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**INTERNATIONAL CENTRE FOR
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**QUANTUM MECHANICAL ANALOGY
FOR SOLVING A COMPETITIVE COEXISTENCE
MODEL IN ECOLOGY**



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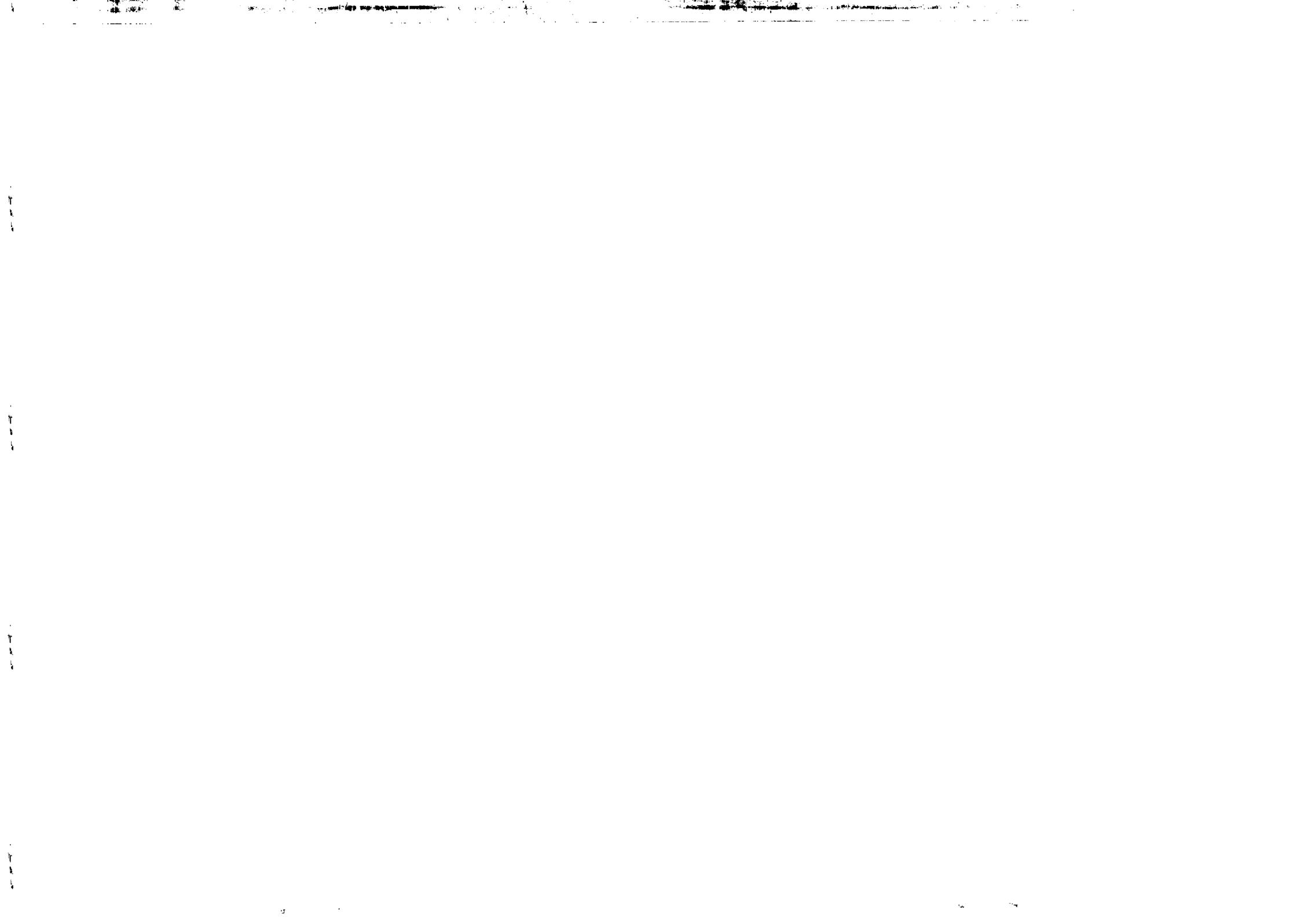
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A COMPETITIVE COEXISTENCE MODEL IN ECOLOGY

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ABSTRACT

We have studied an ecological system of three species: a *strong* and a *weak* one, competing for a single food resource, modelled as a reaction-diffusion process. An exact analytical solution has been found through a quantum mechanical analogy. Such solution indicates that in certain situations the classical results on extinction and coexistence of Lotka-Volterra type equations are no longer valid, essentially, as a consequence of the *weak* species mobility. A stability analysis of this solution against changes in different parameters has been carried out.

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1 Introduction

The mathematical theory of competition was originated, among others in Volterra's 1927 work [1], and since then has become one of the most important problems among those discussed by Mathematical Ecology. Those first results showed that the coexistence of two or more species of predators limited to only one species of prey is impossible. Volterra's results have been generalized, and today are included within the *Competitive Exclusion Principle* (or *ecological theorem*), that states: *N species that compete for $n (< N)$ food resources, cannot coexist* [2, 3].

Several aspects of this problem have been analyzed by different authors, emphasizing, for instance, the conflict between the need to forage and the need to avoid competition; effects of diffusion-mediated persistence; global effects associated with the possibility of refugees; etc. [4, 5, 6, 7].

