

Effect of nonlinear mortality and self-grazing on the dynamics of a marine ecosystem

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Abstract. Do the nonlinear terms arising from mortality or self-grazing of zooplankton have significant effect in suppressing limit cycles or auto-oscillations of marine ecosystem models that are observed under certain conditions? This question is examined with the help of the phase-plane analysis of a class of basic marine ecosystem models. It is found that even a rather small nonlinear term describing nonlinearity in mortality or self-grazing can effectively alter the linear stability conditions and thereby suppress the limit cycles.

Keywords. Nonlinear mortality; self-grazing; zooplankton; marine ecosystem dynamics.

1. Introduction

It has been reported in the literature (Busenberg *et al* 1990) that marine ecosystem models display limit cycles under certain conditions, especially when there is an abundance of nutrients. It has also been suggested that introduction of nonlinear mortality and/or self-grazing suppresses such limit cycles (Steele & Henderson 1992). These types of oscillations of the models are often believed to be unrealistic and are sometimes encountered in simulations for tropical regions. We examine this issue with the help of a class of basic models. The dynamics of some models of this type were examined in detail by Wroblewski *et al* (1988). The present study examines the phase plane trajectories near one of the equilibrium points of the system and also its stability. It follows the phase-plane perspective of Yajnik & Sharada (1992).

2. The class of basic models

We consider a model class that has the least number of variables and yet incorporates some of the essential biology. The model is obtained by describing the biomass of all

autotrophs as the variable P , the biomass of heterotrophs as the variable Z , and the mass of the nutrients as the variable N . The former two are taken in equivalent nutrient mass. It is assumed that all the nutrients limiting the growth of zooplankton are modelled by N . The governing equations for the basic marine ecosystem model take the following form,

$$\frac{dP}{dt} = P\phi(P, Z, N), \quad (1a)$$

$$\frac{dZ}{dt} = Z\psi(P, Z, N), \quad (1b)$$

$$\frac{dN}{dt} = -P\phi(P, Z, N) - Z\psi(P, Z, N) + h(N, t), \quad (1c)$$

where ϕ and ψ are net specific growth rates of phytoplankton and zooplankton respectively. It is a general feature of models of living species that ϕ and ψ lie between maximum and minimum finite values. In the models that we consider, ϕ and ψ have the following forms,

$$\phi(P, Z, N) = f(N) - \varepsilon - g_1(P, Z)Z, \quad (2a)$$

$$\psi(P, Z, N) = (1 - \gamma)g_1(P, Z)P - \omega(Z) - \gamma g_2(P, Z). \quad (2b)$$

Here, f , g_1 , g_2 and ω are respectively the productivity, grazing, self-grazing and zooplankton mortality functions and ε is the mortality coefficient for phytoplankton.

The net input function h depends on physical processes like diffusion, upwelling etc. Since we wish to explore conditions arising from internal nonlinear structure, we take $h(N, t)$ to be zero. It follows from (1) that $P + Z + N$ is a constant and the system is therefore governed by two equations.

The productivity function $f(N, P)$ is governed by Michaelis-Menten law, and is taken to be

$$f = v_p N / (k_1 + N), \quad (3)$$

where v_p and k_1 are the asymptotic growth rate and the half-saturation constant respectively. The effect of changes in light on productivity can be modelled by incorporating a light-dependent term in the above, which would introduce an indirect dependence on time.

The mortality function ω is taken in the form,

$$\omega = \omega_1 + \omega_2 Z, \quad (4)$$

where ω_1 and ω_2 are the linear and quadratic mortality coefficients respectively. ω_2 is zero in the models, where mortality is linear.

Table 1. Models of grazing.

