

Spatially-Structured Three-Species Models for Benthic Predation

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ABSTRACT In a recent study [1], an ordinary differential equation model has been given for one-prey (mussel) and one-predator (sea star) of a benthic community, representing their spatially-structured dynamics. We generalize this model in this paper and extend its scope to the dynamics of three species (one-prey, two-predators) of benthic community namely: mussel, sea star and spiny lobster. We present two models in this paper, one with the assumption that the prey reaches certain size and becomes resistant to both predators and the other when the large size prey becomes resistant to one predator but remains vulnerable to the other. It is seen that these models have the possibility of multiple equilibrium solutions whose existence and stability may be related to the crucial parameters of the two predators.

(Spatially-structured; benthic species; predator-prey interactions)

INTRODUCTION

In a recent study, authors in [1] introduce four models (each model representing a different model class from ordinary differential equation (ODE), stochastic birth-death (SBD), cellular automata (CA) and agent based models (ABMs)) of an intertidal predator-prey system to demonstrate advantages of the multiple model approach. They introduce an experimental system of mussels and their predators. The mussel *Mytilus californianus* is a dominant species of the intertidal zones of the North American continent. This species is found in narrow bands in shore sites of moderate to high wave exposure. The predators of *M. californianus* are the sea star, *Pisaster ochraceus*, in the Pacific Northwest [2, 3], and the spiny lobster, *Panulirus interruptus*, in Southern California [4].

Early experiments suggested that mussels experience a spatial refuge from predation at the upper intertidal zone. It was observed that below the upper intertidal zone there were patches of very large mussels which escaped predation [2]. It has also been observed that sea stars ate mussels smaller than the maximum available size. This suggested that mussels reach a certain size and become resistant to predation. Later

studies contradict the hypotheses of spatial and size refuges [5, 6] terming the refuge hypothesis as an oversimplification of a more complex situation.

Mussel growth depends on the flow of water providing food, resulting in higher growth rates for mussels located in the intertidal zone and on wave exposed shores [7]. The probability of being attacked by a predator decreases when a mussel is surrounded by larger mussels [6, 8]. Thus, the rates of production and mortality in any specific location depend on the location of a mussel in the gradients of tidal height and wave exposure and on the size and density of surrounding mussels.

Authors in [1] incorporate these assumptions in their models considering rates of recruitment, growth, and predation mortality as dynamic spatially explicit process. They take a multiple model approach and develop and analyze four classes of models to study the predation dynamics in benthic communities. Their ordinary differential model is a two-species model that represents the dynamics of a single prey (mussel) and its single predator (sea star) in the Pacific. We generalize this model in this paper and extend its scope to three-species interactions of mussel,

sea star and spiny lobster. Indeed we propose two models designated Model 1 and Model 2. While we develop Model 1 under the assumption that the prey reaches a certain size and becomes resistant to both predators, we formulate Model 2 for a situation when the large size prey becomes resistant to one predator but remains vulnerable to the other. It may be mentioned that while our Model 1 concerns the interactive dynamics of those regions of Pacific where all the three species i.e. prey (mussel) and its two predators (sea star and spiny lobster) may interact, Model 2 can also be applicable to other similar situations of fish interactions.

We find the equilibrium solutions of Model 1 and Model 2 and study their stability. It is found that likewise two-species model of [1], our three-species models still have the possibility of multiple equilibrium solutions whose stability depends on the crucial parameters of the two predators. We plan the rest of the paper as follows. We formulate main models in section 2. Equilibrium solutions of the models are given in section 3. We discuss the stability of the equilibrium solutions in section 4. Section 5 contains the main conclusions of the paper.

MAIN MODELS

We base our three-species interaction model on the work in [1] where "space" is made up of a large number of very small "patches" which can be occupied by, at most, one mussel and predators move randomly among patches. Prey biomass grows in size in each patch until a predator grazes a patch to size zero. In this setting, each patch is either empty or occupied by a mussel. We consider the three-species model to be governed by the following set of equations

$$\frac{\partial n(a, t)}{\partial t} + \frac{\partial n(a, t)}{\partial a} = -\mu(a, t)n(a, t), \quad (1)$$

$$\frac{dP(t)}{dt} = I_P - \alpha_1(t)P(t), \quad (2)$$

$$\frac{dQ(t)}{dt} = I_Q - \alpha_2(t)Q(t), \quad (3)$$

where $n(a, t)$ is the density of prey of age a at time t ; $P(t)$ and $Q(t)$ represent the densities of the two types of predators. Equation (1) is the well known Mckendrick model [9] for removals in an age-structured population with

$\mu(a, t)$ denoting the mortality rate for prey of age a at time t .

We assume that the addition of new individuals into prey population takes place according to

$$n(0, t) = \sigma(1 - N(t)/K) \quad (4)$$

where σ is the constant rate at which the prey settle into empty patches with overall recruitment of prey decreasing linearly until all available space is occupied at a maximum density K .

$N(t)$ represents the overall prey density to be given by $N(t) = \int_0^\infty n(a, t)da$. In the above open system, predators $P(t)$ and $Q(t)$ immigrate at the constant rates I_P and I_Q and emigrate at the per capita rates $\alpha_1(t)$ and $\alpha_2(t)$ respectively.

Considering that the prey (mussel) size plays an important role in its protection from predation, we let $s(a)$ denote the size of a prey of age a and assume growth to be given by the von Bertalanffy [10] formulation

$$s(a) = s_\infty - (s_\infty - s_0) \exp(-\beta a), \quad \text{where } \beta$$

is the growth rate, s_∞ is the maximum size, and s_0 is the size of a newly settled recruit. We assume each prey's vulnerability to predation depends on its size and density and size of prey in some spatial neighbourhood of radius R surrounding the individual. Following authors of [1] in their mean field approximation, we consider the size of the neighbourhood $R = \infty$,

$$\text{and define } S(t) = \int_0^\infty s(a)n(a, t)da, \quad (5)$$

as the mean size of prey weighted by prey density.

Model 1

We develop this model under the assumption that the probability of prey being attacked by either predator decreases when a mussel is surrounded by larger mussels [6, 8] and accordingly we write the mean field approximation for the per capita mortality rate of prey as

$$\mu(a, t) = \mu_0 + [k_{1P}(t)P(t) + k_{1Q}(t)Q(t)] \exp(-cS(t)) \quad (6)$$

which is independent of prey age but decreases exponentially with the weighted mean size of prey, $S(t)$. The parameter μ_0 is the mortality rate due to causes other than predation, c is a measure of how quickly resistance to predation increases with prey size, and k_{1P} and k_{2Q} are the

respective predation coefficients of predators $P(t)$ and $Q(t)$.

For predators, we assume that the emigration rate of each predator from the system is inversely proportional to the per capita rate of prey consumption and consider

$$\alpha_1(t) = \left[\frac{E_{1P}}{k_{1P} S(t) \exp(-c(S(t)))} \right] \quad \text{and} \quad \alpha_2(t) = \left[\frac{E_{1Q}}{k_{1Q} S(t) \exp(-c(S(t)))} \right] \quad (7)$$

where E_{1P} and E_{1Q} are the constants of proportionality relating prey consumption to predator emigration. Taking the time derivative of $S(t)$ in (5) and using equation (1), we get (8). Integrating the first integral on the right by parts and using the fact that μ in the second integral on

the right does not depend on a (see (6)), (8) can be reduced to (9). Next differentiating $N(t)$ with respect to time t and using equation (1) again, it can be shown that $N(t)$ satisfies the following differential equation (10).

$$\frac{dS}{dt} = - \int_0^\infty s(a) \frac{\partial n}{\partial a} da - \int_0^\infty s(a) \mu(a, t) n(a, t) da \quad (8)$$

$$\frac{dS}{dt} = s_0 \sigma + (s_\infty \beta - s_0 \sigma K^{-1}) N(t) - [\beta + \mu_0 + (k_{1P} P + k_{1Q} Q) \exp(-cS(t))] S(t) \quad (9)$$

$$\frac{dN}{dt} = \sigma - [K^{-1} \sigma + \mu_0 + (k_{1P} P + k_{1Q} Q) \exp(-cS(t))] N(t) \quad (10)$$

In the process, we have replaced the Mckendrick equation (1) by a pair of differential equations (9) and (10). Now combining these equations with

equations (2) and (3) along with necessary changes, Model 1 can be seen to comprise of four equations only as given below.