In this work we study the possibility of coexistence in a simplified situation, two species competing for a unique food resource, as a first step to know the role played by the different parameters of the model on the global behavior. The model to be discussed here is similar to the one used by Eigen [8] in relation with problems of prebiological evolution and by Mikhailov [9] in order to describe a noise-induced transition in a biological system with diffusion. We analyze the possibility of coexistence in the case where the food resource has the characteristics of a *solitary wave* with constant velocity. Such a behavior could have, for instance, an stational origin. This spatial inhomogeneity, that at variance with [9] is highly coherent, allows for the coexistence of both species, as a consequence of the mobility of the *weak* species.

2 Mathematical Model

The model, as indicated above, consist of two species competing for the same food resource. We indicate with N the population density of the *strong* species, with n the population density of the *weak* species, and with M the food density. The set of differential equations we use in order to describe the time behavior, for the spatially homogeneous case, of such a system is :

$$\begin{aligned}\partial_t n(t) &= [bM(t) - a]n(t) \\ \partial_t N(t) &= [BM(t) - A]N(t) \\ \partial_t M(t) &= Q(t) - [G + cn(t) + CN(t)]M(t),\end{aligned}\quad (1)$$

These are Malthusian-like *birth-death* equations [10] for each species where $bM(t)$ and $BM(t)$ indicate the growth rate while a and A indicate the death rate (assumed constant) of the species $n(t)$ and $N(t)$ respectively. For the food $M(t)$ the production is given by $Q(t)$, that is assumed to be independent of the population densities, while the decay is due not only to the natural degradation (rotting) with a rate G , but to the consumption by both predator species with rates $cn(t)$ and $CN(t)$. The relevant stationary, asymptotic,

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solutions for these equations are given by:

$$\begin{aligned} M_n &= \frac{a}{b}, & n_n &= \frac{Qb - Ga}{ca}, & N_n &= 0 \\ M_N &= \frac{A}{B}, & N_N &= \frac{QB - GA}{CA}, & n_N &= 0 \end{aligned} \quad (2)$$

Assuming the condition

$$\frac{A}{B} < \frac{a}{b} \quad (3)$$

the threshold for the survival of the species N is lower than the threshold needed for the survival of the species n and after a linear stability analysis it can be shown that the first solution is unstable while the second one is stable. This corresponds to the initial assumption that N will have the characteristics of the *strong* species, the one that survives, while n will be the *weak* species, the one that becomes extinct. Hence, an arbitrary initial condition will evolve, asymptotically, towards the attractor corresponding to the second of the indicated stationary solutions.

If we assume that both, the *strong* and food species, are heavy and immobile, while the *weak* is light and mobile, the possibility of migration of the *weak* species can be included, modeled as a diffusive process [2, 11, 12]. Hence, Eq.(1) becomes:

$$\begin{aligned} \partial_t n(x, t) &= D_n \partial_x^2 n(x, t) + [bM(x, t) - a]n(x, t) \\ \partial_t N(x, t) &= [BM(x, t) - A]N(x, t) \\ \partial_t M(x, t) &= Q(x, t) - [G + cn(x, t) + CN(x, t)]M(x, t). \end{aligned} \quad (4)$$

With the conditions indicated before, Eq.(3), and with a spatially homogeneous source $Q(t)$, the mobility of the *weak* species does not prevent its extinction.

Mikhailov's work [9] has shown that the existence of spatio-temporal fluctuations in the food resource, when larger than certain threshold value, makes possible the coexistence due exclusively to the mobility of the *weak* species. The model is again the same as in Eq.(4), but assuming that $Q(x, t) = Q(x, t) + f(x, t)$, with $f(x, t)$ a random function of space and time. Hence, $f(x, t)$ can be interpreted as an external random factor. His main result is that, due to the mobility of the *weak* species, the increase of its population density in those regions where the fluctuations occurs, compensates for the decay outside these regions, rendering a *noise induced transition* to a phase where coexistence is allowed.

3 Case of a Solitary Wave Like Source [13]

We start from the same original equations indicated in Eq.(4). In order to simplify the algebra we rewrite the equations assuming that $c = b$ and $C = B$, scaling the variables n, N, M, Q , (multiplying each one by b/a), and calling: $g = G/a$, $\beta = B/b$, $\alpha = A/a$ and $q = bQ/a^2$. We also do the following change of spatial and temporal coordinates

$$t \rightarrow \tau = at, \quad x \rightarrow y = x\sqrt{\frac{a}{D_n}}$$

After these changes, Eq.(4) adopts the simplified form

$$\begin{aligned} \partial_\tau n(y, \tau) &= \partial_y^2 n(y, \tau) + [M(y, \tau) - 1]n(y, \tau) \\ \partial_\tau N(y, \tau) &= [\beta M(y, \tau) - \alpha]N(y, \tau) \\ \partial_\tau M(y, \tau) &= q(y, \tau) - [g + n(y, \tau) + \beta N(y, \tau)]M(y, \tau) \end{aligned} \quad (5)$$

As we are interested in the case when the food resource behaves like a *traveling wave* with a constant velocity c , it is more convenient to change to a reference frame that moves with the wave, i.e. $y \rightarrow \xi = y - ct$, rendering

$$\begin{aligned} \partial_\tau n(\xi, \tau) &= \partial_\xi^2 n(\xi, \tau) + c\partial_\xi n(\xi, \tau) + [M(\xi, \tau) - 1]n(\xi, \tau) \\ \partial_\tau N(\xi, \tau) &= c\partial_\xi N(\xi, \tau) + [\beta M(\xi, \tau) - \alpha]N(\xi, \tau) \\ \partial_\tau M(\xi, \tau) &= q(\xi, \tau) - [g + n(\xi, \tau) + \beta N(\xi, \tau)]M(\xi, \tau) + c\partial_\xi M(\xi, \tau). \end{aligned} \quad (6)$$

