0 \quad (5)$$

Let us note:

Since $c_{12}\in(0,1)$ and $c_{21}\in(0,1)$, then obviously $1-c_{12}c_{21}>0$.

The dynamical system (1–2), under the regime $y<\eta$, has another three non-internal equilibrium points

$$x=0,\ y=0 \quad (6)$$
$$x=0,\ y=K_2(r_2-\beta_2)/r_2x$$
$$x=K_1(r_1-\beta_1)/r_1,\ y=0$$

Since the effect produced by grazing is small compared to the major phenomena associated with the intrinsic growth of coral and algae, β_1 and β_2 are assumed to be much smaller than r_1 and r_2, respectively. As a result of such an assumption, all the equilibria (6) have positive x and y-coordinates.

In the next step in our analysis, we will "activate" the Heaviside step-function by choosing positive nonzero values of the boosting parameter α. As a result, as soon as y exceeds η, the rate of growth of the concentration of algae mass will receive a boost, and the latter will have a substantial effect on the location of the equilibria.

Nullclines and analysis

The directional vector field for the dynamical system (1–2) is:

$$\vec{V}=V_x\,\vec{i}+V\vec{j}_y, \quad (7)$$

where:

$$V_x=\frac{r_1c_{12}x}{K_1}\left(\frac{K_1}{c_{12}}-\frac{x}{c_{12}}-y-\frac{\beta_1K_1}{r_1c_{12}}\right)$$
$$V_y=\frac{r_2c_{21}x}{K_2}\left(\frac{K_2}{c_{21}}-\frac{y}{c_{21}}-x+\frac{\alpha K_2}{r_2c_{21}}H(y-\eta)-\frac{\beta_2K_2}{r_2c_{21}}\right). \quad (8)$$

In the regime $y<\eta$ the equations (8) become:

$$V_x=\frac{r_1c_{12}x}{K_1}\left(\frac{K_1}{c_{12}}-\frac{x}{c_{12}}-y-\frac{\beta_1K_1}{r_1c_{12}}\right)$$
$$V_y=\frac{r_2c_{21}x}{K_2}\left(\frac{K_2}{c_{21}}-\frac{y}{c_{21}}-x-\frac{\beta_2K_2}{r_2c_{21}}\right). \quad (9)$$

From (9) we get the x-nullcline and the y-nullcline, respectively:

$$y=-\frac{1}{c_{12}}x+\frac{K_1}{r_1c_{12}}(r_1-\beta_1)$$
$$x=-\frac{1}{c_{21}}y+\frac{K_2}{r_2c_{21}}(r_2-\beta_2). \quad (10)$$

Based on the nullclines (10), the interior equilibrium point (4) is stable if the x-intercept of the x-nullcline is less than the x-intercept of the y-nullcline, i. e.,

$$\frac{K_1(r_1-\beta_1)}{r_1} < \frac{K_2(r_2-\beta_2)}{r_2 c_{21}}. \tag{11}$$

Because (4) is an interior equilibrium point, the condition (11) implies that the following condition will be satisfied as well:

$$\frac{K_2(r_2-\beta_2)}{r_2} < \frac{K_1(r_1-\beta_1)}{r_1 c_{12}}. \tag{12}$$

The condition (12) tells us that y-intercept of the$y$-nullcline is less than the y-intercept of the x-nullcline.