$$\frac{dS}{dt} = s_0 \sigma + (s_\infty \beta - s_0 \sigma K^{-1}) N(t) - [\beta + \mu_0 + (k_{1P} P + k_{1Q} Q) \exp(-cS(t))] S(t)$$

$$\frac{dN}{dt} = \sigma - [K^{-1} \sigma + \mu_0 + (k_{1P} P + k_{1Q} Q) \exp(-cS(t))] N(t)$$

$$\frac{dP}{dt} = I_{1P} - \frac{E_{1P} P(t)}{k_{1P} S(t) \exp(-cS(t))}, \quad \text{Model 1}$$

$$\frac{dQ}{dt} = I_{1Q} - \frac{E_{1Q} Q(t)}{k_{1Q} S(t) \exp(-cS(t))},$$

Here we have replaced the notations I_P and I_Q by I_{1P} and I_{1Q} respectively to relate these immigration rates of predators to Model 1. It may be noted that under the similarity conditions for the two predators in terms of their vital parameters given as

$$k_{1P} = k_{1Q} = \theta, I_{1P} = I_{1Q} = I, \text{ and } E_{1P} = E_{1Q} = e_0 \quad (11)$$

Model 1 reduces to the form of the mean field approximation model of [1] as follows:

$$\begin{aligned} \frac{dS}{dt} &= s_0 \sigma + (s_\infty \beta - s_0 \sigma K^{-1}) N(t) - [\beta + \mu_0 + \theta Z \exp(-cS(t))] S(t) \\ \frac{dN}{dt} &= \sigma - [K^{-1} \sigma + \mu_0 + \theta Z \exp(-cS(t))] N(t) \end{aligned} \quad \text{Model 1A}$$

$$\frac{dZ}{dt} = 2I - \frac{e_0 Z}{\theta S(t) \exp(-cS(t))},$$

where

$Z = Z(t) = P(t) + Q(t)$. We shall refer to this model as Model 1A in this paper.

Model 2

We formulate this model under the assumption that the probability of an individual prey being attacked by the predator P (predator Q)

decreases (increases) if this individual is surrounded by larger preys. In other words it may also be said that while the predator P has preference for smaller size preys the predator Q prefers larger preys. We incorporate this assumption by considering the per capita mortality rate of prey as

$$\mu(a, t) = \mu_0 + k_{2P} P(t) \exp(-cS(t)) + k_{2Q} Q(t)(1 - \exp(-cS(t))) \quad (12)$$

where k_{2P} and k_{2Q} are the attack coefficients of predators P and Q respectively, c and μ_0 carry the same meanings as in Model 1.

Again assuming that the emigration rate of each predator from the system is inversely proportional to the per capita rate of prey consumption, we consider

$$\alpha_1(t) = \left[\frac{E_{2P}}{k_{2P} S(t) \exp(-cS(t))} \right] \text{ and } \alpha_2(t) = \left[\frac{E_{2Q}}{k_{2Q} S(t) (1 - \exp(-cS(t)))} \right] \quad (13)$$

Here E_{2P} and E_{2Q} are the constants of proportionality relating prey consumption to predator emigration. Following same steps as for

Model 1, it can be shown that Model 2 consists of following four governing equations.

$$\begin{aligned} \frac{dS}{dt} &= s_0 \sigma + (s_\infty \beta - s_0 \sigma K^{-1}) N(t) - [\beta + \mu_0 + k_{2P} P \exp(-cS(t)) + k_{2Q} Q(1 - \exp(-cS(t)))] S(t) \\ \frac{dN}{dt} &= \sigma - [K^{-1} \sigma + \mu_0 + k_{2P} P \exp(-cS(t)) + k_{2Q} Q(1 - \exp(-cS(t)))] N(t) \\ \frac{dP}{dt} &= I_{2P} - \frac{E_{2P} P(t)}{k_{2P} S(t) \exp(-cS(t))}, \\ \frac{dQ}{dt} &= I_{2Q} - \frac{E_{2Q} Q(t)}{k_{2Q} S(t) (1 - \exp(-cS(t)))} \end{aligned} \quad \text{Model 2}$$

This time we have replaced the notations I_P and I_Q by I_{2P} and I_{2Q} respectively to relate these immigration rates of predators to Model 2. It may

be pointed out at this stage that Model 2 in addition to benthic communities may also represent the dynamics of those sea populations (e.g. fish populations) which may have

interactions similar to these communities. Likewise (11), if the two predators have similar vital parameters such as

$$k_{2P} = k_{2Q} = \theta', I_{2P} = I_{2Q} = I', \text{ and } E_{2P} = E_{2Q} = e_0', \quad (14)$$

then Model 2 takes the simplified form as under

$$\begin{aligned} \frac{dS}{dt} &= s_0\sigma + (s_\infty\beta - s_0\sigma K^{-1})N(t) - [\beta + \mu_0 + \theta'\{P \exp(-cS(t)) + Q(1 - \exp(-cS(t)))\}]S(t), \\ \frac{dN}{dt} &= \sigma - [K^{-1}\sigma + \mu_0 + \theta'\{P \exp(-cS(t)) + Q(1 - \exp(-cS(t)))\}]N(t), \quad \text{Model 2A} \\ \frac{dP}{dt} &= I' - \frac{e_0' P(t)}{\theta' S(t) \exp(-cS(t))}, \\ \frac{dQ}{dt} &= I' - \frac{e_0' Q(t)}{\theta' S(t)(1 - \exp(-cS(t)))}, \end{aligned}$$

which we shall refer to Model 2A in this paper.

EQUILIBRIUM SOLUTIONS

Model 1

An equilibrium solution (S^*, N^*, P^*, Q^*) of Model 1 will satisfy

$$s_0\sigma + (s_\infty\beta - s_0\sigma K^{-1})N^* - [\beta + \mu_0 + (k_{1P}P^* + k_{1Q}Q^*) \exp(-cS^*)]S^* = 0, \quad (15)$$

$$[K^{-1}\sigma + \mu_0 + (k_{1P}P^* + k_{1Q}Q^*) \exp(-cS^*)]N^* = \sigma, \quad (16)$$

$$\frac{E_{1P} P^*}{k_{1P} S^* \exp(-cS^*)} = I_{1P}, \quad (17)$$

$$\frac{E_{1Q} Q^*}{k_{1Q} S^* \exp(-cS^*)} = I_{1Q}. \quad (18)$$

Equations (16), (17) and (18) can be used to find N^* , P^* and Q^* in terms of S^* as

$$N^* = \left[\frac{\sigma}{K^{-1}\sigma + \mu_0 + (A_1 + B_1)S^* \exp(-2cS^*)} \right] \quad (19)$$

$$P^* = A_1 S^* \exp(-cS^*) / k_{1P} \quad (20)$$

$$Q^* = B_1 S^* \exp(-cS^*) / k_{1Q}, \quad (21)$$

where $A_1 = I_{1P}k_{1P}^2 / E_{1P}$ and $B_1 = I_{1Q}k_{1Q}^2 / E_{1Q}$.

Substituting for N^* , P^* and Q^* from (19), (20) and (21) into (15), S^* can be found as a real

$$f(S) = s_0\sigma[K^{-1}\sigma + \mu_0 + (A_1 + B_1)S \exp(-2cS)] + [\beta s_\infty - K^{-1}s_0\sigma]\sigma - S[\beta + \mu_0 + (A_1 + B_1)S^* \exp(-2cS^*)][K^{-1}\sigma + \mu_0 + (A_1 + B_1)S^* \exp(-2cS^*)] = 0, \quad 0 \leq S \leq s_\infty \tag{22}$$

For the prey N we use the same data as given in [1] and reproduced here in Table 1. For predators P and Q , we consider parameter values from Table 2. We find that under both conditions (i) when the two predators have their vital parameters equal (see (11)) and (ii) when the two predators differ in their vital parameters, *Model 1* has the possibility of multiple equilibrium solutions depending on the number of roots of equation (22). More specifically, *Model 1* has either single equilibrium or three equilibriums.

For illustration purposes the parameters from Tables 1 and 2 are fixed as follows –

$$s_0 = 1.0, \sigma = 1.0, s_\infty = 200.0, K = 1.0, \mu = 0.0001, c = 0.04, \beta = 0.0004, I_{1P} = I_{1Q} = I = 0.01, E_{1P} = E_{1Q} = e_0 = 5.0.$$

Then the two cases when the two predators have equal parameters and when they differ in vital parameters can be categorized by whether $k_{1P} = k_{1Q} = \theta$ or $k_{1P} \neq k_{1Q}$. For the case when the two predators have equal parameters, it can be shown that *Model 1* has a single (upper) equilibrium denoted S_3 if $\theta = 1.0$; three

positive root of the function -

equilibriums (denoted S_1 as lower equilibrium, S_2 as middle equilibrium and S_3 as upper equilibrium) if $\theta = 0.44$ and a single (lower) equilibrium S_1 if $\theta = 3.0$. It can also be shown for the case when the two predators differ in their vital parameters that *Model 1* has a single (upper) equilibrium denoted S_3 if $k_{1P} = 0.2, k_{1Q} = 0.4$; three equilibriums (denoted S_1 as lower equilibrium, S_2 as middle equilibrium and S_3 as upper equilibrium) if $k_{1P} = 0.3, k_{1Q} = 0.5$ and a single (lower) equilibrium S_1 if $k_{1P} = 4.0, k_{1Q} = 3.0$. For want of space we illustrate only the case when the two predators differ in their vital parameters in Figure 1 (a - c).