The possibility of solving analytically this problem hinges on the fact that, with an adequate transformation, the equation for $n(\xi, \tau)$ adopts the form of a Schrödinger like equation, where the potential is associated with the food wave. If we propose for $n(\xi, \tau)$

$$n(\xi, \tau) = e^{(-c\xi/2)} \phi(\xi, \tau), \quad (7)$$

the resulting equation for $\phi(\xi, \tau)$ is

$$\frac{\partial^2 \phi}{\partial \xi^2} + (M(\xi) - 1 - \frac{c^2}{4})\phi = \frac{\partial \phi}{\partial \tau}. \quad (8)$$

Assuming the stationary case: $\frac{\partial \phi}{\partial \tau} = 0$, all the time dependence comes through the variable ξ . Comparing with the one-dimensional Schrödinger equation [14]

$$\frac{\partial^2 \psi}{\partial \xi^2} + (E - V(\xi))\psi = 0 \quad (9)$$

we can identify the potential and the energy eigenvalue as

$$V(\xi) \rightarrow -M(\xi), \quad E \rightarrow -1 - \frac{c^2}{4}.$$

On the other hand, as we are considering population densities, n must be positive. Hence, the only relevant solution is the one corresponding to the ground state of the potential $-M(\xi)$, a wave function $\psi_s(\xi)$ without nodes and energy E_s , determining the value for the velocity c , given by $c^2 = -4(1 + E_s)$, univocally. The form of the density $n(\xi)$ is fixed by Eq.(7), corresponding to the ground state wave function times an exponential decreasing factor that shifts the maximum of $\psi_s(\xi)$ backwards.

Hence, it is clear that the possibility of survival of the *weak* species as a wave like density is determined by an adequately chosen behavior of the density $M(\xi, \tau)$. In this work we have adopted for $M(\xi, \tau)$ the form of a localized perturbation moving on top of the homogeneous distribution corresponding to the threshold $M_N = \alpha/\beta$ (i.e. the second value in Eq.(2) with the scaled parameters). Hence, a grow of both $N(\xi)$ and $n(\xi)$ inside the disturbed region, can be expected. Outside this region some given values will be reached. The general result for N is

$$N_s(\xi) = N^* \exp\left[-\frac{1}{c} \int_{\xi}^{\infty} (\beta M(\xi') - \alpha) d\xi'\right] \quad (10)$$

for $\xi \in [-\xi_c, \xi_c]$, $N_s(\xi) = N^*$ for $\xi > \xi_c$, and (in principle) a different constant value, to be determined, for $\xi < -\xi_c$. Here $[-\xi_c, \xi_c]$ indicates the region where M departs from its *standard* value.

Finally, the source q consistent with the stationary state $(M_s(\xi), N_s(\xi), n_s(\xi))$ we have just obtained, is given by

$$q_s(\xi) = (g + \beta N_s(\xi) + n_s(\xi)) M_s(\xi) + c \frac{\partial}{\partial \xi} M_s(\xi). \quad (11)$$

All the external influence will be included in the function $q_s(\xi)$ that now plays the role of an external parameter keeping the system far from equilibrium.

Here it is worth to make a comment concerning the form found for n : in the above indicated solution we expect the wave function $\phi(\xi, \tau)$ to decay exponentially outside the support of the *potential function* $\frac{\beta}{2} - M(\xi)$. The rate of decay, as it is known from quantum mechanics, is $\gamma = \sqrt{-E_s}$, whereas from the indicated solution $\frac{\xi}{2} = \sqrt{-(1 + E_s)}$. Hence, the sign of the combined exponent $-\gamma|\xi| - \frac{\xi}{2}$ is effectively negative as $\xi \rightarrow -\infty$, since $\gamma > \frac{\xi}{2}$. The fact that $n \neq 0$ in a localized region of the ξ -space is to be interpreted in the following way: before the food wave reaches the point x , there is a negligible number of individuals of the *weak species* (*extinction* situation); but because their *ability* to follow the wave (as opposite to the *strong species*) their population can grow to a non-negligible value, but only around the wavefront. Those individuals which are lagged behind, are condemned to extinction by competition with the *apter* species in the homogeneous situation.

For the form of the wave $M(\xi)$ mounted on top of the homogeneous value M_s , we can choose several different possibilities. In [13] we have adopted a truncated parabola, however, there are several other possibilities corresponding to all known cases of exactly (or quasi-exactly) solvable potentials [16].