	$g_1(P, Z)$	$g_2(P, Z)$
A. Without self-grazing		
A1. Michaelis-Menten	$v_g / (k_2 + P)$	0
A2. Ivlev	$R_m (1 - \exp(-\lambda P))$	0
A3. Mayzaud & Poulet	$R_m \lambda P (1 - \exp(-\lambda P))$	0
B. With self-grazing		
B1. Nonswitching	$v_g p_1 / (k_2 + p_1 P + p_2 Z)$	$v_g p_2 / (k_2 + p_1 P + p_2 Z)$
B2. Switching	$\frac{v_g p_1 P}{k_2(p_1 P + p_2 Z) + p_1 P^2 + p_2 Z^2}$	$\frac{v_g p_2 Z}{k_2(p_1 P + p_2 Z) + p_1 P^2 + p_2 Z^2}$

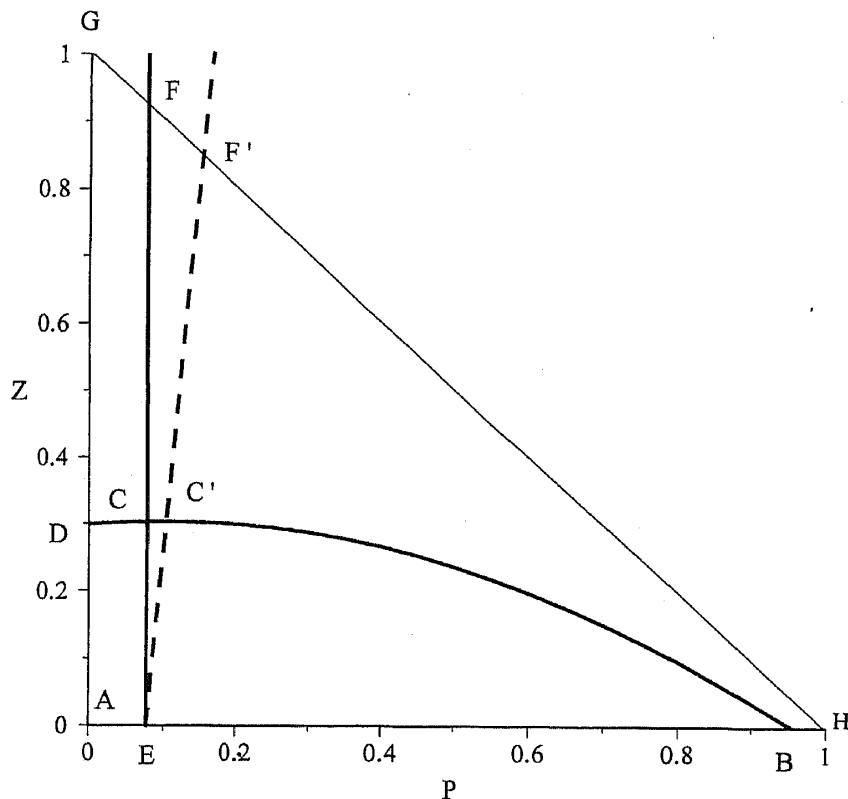


Figure 1. Phase plane of the basic model A1 ($k_1 = 0.5$, $k_2 = 1$, $\varepsilon = 0.05$, $v_g = 1$, $\gamma = 0.3$, $v_p = 0.6$, $\omega_1 = 0.05$). The equilibrium point C shifts to C' when ω_2 changes from zero to 0.05 and its linear stability characteristics are altered.

Several approaches have been tried in modelling grazing and self-grazing. They are given in table 1. p_1 and p_2 are preference parameters respectively for phytoplankton and zooplankton ($p_1 + p_2 = 1$) in the models with self-grazing. Clearly, the models B₁ and B₂ reduce to A₁ when p_2 is set to zero.

3. Phase plane analysis

Qualitative aspects of the dynamics of the model A₁ can be readily understood with the help of a phase plane plot. Figure 1 shows the phase plane. The state of the system lies in the triangle AHG as the total biomass ($P + Z$) cannot exceed the total nutrient, which is normalized to unity, and P and Z cannot become negative. Three types of equilibrium points can occur where dP/dt and dZ/dt are zero. dP/dt is zero on the x -axis and on BCD where $\phi = 0$, and dZ/dt is zero on the y -axis and on ECF where $\psi = 0$. Figure 1 shows the three types of equilibrium points A, B and C. A is the intersection of x - and y -axes, B, the intersection of BCD and x -axis, and C, the intersection of BCD and ECF. Limit cycles arise when the point C becomes unstable, A and B not being relevant to the limit cycles.