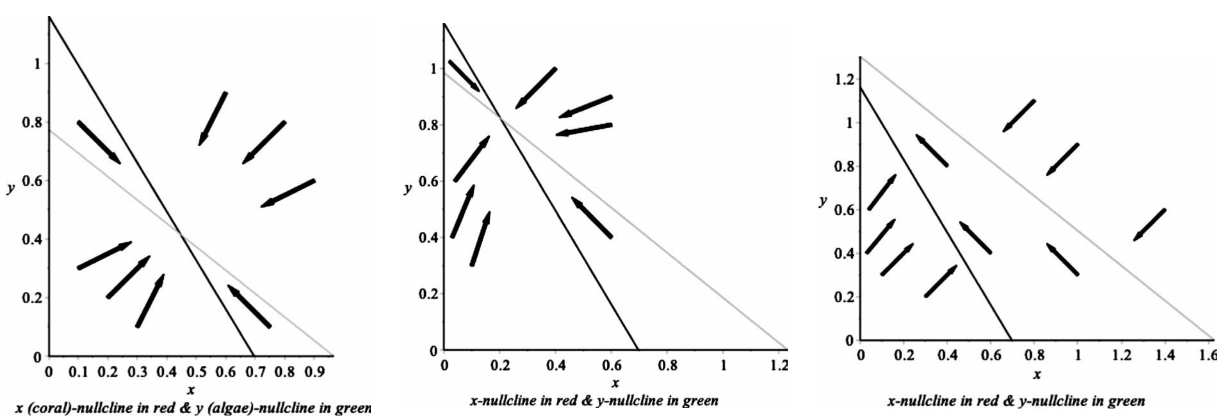
Figure 1 shows the nullclines (10) of the dynamical system (1–2). In both Figures 1a & 1b, the nullclines intersect in the interior of the first quadrant, and the interior equilibrium points are stable either in case of no boosting ($\alpha = 0$) or when the boosting term is sufficiently small ($\alpha = 0.08$). In Figure 1a there is no algae boosting effect: $\alpha = 0$, and in Figure 1b the algae boosting effect has been added by assigning $\alpha = 0.08$. We notice that, as a result of increasing α, the interior equilibrium points hifts in the upper left direction of the nullclines-plane. Further increase in the value of α results in the motion of the nullclines intersection beyond the first quadrant, which means the disappearance of the interior equilibrium. We illustrated this situation in Figure 1c, which corresponds to $\alpha = 0.2$. Thus, a sufficiently high value of the boosting term results in the extinction of coral.

The numerical values for the parameters r_1, r_2, K_1, K_2, c_{12} and c_{21} are taken from the tables provided in [21]. In this article, for our numerical simulations we used our own program written in the MAPLE programming software. In all the figures, we will use the same values for the aforementioned parameters. The parameters α, β_1, and β_2 will play the decisive role in the preservation or extinction of coral.

Figure 2 shows the directional field plot (Fig. 2a) and the phase trajectories for 500 solutions, with randomly selected initial conditions, of the dynamical system (1–2) in presence of grazing. Based on observations, we assumed grazing on coral ($\beta_2 = 10\beta_1$). As we can see from Figure 2, such a system has a stable interior equilibrium; thus, grazing in the above proportion does help coral to survive and sustain a well-balanced reef ecosystem.

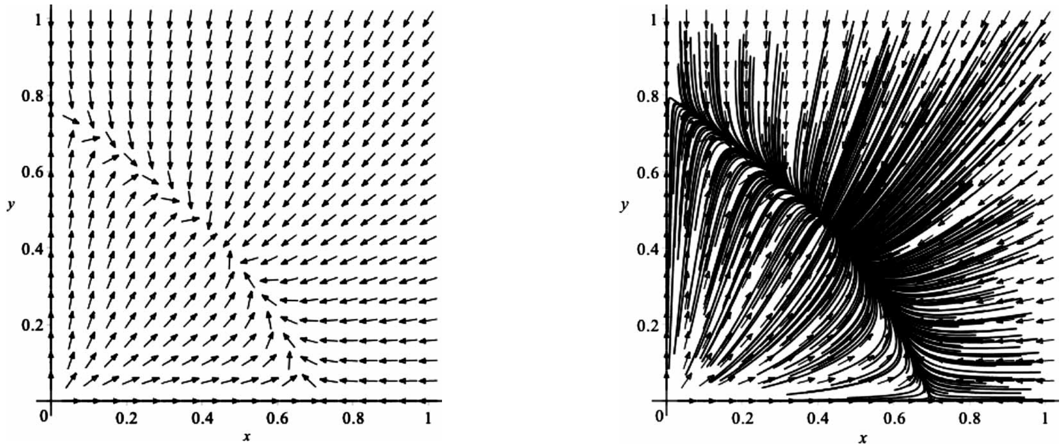
Figure 3 shows the time plots of the behavior of the dynamical system (1–2) for the same set of parameters. In Figure 3a, we assume no grazing, whereas, in Figure 3b, we assume grazing occurs, and there is much more grazing on algae than on corals. In either case, the system has an interior equilibrium, and in the grazing case, the biomass of corals stabilizes at a higher level. Thus, we can conclude that grazing in the proportion suggested does help corals to survive.

