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"Seasonality and Chaos in a Plankton-Fish Model"

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These are preliminary lecture notes, intended only for distribution to participants.

SEASONALITY AND CHAOS IN A PLANKTON-FISH MODEL

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Abstract

The dynamics of a plankton-fish model comprising phosphorus, algae, zooplankton and young fish are analyzed for different values of average light intensity, phosphorus concentration in the inflow and adult fish biomass. Light intensity and water temperature are periodically varied during the year, while the other parameters are fixed at realistic values. The analysis is carried out with a continuation method for the study of the bifurcations of periodically forced continuous-time nonlinear systems. The large number of bifurcations of different types indicates that the dynamics of the model can be very complex. In fact, multiplicity of attractors, catastrophic transitions, subharmonics of various periods, cascades of period doublings and strange attractors arise for suitable values of the parameters. The results are in agreement with the most recent theories on food chain systems and periodically forced predator-prey systems. They also suggest that large year-to-year differences in food chain dynamics need not always be attributable to external factors like interannual weather variability.

1 INTRODUCTION

Historical time series of plant, animal and human populations are often so irregular that it is hard to imagine that these populations are near an equilibrium. Nevertheless, some sort of periodicity is sometimes detectable in these time series. Examples of this kind are insect-pest outbreaks in forests (Royama, 1984), algae blooms in artificial reservoirs and lakes (Harris, 1986), fluctuations of some animal populations (Schaffer,1984), dynamics of childhood diseases (Schaffer and Kot, 1985) and many others. Nevertheless, also in these cases, the deviations from a periodic pattern are conspicuous. Such deviations were attributed to various difficulties that arise when collecting data (measurement noise), or to fluctuations of environmental factors influencing the populations (process noise). In other words, scientists believed that, in the absence of measurement and process noise, populations would be constant or periodic and that all deviations from these modes of behavior would be due to random accidents.

The discovery that nonlinear dynamical systems can behave in a purely chaotic way in the absence of exogenous noise sources has radically modified this belief. In other words, it could be that many of the deviations of a population from an equilibrium or a cycle are due to the internal mechanisms of reproduction and growth of the population and not to the influence of external forces. May (1974) was the first to point out this possibility in a study on insect populations with nonoverlapping generations. Since then, the problem of deterministic chaos in population dynamics has been intensely investigated. The analysis of many classical models has proved that chaos may arise for suitable values of the parameters characterizing the population. Among these studies we can recall those on parasitism (May, 1985; Lauwerier and Metz, 1986), competition (Gilpin, 1979), sex (Caswell and Weeks, 1986) and predation (Inoue and Kamifukumoto, 1984; Schaffer, 1988; Rinaldi *et al.*, 1991) and the recent investigations on food chains (Scheffer, 1990; Hastings and Powell, 1991) and on a chemostat with a predator, a prey and a periodically forced inflowing substrate (Kot *et al.*, 1991). However, detecting chaos from real population data, which are, in any case, affected by some kind of noise, is, at least equivocal. Identifying the presence of deterministic chaos in such time series requires the capability of distinguishing between non chaotic time series affected by noise and chaotic time series affected by noise. Nevertheless, the use of numerical techniques has allowed different authors to conjecture the presence of chaos, for example, in the dynamics of the

Canadian Lynx population (Schaffer, 1984), in the growth of some species of trees (Gutierrez and Almiral, 1989), and in certain childhood disease epidemics (Schaffer and Kot, 1985; Olsen, 1987; Kot *et al.*, 1988; Sugihara and May, 1990). As a result population communities have all the ingredients of strongly nonlinear dynamics (for a debate on the importance of chaos in biology see Schaffer and Kot, 1986; Berryman and Millstein, 1989; Pool, 1991a,b).

This paper is devoted to the study of a model of plankton dynamics in a seasonal environment. In addition to the effects of light, temperature and nutrients on the planktonic system, we take the impact of planktivorous fish into account. Traditionally, this aspect is rarely considered in plankton models (see, *e.g.*, Jorgensen (1983) for a review), although the dominant influence of fish on plankton in many aquatic systems is now documented by a large number of studies (*e.g.*, Lamarra, 1975; Leah *et al.*, 1980; Cronberg, 1982; Shapiro and Wright, 1984; Reinertsen and Olsen, 1984; Levitan *et al.*, 1985). Field data and laboratory experiments show that the dynamics of the populations coexisting in a water body are rather complex, although some general patterns are mostly identifiable. A well known scenario is the occurrence of a spring bloom of algae followed by a zooplankton peak inducing a clear water

phase, which, subsequently, changes to a more turbid situation with low zooplankton densities (Sommer *et al.*, 1986). In other cases continuing regular density oscillations are found, especially of large Cladocerans (McCauley and Murdoch, 1987). Often, however, field data on plankton show considerable irregularity. Algae do peak in early Summer (blooms), but the amplitude and the time of occurrence of these blooms and subsequent zooplankton peaks are often quite different from one year to the next. The concentration of the limiting nutrient (in general phosphorus), as well as the biomass of young fish feeding on zooplankton, follows a simpler pattern during the year, but these patterns often vary conspicuously and aperiodically through years. In short, recorded time series of phosphorus, algae, zooplankton and fish clearly point out two characteristic frequencies. A low frequency (one year period) obviously due to the one-year periodicity of the environmental factors (light intensity, water temperature,...) regulating the growth of all species involved in the process, and a high frequency (1-2 months period). Nevertheless, random deviations from the average periodic pattern are not negligible. These deviations have been, until now, explicitly attributed to the unpredictable fluctuations of environmental factors. In other words, algae, zooplankton, and fish populations would have exactly the same pattern repeating each year (periodic solution of "period one") if the environment were perfectly periodic.

Without having the intention of underestimating the role of the environmental randomness, this paper presents the results of a study which shows that plankton dynamics can be intrinsically chaotic. This fact could have been somehow conjectured by a naive analogy with the most recent results on periodically forced predator-prey systems (Rinaldi *et al.*, 1991; Kot *et al.*, 1991). But the models discussed in these contributions are not suited for describing the planktonic system. For this reason we have performed a systematic and detailed analysis of all possible modes of behavior of a more complex model. Our model is composed by five compartments, namely, phosphorus, algae, zooplankton, young fish and adult fish (the last considered as a parameter), and encapsulates the most important processes (influence of light intensity and nutrient concentration on algal growth, functional response of zooplankton and fish, recycling of phosphorus through excretion, decomposition and mineralization, temperature dependence of growth and mortality rates,...). The discussion is carried out with respect to three parameters: latitude, phosphorus concentration of the inflow and fish biomass. Light intensity, water temperature, and recruitment of young fish are taken

as periodically varying input functions of the model, while all other parameters are fixed at realistic values. The analysis shows that such a model has very complex dynamics, comprising multiple attractors, catastrophes, subharmonics and chaos. Multiplicity of attractors can lead to high sensitivity to noise; catastrophes imply conspicuous variations of the populations for small variations of strategic parameters; subharmonics correspond to periodic behavior with long periods (3,4,... years); chaos implies no periodicity whatsoever although patterns may look periodic at first sight.

The paper is organized in sections. In the next section we present our model and outline its limitations. In Section 3 the continuation method used to compute the bifurcations of the model is described. In the fourth section we present the results of the analysis in terms of bifurcation curves in two dimensional parameter spaces. The presence of chaos is detected by means of Poincaré sections which point out the fractal geometry of the attractors. Finally, in Section 5 we summarize the results and outline the most important directions for further research.