The following conditions hold at C.

$$\phi(P, Z) = 0, \quad (5a)$$

$$\psi(P, Z) = 0. \quad (5b)$$

The linear stability is determined by the trace of the Jacobian

$$J = \begin{bmatrix} \phi + P \frac{\partial \phi}{\partial P} & P \frac{\partial \phi}{\partial Z} \\ Z \frac{\partial \psi}{\partial P} & \psi + Z \frac{\partial \psi}{\partial Z} \end{bmatrix}. \quad (6)$$

Let T be the trace of the Jacobian J . Then,

$$T = (\phi + \psi) + P \frac{\partial \phi}{\partial P} + Z \frac{\partial \psi}{\partial Z}, \quad (7)$$

where the first two terms vanish at the equilibrium point C. If T is positive, the point C is unstable. Under such conditions limit cycle occurs in the model. When T is negative, the point C is stable and there is no question of limit cycles arising.

To examine what happens to the trace T at the equilibrium point C when ω_2 is varied, we consider the total derivative of T keeping all other parameters such as $v_p, v_g, k_1, k_2, \varepsilon, \omega_1$ fixed

$$\begin{aligned} \frac{dT}{d\omega_2} &= \frac{\partial P}{\partial \omega_2} \frac{\partial \phi}{\partial P} + P \frac{\partial^2 \phi}{\partial P^2} \frac{\partial P}{\partial \omega_2} + P \frac{\partial^2 \phi}{\partial P \partial Z} \frac{\partial Z}{\partial \omega_2} \\ &\quad + \frac{\partial Z}{\partial \omega_2} \frac{\partial \psi}{\partial Z} + Z \frac{\partial^2 \psi}{\partial P \partial Z} \frac{\partial P}{\partial \omega_2} + Z \frac{\partial^2 \psi}{\partial Z^2} \frac{\partial Z}{\partial \omega_2}. \end{aligned} \quad (8)$$

Since the trace is calculated at the equilibrium point C which changes as ω_2 changes, it follows from (5a) and (5b) that

$$\frac{\partial \phi}{\partial P} \frac{\partial P}{\partial \omega_2} + \frac{\partial \phi}{\partial Z} \frac{\partial Z}{\partial \omega_2} + \frac{\partial \phi}{\partial \omega_2} = 0, \quad (9a)$$

$$\frac{\partial \psi}{\partial P} \frac{\partial P}{\partial \omega_2} + \frac{\partial \psi}{\partial Z} \frac{\partial Z}{\partial \omega_2} + \frac{\partial \psi}{\partial \omega_2} = 0. \quad (9b)$$

In the case of model A1,

$$\frac{\partial \phi}{\partial \omega_2} = 0 \quad \text{and} \quad \frac{\partial \psi}{\partial \omega_2} = -Z, \quad (10)$$

$$\frac{dT}{d\omega_2} = \left[P \frac{\partial^2 \phi}{\partial P^2} + \frac{\partial \phi}{\partial P} \right] \frac{\partial P}{\partial \omega_2} + \left[P \frac{\partial^2 \phi}{\partial P \partial Z} + \frac{\partial \psi}{\partial Z} \right] \frac{\partial Z}{\partial \omega_2},$$