Figure 4 shows the time plot sin the presence of the boosting term, i. e., for $\alpha > 0$. We notice that, even when α is very small, the boosting effect, α, affects the coral quite dramatically; when α exceeds some (bifurcation) value between α=0.04 and $\alpha = 0.08$, the coral dies out. In case of $\alpha = 0.04$ (Fig. 4b), the system still possesses an interior equilibrium, whereas for $\alpha = 0.08$ (Fig. 4c),



(a) Stable interior equilibrium point (b) Stable interior equilibrium point (c) No longer interior equilibrium points

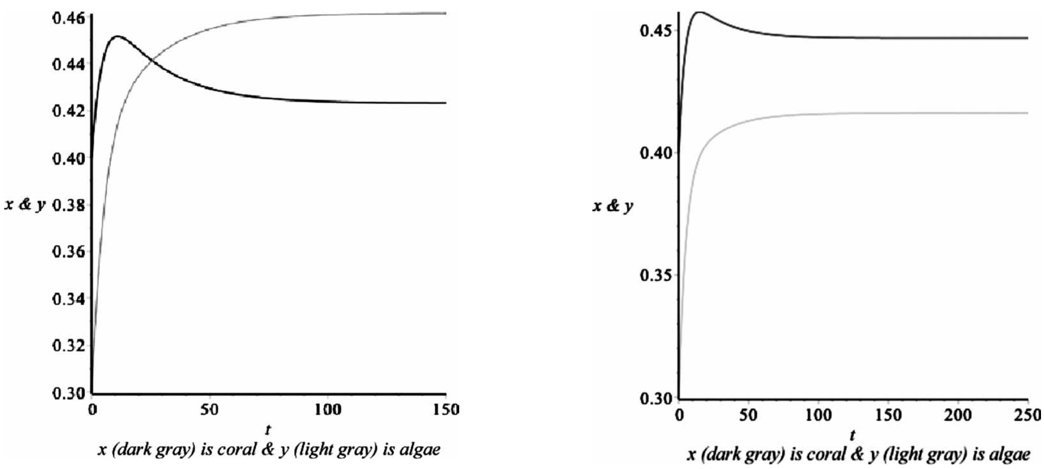
Fig. 1. Null clines showing stable interior equilibrium points (a) & (b), and no interior equilibrium point (c), for the dynamical system (1–2), for $r_1 = 0.2$, $r_2 = 0.3029279759$, $K_1 = 0.7$, $K_2 = 0.8$, $c_{12} = 0.6$, $c_{21} = 0.8$, $\beta_1 = 0.001$, $\beta_2 = 0.01$



(a) Directional field $\vec{V}$

(b) Solution curves

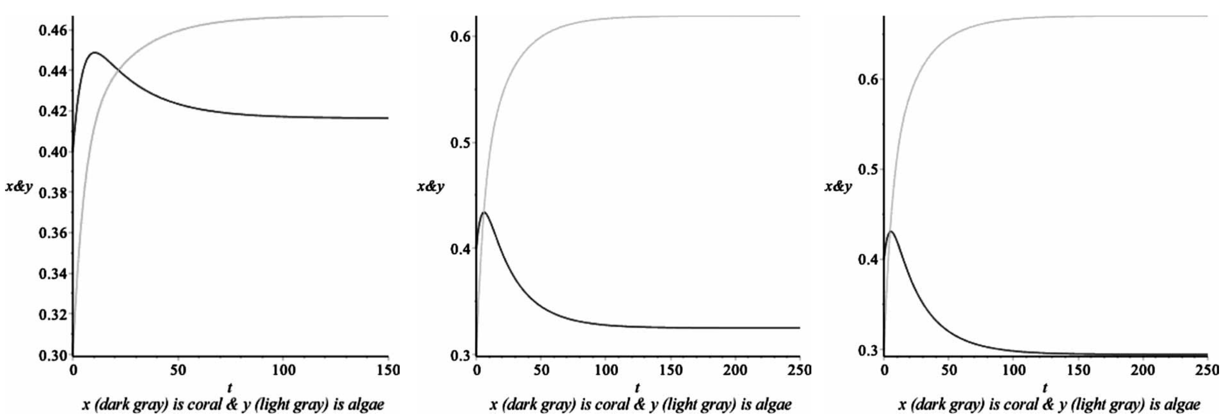
Fig. 2. Directional field plot (a), and 500 solution curves of the dynamical system (1–2) for random initial values for x and y (b), for $r_1 = 0.2$, $r_2 = 0.302928$, $K_1 = 0.7$, $K_2 = 0.8$, $c_{12} = 0.6$, $c_{21} = 0.8$, $\alpha = 0$, $\beta_1 = 0.001$, $\beta_2 = 0.01$