Here, we start dividing the space in five different zones

$$\begin{array}{ll} \text{zone I} & 2\xi_0 \leq \xi < \infty \\ \text{zone II} & \xi_0 \leq \xi < 2\xi_0 \\ \text{zone III} & -\xi_0 \leq \xi < \xi_0 \\ \text{zone IV} & -2\xi_0 \leq \xi < -\xi_0 \\ \text{zone V} & -\infty \leq \xi < -2\xi_0 \end{array} \quad (12)$$

We have chosen for the potential the following form

$$V(x) = \begin{cases} -M_0 & \text{zone I,} \\ -M_0 - 2mx_0 + mx & \text{zone II,} \\ -M_0 - mx & \text{zone III,} \\ -M_0 + 2mx_0 + mx & \text{zone IV,} \\ -M_0 & \text{zone V.} \end{cases} \quad (13)$$

Hence, the food resource adopts the form

$$M_s(\xi) = \begin{cases} \alpha/\beta = M_0 & \text{zone I,} \\ M_0 + 2m\xi_0 - m\xi & \text{zone II,} \\ M_0 + m\xi & \text{zone III,} \\ M_0 - 2m\xi_0 - m\xi & \text{zone IV,} \\ M_0 & \text{zone V.} \end{cases} \quad (14)$$

The corresponding stationary Schrödinger like equation (9) has the following ground state wave function ,

$$\psi_s(\xi) = \begin{cases} B_1 e^{-\alpha_1 \xi}, & \text{zone I,} \\ A_2 \text{AyAi}[a_2(\xi)] + B_2 \text{AyBi}[a_2(\xi)] & \text{zone II,} \\ A_3 \text{AyAi}[a_3(\xi)] + B_3 \text{AyBi}[a_3(\xi)] & \text{zone III,} \\ A_4 \text{AyAi}[a_4(\xi)] + B_4 \text{AyBi}[a_4(\xi)] & \text{zone IV,} \\ A_5 e^{\alpha_1 \xi}; & \text{zone V.} \end{cases} \quad (15)$$

where

$$\begin{aligned} a_2(\xi) &= l^2(a_1^2 - 2m\xi_0) + \xi/l, \\ a_3(\xi) &= (la_1)^2 - \xi/l, \\ a_4(\xi) &= l^2(a_1^2 + 2m\xi_0) + \xi/l. \end{aligned} \quad (16)$$

with $l = m^{-1/3}$ and $\text{AyAi}[z]$, $\text{AyBi}[z]$ are Airy functions.

On the other hand, replacing the form of $M(\xi)$ into the expression for the *strong* species $N(\xi)$ we obtain:

$$N_s(\xi) = \begin{cases} \mathcal{A}_1 & \text{zone I,} \\ \mathcal{A}_2 e^{\frac{m\beta\xi(\xi-4)}{2c}} & \text{zone II,} \\ \mathcal{A}_3 e^{-\frac{m\beta\xi^2}{2c}} & \text{zone III,} \\ \mathcal{A}_4 e^{\frac{m\beta\xi(\xi+4)}{2c}} & \text{zone IV,} \\ \mathcal{A}_1 & \text{zone V.} \end{cases} \quad (17)$$

In Figure (1) we show the results for the indicated M_s , N_s , and n_s for a particular set of parameters, while in Figure (2) we show the form of the associated source $q_s(\xi)$.

4 Stability of solutions

In this section we study the stability of the above indicated solution by means of two approaches: an adiabatic elimination scheme and a numerical method.

In order to proceed with the adiabatic elimination scheme, we assume that the food resource M is a fast variable, such that it accommodates rapidly to the variations of the other two variables: N and n . If this situation is right, we can write for the *slow variables*: $N(\xi, \tau) = N_0(\xi) + \delta N(\xi, \tau)$ and $n(\xi, \tau) = n_0(\xi) + \delta n(\xi, \tau)$, where $\delta N(\xi, \tau)$ and $\delta n(\xi, \tau)$ are small variations of the fields. Up to linear contributions in these variations we obtain:

$$\begin{aligned} M(\xi) &= Q(\xi) \int [e^{\int [G+n(\xi'')+\beta N(\xi'')d\xi''] / c} d\xi''] e^{-\int [G+n(\xi')+\beta N(\xi')d\xi'] / c} \\ \delta \dot{N}(\xi, \tau) &= [\beta Q(\xi) M_0(\xi) - \alpha + c\partial_\xi + Q(\xi)\beta M_{1s}(\xi)] \delta N + \beta Q(\xi) M_{1w}(\xi) \delta n \\ \delta \dot{n}(\xi, \tau) &= [Q(\xi) M_0(\xi) - 1 + c\partial_\xi + \partial_\xi^2 + Q(\xi) M_{1w}(\xi)] \delta n + Q(\xi) M_{1s}(\xi) \delta N \end{aligned} \quad (18)$$

where

$$M_0(\xi) = \frac{ce^{G\xi+I_1(\xi)/c}}{Q(\xi)I_2(\xi)}$$

$$M_{1s}(\xi) = \frac{\beta\xi e^{G\xi/c+I_1(\xi)}}{Q(\xi)I_2(\xi)} - \frac{\beta e^{G\xi/c+I_1(\xi)} I_3(\xi)}{Q(\xi)I_2(\xi)^2} \quad (19)$$

$$M_{1w}(\xi) = \frac{\xi e^{G\xi/c+I_1(\xi)}}{Q(\xi)I_2(\xi)} - \frac{e^{G\xi/c+I_1(\xi)} I_3(\xi)}{Q(\xi)I_2(\xi)^2}$$

$$I_1(\xi) = \int [n(\xi) + \beta N(\xi)] d\xi'$$

$$I_2(\xi) = \int [e^{G\xi'+\int [n(\xi'')+\beta N(\xi'')d\xi'']/c} d\xi'] \quad (20)$$

$$I_3(\xi) = \int [\xi' e^{G\xi'+\int [n(\xi'')+\beta N(\xi'')d\xi'']/c} d\xi']$$

The eigenvalue analysis of such system is standard. In Figure (3) we show the real part of the eigenvalues of the system. As such real part, within the precision of our calculation, results to be negative, we can conclude that the above indicated solution is linearly stable.