$$\frac{dT}{d\omega_2} = \frac{-Z(ax^2 + bxy + cy^2)}{d}, \quad (11)$$

where

$$a = c_1 c_2^2,$$

$$b = 2Pc_1[c_2^2 + (c_1 + c_2)Z] + c_1^2 c_2(P - Z + c_2),$$

$$c = c_1^3 Z(P - c_2),$$

$$d = c_1^3 c_2(x + y c_1) v_g k_2 (1 - \gamma),$$

$$c_1 = k_1 + 1 - P - Z, \quad c_2 = k_2 + P,$$

$$x = v_p k_1 c_2, \quad y = v_g c_1.$$

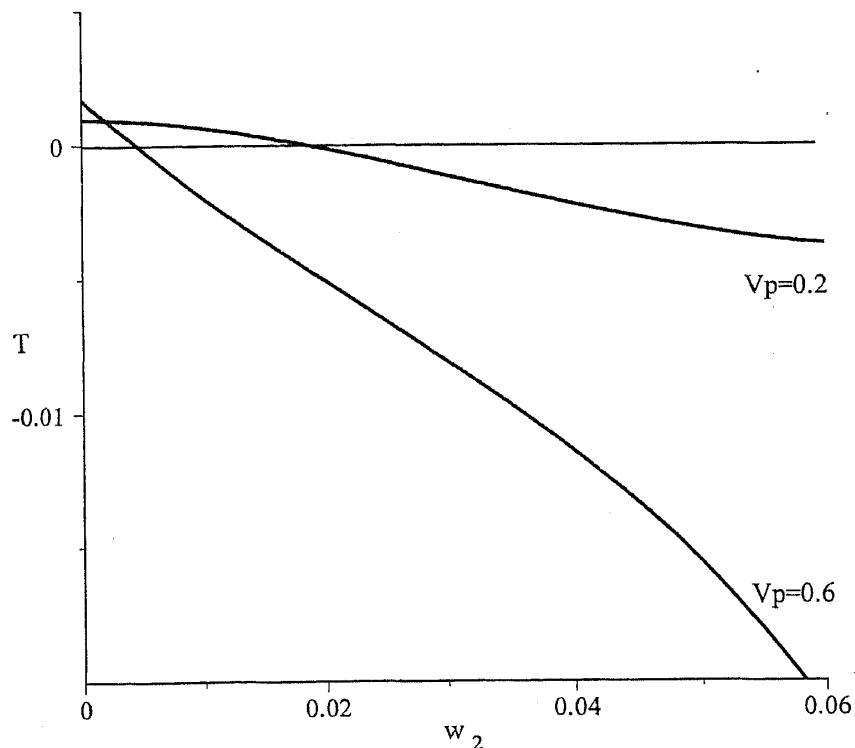


Figure 2. Effect of nonlinear mortality coefficient ω_2 on the trace T for two values of v_p (0.2 and 0.6) ($k_1, k_2, \varepsilon, v_g, \gamma, \omega_1$ as in figure 1).

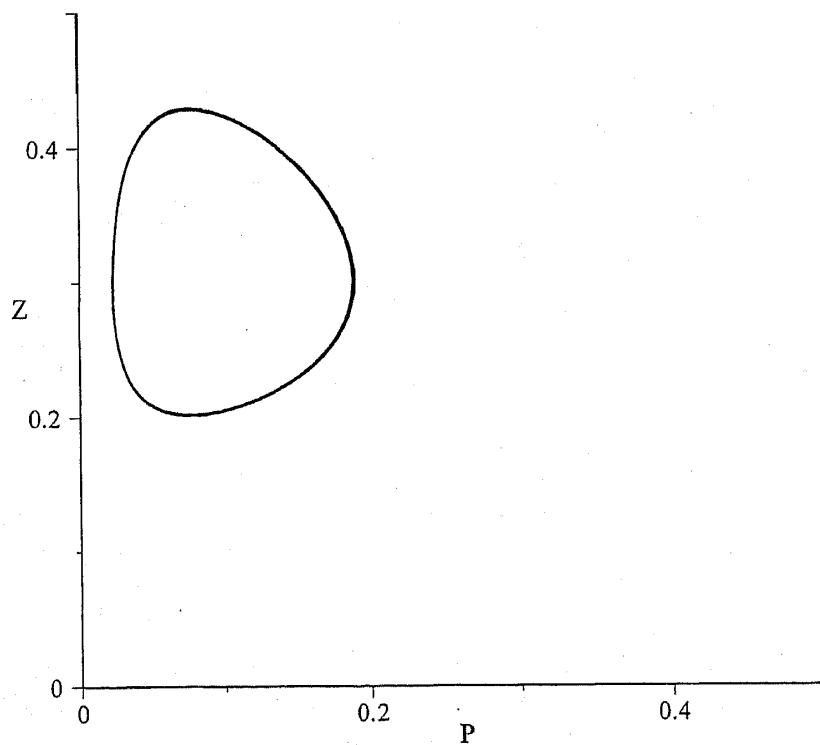


Figure 3. Limit cycle in absence of nonlinear mortality ($k_1, k_2, \varepsilon, v_g, \gamma, \omega_1$ as in figure 1; $v_p = 0.6, \omega_2 = 0$).

