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"Simulating Aquatic Systems: A Model of Ecological Processes"

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SIMULATING AQUATIC SYSTEMS: A MODEL OF ECOLOGICAL PROCESSES

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Abstract. Process equations of a deterministic model simulating multi-species plankton dynamics in aquatic ecosystems are discussed. Formulations include micro and macroalgae, benthic macrophytes and zooplankton growth processes, interactions with nutrients and oxygen fluxes, dissolved and particulate organic matter formation and sedimentation.

Results with simulated data are shown to designate model capabilities and different compartments influencing plankton dynamics and growth. Simulations with field data are discussed to evaluate ecological stability of the analyzed system and various impact scenarios.

Introduction

Historical documentation of ecological instability in localized areas of the Italian coasts and lagoons date back to the eighteenth century. In the last few years much effort has been devoted to bridge the gaps of understanding trophic processes, which lead, in some cases, to serious damages to the environment.

Ecological models are one of the most important tools for ecologists involved in impact studies, for their capability to reduce the high grade of complexity of the natural systems. Complexity and inter-relationships in ecosystems are well known to be prominent: uptake of nutrients by vegetal communities, predation rates of predators, microbial degradation of organic matter are some examples. It seemed therefore a priority to define a device able to test the conceptual framework of the research and to center the further measures on the field which the Laboratorio Centrale di Idrobiologia is carrying out in the lagoons of the Pontine areas (this will be discussed later herein).

In this context a cooperation plan was set up with the Department of Biology of the Trieste University, in order to implement a proper software and develop it alongside in the experimental procedures and results.

A very early result of this work was a first simple microcomputer BASIC language program (Hull and Lagonegro 1988) also reported by this journal. The model, called AQUAMOD, has then been consistently implemented in the mathematical formulations while field experiments became more precise (Hull, Lagonegro and Falcucci 1988, and Lagonegro and Hull 1989), and was also translated into FORTRAN programming language.

The latest version, that will be discussed herein, has been developed to be used as a block of subroutines for the dynamics of the ecological components within a more wide circulation model of the treated ecosystem; for which it is still necessary to provide the proper connections between the nutrient fluxes and those of the circulation model. Besides, it can also be satisfactorily used by itself for aquatic systems showing very slow circulation and mixing processes.

Developing the model, suggestions were taken from many different sources (UNESCO 1983, Kremer and Nixon 1978, Di Toro *et al.* 1971, Platt *et al.* 1982) and some parts of our own were added: with the first models AQUAMOD still shows some relations, while the additions were mostly suggested by the applications of the various versions with experimental data.

The first small ecological model was developed (Lagonegro and Hull 1987 Hull, Lagonegro and Puccia 1988, Hull and Lagonegro 1988, Hull, Lagonegro and Falcucci 1988) to test the equations for nutrients and the phyto and zooplanktonic community (zooplankton being purely herbivorous or purely carnivorous, as well as omnivorous). An intermediate version has then been written in FORTRAN, taking into account the oxygen flux, the indirect sediment effect, important in shallow waters, the day-night cycle for light (Lagonegro and Hull 1989). Further experimenting suggested to add the day- night cycle for water temperature, the dead organic matter equation, the whole sediment direct equation, as well as the benthic macrophytes. The novelties of this latest version of the model are so many that persuaded us to prepare this paper with the aim to explain

old and new equations, and to show the model performances with field and simulated data.

One last information concerns the hardware that must be used to run the program. An IBM or compatible microcomputer can perform computations, but each run takes a lot of time, even if the machine is equipped with a mathematical co-processor. For more suitable performances it is better to dispose of some kind of mini computer (*i.e.* micro VAX) compatible with the FORTRAN of the MS-DOS operating system.

Model equations

The general form of the equations is

$$\frac{dX(t)}{dt}=kX(t) \qquad (1)$$

where X(t) represents one of the model variables, such as phytoplankton biomass or nutrient concentrations, etc. With k constant during the time span involved for the simulation, the solution of equation (1) would be quite easy and yield of X(t) at every time would be computed. Unfortunately this is almost never the case and a way around must be found. So we can say that:

$$dX(t) = k\,X(t)\,dt \qquad (2)$$

by assuming that

$$dX(t) = X(t+dt) - X(t)$$

we have

$$X(t+dt) = X(t) + k\,X(t)\,dt = X(t)\,(1 + k\,dt) \qquad (3)$$

the condition k=0 holds when the quantity X(t) is in a stationary state, constant in value.

As just suggested, in systems as those described by the model, the quantity k is generally a complicated function of time and of other variables, such as light, temperature, nutrients and biomasses, both through the forcing function written in the model and through their dependence on the quantity X(t) itself. For example, light and nutrients, at a given point in the water column, strongly depend on the overlying biomass present above, because of transmission and recycling. Besides, in those equations where X(t) stands for biomass, some vital parameters, as grazing and/or preying coefficients, present as parts of k in the equation itself, are described by other equations where X(t) and quantities like X(dt) are also used (*i.e.* equation 4). In these cases non-linearity arises, and makes equation (1) quite difficult, if not impossible, to solve exactly.