2 MODEL DESCRIPTION

The model considers the part of the aquatic ecosystem depicted in Fig.1. Each compartment shown in the figure corresponds to one state variable in the model, except for the biomass of 'adult fish' which is kept constant, as will be discussed later. Obviously, the variables represent complex groups of species. Assuming that hydrology is constant the formulation of the model is as follows:

$$\begin{aligned} \dot{P} &= \delta(P_0 - P) - A\Psi_A + \rho_A m_A^* A + \rho_Z m_Z^* Z + \rho_F m_F^* F + \\ &\quad \xi_Z Z \Psi_Z + \xi_F F \Psi_F \qquad (1) \\ \dot{A} &= e_A A \Psi_A - Z\Psi_Z - m_A^* A - \delta A \qquad (2) \\ \dot{Z} &= e_Z Z \Psi_Z - F\Psi_F - V_0 \Psi_{V_0} - m_Z^* Z - \delta Z \qquad (3) \\ \dot{F} &= e_F F \Psi_F - m_F^* F + V_0 i(t, L_0) - F d(t, L_0) \qquad (4) \end{aligned}$$

where the four functional responses Ψ are given by

$$\begin{aligned} \Psi_A &= \beta_A^* \frac{P}{k_A + P} \cdot \frac{L}{\gamma A + L} \\ \Psi_Z &= \beta_Z^* \frac{A}{k_Z + A} \\ \Psi_F &= \beta_F^* \frac{Z}{k_F + Z} \end{aligned}$$

$$\Psi_{V_0} = \beta_{V_0}^* \frac{Z^2}{k_{V_0}^2 + Z^2}$$

and

P = phosphorus concentration

A = algal concentration

Z= zooplankton concentration

F = young fish biomass

V_0 = adult fish biomass

P_0 = phosphorus concentration of the inflow

L_0 = average light intensity

L = light intensity

ρ_A (ρ_Z) (ρ_F) = amount of nutrient released by decomposition of a unit of dead algae (zooplankton) (young fish)

ξ_Z (ξ_F) = amount of phosphorus excreted by zooplankton (fish) per unit of algae (zooplankton) eaten

m_A^* (m_Z^*) (m_F^*) = mortality rate of algae (zooplankton) (young fish)

δ = inverse of retention time

e_A (e_Z) (e_F) = efficiency of algae (zooplankton) (young fish)

$i(t, L_0)$ = recruitement rate of young fish

$d(t, L_0)$ = aging rate of young fish

γ = self-shading capacity of algae

β_A^* = maximum rate of phosphorus uptake

β_Z^* = maximum grazing rate of zooplankton

β_F^* ($\beta_{V_0}^*$)= maximum predation rate of young (adult) fish

k_A, k_Z, k_F, k_{V_0} = half saturation constants (i.e. values of $A, Z, F,$ and V_0 at which the corresponding functional responses are half maximum)

Table 1 gives the dimensions of parameters, the range of realistic values, and the relevant sources of this information. In all figures which follow phosphorus concentration (P) is in $mgPl^{-1}$, while algal (A), zooplankton (Z) and young fish (F) concentrations are in $mgdwl^{-1}$. The stars '*' appearing in equations (1)-(4) denote a temperature dependence. In accordance with the most commonly used Q_{10} approximation of Arrhenius law, all parameters varying with temperature are assumed to double every 10 degrees. The corresponding values at 20 degree Celsius are indicated in Tab.1 without '*'.

Light intensity L and water temperature T are assumed to be sinusoidal

functions of t(day):

$$L(t) = L_0(1 + \epsilon_L sin\frac{2\pi}{365}t)$$

$$T(t) = T_0(1 + \epsilon_T sin\frac{2\pi}{365}(t - \tau_T))$$

where t=0 at Spring Equinox. In order to reduce the number of parameters, the average light intensity L_0, obviously inversely related to latitude, has been selected as an independent parameter, while τ_T has been fixed to 80 days and ϵ_L, T_0 and ϵ_T have been related through linear regression to L_0 using data of lakes at different latitudes. The result is

$$\epsilon_L = 2.3027 - 0.0048L_0$$

$$T_0 = 0.034L_0$$

$$\epsilon_T = 0.8\epsilon_L = 1.8421 - 0.0038L_0$$

In the following we shortly describe the rationale behind the model formulation, concentrating on the less traditional aspects of it.

The phosphorus equation (1) contains the following terms: net input, uptake by algae, release from decomposing algae, zooplankton and fish and finally excretion by zooplankton and fish. The concentration P_0 is kept constant and is used to set the nutrient level in the system. Seasonal variations in processes like uptake by and release from sediments and aquatic macrophytes are neglected. Nutrient release from decomposing organisms is considered an instantaneous process, and excretion by zooplankton and fish is taken proportional to their consumption rates.

The algal equation (2) consists of a growth term, mortality due to zooplankton grazing, basic mortality and an outflow from the system. The growth Ψ_A, obviously dependent upon phosphorus concentration, is also a function of light. The Monod function for light dependence can be easily justified (Cornelli, 1989) and serves to describe the competition effect due to self shading. The grazing Ψ_Z by zooplankton is also written as a Monod formulation (type II functional response).

Zooplankton, in the model, should be thought of as large Cladocerans like Daphnia species. This group represents the most dominant grazers of algae and is also most vulnerable to fish predation (Scheffer, 1991, and references therein). Concerning the zooplankton equation (3) it should be noted that there are two different predation losses, one for adult fish, and one for 'young of the year' fish. Young fish are supposed to have a type II Ψ_F functional response, whereas the adult fish have a type III functional response Ψ_{Y_0}, because unlike the young fish, the larger animals are able to switch to

alternative prey (Scheffer, 1991).

The equation for fish (4) is probably the least traditional part of the model. Generally, plankton and fish dynamics are not described in the same model. The rationale behind this is that the characteristic time scales of these groups differ quite substantially. This might be true if one focuses on the total biomass of the fish population, but certainly not if the planktivorous capacity is of interest. Young fish of almost all species go through a stage at which they are obligatory planktivores. Therefore, the yearly recruitment which often gives rise to massive peaks of young fish, causes the predation pressure of the fish community on zooplankton to show a pronounced seasonal peak. Unfortunately, it is not reasonable to put this peak into the model as a forcing function, since it is known that there are large interannual differences in young fish survival, depending on the availability of plankton at the moment that young fish are in their planktivorous stage. Equation (4) shows how this complex interaction with fish is incorporated in the model. The amount of adult fish, as mentioned before, is treated as constant with respect to the time scale of interest. Young fish have a consumption dependent biomass growth and a fixed mortality. In addition, there is an input, proportional to the amount of adult fish representing recruitment, and an output representing the aging of young fish. Obviously, the latter process would put them in the adult fish class, if this class were modelled dynamically. The input and output of young fish is uniformly spread over some time. The timing of recruitment is especially relevant in this context. It is formulated in such a way that the input process is finished 6 weeks after the temperature reaches 14 degrees Celsius, which is the moment that, on average, young fish start to forage heavily on large zooplankters. More precisely, the recruitment function $i(t, L_0)$ is equal to 0.005 for 20 days starting from day $\tau_i = 158 - 0.26\ L_0$ (typically the beginning of May) and 0 otherwise, while the aging function $d(t, L_0)$ is equal to 0 for 120 days starting from day τ_i, and to 0.05 for the rest of the year.

The model is rather complex compared to traditional models used up to now . Although, crude simplifications are made, and many potentially interesting factors are still left out of consideration, the number of parameters is large. This prohibits an extensive analysis over the complete parameter space. After having checked that the qualitative behavior of the model is sound for all realistic values of the parameters, the strategy has therefore been to analyze the behavior of the model with respect to just three parameters: the light intensity (L_0), the phosphorus loading (P_0) and the adult fish

biomass (V_0). All other parameters are fixed in the middle of the realistic ranges given in Table 1.