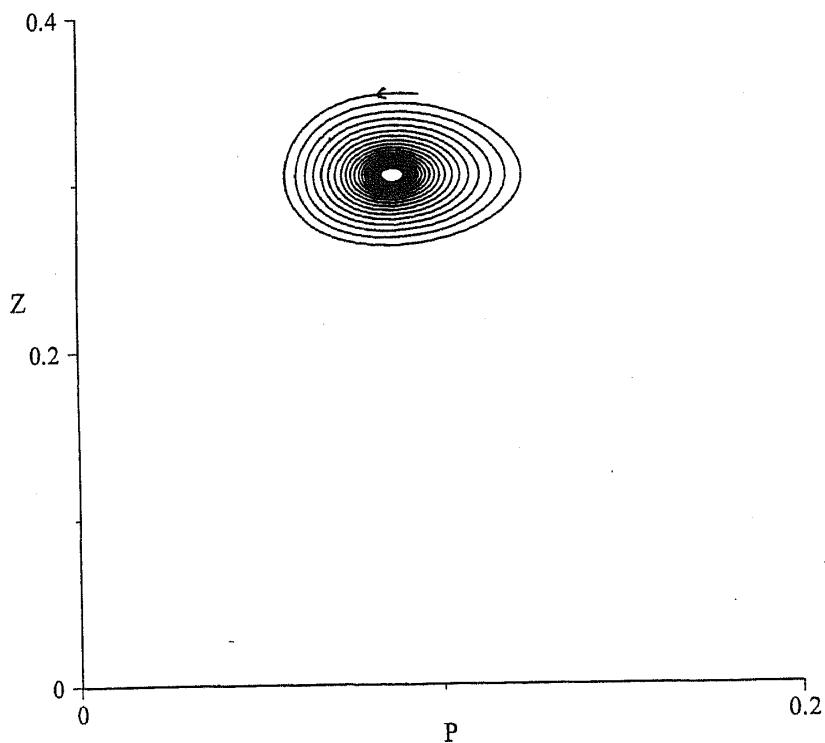


Figure 4. Disappearance of limit cycle due to nonlinear mortality ($k_1, k_2, \varepsilon, v_g, \gamma, \omega_1$ as in figure 1; $v_p = 0.6, \omega_2 = 0.02$).