In order to perform the numerical analysis, we have adapted an evolution scheme previously applied to another reaction-diffusion systems [15]. We have considered as our initial condition the solution we have found in the previous section, and have studied its evolution when some variation of parameters occurs: variations in the propagation velocity c of the source q as well as in the amplitude of the initial conditions. The results are shown in Figures (4a,b,c) in one case and in Figures (5a,b,c) in the other. In the latter case it is possible to see a relaxation towards the stable (initial) condition. It is clear from these graphical results that the solution is robust against the indicated perturbations.

5 Conclusions

The study of simplified models could help in the understanding of the role played by some *environmental* parameters in situations where the complexity of the ecological reality makes its complete modelization very hard. In our case, the model so far studied could give some hints on the behavior of systems of species in competence and the possibility of coexistence. Here we have analyzed an aspect that is usually neglected in models related with competence, that is the inclusion of spatial dependence and the dynamical aspects associated with it (see however ref. [4, 17]). Through a quantum analogy, we have shown that the existence of spatial non homogeneity of the shared food source (of seasonal or artificial origin) can be a possible origin of coexistence of competing species. However, the solution indicated in Eqs.(13), (15) and (17) would be relevant from an ecological point of view as far as it is stable against non-extremal variations of environmental parameters (for instance velocity or intensity of the food source). in order to test the stability, we have not only performed an analytical study of the stability of the solutions, but also a numerical one. The first indicates that the solution is linearly stable while the second gives clues on the stability against the indicated parameter variations. The robustness of our solution against the indicated perturbations arise from the fact that the form of q , that now plays the role of an external control parameter, is kept essentially fix.

So far we have only considered a heavy and immobile *strong* species and a mobile *weak* one. A natural question is: how could the inclusion of the mobility of the *strong* species influence the above indicated results? That means to consider again the scaled Eq.(5), that when we include diffusion of the *strong* species adopts the form

$$\partial_\tau n(y, \tau) = d_y^2 n(y, \tau) + [M(y, \tau) - 1] n(y, \tau)$$

$$\partial_\tau N(y, \tau) = d_N^2 N(y, \tau) + [\beta M(y, \tau) - \alpha] N(y, \tau)$$

$$\partial_\tau M(y, \tau) = q(y, \tau) - [g + n(y, \tau) + \beta N(y, \tau)] M(y, \tau) \quad (21)$$

with $d = D_N/D_n$. A possible via of treating this system, at least for small d values, is through some kind of singular perturbation approach [18].

The study of such a case, as well as other possible extensions of the present model (including contributions corresponding to the *struggle for life* within each species; inclusion of *cleverness* of the *weak* species -for instance through a *chemotaxis* like mechanism [2, 12]-; increasing the number of species or the number of spatial dimensions) will be discussed elsewhere [19]

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FIGURE CAPTIONS

FIGURE 1 : Stationary solutions M_s , N_s and n_s for the set of parameters: $m = 0.85$, $a_1 = 0.28100$, $v_1 = 0.921039$, $A_1 = 1$, $A_2 = 1.15498$, $B_2 = 0.28463$, $A_3 = 1.23793$, $B_3 = 0.0488288$, $A_4 = 0.1193055$, $B_4 = 0.165790$, $A_5 = 0.259872$, $c = 0.340359$.

FIGURE 2 : Source $q_s(\xi)$ for the same set of parameters as in Fig.(1).

FIGURE 3: Real part of the eigenvalues for the adiabatically reduced stability analysis as function of the a wavenumber-like parameter.

FIGURE 4: Evolution of the populations for M , N and n , for the initial conditions given by M_s , N_s and n_s , as indicated in Fig.(1). We have considered a variation of the velocity c_0 given before of: $c = c_0 \pm c_0/10$

FIGURE 5: Evolution of the populations for M , N and n , when the initial conditions given by M_s , N_s and n_s , as indicated in Fig.(1), have been slightly varied in amplitude: $n_0 = 5n_s$, $M_0 = .9M_s$ and $N_0 = N_s$. Relaxation towards the solution in Fig.(1) is clearly seen.