3 THE METHOD OF INVESTIGATION

The model, adding the equation $\dot{t} = 1$ (t mod 1 year), can be transformed into an autonomous five-dimensional system for which four-dimensional Poincaré section and four-dimensional first return map

$$(P(0), A(0), Z(0), F(0)) \mapsto (P(1), A(1), Z(1), F(1))$$

can be defined (Arnold, 1982; Guckenheimer and Holmes, 1983). This map specifies the values $P(1), A(1), Z(1), F(1)$ that the four state variables have at the end of the year, once the values $P(0), A(0), Z(0), F(0)$ that the same variables have at the beginning of the year are known. Fixed points of the k-th iterate of the map correspond to periodic solutions with period k years. We will refer to these points as period k fixed points. It should be noted that a periodic solution with period k corresponds to a k-ple of period k fixed points of the Poincaré map. Closed and regular curves (invariant tori) on the Poincaré section correspond to quasi-periodic solutions, while irregular invariant sets (strange attractors) correspond to chaotic solutions. Fixed points of the Poincaré map can bifurcate at some parameter values. In the following we will discuss bifurcations in two-dimensional parameter spaces and will therefore talk of bifurcation curves. In all our figures we will only display bifurcations involving at least one attractor because only these bifurcations are of biological interest.

We use the following notation for fixed point codimension one bifurcations.

$f^{(k)}$ - flip (period doubling) bifurcation curve. For parameter values on this curve the map has a period k fixed point with a multiplier $\mu_1^{(k)} = -1$. When this curve is approached, a stable cycle of period k loses stability and smoothly becomes a stable cycle of period 2k.

$t^{(k)}$ - tangent (fold) bifurcation curve. For parameter values on this curve the map has a period k fixed point with a multiplier $\mu_1^{(k)} = 1$. On this curve a stable and an unstable cycle of period k collide and disappear.

The bifurcation curves presented in the following section have been computed by means of a continuation method interactively supported by the program LOCBIF developed by A. Khibnik, Yu.A. Kuznetsov, V. Levitin and E. Nikolaev at the Research Computing Centre of the USSR Academy

of Sciences at Pushchino. The method can be briefly described as follows (Khibnik, 1990a,b). Each bifurcation curve is computed by projecting a one-dimensional manifold located in the six-dimensional space (P, A, Z, F, p_1, p_2) on the (p_1, p_2) plane, where p_1 and p_2 are two parameters (for example P_0 and L_0). The manifold is determined by the four fixed point equations and by a bifurcation condition imposed on the multipliers of the fixed point. This condition is written using the characteristic polynomial $det(J - \mu I)$, where J is the Jacobian matrix of the proper iterate of the Poincaré map at point (P, A, Z, F) and I is the 4x4 unit matrix. More precisely, the bifurcation conditions are $det(J + I) = 0$ for flip bifurcation and $det(J - I) = 0$ for tangent bifurcation. In the program LOCBIF the bifurcation curves are computed by means of an adaptive prediction-correction continuation procedure with tangent prediction and Newton correction. All relevant derivatives, as well as the Poincaré map, are evaluated numerically.

4 ANALYSIS OF THE RESULTS

In this section we present and interpret bifurcation curves in the parameter spaces (P_0, L_0) and (V_0, L_0). These curves are only some of the bifurcation curves we have obtained. In particular, we do not display bifurcation curves involving only unstable modes of behavior, because they are of no biological interest. (They are needed only if one likes to fully understand the global bifurcation structure of the system from a purely formal point of view (Kuznetsov *et al.*, 1992).) We also do not show bifurcation curves that we have detected only in very small regions of the parameter space because we are not sure whether they correspond to relevant phenomena. For these reasons, the analysis is not complete and the modes of behavior we point out are only samples of the dynamics of our plankton-fish model. Nevertheless, these samples are quite interesting and refer to characteristic phenomena that we have checked to be robust with respect to parameter perturbations.

In order to be as clear as possible, we present the results in three different subsections dedicated, respectively, to multiplicity of attractors, catastrophes and chaos.

4.1 Multiplicity of attractors

It is already known (Muratori and Rinaldi, 1989; Scheffer, 1991) that even the most rudimentary food chain model composed of a prey, a predator and

a constant superpredator has multiple attractors in the absence of seasonalities. On the other hand, it has been pointed out recently (Rinaldi *et al.*,1991) that periodic variations of environmental factors can easily give rise to multiple attractors even in the simple predator-prey models which have only one attractor in a constant environment. Thus, multiplicity of attractors may also be expected in our plankton-fish model, which is more complex than a simple food chain and has many periodically varying factors.

Fig. 2 shows two sets of bifurcation curves in the parameter space (P_0, L_0). In Fig. 2a we have two branches of a tangent bifurcation of period 1. In the shaded region delimited by the two curves, the system has two stable cycles of period 1 and an unstable cycle of period 1. When a bifurcation curve $t^{(1)}$ is crossed coming from inside the shaded region , one of the two stable cycles collides with the unstable one and disappears. Thus, in the shaded region we have coexistence of two distinct stable cycles of period 1, while outside that region we have only one stable mode of behavior. Fig. 3 shows the two coexisting attractors for point 1 of Fig. 2a. In both cases algae peak three times per year and zooplankton peaks (essentially) two times per year, but the amplitudes of the oscillations

are quite different. Of course, each of these attractors has its own basin of attraction, so that, in the presence of heavy intermittent noise, the system will randomly visit the two attractors.

Fig. 2b shows another set of bifurcation curves, namely flip of period 1 and tangent of period 1. When the flip bifurcation curve $f^{(1)}$ is crossed from below, a stable cycle of period 1 loses stability and becomes a stable cycle of period 2. In the shaded region of Fig. 2b we have two attractors: a cycle of period 1 and a cycle of period 2. Fig. 4 shows these two attractors for point 1 of Fig. 2b. Recognizing that the second attractor is not a cycle of period 1 requires a close look: this is because point 1 in Fig. 2b is situated near the flip bifurcation curve $f^{(1)}$ where cycles of period 2 degenerate into cycles of period 1. The period 2 behaviour shown in Fig. 4b is an example of subharmonic behaviour. The occurrence of subharmonics in the model suggests that plankton communities can vary periodically with period k=2,3,... years even if environmental factors do vary periodically with period 1.

4.2 Catastrophes

Macroscopic transitions can easily occur for small variations of a parameter in a nonlinear system with multiple attractors (May, 1977). Perhaps the best

known example (Noy-Meir, 1975) in population dynamics is the crash of food chain systems for an increase of the exploitation rate of the top predator (adult fish in our case). On the other hand, it has been recently ascertained (Rinaldi *et al.*, 1991) that seasonalities can favor catastrophic transitions in simple predator-prey models. Thus, it may be expected that our plankton-fish model can also undergo substantial transitions when parameters like phosphorus or adult fish biomass are slightly perturbed. Confirmations of this conjecture can be found in Figs. 5,6. In each one of these figures the two stable modes of behavior are shown. In Fig. 5 the transition is obtained by lowering the phosphorus concentration of the inflow (see points 2 and 3 in Fig. 2a). Since the catastrophe is associated with a tangent bifurcation of period 1, the system "jumps" from a cycle of period 1 (Fig. 5a) to another cycle of period 1 (Fig. 5b). Nevertheless, the two cycles are different, the first one having much more pronounced oscillations. In Fig. 6 the catastrophe is obtained by increasing the biomass of adult fish so that a curve of tangent bifurcations of period 3 (see curve $t^{(3)}$ of Fig. 12 below) is crossed. The attractor, just before the bifurcation, is therefore a cycle of period 3 (Fig. 6a), while, just after the bifurcation, the system behaves aperiodically on a strange attractor (Fig. 6b). Notice that the aperiodicity of the strange attractor is more easily seen in the dynamics of the higher trophic levels (fish) then, for instance, in phosphorus and algae.

4.3 Deterministic chaos

Deterministic chaos has been shown to be possible in many simple continuous-time population models. Food chain systems have been proved to be chaotic even in the constant parameter case (Hogeweg and Hesper, 1978; Schef-fer, 1990; Hastings and Powell, 1991). The classical predator-prey model can become chaotic when one of its parameters is varied periodically (Inoue and Kamifukumoto, 1984; Schaffer, 1988; Toro and Aracil,1988; Allen, 1989; Kuznetsov *et al.*, 1992; Rinaldi *et al.*,1991) and the lowest amplitude of the seasonal variation needed to generate chaos can become quite small if there are many periodic factors acting on the system (Rinaldi and Muratori, 1991). Finally, a chemostat model composed by nutrient, prey and predator has also been shown to be chaotic for suitable amplitudes of the periodically varying inflow concentration of the nutrient (Kot *et al.*, 1991). It would, therefore, be at least surprising if our plankton-fish model would not be chaotic in some subregions of the parameter space.