It may be mentioned that in our illustration we use variations in predation coefficients only. Obviously variations in other parameters such as immigration or emigration rates of predators can be considered as well for such illustrations.

Table 1. Model parameters and their default values from [1]

SYMBOL	DEFINITION	VALUE	SYMBOL	DEFINITION	VALUE
area	Unit area	25 cm ²	s_∞	Maximum prey size	200 mm
A_r	Total system area	4×10^4 units of area	K	Maximum prey density	1 prey/unit area
t	Time	1 day	μ_0	Per capita prey mortality rate	0.0001 day ⁻¹
a	Age	1 day	c	Resistance to predation with prey size	0.04 unit area mm ⁻¹
σ	Prey recruitment rate	1 prey (unit area) ⁻¹ day ⁻¹	β	Decrease in prey growth rate with size	0.0004 day ⁻¹
s_0	Size of newly settled prey	1 mm			

Table 2. Parameter values for predators P and Q of Model 1.

SYMBOL	DEFINITION	VALUES	UNITS
k_{1P}	Attack coefficient of predator P	< 1.0, 1.0*, > 1.0	unit area predator ⁻¹ day ⁻¹
k_{1Q}	Attack coefficient of predator Q	< 1.0, 1.0, > 1.0	unit area predator ⁻¹ day ⁻¹
I_{1P}	Immigration rate of predator P	< 0.01, 0.01*, > 0.01	predator (unit area) ⁻¹ day ⁻¹
I_{1Q}	Immigration rate of predator Q	< 0.01, 0.01, > 0.01	predator (unit area) ⁻¹ day ⁻¹
E_{1P}	Emigration rate of predator P	< 5.00, 5.0*, > 5.0	mm predator ⁻¹ day ⁻²
E_{1Q}	Emigration rate of predator Q	< 5.00, 5.0, > 5.0	mm predator ⁻¹ day ⁻²

*Values used by Donalson, *et al* in [1]

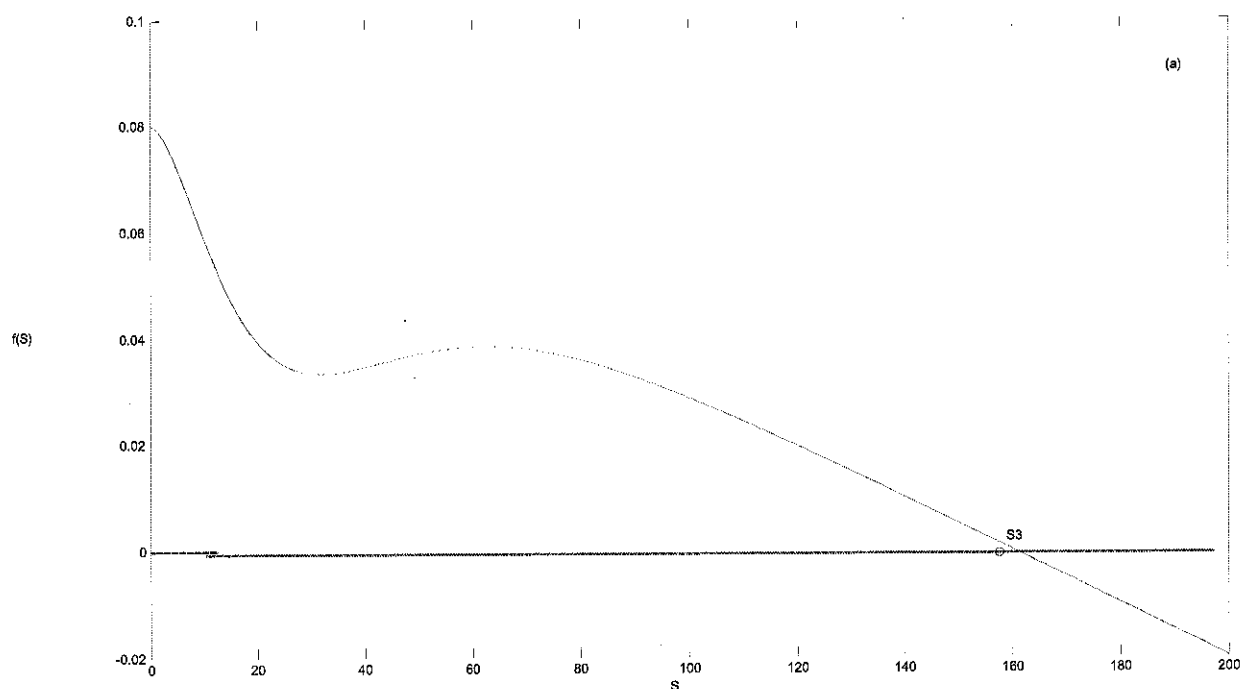


Figure 1a. Multiple equilibria of Model 1 with different parameters e.g. $k_{1P} \neq k_{1Q}$.

$I_{1P} = I_{1Q} = I = 0.01, E_{1P} = E_{1Q} = e_0 = 5.0; s_0 = 1.0, \sigma = 1.0, s_\infty = 200.0, K = 1.0,$
 $\mu = 0.0001, c = 0.04, \beta = 0.0004, k_{1P} = 0.2, k_{1Q} = 0.4$ or $k_{1P} = 0.4, k_{1Q} = 0.2$

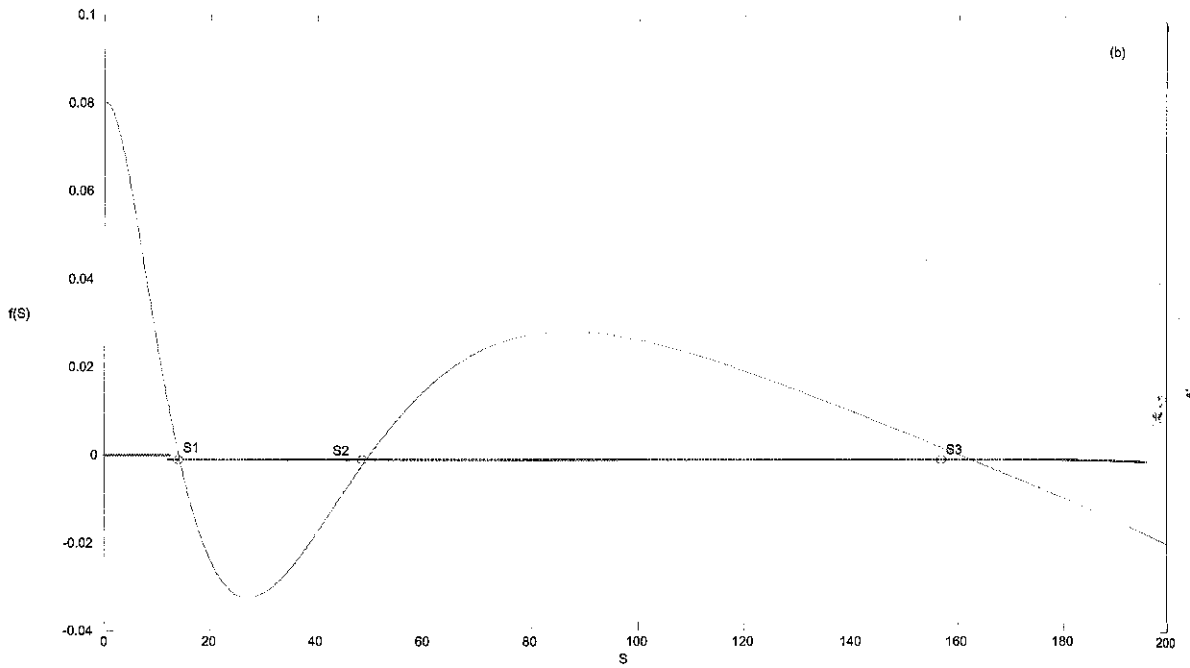


Figure 1b. Multiple equilibriums of Model 1 with different parameters e.g. $k_{1P} \neq k_{1Q}$.