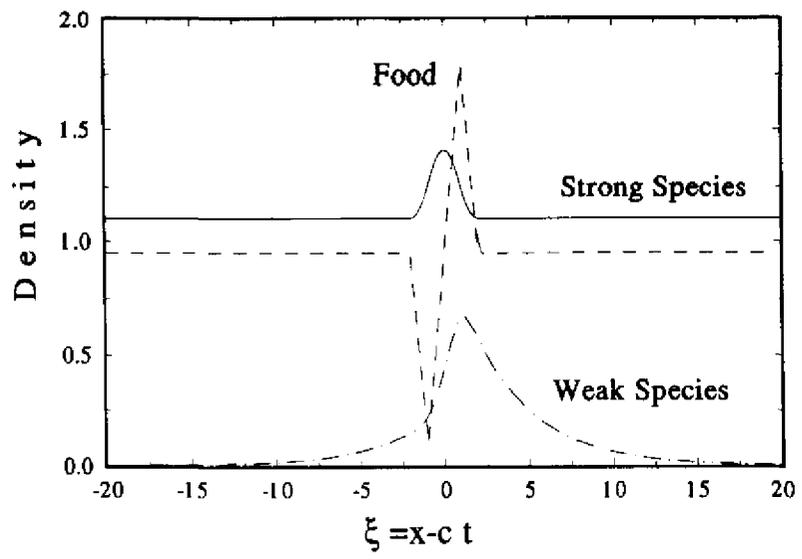


Fig.1

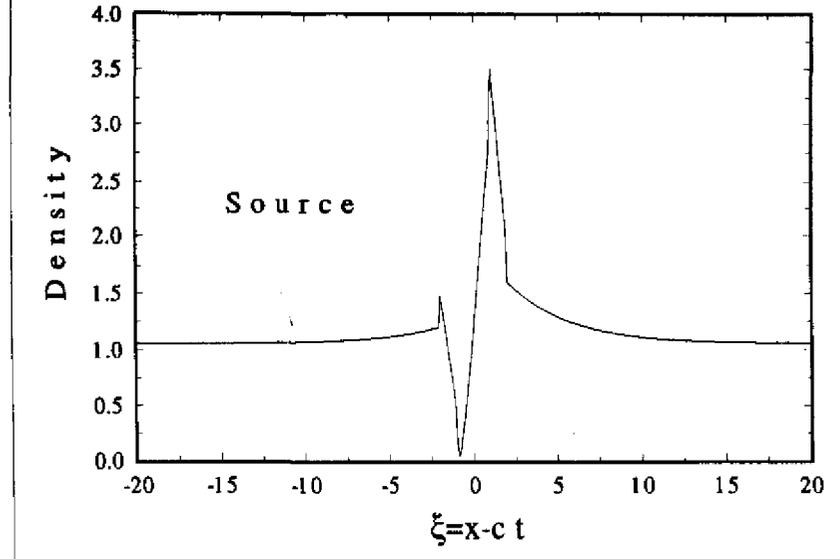


Fig.2

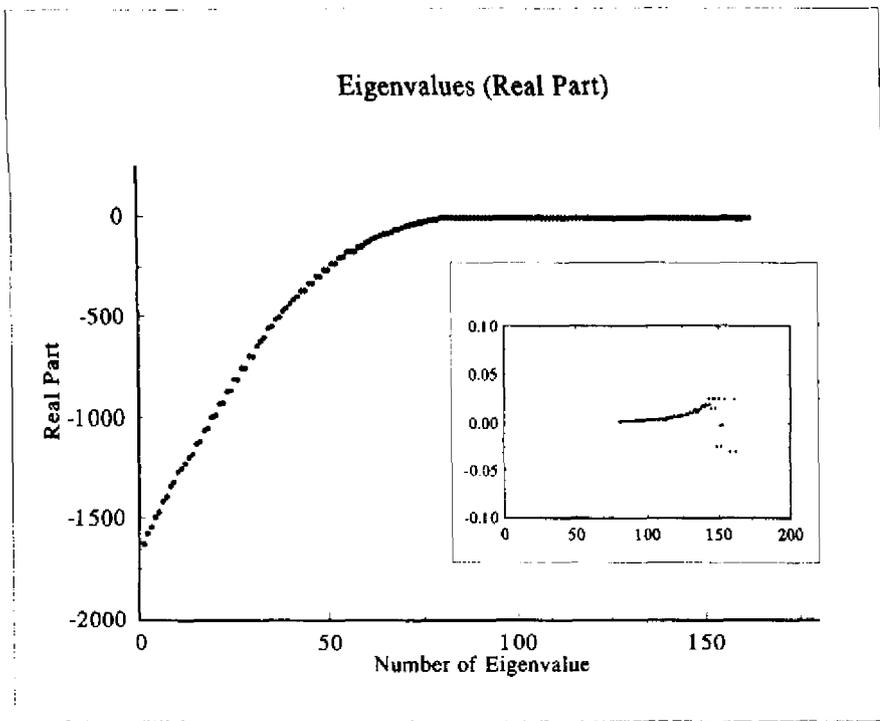


Fig. 3