Fig. 7 shows a complete set of flip bifurcation curves in the parameter space (P_0, L_0) and three distinct regions in which chaos may arise. If the phosphorus concentration of the inflow P_0 is slowly increased over time and the average light intensity L_0 is fixed at a high value (*e.g.*, L_0=390), the model predicts that the standard period 1 periodic solution will first bifurcate into a period 2 periodic solution (on curve $f^{(1)}$) and then, for a slightly bigger value of P_0, double again its period (on curve $f^{(2)}$) and continue like so until the periodicity is lost. At that point the attractor becomes a genuine chaotic attractor. This region of chaos is characterized by high concentrations of phosphorus (eutrophic lakes) so that algae are not nutrient limited. This is equivalent to saying that plankton and fish are independent of phosphorus concentration and that the model, in fact, reduces to a three stage food chain. The amplitudes of the light and temperature seasonal variations in this food chain are rather small because L_0 is high. Nonetheless, the existence of chaos in this region of the parameter space is not a surprise, since food chain systems can be chaotic in a constant environment especially if growth rates are high. The closed region of chaos at lower values of P_0 and L_0 is also interesting because it shows that chaos can be obtained either by increasing or by decreasing the concentration of nutrient, a result similar to that found by Kot *et al.* (1991) for a much simpler model. Finally, Fig. 7 shows that there are very large regions, in particular in eutrophic lakes, where the system behaves periodically with period 2.

The strange attractors corresponding to the three points named 1, 2, 3 in Fig. 7 are shown in Figs. 8, 9, 10. The upper part ((a) and (b)) of these figures shows two different projections of the Poincare' sections. Each dot in these figures is a sample of the variables indicated on the axis, taken the same day once a year for 500 times. The lower part (c) of the figures shows the corresponding time series of one of the populations: as already remarked for Fig. 6b, the irregularity of the attractor is at first sight more evident for fish than for algae. An explanation for the large interannual differences in fish becomes apparent if one samples the zooplankton population at the first day at which the young fish cohort is fully foraging on large zooplankton (see dots on Fig. 10c). The density of zooplankton which is of critical importance to fish at this life stage is highly variable. The match or mismatch of the appearance of young fish and the peak in their food availability has been suggested as the main cause of the huge year-to-year differences in young fish survival of natural fish populations (Cushing and Dickson, 1976; Cushing, 1982). Our analysis suggests that in addition to meteorological variability the

intrinsic chaos in the aquatic ecosystem is a likely cause of this mechanism.

The fractal geometry of the attractors is very clear in Figs. 8,9, while Fig. 10 displays an attractor which, at a first glance, seems to represent some kind of quasi-periodicity (behavior on torus). Nevertheless, the fractal nature of this attractor can be revealed by changing the scale of observation. Fig.11 illustrates the results of two successive zoomings into the attractor and points out the classical selfsimilarity property of fractal sets.

To conclude our analysis of chaos, we show in Fig. 12 two other period doubling routes to chaos in the parameter space (V_0, L_0). The figure indicates that adult fish biomass might be a critical control variable, because an increase of this variable can cause either the appearance or the disappearance of chaos. The strange attractors corresponding to points 1 and 2 of Fig. 12 are shown in Figs. 13, 14. Also in these cases, the variability of the young fish peaks is greater than that of the algal blooms.

5 CONCLUDING REMARKS

We have shown in this paper that the variability of the yearly patterns of plankton and fish populations (usually attributed to some environmental randomness) can be a direct consequence of the biological and physical processes characterizing the model. This conclusion is based upon the results obtained by analyzing the stable modes of behavior of a model with periodically varying light intensity, water temperature, and fish recruitment and aging. From a technical point of view, the analysis has required the study of the bifurcations of a periodically forced four-dimensional dynamical system: a quite difficult problem that could not have been solved by standard simulation techniques. We have used, instead, a package implementing a powerful continuation method producing flip and tangent bifurcation curves of periodic solutions of any period. The package also detects "codimension two" bifurcation points, a fact that has not been emphasized in the paper but which is of strategic importance for successfully organizing the analysis (Kuznetsov *et al.*, 1992).

Some of the results we have obtained confirm many of the conclusions recently obtained by different authors who have analyzed the dynamics of simple ecological models. The chaos predicted by our model in eutrophic lakes at low latitudes seems to be originated by the possibility that three stage food chains behave aperiodically even in a constant environment (Scheffer, 1990; Hastings and Powell, 1991). The existence of subharmonics and of

strange attractors obtained through cascade of period doublings is in line with the analysis carried out in Rinaldi *et al.*, (1991), while the rarity of quasi-periodic behavior is perhaps due to the high ratio between the period (1 year) of the forcing functions and the period (1-2 months) of the autonomous oscillations of phytoplankton- zooplankton communities.

There are many caveats when interpreting the results of rather abstract models like the one discussed in this paper in terms of real world biology. Nonetheless, a number of significant inferences can be made. Firstly, the analysis shows that the normal seasonal cycle of light and temperature can easily lock the relatively fast cycling plankton system into yearly repeated patterns. This result will probably be in accordance with general biological intuition. More remarkable is the observation that the interplay of the season with the intrinsic rhythms caused by food chain interactions, can give rise to more irregular patterns. Sometimes the same seasonal pattern may repeat every two or three years, but more often no repetition is found whatsoever. The pattern is chaotic, although, at first glance, the time series often look more or less like yearly repeated patterns. This mix of regularity and randomness is, of course, in perfect accordance with observations on seasonal dynamics in nature. However, the real world randomness will, no doubt, be also caused by external perturbations like yearly differences in weather. Nevertheless, it can be stated that observed interannual differences in the ecosystem dynamics need not be always attributable to weather or other external forces. The detected kind of deterministic irregularity offers a good explanation of a phenomenon that has bothered aquatic ecologists for many years: the extremely large year-to-year variation in young fish survival. Although, the generated zooplankton patterns often look rather similar in different years, the timing of their peaks appears to vary. Since the timing of fish spawning is triggered by temperature, and not by food availability, this can cause the young fish to be born in a period of either very high or extremely low food abundance, resulting in large differences in survival. The fact that 'time shift irregularities' causing this match-mismatch process typically arise from the model suggests that it might be impossible to properly relate the natural variation in recruitment success to weather conditions.

The relationship between the investigated control parameters and the occurrence of phenomena like chaos, catastrophes and subharmonics in the model is rather complex, but some broad patterns can be detected. The results suggest, for instance, that oligotrophic systems tend to show regular, yearly repeating, seasonal patterns. Chaos only arises in more eutrophic situations. The temperature-light regime of northern countries seems also to be in favor of yearly repeating patterns. The model generates chaos more easily in conditions associated with warm climates. Of course, these conclusions are only based on observations of the behavior in a limited part of the parameter space, and should therefore be interpreted with care.

Obviously, the work presented in this paper is merely a starting point for further research. The bewildering range of behavior suggests that a detailed analysis of simplified submodels might be informative. On the other hand, many sources of seasonal variation are still left out of consideration, and the effects of including these extra perturbations would be worth studying. Especially challenging seems the search for patterns predicted by the model in real world data sets (Sugihara and May, 1990). However, in view of the noisy character of most ecological data this is an ambitious target.

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TABLE CAPTION

Table 1. The parameters of the model, their units, their minimum and maximum values and the sources of information supporting these data. In all figures of the paper, unless explicitly stated, the parameters are equal to the central value of the range indicated in this table.