$I_{1P} = I_{1Q} = I = 0.01$, $E_{1P} = E_{1Q} = e_0 = 5.0$; $s_0 = 1.0$, $\sigma = 1.0$, $s_\infty = 200.0$, $K = 1.0$,
 $\mu = 0.0001$, $c = 0.04$, $\beta = 0.0004$, $k_{1P} = 0.3$, $k_{1Q} = 0.5$ or $k_{1P} = 0.5$, $k_{1Q} = 0.3$

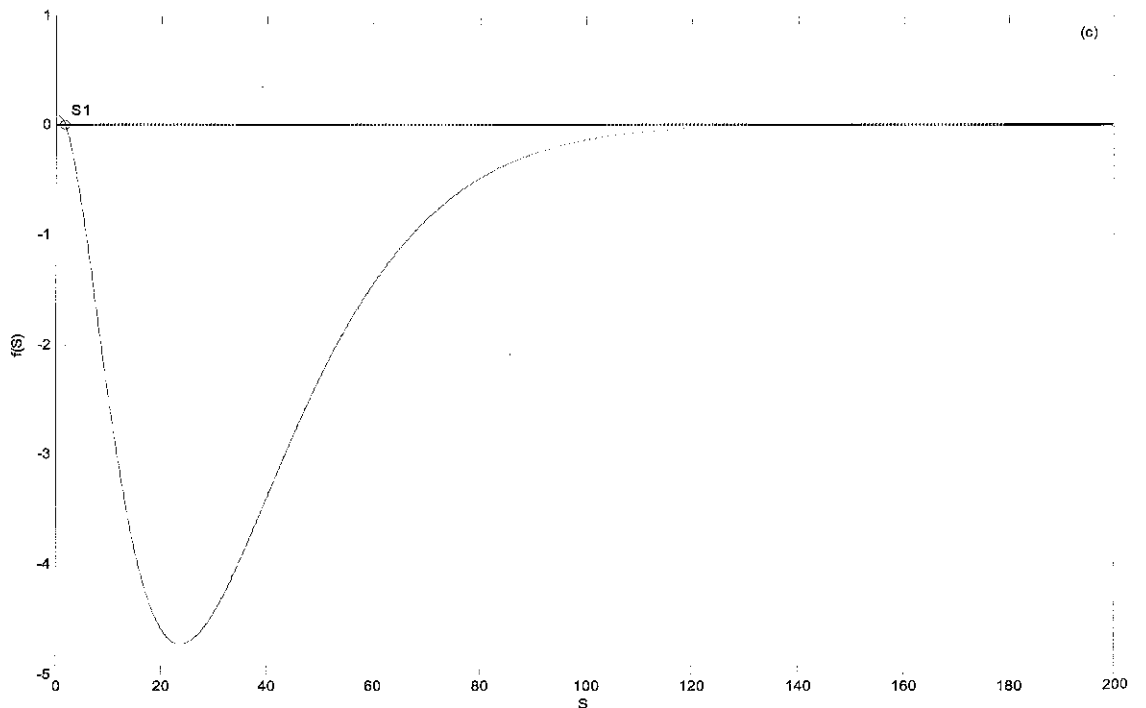


Figure 1c. Multiple equilibriums of Model 1 with different parameters e.g. $k_{1P} \neq k_{1Q}$.

$I_{1P} = I_{1Q} = I = 0.01$, $E_{1P} = E_{1Q} = e_0 = 5.0$; $s_0 = 1.0$, $\sigma = 1.0$, $s_\infty = 200.0$, $K = 1.0$,
 $\mu = 0.0001$, $c = 0.04$, $\beta = 0.0004$, $k_{1P} = 4.0$, $k_{1Q} = 3.0$ or $k_{1P} = 3.0$, $k_{1Q} = 4.0$

Model 2

Following the same steps as for *Model 1*, it can be shown that an equilibrium solution

$(S^{**}, N^{**}, P^{**}, Q^{**})$ of *Model 2* is given by equations

$$N^{**} = \sigma / [K^{-1}\sigma + \mu_0 + A_2 S^{**} \exp(-2cS^{**}) + B_2 S^{**} (1 - \exp(-cS^{**}))^2], \quad (23)$$

$$P^{**} = A_2 S^{**} \exp(-cS^{**}) / k_{2P}, \quad (24) \quad Q^{**} = B_2 S^{**} (1 - \exp(-cS^{**})) / k_{2Q}, \quad (25)$$

where

$A_2 = I_{2P} k_{2P}^2 / E_{2P}$, $B_2 = I_{2Q} k_{2Q}^2 / E_{2Q}$ and S^{**} is a positive real root of

$$F(S) = s_0 \sigma [K^{-1}\sigma + \mu_0 + A_2 S \exp(-2cS) + B_2 S (1 - \exp(-cS))^2] +$$

$$[\beta s_\infty - s_0 \sigma K^{-1}] \sigma - S [\mu_0 + \beta + A_2 S \exp(-2cS) + B_2 S (1 - \exp(-cS))^2] \times$$

$$[K^{-1}\sigma + \mu_0 + A_2 S \exp(-2cS) + B_2 S (1 - \exp(-cS))^2] = 0 \quad 0 \leq S \leq s_\infty \quad (26)$$

Again choosing parameter values for the prey N from Table 1 and for the two predators from Table 2, it can be seen that *Model 2* also has the possibility of multiple equilibrium solutions depending on the number of roots of equation (26). Choosing the parameter values as $k_{2Q} = 1.0$, $I_{2P} = 0.001$, $I_{2Q} = 0.00001$, $E_{2P} = 1.0$, $E_{2Q} = 5.0$; $s_0 = 1.0$, $\sigma = 1.0$, $s_\infty = 200.0$, $K = 1.0$, $\mu = 0.0001$, $c = 0.04$, $\beta = 0.0004$, it can be shown that *Model 2* has a single (upper) equilibrium S_3 if $k_{2P} = 0.7$, three equilibriums (S_1 , S_2 and S_3)

if $k_{2P} = 1.0$ and a single (lower) equilibrium S_1 if $k_{2P} = 5.0$. Again just for an illustration, we display the possibility of three equilibriums in Figure 2. It can also be seen that under the similarity conditions (14), *Model 2* (or more specifically *Model 2A*) has the possibility of one equilibrium solution only. We illustrate this in Figure 3 for different values of immigration rates i.e. $I' = 0.00001$, 0.01 and 1.0 . Similar result can be shown for different values of predation coefficients θ' or emigration rates e_0' . This single equilibrium can be either lower equilibrium S_1 or upper equilibrium S_3 .

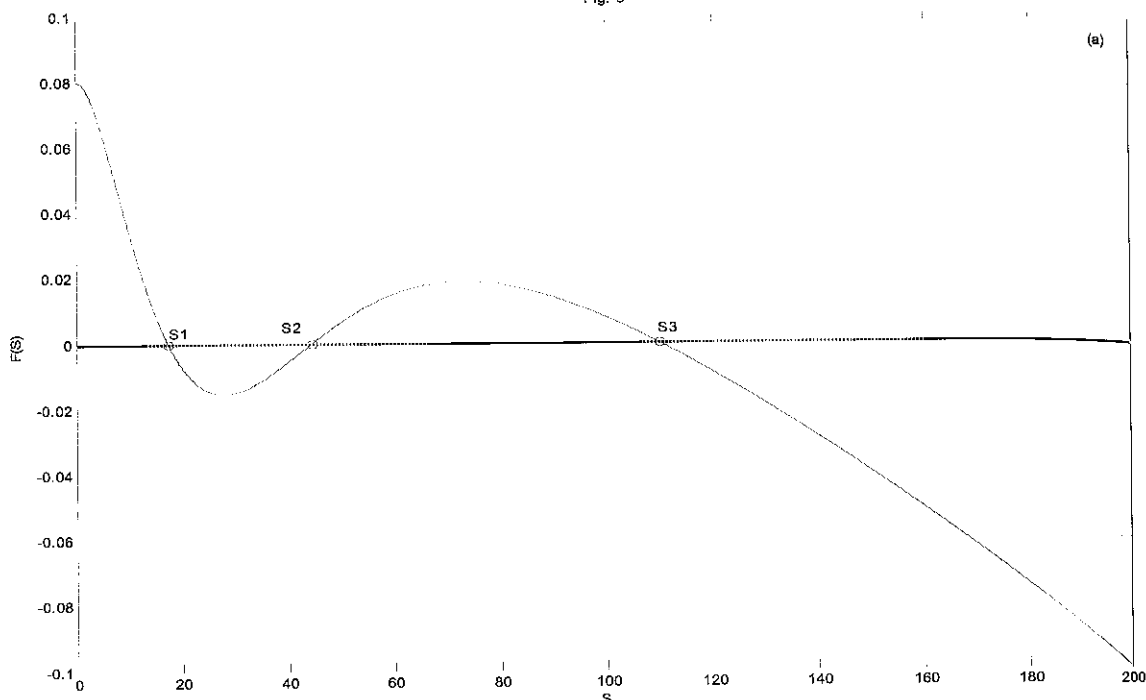


Figure 2. Multiple equilibriums of *Model 2* for different values of attack coefficient k_{2P} of Predator P. $k_{2Q} = 1.0, I_{2P} = 0.001, I_{2Q} = 0.00001, E_{2P} = 1.0, E_{2Q} = 5.0; s_0 = 1.0, \sigma = 1.0, s_\infty = 200.0, K = 1.0, \mu = 0.0001, c = 0.04, \beta = 0.0004, k_{2P} = 1.0$.