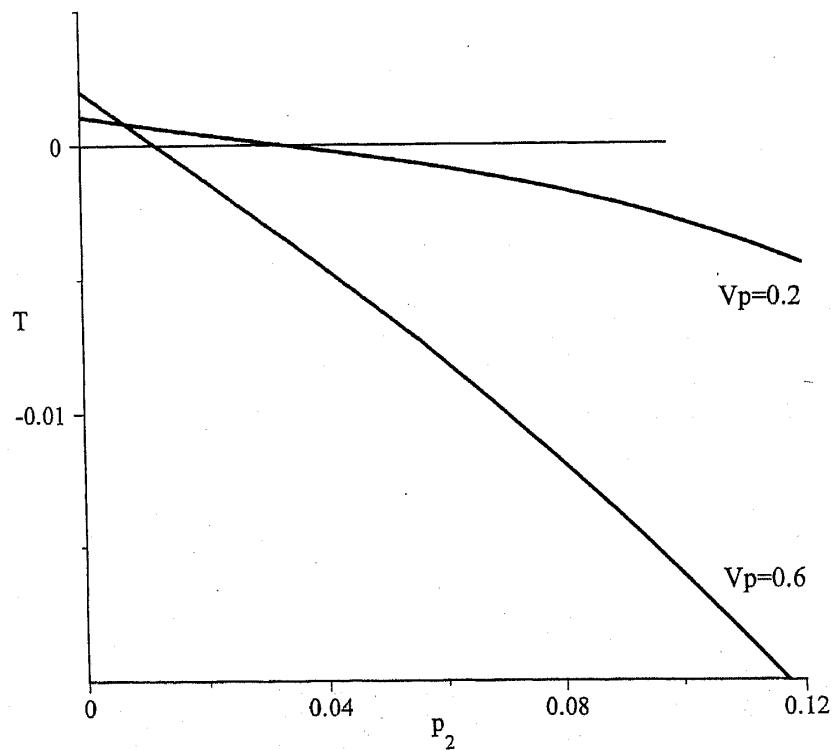


Figure 5. Effect of self-grazing on the trace T ($k_1, k_2, \varepsilon, v_g, \gamma, \omega_1$ as in figure 1; $v_p = 0.2$ and 0.6).

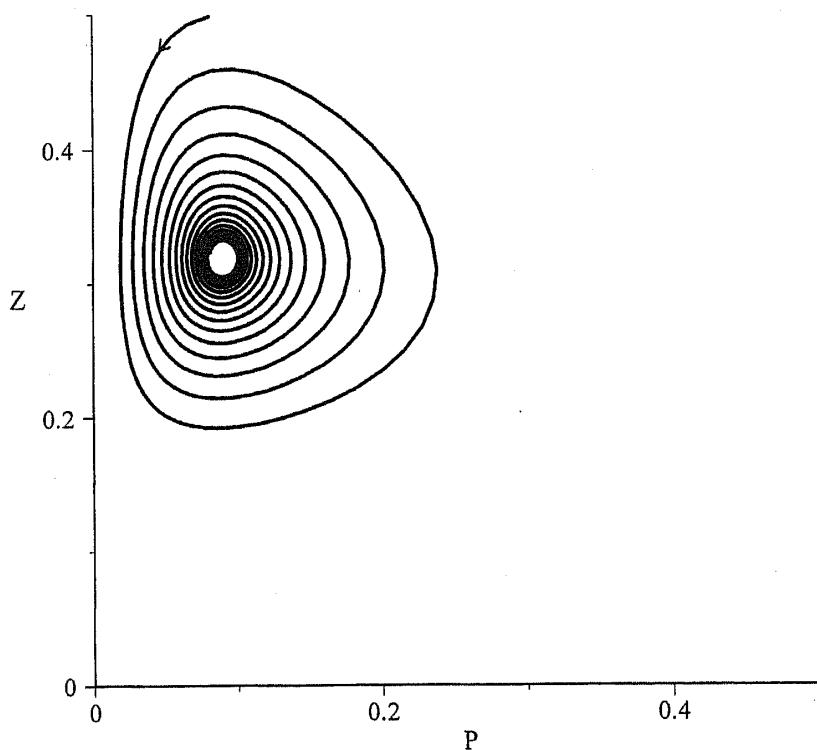


Figure 6. Suppression of limit cycles due to self-grazing ($k_1, k_2, \varepsilon, v_g, \gamma, \omega_1$ as in figure 1; $v_p = 0.6, p_2 = 0.05$).

For example, for $v_p = 0.6, v_g = 1, k_1 = 0.5, k_2 = l, \gamma = 0.3, \omega_1 = 0.05$ and $\varepsilon = 0.05$, the equilibrium point C is at $P^* = 0.077, Z^* = 0.3039, dT/d\omega_2$ is -0.028 .

So the effect of ω_2 in this typical case is to decrease the value of trace and hence the stability. In general, the sign of $dT/d\omega_2$ depends on $(ax^2 + bxy + by^2)$. Similarly, an expression for variation of the trace with p_2 can be obtained for the model B₁.

Figure 2 shows how the sign of the trace changes in the model A₁ from positive to negative when nonlinear mortality is introduced, that is, ω_2 changes from zero to a positive value and figures 3 and 4 show how the limit cycles disappear. Similarly when self-grazing is introduced, p_2 in the model B₁ changes from zero to a positive value and figure 5 shows the consequential effect on the trace. The resulting suppression of limit cycles is shown in figure 6.

4. Conclusion

It is shown by using phase-plane analysis how nonlinear mortality or self-grazing of zooplankton imparts stability to a class of ecosystem models and suppresses limit cycles.

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