TABLE 1

Parameter	Units	Min Value	Max Value	Source of information
L_0	$cal\,cm^{-2}day^{-1}$	300	400	*Hutchinson* 1957
V_0	$mgdw\,l^{-1}$	0.5	3	*Scheffer* 1991
P_0	$mgP\,l^{-1}$	0	2	*Vendegna and Teruggi* 1984
m_A	day^{-1}	0.05	0.4	*Scheffer* 1991
m_Z	day^{-1}	0.1	0.25	*Scheffer* 1991
m_F	day^{-1}	0.01	0.03	*Scheffer* 1991*
e_A	$mgdw(mgP)^{-1}$	70	125	*Scheffer* 1991*
e_Z	$---$	0.5	0.7	*Scheffer* 1991
e_F	$---$	0.4	0.6	*Scheffer* 1991*
ρ_A	$mgP(mgdw)^{-1}$	$2.85 \cdot 10^{-3}$	$4.65 \cdot 10^{-3}$	*Scheffer* 1991*
ρ_Z	$mgP(mgdw)^{-1}$	$2.85 \cdot 10^{-3}$	$4.65 \cdot 10^{-3}$	*Scheffer* 1991*
ρ_F	$mgP(mgdw)^{-1}$	$2.85 \cdot 10^{-3}$	$4.65 \cdot 10^{-3}$	*Scheffer* 1991*
ξ_Z	$mgP(mgdw)^{-1}$	$4.5 \cdot 10^{-3}$	$9.5 \cdot 10^{-3}$	*Scheffer* 1991*
ξ_F	$mgP(mgdw)^{-1}$	$4.5 \cdot 10^{-3}$	$7.5 \cdot 10^{-3}$	*Scheffer* 1991*
γ	$cal\,cm^{-2}day^{-1}(mgdw)^{-1}l$	120	180	*Steemann and Hansen* 1959
δ	day^{-1}	0	0.05	*Matsamura and Sakawa* 1980
β_A	$mgP\,day^{-1}(mgdw)^{-1}$	0.005	0.015	*Scheffer* 1991
β_Z	day^{-1}	0.5	0.7	*Matsamura and Sakawa* 1980
β_F	day^{-1}	0.10	0.20	*Scheffer* 1991*
β_{V_0}	day^{-1}	0.4	0.6	*Scheffer* 1991
k_A	$mgP\,l^{-1}$	0.01	0.03	*Matsamura and Sakawa* 1980
k_Z	$mgdw\,l^{-1}$	0.05	0.13	*Matsamura and Sakawa* 1980
k_F	$mgdw\,l^{-1}$	0.25	0.75	*Scheffer* 1991*
k_{V_0}	$mgdw\,l^{-1}$	0.8	1.2	*Scheffer* 1991

* and references therein.

FIGURE CAPTIONS

Fig.1 The flow of material in the phosphorus-plankton-fish model. Connections between the two fish compartments represent recruitment and aging processes. In the model each compartment is described by a single variable and adult fish V_0 is assumed to be constant. while all other variables $(P.A.Z.F)$ vary in accordance with a differential equation (mass balance).

Fig.2 Bifurcation curves in the two parameters space $(P_0.L_0)$ with V_0=1.00. Fig.(a): tangent bifurcations of period 1 (on the two curves $^{(1)}$ a stable and an unstable periodic solution of period 1 collide and disappear). Fig.(b): tangent and flip bifurcations of period 1 (crossing the flip curve $f^{(1)}$ from the left to the right a stable periodic solution of period 1 loses stability and becomes a stable periodic solution of period 2). Units are as in Table 1.

Fig.3 Coexistence of attractors. Two stable periodic (a) and (b) solutions of period 1 corresponding to the same parameter values. P_0=0.346. L_0=308. V_0=1.00. See point 1 of Fig.2a. In the second attractor (b) algae and zooplankton blooms are much more marked. Concentrations are in $mgdwl^{-1}$.

Fig.4 Coexistence of attractors. The attractor (a) is a cycle of period 1. while the attractor (b) is a cycle of period 2. The parameter values are P_0=1.710. L_0=379.5. V_0=1.00. See point 1 of Fig.2b. Algal concentration and young fish biomass are in $mgdwl^{-1}$.

Fig.5 Catastrophic transitions. Two stable cycles of period 1 for the same average light intensity (L_0=308) and adult fish biomass (V_0=1.00). and for slightly different phosphorus concentrations of the inflow (P_0=0.330 in Fig. (a) and P_0=0.325 in Fig. (b)). See points 2 and 3 in Fig.2a. Lowering the concentration of phosphorus in the inflow generates a catastrophic transition from a cycle with marked algae and zooplankton blooms to a smoother cycle.

Fig.6 Catastrophic transitions. A stable cycle of period 3 and a strange attractor for the same average light intensity (L_0=340.7) and phosphorus concentration of inflow (P_0=1.00) and for slightly different values of adult fish biomass (V_0=2.115 in Fig. (a) and V_0=2.150 in Fig. (b)). Increasing the adult fish biomass gives rise to a catastrophic transition from a cycle to a strange attractor.

Fig.7 Flip bifurcations curves $f^{(1)}$. $f^{(2)}$. $f^{(4)}$ in the two parameter space (P_0.L_0). with V_0=1.00. In the three dotted regions chaotic behavior is possible (see also the next three figures showing the strange attractors of points 1. 2 and 3).

Fig.8 Chaotic behavior of the model. Figs. (a) and (b) show two projections of the strange attractor on the Poincaré section. The fractal structure of the attractor is clearly displayed. Fig. (c) shows the irregular fluctuations of the biomass of young fish during a period of 10 years (the year starts the first day at which all the young fish forage on zooplankton). The parameter values identifying the attractor are P_0=0.887. L_0=390. and V_0=1.00. See point 1 of Fig.7.

Fig.9 Chaotic behavior of the model. Figs. (a) and (b) show two different projections of the strange attractor. Fig. (c) shows the irregular fluctuations of the algal concentration during a period of 5 years (the year starts the first day at which all the young fish forage on zooplankton). Chaos can be detected by comparing the minor blooms of each year. The parameter values identifying the attractor are P_0=1.192. L_0=384. and V_0=1.00. See point 2 of Fig.7.

Fig.10 Chaotic behavior of the model. Figs. (a) and (b) show two different projections of the strange attractor. The fractal structure of the attractor cannot be perceived at this scale (see next figure for two successive zoomings). Fig. (c) shows the irregular fluctuations of the zooplankton concentration during 5 successive years starting the day at which all the young fish forage on zooplankton. The parameter values identifying the attractor are P_0=0.390. L_0=364.8. and V_0=1.00. See point 3 of Fig.7.

Fig.11 The selfsimilarity property of a strange attractor. When zooming into a small square around point X of Fig.10a. the "line" representing the attractor appears as the double line of Fig. (a). Zooming more deeply on point X the upper "line" of Fig. (a) becomes the double line of Fig. (b).

Fig.12 Flip and tangent bifurcation in the two dimensional parameter space (V_0.L_0) with P_0=1.00. The strange attractors present in the shaded regions are obtained through cascade of period doublings $f^{(1)}$. $f^{(2)}$.... and $f^{(3)}$. $f^{(6)}$..... (see also the next two figures showing the strange attractors of points 1 and 2).

Fig.13 Chaotic behavior of the model. Figs. (a) and (b) show two different projections of the strange attractor of point 1 of Fig.12 (V_0=1.15.L_0=360. P_0=1.00). Fig. (c) shows the irregular fluctuations of young fish biomass during 5 successive years.

Fig.14 Chaotic behavior of the model. Figs. (a) and (b) show two different projections of the strange attractor of point 2 of Fig.12 (V_0=2.11. L_0=345.9. P_0=1.00). In Fig. (c) the randomness of the algae blooms is particularly evident on the secondary peaks.