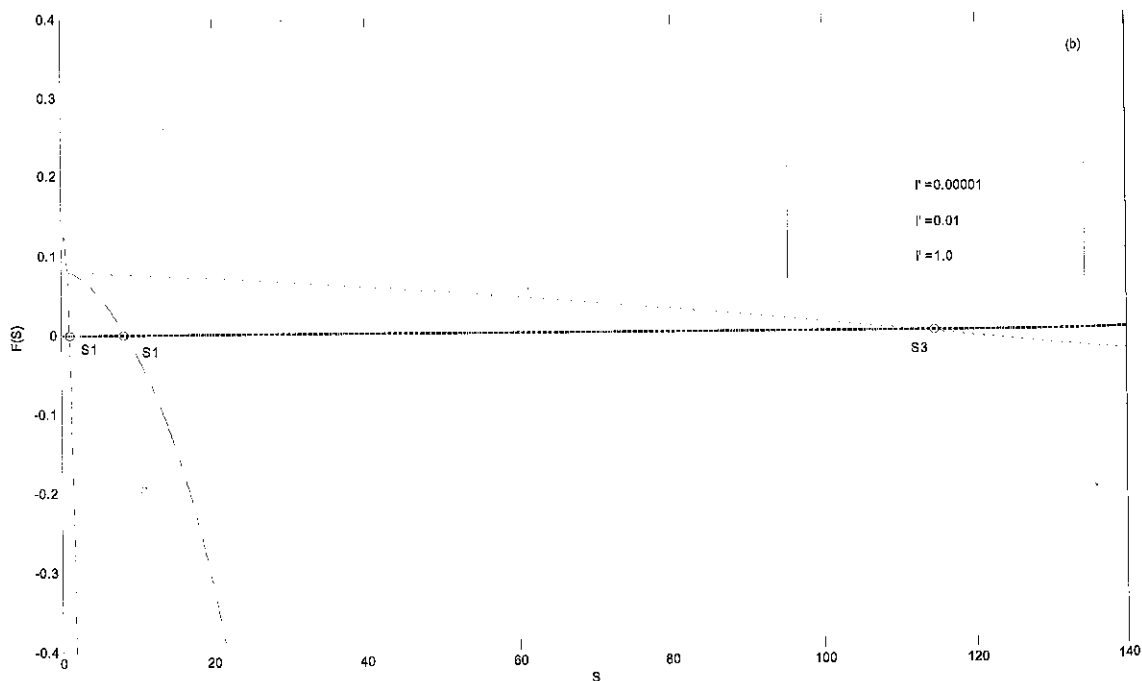


Figure 3. Single equilibriums of *Model 2* under similarity conditions (14) $k_{2P} = k_{2Q} = \theta'$, $I_{2P} = I_{2Q} = I', E_{2P} = E_{2Q} = e'_0; s_0 = 1.0, \sigma = 1.0, s_\infty = 200.0, K = 1.0, \mu_0 = 0.0001, c = 0.04, \beta = 0.0004, \theta' = 1.0, e'_0 = 5.0, (i) I' = 0.00001, (ii) I' = 0.01, (iii) I' = 1.0$

STABILITY OF EQUILIBRIUM SOLUTIONS

Model 1

Using the default values of Table 1 for prey N , taking any suitable choice of values for parameters $k_{1P}, k_{1Q}, I_{1P}, I_{1Q}, E_{1P}$ and E_{1Q} of the two predators P and Q from Table 2 and integrating the system of equations of Model 1, it can be seen that the lower equilibrium $(S_1^*, N_1^*, P_1^*, Q_1^*)$ and the upper equilibrium $(S_3^*, N_3^*, P_3^*, Q_3^*)$ of Model 1 are stable where as the middle equilibrium $(S_2^*, N_2^*, P_2^*, Q_2^*)$ is unstable. Here S_i^* is a positive real root of equation (22), N_i^*, P_i^* and Q_i^* are the corresponding equilibrium values for prey N , predator P and predator Q obtained from (19), (20) and (21) respectively. The unstable equilibrium $(S_2^*, N_2^*, P_2^*, Q_2^*)$ lies in between the two stable equilibriums. A solution of Model 1 would tend to which of the two stable equilibriums $(S_1^*, N_1^*, P_1^*, Q_1^*)$ and $(S_3^*, N_3^*, P_3^*, Q_3^*)$ depends on the initial point.

For the default values of Table 1 and using the similarity conditions (11) with $I_{1P} = I_{1Q} = I = 0.01$, and $E_{1P} = E_{1Q} = e_0 = 5.0$ (values considered in [1] for benthic communities) Model 1 has only the upper stable equilibrium $(S_3^*, N_3^*, P_3^*, Q_3^*)$ with $P_3^* = Q_3^*$ if $k_{1P} = k_{1Q} = \theta < 0.4$ (approximate), two (lower and upper) stable equilibriums if $0.46 < \theta < 3.0$ (approximate) and only the lower stable equilibrium $(S_1^*, N_1^*, P_1^*, Q_1^*)$ with $P_1^* = Q_1^*$ if $\theta \geq 3$ (approx.). Obviously these results correspond to variation in the attack coefficients of the two predators. Similar results for the variation in the immigration rates or the emigration rates of the two predators can be stated. We mention here only the results for the variation in immigration rates. For the default values of Table 1 and fixing $k_{1P} = k_{1Q} = \theta = 1.0$,

and $E_{1P} = E_{1Q} = e_0 = 5.0$, Model 1 has only the upper stable equilibrium with $P_3^* = Q_3^*$ if $I_{1P} = I_{1Q} = I < 0.002$ (approximate), two (lower and upper) stable equilibriums if $0.0025 < I < 0.1$ (approximate) and only the lower stable equilibrium $(S_1^*, N_1^*, P_1^*, Q_1^*)$ with $P_1^* = Q_1^*$ if $I \geq 0.1$ (approximate).

For dissimilar predators, we assume that the two predators differ either in their attack coefficients or immigration rates or emigration rates. Setting $I_{1P} = I_{1Q} = I = 0.01$ and $E_{1P} = E_{1Q} = e_0 = 5.0$, it is seen that Model 1 has only the upper stable equilibrium $(S_3^*, N_3^*, P_3^*, Q_3^*)$

if $k_{1P} + k_{1Q} < 0.8$, two stable equilibriums if $0.92 < k_{1P} + k_{1Q} < 6.0$ and only the lower stable equilibrium $(S_1^*, N_1^*, P_1^*, Q_1^*)$ if $k_{1P} + k_{1Q} > 6.0$. (These results may be easily compared with the corresponding results given above for similarity conditions). Now fixing $k_{1P} = k_{1Q} = \theta = 1.0$, $E_{1P} = E_{1Q} = e_0 = 5.0$ and considering the variation in immigration rates only, it is found that Model 1 has only the upper stable equilibrium $(S_3^*, N_3^*, P_3^*, Q_3^*)$ if $I_{1P} + I_{1Q} < 0.004$, two stable equilibriums if $0.005 \leq I_{1P} + I_{1Q} < 0.2$ and only the lower stable equilibrium $(S_1^*, N_1^*, P_1^*, Q_1^*)$ if $I_{1P} + I_{1Q} > 0.2$. In regards to equilibrium solutions of Model 1 based on the emigration rates of the two predators, it can be shown that while large sum $E_{1P} + E_{1Q}$ of the emigration rates may lead to upper stable equilibrium, small sums may produce only lower equilibrium. For moderate values of the sum $E_{1P} + E_{1Q}$, lower and upper both equilibriums may exist. To illustrate, we display in Figure 4 the results based on the sum $I_{1P} + I_{1Q}$ of the immigration rates of the two predators.

