



Original Research Article

Algae-herbivore interactions with Allee effect and chemical defense



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ABSTRACT

Macroalgae exhibit a variety of characteristics that provide a degree of protection from herbivores. One characteristic is the production of chemicals that are toxic to herbivores. The toxic effect of macroalgae on herbivorous reef fish is studied by means of a spatiotemporal model of population dynamics with a nonmonotonic toxin-determined functional response of herbivores. It is assumed that the growth rate of macroalgae is mediated by Allee effect. We see that under certain conditions the system is uniformly persistent. Conditions for local stability of the system is obtained with weak and strong Allee effects. We observe that in presence of Allee effect on macroalgae, the system exhibits complex dynamics including Hopf bifurcation and saddle-node bifurcation. The obtained results show that the spatiotemporal system does not exhibit diffusion-driven instability. Computer simulations have been carried out to illustrate different analytical results.

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1. Introduction

Macroalgae-herbivore interactions are important in all ecosystems. Macroalgae can defend themselves against herbivores through a variety of chemicals that are toxic to herbivores (Appelhans et al., 2010). Toxin-mediated interactions between macroalgae and herbivores play an important role in marine ecology.

Several algae species are known to produce chemical compounds that reduce the growth and reproduction of fishes. Dinoflagellates are a major marine phytoplankton group which are frequently found as epiphytes on macroalgae and corals. Ciguatoin (CTX) originates in dinoflagellate species *Gambierdiscus toxicus* which reduces the growth and reproduction of herbivorous reef fish (Yasumoto et al., 1987). The adverse effects of CTX on fish embryos are studied by (Edmunds et al., 1999). On tropical coral reefs, herbivorous fish promote coral dominance by suppressing competing macroalgae (Rotjan and Lewis, 2006). Toxic-macroalgae reduce herbivory by satiating the detoxification system of herbivores (De Lara-Isassi et al., 2000). Interactions with toxic-macroalgae and herbivorous fish reduce herbivory by slowing the rate of digestion leading to reduced growth rates of herbivores and proliferation of macroalgae in coral reef ecosystem (Hay, 1997).

In population dynamics an Allee effect describes the reduction in per capita population growth rate in a low density population level

(Mistro et al., 2012). Under an Allee effect for large populations, reproduction and survival rates are inversely proportional to increased population density (González-Olivares et al., 2011; Sen et al., 2012). A strong Allee effect introduces a population threshold, and the population must surpass this threshold to grow. In contrast, a population with a weak Allee effect does not have a threshold. An Allee effect may arise from difficulties in finding mates, reproductive facilitation and predation (Holt et al., 2004). Increase in herbivory in coral reef keeps macroalgae population in control. Field observations by (Momo, 1995; Wear et al., 1999) suggest that a threshold concentration of macroalgal population is required for its cell division. This means, under excessive herbivory, macroalgae can experience an Allee effect.

We have considered a bi-trophic food chain model where toxic-macroalgae are subject to Allee effect and herbivorous fish are growing on toxic-macroalgae at the second trophic level. A toxin-determined functional response is considered to explore how toxic-macroalgae affect herbivore dynamics (Li et al., 2006). We assumed that herbivorous fish are harvested at a rate proportional to its population density.

In the present paper the main emphasis will be put on studying dynamics of the system with an Allee effect. We have studied the model analytically as well as numerically. The proofs are all deferred to the Appendix.

2. The basic model

We consider a two compartmental system of differential equations in which the concentrations of toxic-macroalgae and

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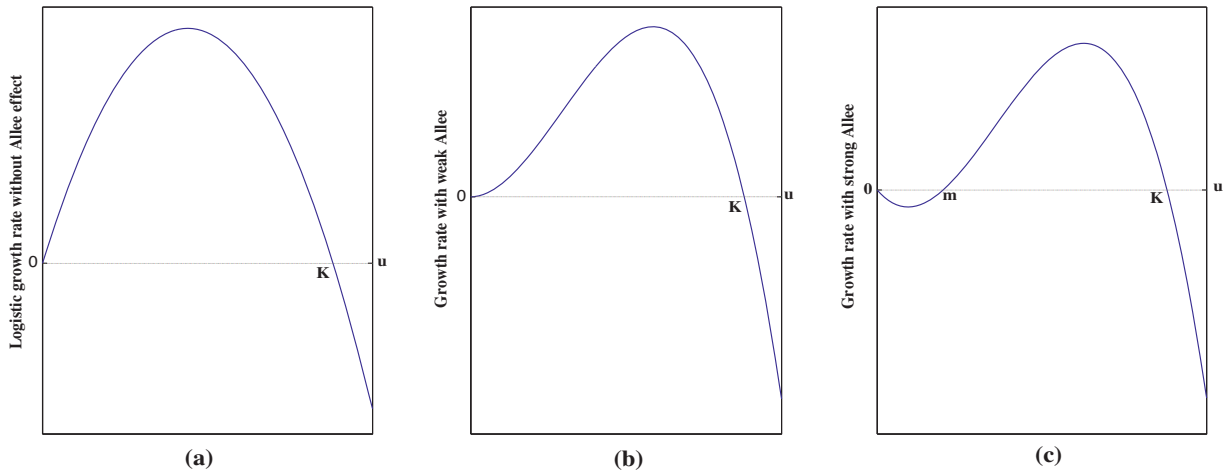