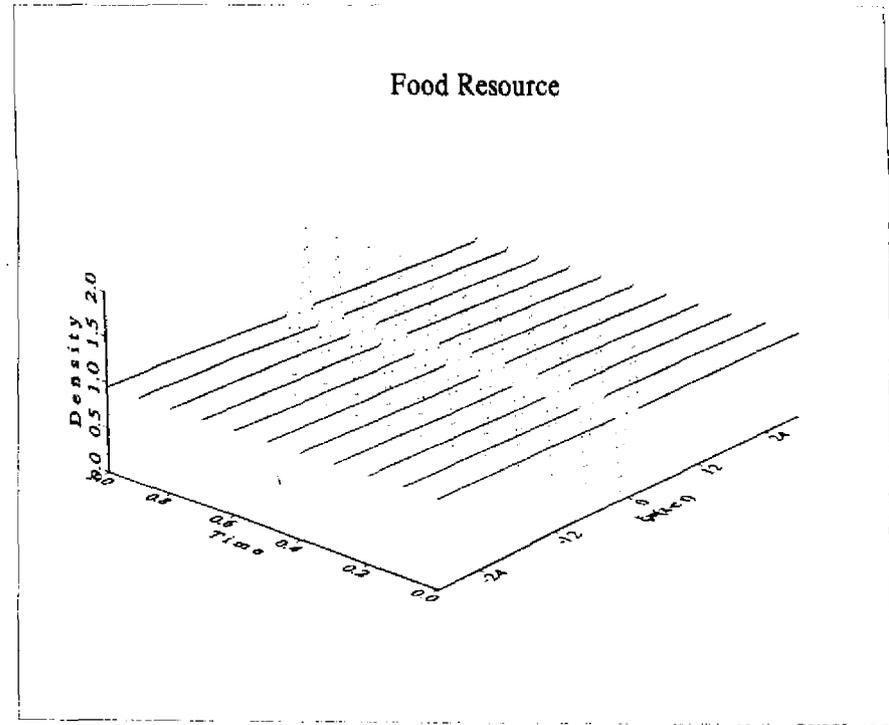


Fig. 4a

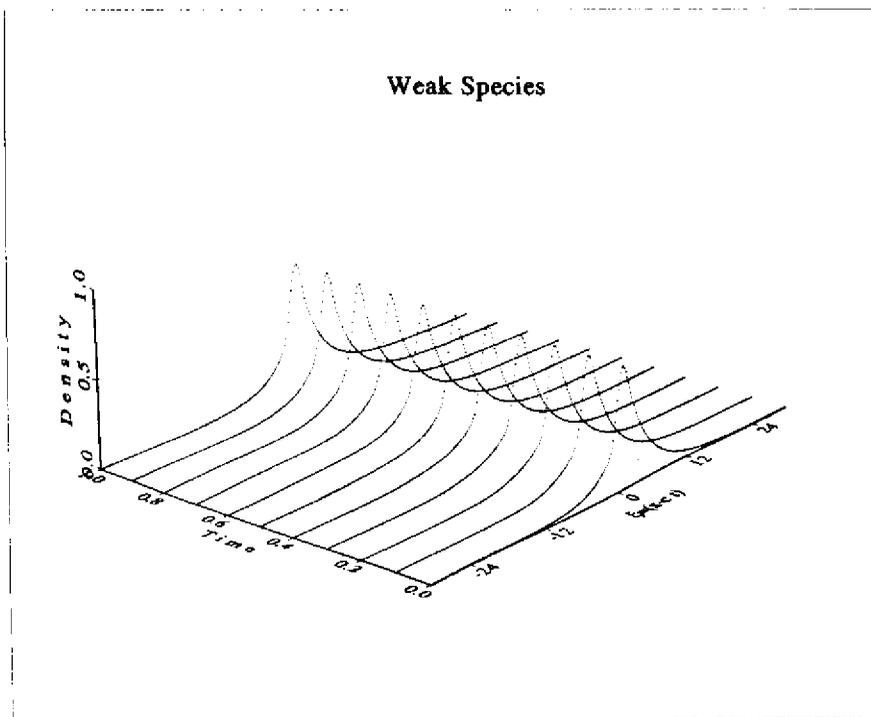


Fig.4b

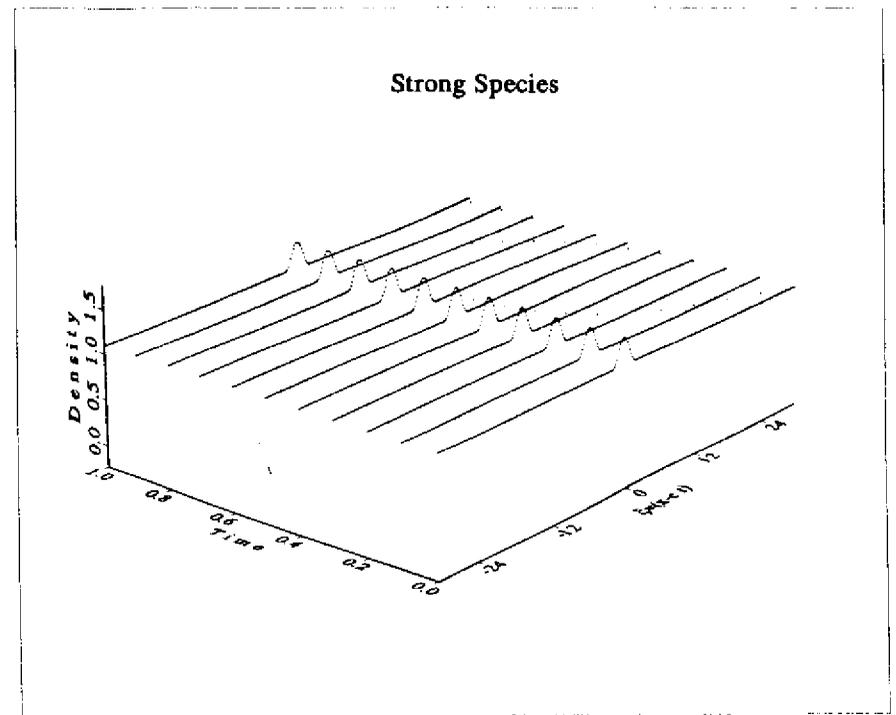


Fig.4c