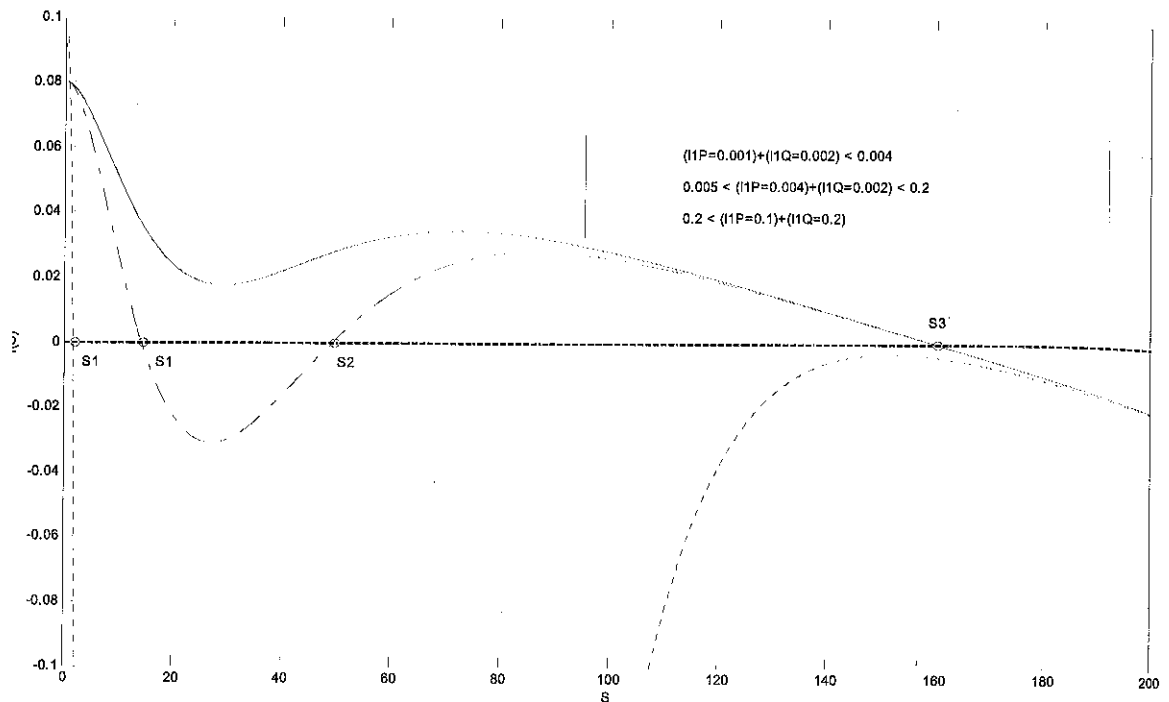


Figure 4. Multiple equilibriums of *Model 1* for different values of $(I_{1P} + I_{1Q})$ the sum of predation coefficients of P and Q with $s_0 = 1.0, \sigma = 1.0, s_\infty = 200.0, K = 1.0, \mu = 0.0001, c = 0.04, \beta = 0.0004, k_{1P} = k_{1Q} = 1.0, E_{1P} = E_{1Q} = 5.0$: (i) $I_{1P} = 0.001, I_{1Q} = 0.002 \Rightarrow I_{1P} + I_{1Q} < 0.004$; (ii) $I_{1P} = 0.004, I_{1Q} = 0.002 \Rightarrow 0.005 < I_{1P} + I_{1Q} < 0.2$; (iii) $I_{1P} = 0.1, I_{1Q} = 0.2 \Rightarrow 0.2 < I_{1P} + I_{1Q}$.

The general features noticed at the stable equilibriums are as follows. At the lower stable equilibrium $(S_1^*, N_1^*, P_1^*, Q_1^*)$ prey sizes are kept low by relatively high levels of total predation (in reference to $k_{1P} = k_{1Q} = 1.0$) by both predators or by relatively high levels of total immigration rates (in reference to $I_{1P} = I_{1Q} = 0.01$) by both predators or by relatively low levels of total emigration rates (in reference to $E_{1P} = E_{1Q} = 5.0$) by both predators. At the upper stable equilibrium $(S_3^*, N_3^*, P_3^*, Q_3^*)$ there is a relatively high density of large prey which are resistant to predation. For this reason, two predators sustain at this equilibrium only with low equilibrium values. It is seen that the predator whose attack coefficient (k_{1P} or k_{1Q}) or immigration rate (I_{1P} or I_{1Q}) is higher or emigration rate (E_{1P} or E_{1Q}) is lower maintains its higher

value at either equilibrium. For chosen feasible parameter values as those in Tables 1 and 2, there is no evidence of exotic dynamics such as limit cycles or chaos.

Model 2

It is obvious from Figures 3 and 4 that Model 2 has possibilities of having multiple equilibrium solutions. More specifically it can have either lower equilibrium $(S_1^{**}, N_1^{**}, P_1^{**}, Q_1^{**})$ or upper equilibrium $(S_3^{**}, N_3^{**}, P_3^{**}, Q_3^{**})$ or three equilibriums with an additional equilibrium $(S_2^{**}, N_2^{**}, P_2^{**}, Q_2^{**})$ in between. For the default parameter values for prey chosen from Table 1 and considering any suitable parameter values for the two predators from Table 2, it is seen that lower and upper equilibriums of Model 2 are stable where as the middle equilibrium is always unstable. A solution of Model 2 would approach to which stable equilibrium depends on the initial point considered. Under the similarity conditions (14) based on the benthic community

data considered in [1] it looks more likely (see Figure 4) that Model 2 has only single stable equilibrium. It can be either lower or upper equilibrium depending on the particular set of parameter values. In accordance with the benthic community data considering equal immigration rates for the two predators as $I_{2P} = I_{2Q} = 0.01$ and emigration rates as $E_{2P} = E_{2Q} = 5.0$ and assuming two predators differing in their attack rates, it is found that if predator Q has the attack coefficient $k_{2Q} = 1.0$ then any variation in the attack coefficient k_{2P} of predator P

increasing or decreasing from 1.0 does not affect the number of equilibriums of Model 2. It still has only single equilibrium as under similarity conditions (14) though overall size of the prey decreases with the increase in the attack coefficient k_{1P} from 1.0 and again the predator which has higher attack coefficient maintains its relatively higher population. On the other hand it can be noticed that a decrease in the attack coefficient of the predator Q from 1.0 causes a change in the equilibriums for Model 2 from one to two stable equilibriums. We illustrate this fact in Figure 5.

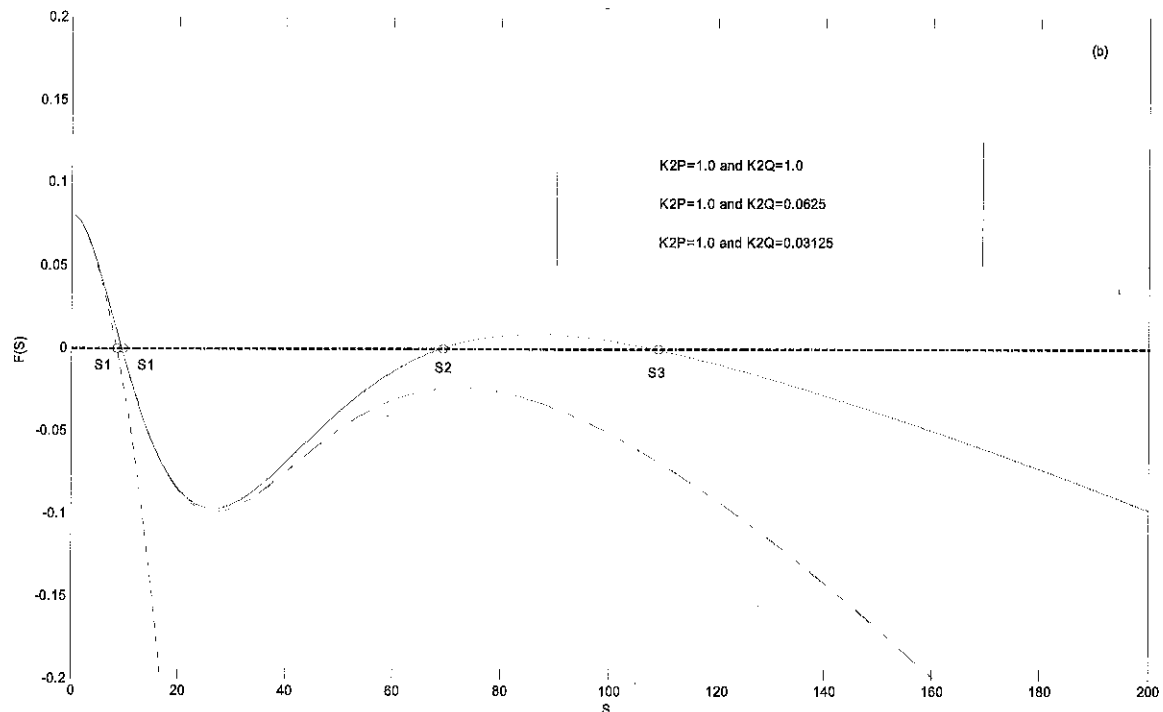


Figure 5. Single and multiple equilibriums of Model 2 for different attack coefficient k_{2Q} of Predator Q.

$s_0 = 1.0, \sigma = 1.0, s_\infty = 200.0, K = 1.0, \mu = 0.0001, c = 0.04, \beta = 0.0004.$

$I_{2P} = I_{2Q} = 0.01, E_{2P} = E_{2Q} = 5.0: k_{2P} = 1.0$ (i) $k_{2Q} = 1.0$, (ii) $k_{2Q} = 0.0625$,

(iii) $k_{2Q} = 0.03125$

We consider default parameter values for prey from Table 1 and assign different sets of definite values to the parameters $k_{2P}, k_{2Q}, I_{2P}, I_{2Q}, E_{2P}$ and E_{2Q} of the two predators such that Model 2 has two stable equilibriums i.e. lower stable equilibrium $(S_1^{**}, N_1^{**}, P_1^{**}, Q_1^{**})$ and upper stable

equilibrium $(S_3^{**}, N_3^{**}, P_3^{**}, Q_3^{**})$. Now, numerous computer simulations are used to see how any change (from the previous value) in a single parameter of either predator affects the equilibriums of Model 2. We summarize these results in Table 3 below.