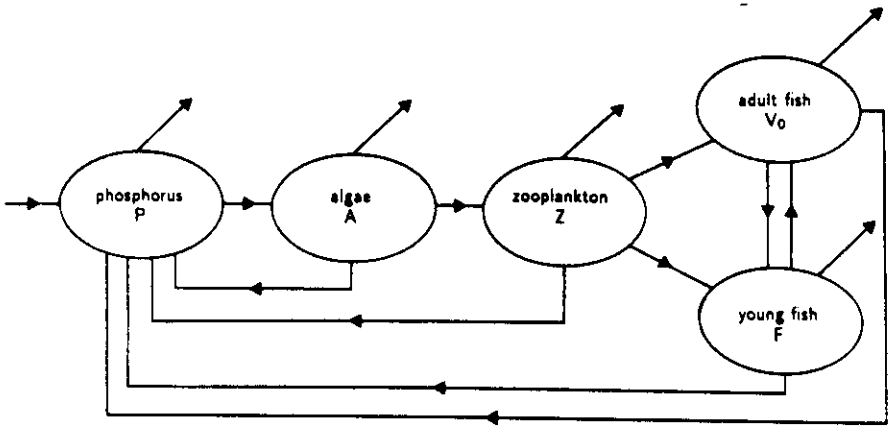
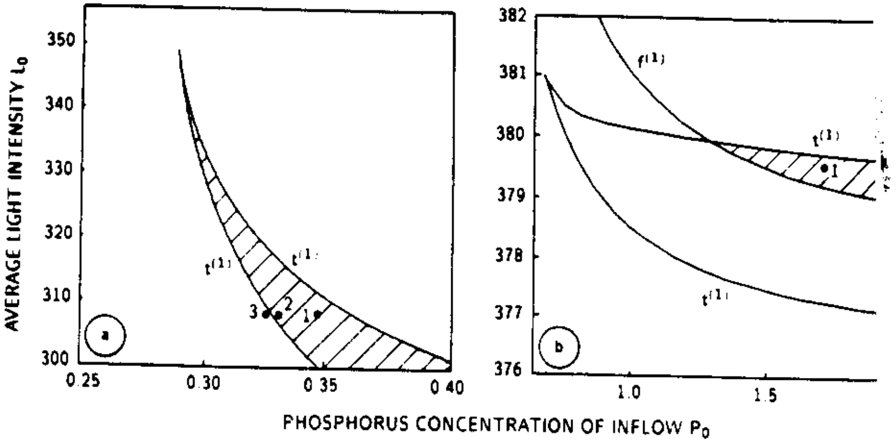

phosphorus
P
algae
A
zooplankton
Z
adult fish
V_0
young fish
F

Figure 1


AVERAGE LIGHT INTENSITY L_0
350
340
330
320
310
300
0.25
0.30
0.35
0.40
$t^{(1)}$
$t^{(1)}$
3
2
1
a
382
381
380
379
378
377
376
1.0
1.5
$f^{(1)}$
$t^{(1)}$
1
$t^{(1)}$
b
PHOSPHORUS CONCENTRATION OF INFLOW P_0