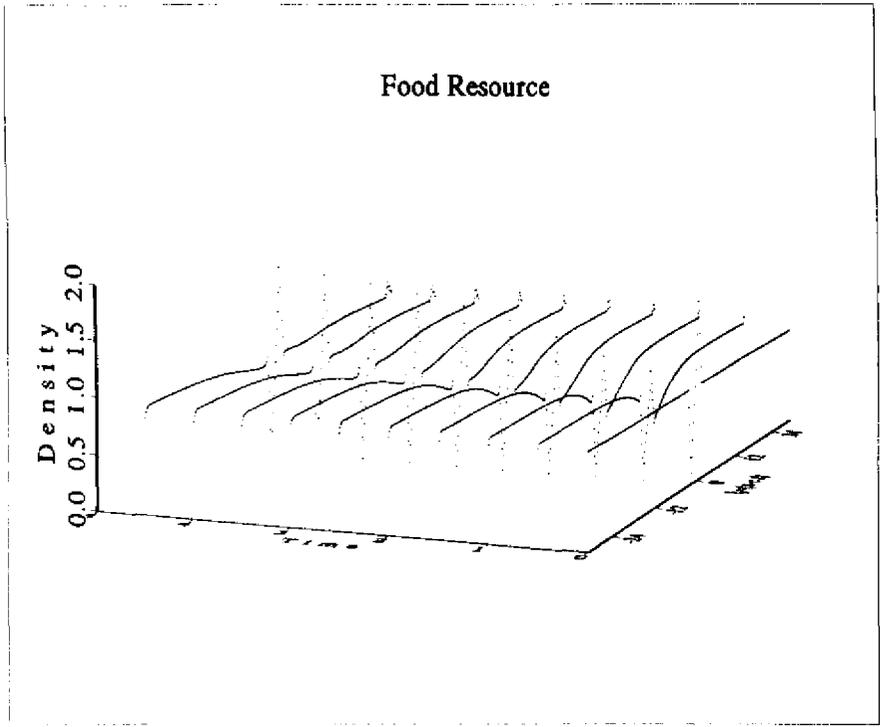


Fig. 5a

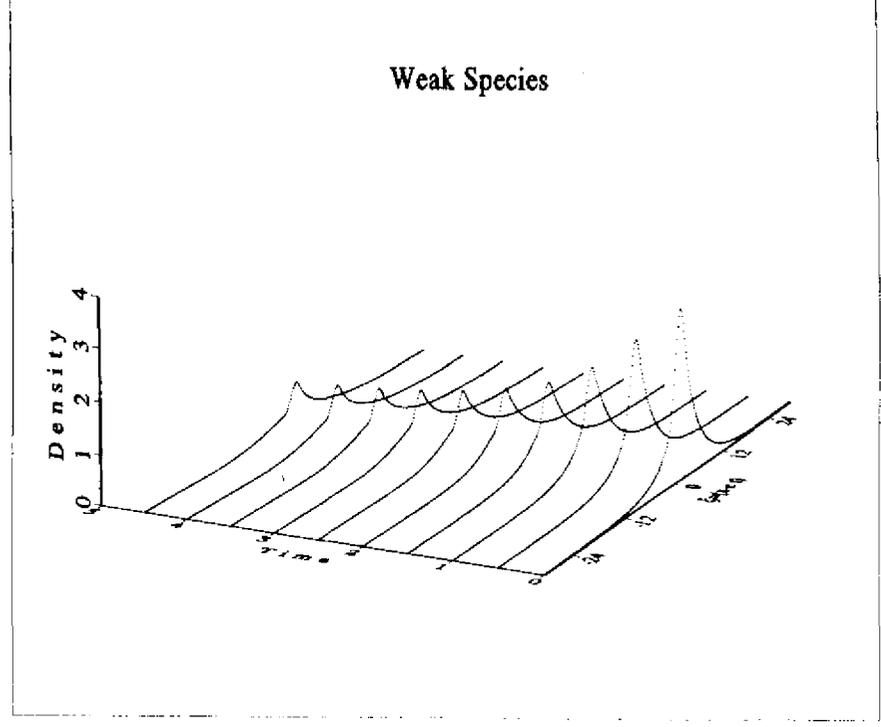


Fig. 5b

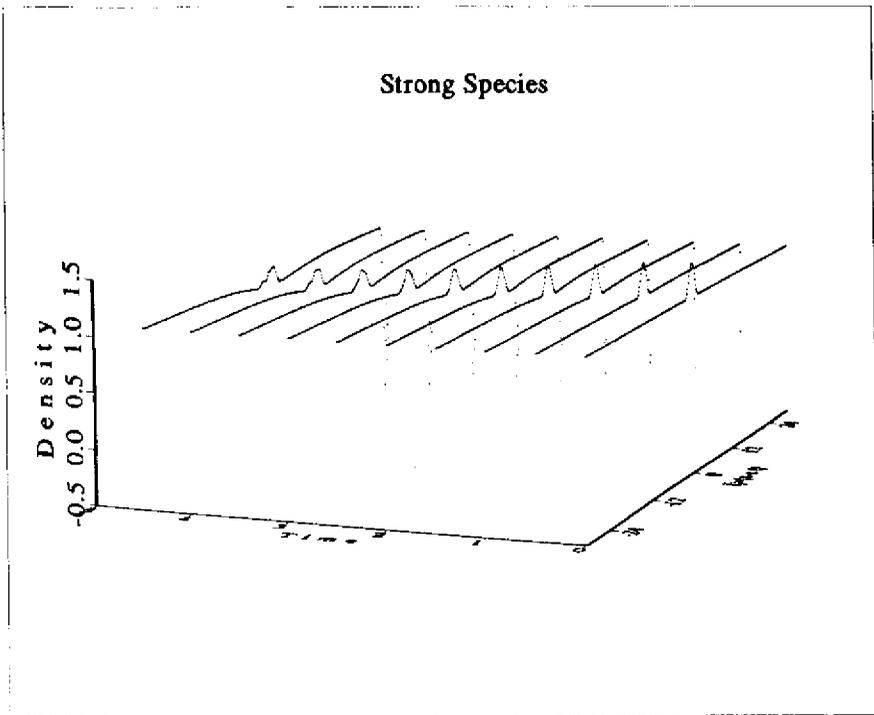


Fig. 5c