Table 3. Change in the equilibriums of Model 2 from two stable equilibriums with variation in a single parameter of a predator.

DIFFERENT CASES CONSIDERED	PARAMETER	TYPE OF VARIATION	EXISTING STABLE EQUILIBRIUM(S)
$k_{2P} < k_{2Q}$	I_{2P}	Increasing ↑	Lower equilibrium
	I_{2P}	Decreasing ↓	Upper equilibrium
	I_{2Q}	Increasing ↑	Lower equilibrium
$k_{2P} = k_{2Q}$	I_{2Q}	Decreasing ↓	Lower and upper equilibriums
	$k_{2P} > k_{2Q}$	E_{2P}	Increasing ↑
E_{2P}		Decreasing ↓	Lower equilibrium
E_{2Q}		Increasing ↑	Lower and upper equilibriums
	E_{2Q}	Decreasing ↓	Lower equilibrium

Table 3 seems to be suggesting a generic type of picture from where outcomes for many other combinations of parameter values may be predicted. For example disturbing the various parameter values in pairs from the two equilibrium situation following may occur.

(a) Only lower stable equilibrium

$(S_1^{**}, N_1^{**}, P_1^{**}, Q_1^{**})$ may be more likely expected if

$$\begin{aligned}
 &I_{2P} \uparrow \text{ and } I_{2Q} \uparrow \text{ or } I_{2P} \uparrow \text{ and } E_{2P} \downarrow \text{ or} \\
 &I_{2P} \uparrow \text{ and } E_{2Q} \downarrow \text{ or } I_{2Q} \uparrow \text{ and } E_{2P} \downarrow \text{ or} \\
 &I_{2Q} \uparrow \text{ and } E_{2Q} \downarrow \text{ or } E_{2P} \downarrow \text{ and } E_{2Q} \downarrow
 \end{aligned}
 \tag{27}$$

(b) Only upper stable equilibrium

- (i) $k_{2P} = 1.0$ $k_{2Q} = 2.0$ $I_{2P} = 0.001$ $I_{2Q} = 0.000001$ $E_{2P} = 1.0$ $E_{2Q} = 2.0$.
- (ii) $k_{2P} = 1.0$ $k_{2Q} = 1.0$ $I_{2P} = 0.001$ $I_{2Q} = 0.00001$ $E_{2P} = 1.0$ $E_{2Q} = 5.0$. (30)
- (iii) $k_{2P} = 2.0$ $k_{2Q} = 1.0$ $I_{2P} = 0.001$ $I_{2Q} = 0.000001$ $E_{2P} = 1.0$ $E_{2Q} = 5.0$.

It can be seen that for each of these sets, Model 2 has three equilibriums i.e. lower stable equilibrium $(S_1^{**}, N_1^{**}, P_1^{**}, Q_1^{**})$, upper stable equilibrium $(S_3^{**}, N_3^{**}, P_3^{**}, Q_3^{**})$ and middle unstable equilibrium $(S_2^{**}, N_2^{**}, P_2^{**}, Q_2^{**})$. Further for each of these sets it can be shown that any single situation from (27) causes Model 2 to

$(S_3^{**}, N_3^{**}, P_3^{**}, Q_3^{**})$ may be more likely expected if

$$I_{2P} \downarrow \text{ and } E_{2P} \uparrow$$

(c) Both lower and upper equilibriums may persist if

$$I_{2Q} \downarrow \text{ and } E_{2Q} \uparrow$$

We consider the following set of parameter values for prey from Table 1: $s_0 = 1.0$, $\sigma = 0.0001$, $s_\infty = 200.0$, $K = 1.0$, $\mu = 0.0001$, $c = 0.04$, $\beta = 0.01$. Now we consider three sets of parameter values for predators representing three cases $k_{2P} < k_{2Q}$, $k_{2P} = k_{2Q}$ and $k_{2P} > k_{2Q}$.

have only lower stable equilibrium. We consider only set (i) from (30) just as an illustration and three situations from (27) namely $I_{2P} \uparrow$ and $I_{2Q} \uparrow$, $I_{2P} \uparrow$ and $E_{2Q} \downarrow$ and $E_{2P} \downarrow$ and $E_{2Q} \downarrow$ and shown in Figure 6 that under these situations Model 2 indeed has only lower stable equilibrium.

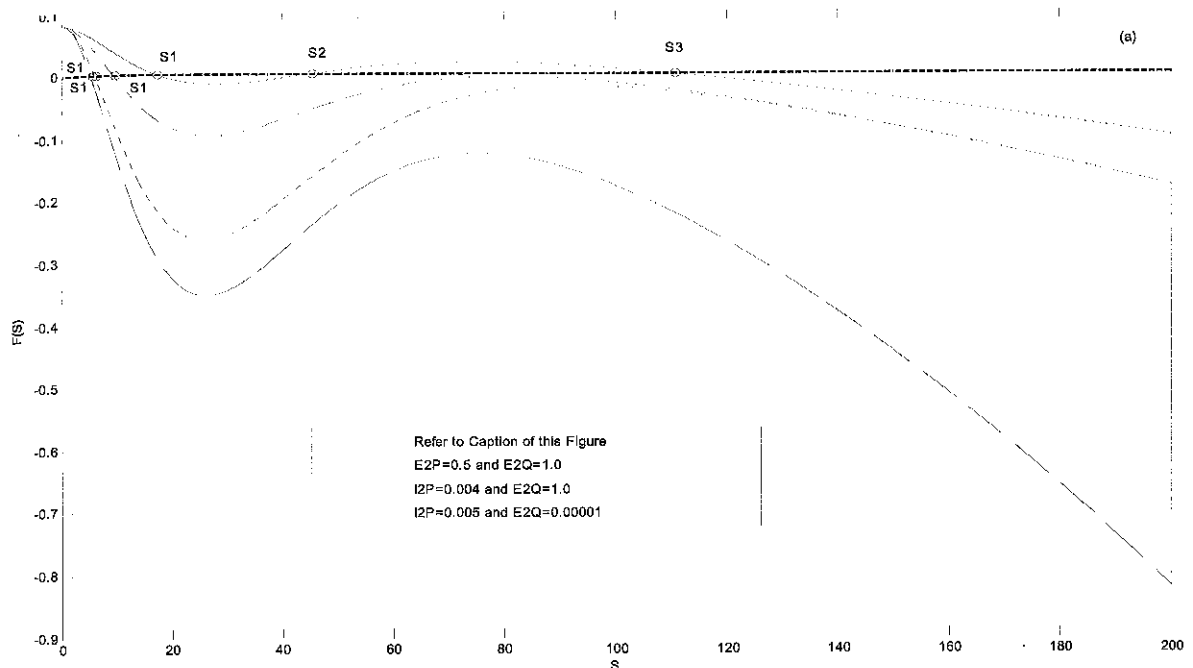


Figure 6. Some situations when Model 2 has lower equilibrium only. $s_0 = 1.0$, $\sigma = 1.0$, $s_\infty = 200.0$, $K = 1.0$, $\mu = 0.0001$, $c = 0.04$, $\beta = 0.0004$. Continuous line graph corresponds to the set of parameters $k_{2P} = 1.0$, $k_{2Q} = 2.0$, $I_{2P} = 0.001$, $I_{2Q} = 0.000001$, $E_{2P} = 1.0$, and $E_{2Q} = 2.0$. Other graphs correspond to changes in a pair of parameters as indicated.