Fig

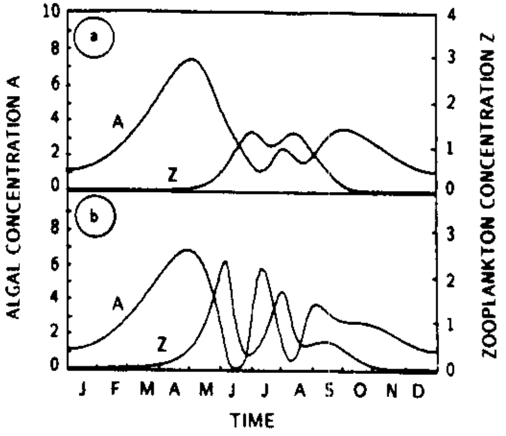


Figure 3

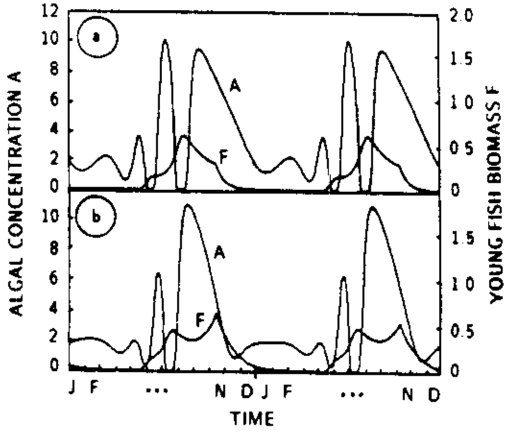


Figure 4

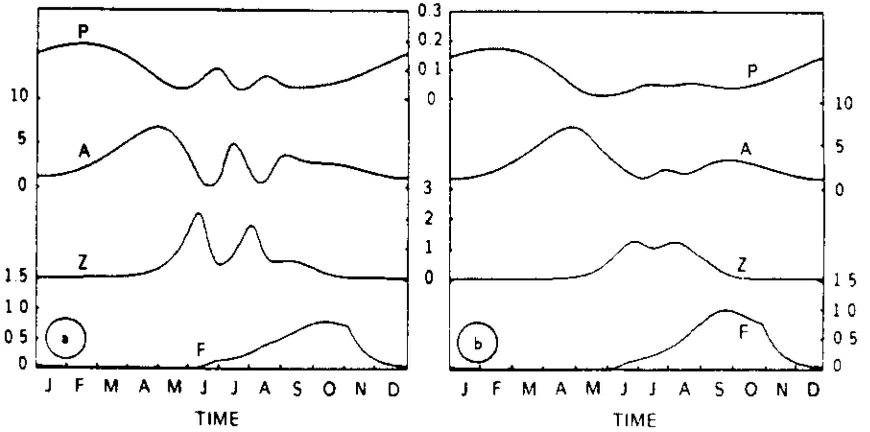


Figure 5

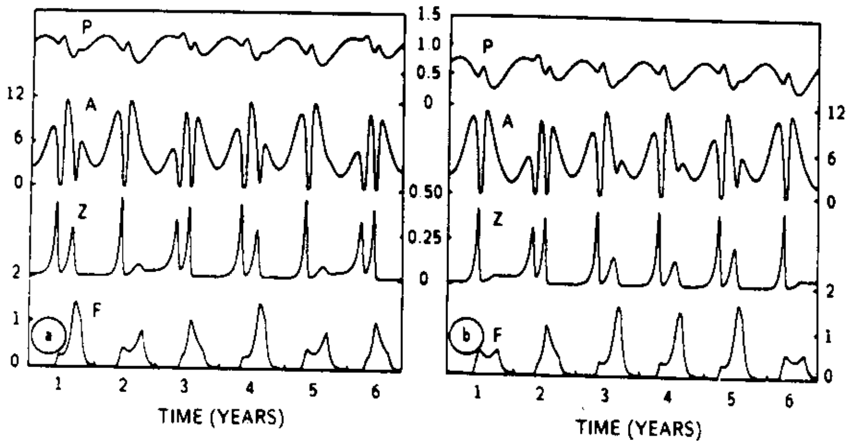


Figure 6

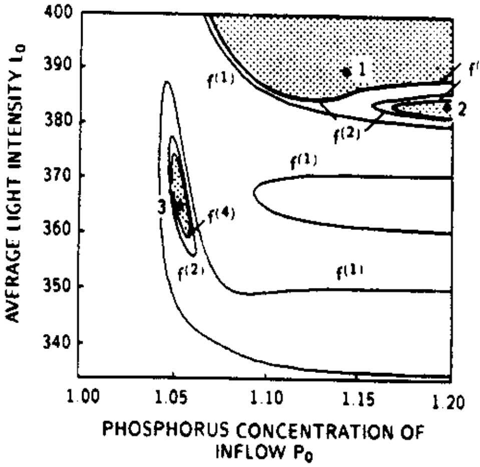
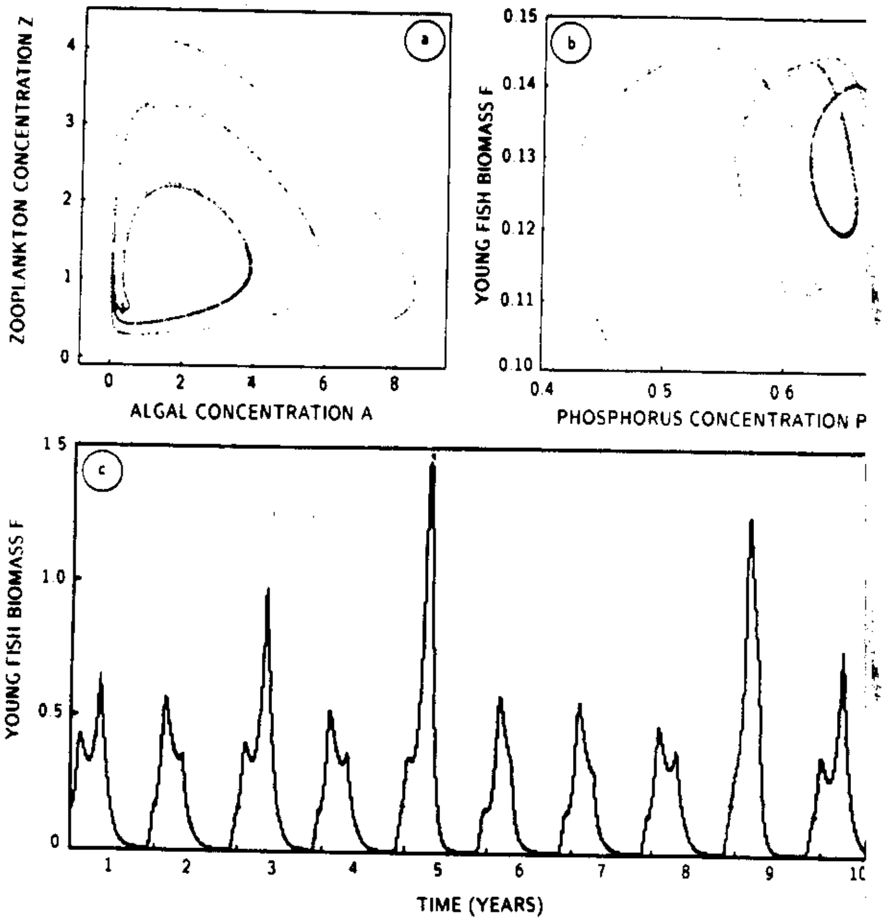


Figure 7



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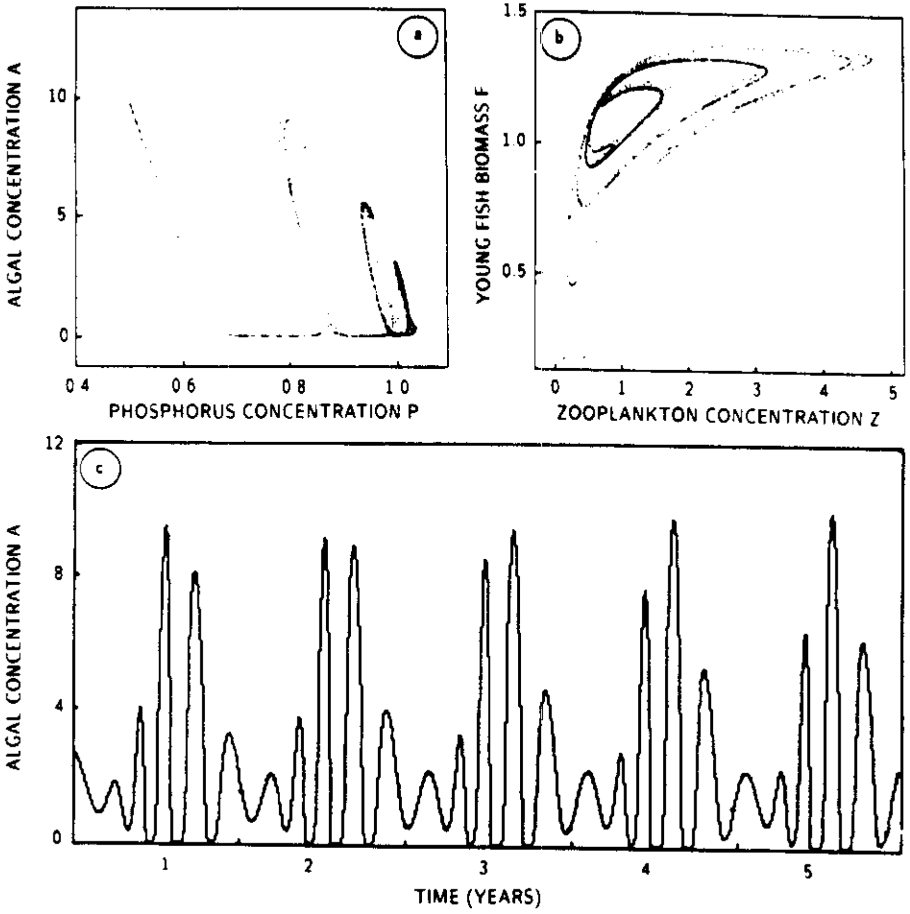