(a) $\beta_1 = \beta_2 = 0$

(b) $\beta_1 = 0.001$, $\beta_2 = 0.01$

Fig. 3. Coral-algae interaction for initial values $x(0) = 0.4$ and $y(0) = 0.3$, for $r_1 = 0.2$, $r_2 = 0.302928$, $K_1 = 0.7$, $K_2 = 0.8$, $c_{12} = 0.6$, $c_{21} = 0.8$, $\alpha = 0$

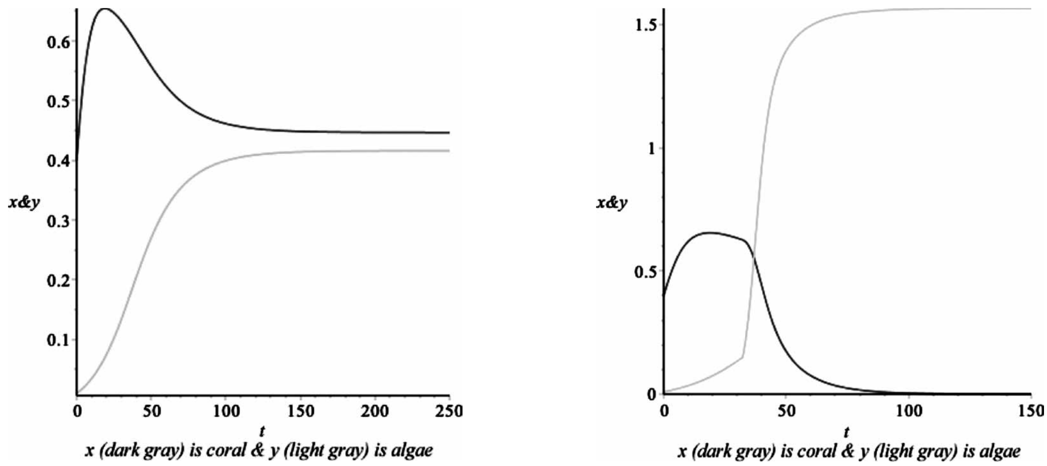


(a) $\alpha = 0.01$

(b) $\alpha = 0.04$

(c) $\alpha = 0.08$

Fig. 4. Coral-algae interaction for initial values $x(0) = 0.4$ and $y(0) = 0.3$, for $r_1 = 0.2$, $r_2 = 0.302928$, $K_1 = 0.7$, $K_2 = 0.8$, $c_{12} = 0.6$, $c_{21} = 0.8$, $\eta = 0.15$, $\beta_1 = 0.001$, $\beta_2 = 0.01$



(a) $\alpha = 0$ (b) $\alpha = 0.3$

Fig. 5. Coral-algae interaction for initial values $x(0) = 0.4$ and $y(0) = 0.01$, for $r_1 = 0.2$, $r_2 = 0.302928$, $K_1 = 0.7$, $K_2 = 0.8$, $c_{12} = 0.6$, $c_{21} = 0.8$, $\eta = 0.15$, $\beta_1 = 0.001$, $\beta_2 = 0.01$

even if the is still an interior equilibrium point, 1b, the coral is diminished to nearly its extinction.

If $\alpha = 0.2$, Figure1c, there is no longer an interior equilibrium point and the coral is extinct.

Figure 5 is another illustration of the boosting effect: when $\alpha = 0$ (Fig. 5a) both coral and algae survive, whereas for $\alpha = 0.3$ (Fig. 5b), even in the presence of grazing, coral gets extinct.

Conclusion

We have considered, both analytically and numerically, the dynamics of the coral-algae competition. We have based our analysis on the dynamical system (1–2), which takes into account specific features of the coral reef ecosystem. These features are:

The "boosting effect" of the algal accelerated growth associated with the shift from the turf algae into the macroalgae state.

The effect of grazing of the algae and the corals by the herbivorous fish and other forms of marine life associated with coral reefs.

The results obtained have shown that the ecosystem may end up in a stable equilibrium, where both corals and algae survive at some levels, thus supporting the existence of the reef, or it may come to the situation where the coral gets extinct. This result eventually leads to the extinction of the coral reef.

We showed that the boosting effect of algae if it is sufficiently intense, it may result in the extinction of the corals. At the same time, the inclusion of the grazing effect, with the realistic assumption that algae are subjected to grazing more intensely than corals, may help corals to survive in this competition. The results of the study may have some practical applications: an endangered coral reef can be saved by encouraging the presence in its neighborhood large numbers of such herbivory as parrotfish, which feeds on algae and dead corals, thus helping corals to compete and cleaning the reef, which results in the healthy reef ecosystem.

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