Fig. 1. (a) Logistic growth rate. (b) Growth rate with weak Allee effect ($-K < m \leq 0$). (c) Growth rate with strong Allee effect ($0 < m < K$).

herbivores are respectively $u(t)$ and $v(t)$ at time t . The growth rate of toxic-macroalgae in the absence of herbivorous fish is subject to an Allee effect with per capita growth rate $f_1(u) = r(u - m)(1 - \frac{u}{K})$, where m is the Allee threshold i.e., the minimum biomass concentration of macroalgae required to begin a positive growth in absence of herbivorous fish, r is the intrinsic growth rate of macroalgae and K is the carrying capacity, $-K < m < K$. When $m > 0$, the macroalgal-growth rate decreases if the population size is below the threshold level m and macroalgae goes to extinction, describing strong Allee effect. If $-K < m \leq 0$, it is said that the macroalgal-population is affected by a weak Allee effect (cf. Fig. 1).

The toxin generated by macroalgae decreases the growth rate of herbivorous fish. The consumption rate of herbivorous fish is given by $f_2(u) = f(u)(1 - \frac{f(u)}{4G})$, where $f(u) = \frac{eu}{1+heu}$, e is the encounter rate per unit of macroalgae, h is the handling time per unit of macroalgae in the absence of toxin and G is the toxin-adjusted maximal amount of toxic-macroalgae a herbivorous fish can ingest per unit time and so, it is a measure of macroalgal-toxicity level (Feng et al., 2011).

Since $0 \leq f_2(u) \leq f(u) \leq \frac{1}{h}$, it follows that $\frac{1}{4h} < G < \frac{1}{h}$. It is observed that $f_2(u)$ is monotonic increasing for $\frac{1}{2h} \leq G < \frac{1}{h}$ and is decreasing for $\frac{1}{4h} < G < \frac{1}{2h}$. In the non-monotone case $f_2(u)$ reaches its maximum at $u_m = \frac{2G}{e(1-2Gh)}$ with $f_2(u_m) = G$ (cf. Fig. 2).

Considering the drift of macroalgae on ocean currents and the movement of herbivorous fish, a reaction-diffusion system, under the assumption that macroalgae and herbivorous fish are diffusing according to Fick's law in a rectangular domain $\Omega = [0, L_1] \times [0, L_2] \subseteq \mathbf{R}^2$ is as follows:

$$\frac{\partial u}{\partial t} = uf_1(u) - vf_2(u) + d_1 \nabla^2 u, (x, y, t) \in \Omega \times (0, \infty) \tag{1}$$

$$\frac{\partial v}{\partial t} = \alpha vf_2(u) - (D + H)v + d_2 \nabla^2 v, (x, y, t) \in \Omega \times (0, \infty)$$

with the initial conditions $u(x, y, 0) \geq 0, v(x, y, 0) \geq 0$, for all $(x, y) \in \Omega$ and the zero-flux boundary conditions $\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0$ in $\partial\Omega \times (0, \infty)$, where n is the outward unit normal vector of the boundary $\partial\Omega$, which is assumed to be smooth. Also, ∇^2 is the Laplacian operator in two-dimensional space, which describes random movement. The zero-flux boundary conditions imply the

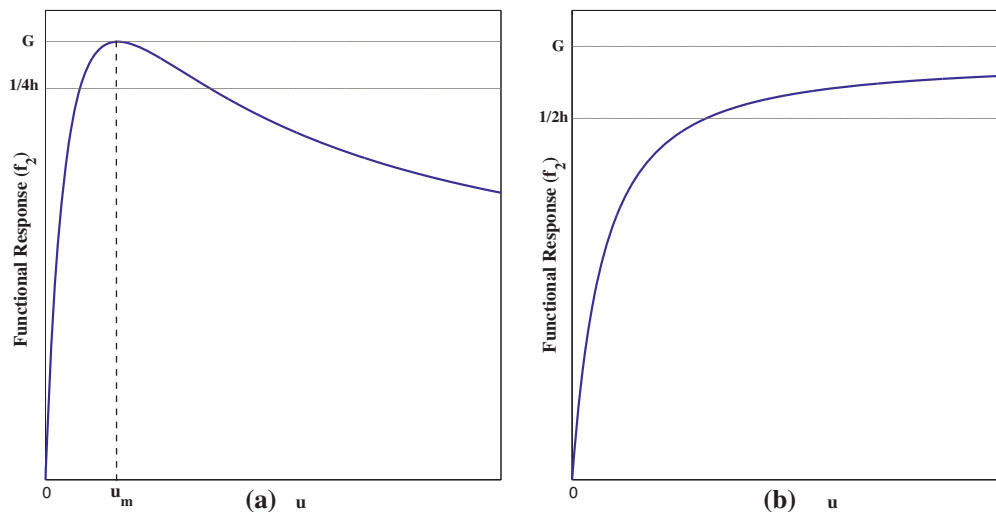


Fig. 2. (a) The functional response of herbivorous fish for $\frac{1}{4h} < G < \frac{1}{2h}$ is unimodal and reaches maximum at $u_m = \frac{2G}{e(1-2Gh)}$. (b) For $\frac{1}{2h} \leq G < \frac{1}{h}$ the functional response is monotonically increasing with the asymptote below G .

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