Figure 9

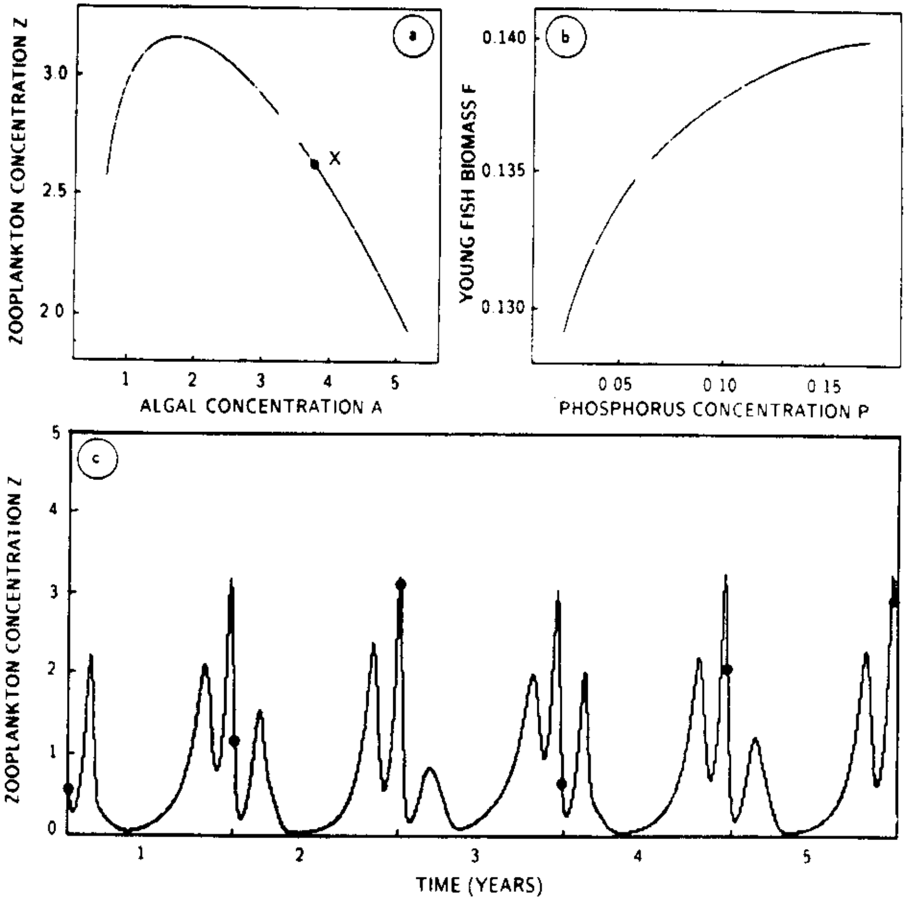


Figure 10

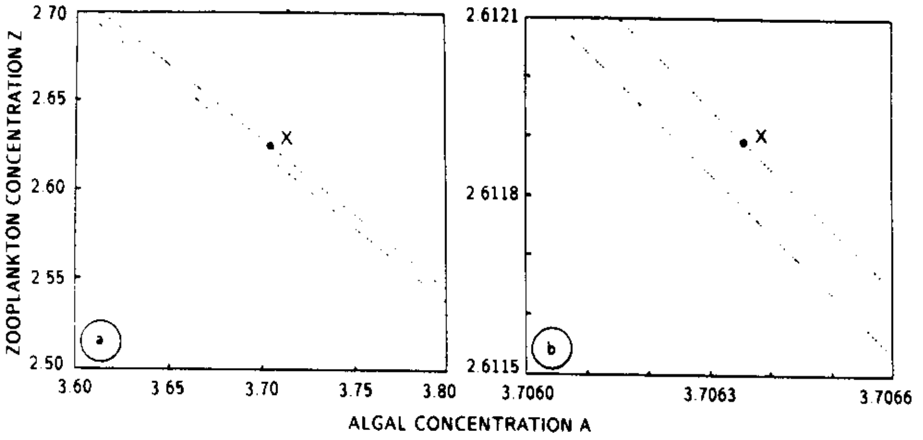


Figure 11

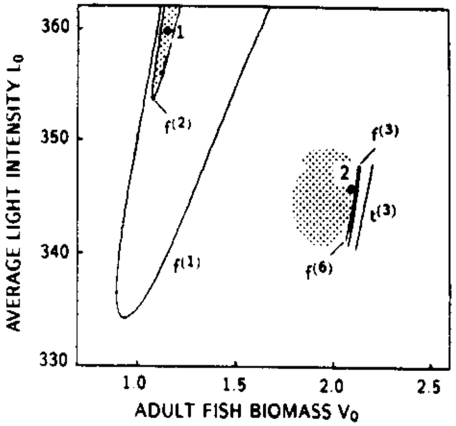
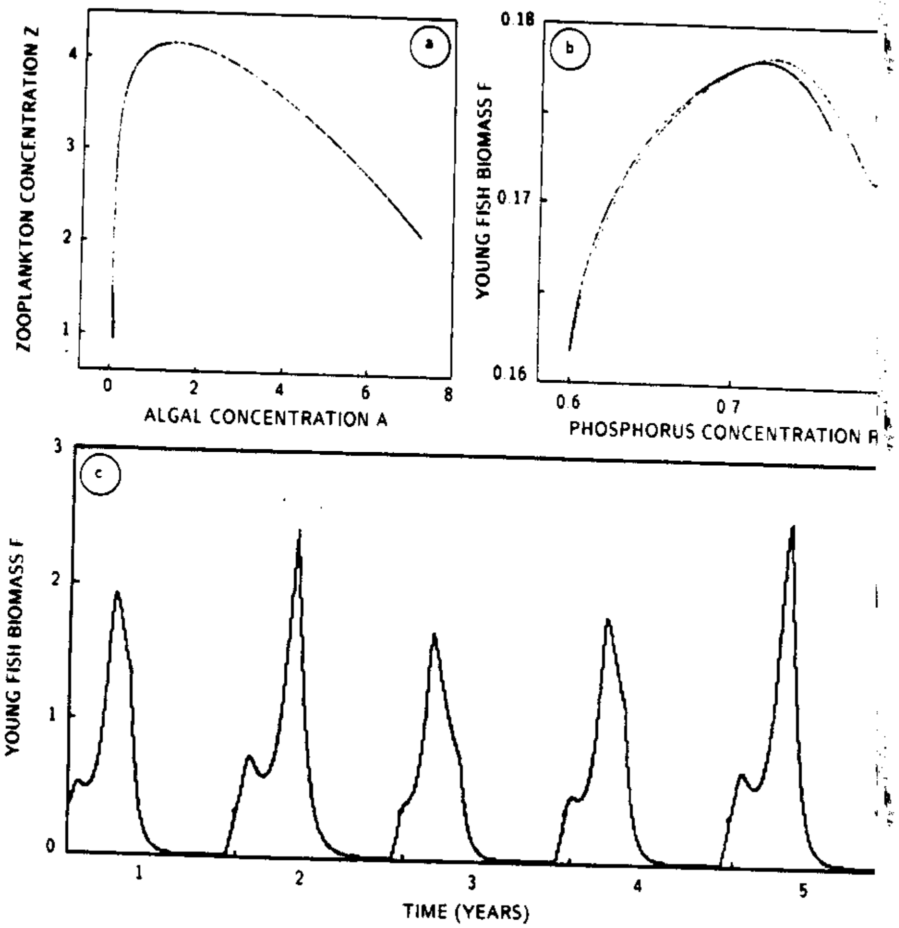


Figure 12



Figur

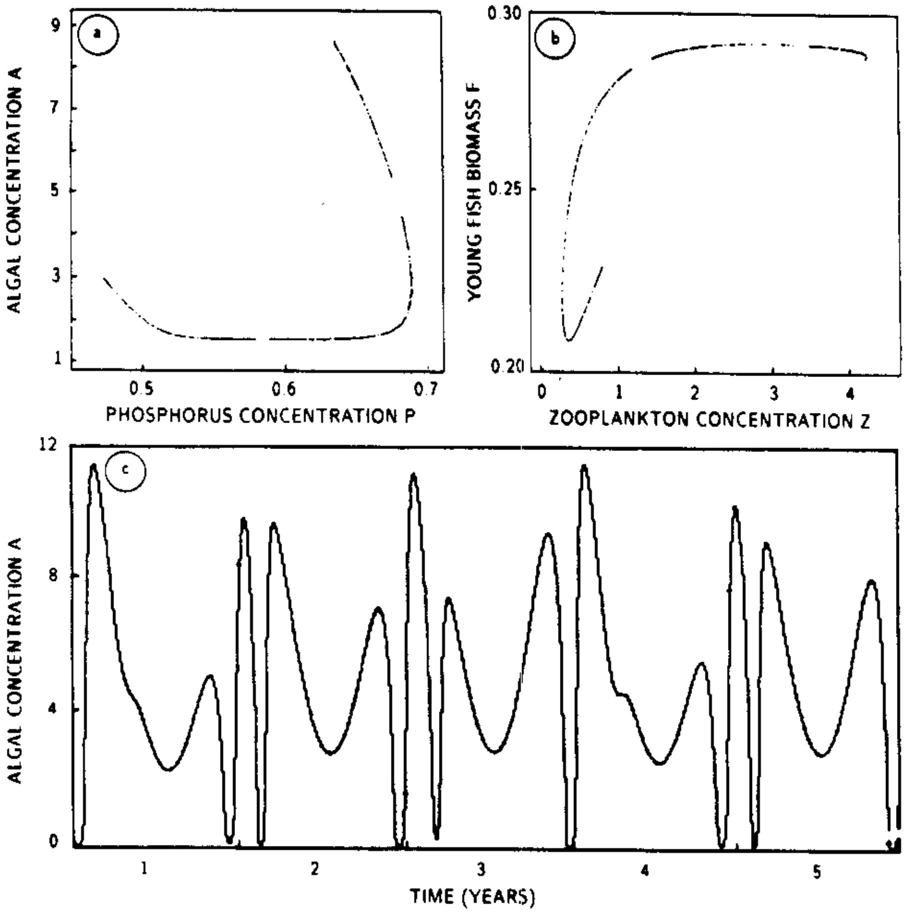

a
ALGAL CONCENTRATION A
9
7
5
3
1
0.5
0.6
0.7
PHOSPHORUS CONCENTRATION P
b
YOUNG FISH BIOMASS F
0.30
0.25
0.20
0
1
2
3
4
ZOOPLANKTON CONCENTRATION Z
c
ALGAL CONCENTRATION A
12
8
4
0
1
2
3
4
5
TIME (YEARS)

Figure 14