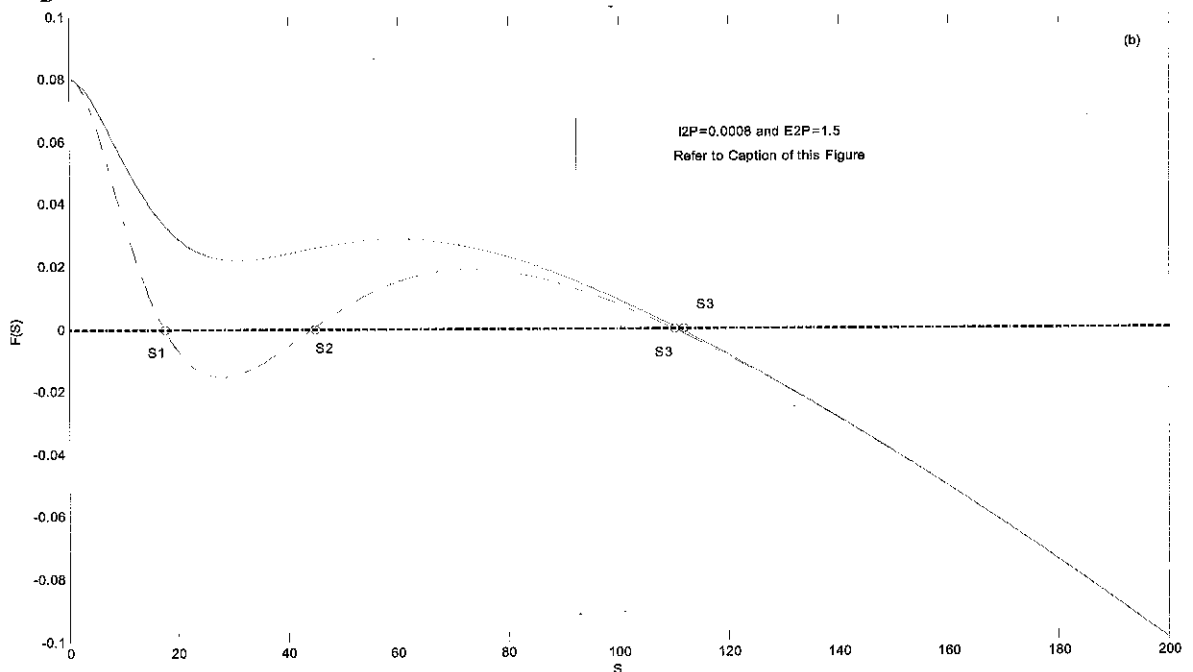


Figure 7. Some situations when Model 2 has upper equilibrium only. $s_0 = 1.0$, $\sigma = 1.0$, $s_\infty = 200.0$, $K = 1.0$, $\mu = 0.0001$, $c = 0.04$, $\beta = 0.0004$. Dash-dot line graph corresponds to the set of parameters $k_{2P} = 1.0$, $k_{2Q} = 1.0$, $I_{2Q} = 0.000001$, $E_{2P} = 1.0$, and $E_{2Q} = 5.0$. Other graph corresponds to changes in a pair of parameters as indicated.

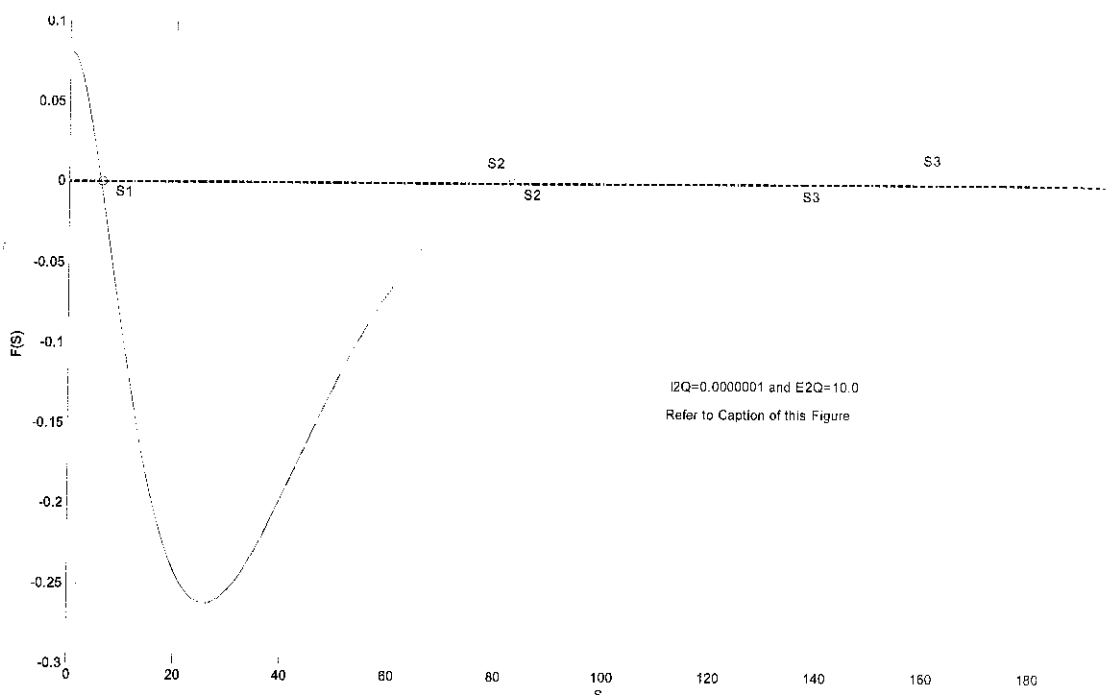


Figure 8. Some situations when for Model 2 two stable equilibriums persist. Dash-dot line graph corresponds to the set of parameters $k_{2P} = 2.0$, $k_{2Q} = 1.0$, $I_{2P} = 0.001$, $I_{2Q} = 0.000001$, $E_{2P} = 1.0$, and $E_{2Q} = 5.0$. Other graph corresponds to changes in a pair of parameters as indicated

Again as an illustration, possibilities of upper stable equilibrium and persistence of two stable equilibriums of Model 2 under conditions (28) and (29) are displayed in Figures 7 and 8 for the sets (ii) and (iii) from (30) respectively.

CONCLUSIONS

We consider predation dynamics of spatially-structured species of benthic community in this paper. We generalize a model of [1] and extend its scope to three species of benthic community namely: mussel (as prey), sea star (as one predator) and spiny lobster (as second predator). We analyze two models designated Model 1 and Model 2. Model 1 is developed under the assumption that the prey (mussel) reaches a certain size and becomes resistant to both predators. Model 2 represents a situation when the large size preys become resistant to one predator but remain vulnerable to the other. It is seen that for the default data of benthic community reported in [1] and reproduced in this paper in Table 1 and 2, both Model 1 and 2 have possibility of multiple equilibrium solutions. More specifically, each model may have one or three equilibriums. One may refer to sections 3 and 4 for some of the important features of the

results of these models which may summarized as follows -

Model 1 (when the prey grows to a certain size and becomes resistant to both predators)

- Whenever Model 1 has single equilibrium (designated lower or upper in this paper) is stable.
- Whenever Model 1 has three equilibriums (designated lower, middle and upper in this paper) the lower and upper equilibriums are stable while the middle one is unstable.
- Under the similarity conditions (11) when the two predators have equal predation coefficients $k_{1P} = k_{1Q} = \theta$, equal immigration rates $I_{1P} = I_{1Q} = I$ and equal emigration rates $E_{1P} = E_{1Q} = e_0$, it is found that the variation in one of the parameters $\{\theta, I, e_0\}$ while fixing the other two may cause a change in the equilibriums from one to two stable equilibriums or vice versa.
- For dissimilar predators, it is seen that the change in the equilibriums of the model from one to two stable equilibriums or vice versa

may occur by the variation in the values of one of the sums $\{(k_{1P} + k_{1Q}), (I_{1P} + I_{1Q}), (E_{1P} + E_{1Q})\}$ while having the other two fixed.

- It is seen that at the lower stable equilibriums, the prey sizes are kept low by relatively high levels of predation by both predators or high levels of immigration rates of predators.
- It is found that at the upper stable equilibriums, there is a relatively high density of large prey which are resistant to predation.
- It is observed that the predator whose attack rate or immigration rate is higher or emigration rate is lower maintains its higher population at either equilibrium.

Model 2 (when the large size preys become resistant to one predator but remain vulnerable to the other predator)

- Whenever Model 2 has single equilibrium (designated lower or upper in this paper) it is stable.
- Whenever Model 2 has three equilibriums (designated lower, middle and upper in this paper) the lower and upper equilibriums are stable while the middle one is unstable.
- Under the similarity conditions (14) when the two predators have equal predation coefficients $k_{2P} = k_{2Q} = \theta'$, equal immigration rates $I_{2P} = I_{2Q} = I'$ and equal emigration rates $E_{2P} = E_{2Q} = e_0'$, it is found that the model has the possibility of a single equilibrium only. It may be either lower or upper stable equilibrium.
- For dissimilar predators it is observed (in reference to the benthic community data of [1]) that any variation in the attack coefficient of the predator to which large size preys become resistant does not affect the number of equilibriums of the model. On the other hand a variation in the attack coefficient of the predator to which large size preys remain vulnerable may cause a change in the equilibriums from one to two stable equilibriums or vice versa.
- It is seen that a variation in the immigration rate or emigration rate of any one predator may also affect the number of equilibriums of the model. We give a generic type picture for change in equilibriums for such

variations in Table 3. From these results we present some other combinations of parameters which can also effect the change in the equilibriums of the model.

It may be mentioned that we observe no evidence of any exotic dynamics such as limit cycles or chaos for both of our models for the chosen data of benthic community from [1].

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