The method to compute values of X(t) at all desired times is then the forward step method which fully exploits equation (3). It uses a finite step dt and, given some starting values for variables and parameters, performs iteration on the equation for defined simulation time. At every step the X(t+dt) just computed becomes the X(t) for the successive X(t+dt). This because the time quantum dt is considered 'small' enough to assume that k has a 'constant value' during each iteration, and that the product (k*dt) in any case is small. The method is particularly suitable for digital computers. The implementation must in any case provide some escape mechanism for those cases when the product (k*dt) has value -1. This means indeed that the new value for X(t) will be zero and so the following ones: quite correct if some nutrient is concerned, with the system waiting for some input, quite dangerous for biological entities which generally never disappear completely. The model provides an inner threshold value for biomass concentration which corresponds to undetectability and ensures this survival and which holds 1 mg/m^3. Should a user find this value unproper, he can change it when starting the program.

The choice of dt is sometimes a hard one to make. It can be 'large' if X(t) is thought of as a smooth function, with soft peaks and valleys, that is both increase and decrease of quantities are slow enough to ensure the (k*dt) product to be small. Otherwise it has to be 'small' enough to allow the hope that the computing accuracy will not be affected within the time range of interest, or that important details will not be lost to obviate at very long waitings for computer time. The risk of strong dependence of the results on this approximation can be significantly reduced by some test runs of the model in the time range of interest with carefully chosen different values of dt.

According to our experience, we could choose it from a wide range of values when using the simple BASIC version of the model, with limited internal exchanges; this is not as easy to do when using the more complex FORTRAN version this paper is concerned with. In this case dt has to be small; how small depends on the parameters and on the time the simulation lasts. The shorter the time, the easier will be the choice, because the possible distortions do not modify it enough to allow us to say it behaves like a completely different system. A sound criterion is to use a twentieth or less of the smallest time period of the forcing functions implemented in the model. We used one hour or less, very often 30 minutes only, having found, in testing our samples, that the outcoming yield curves were quite the same, as far as their trend was concerned, for time ranging from a few seconds to one hour, over a year-long simulation. Our model shortest time period is in fact 24 hours, for the day-night cycle of light and temperature.

This suggests that long-term predictions are quite hazardous, except for very simple or very stable ecosystems. In any case, the program includes the possibility to stop the computation, and to change the parameters influencing the equations which describe the internal interactions, so that a more flexible use of the model can be made.

The equations which follow, with the exception of those for macrophytes and sediment organic matter, describe the evolution of the system at a given depth in

the water. If one wants to consider what happens at more points along the same vertical water column axis (that is at more depth values), the model is able to do it, because it also takes into account the shadow effect due to the light absorption along the overlaying layers.

1. Phytoplankton equations

Speaking of phytoplankton equations does not mean that we cannot use them for different species (*i.e.* macroalgal species); they are so diffused in the water that we can sensibly speak of their 'density'.

Density, more precisely nitrogen equivalent density, is the unity homogenizing all the matter fluxes in the model. It will be given in mg/m^3, with the exception of the sediment organic matter, given in mg/m^2.

The equations are

$$\frac{d\,P(i,t)}{dt} = kP(i,t)$$

with

P(i,t): i-th phytospecies mass, described as nitrogen concentration, evolving with time;

i = 1,2, ... ,Np

Np: number of phytospecies in the modelled ecosystem.

The k quantity for phytoplankton is:

$$k = [g(i,t) - R(i) - D(i)] - \sum_{j=1}^{Nz} Z(j,t) * Gr(j,i) * \frac{Tz[T(t)]}{S(j) + Pht(t)} \qquad (4)$$

with

g(i,t): growth function for phytospecies i; it depends on light, nutrients, temperature and is a forcing function in the model.

R(i),D(i): respiration rate and natural mortality rate for the i-th phytospecies. They are given in input to the model.

Z(j,t): j-th zoospecies mass, always as nitrogen concentration, at time t.

j = 1,2, ... ,Nz.

Nz: number of zoospecies in the modelled ecosystem.

Gr(j,i): grazing rate of zoospecies j on phytospecies i. It is the element of a grazing matrix of (Nz*Np) elements, given in input to the model. Thus it is possible to characterize the grazing tastes of the zoospecies; pure carnivores will have a zero value.

S(j): grazing half saturation constant for zoospecies j; it is given in input to the model.

Tz[T(t)]: temperature dependent factor for the efficiency in feeding of all the zoospecies (see zooplankton section).

$Pht(t) = \sum_{i=1}^{Np} P(i,t)$: total phytoplankton mass at time t.

The forcing function g(i,t) can be written as the product of a growth function Gmx(i,t), computed as if the nutrients supply was always adequate, for algal growth and a factor A(i,t), also computed at every step, which is a function of the fractions between availability and needs. This factor is obviously dependent on the nutrients spectrum used by each species and has the value of the minimum fraction for that species, if one of them is less than 1; otherwise it holds 1. So we can write that:

$$g(i,t) = Gmx(i,t) * A(i,t) \qquad (5)$$

with

$$Gmx(i,t) = G_1(i,T) * G_2(i,I) * G_3(i,Nut) \qquad (6)$$

where

$G_1(i,T)$: part dependent on temperature T; dependency on time comes through T, a forcing function.

$G_2(i,I)$: part dependent on light intensity I, also a forcing function of time, through intensity Is on the surface and biomass filtering it through the water at deeper levels.

$G_3(i,nut)$: part dependent on nutrients, based on Liebig's rule. Actual nutrient concentrations and species related half saturation constants are used. The constants are given in input to the model.

Let us see separately each of these functions.

1.1. First we have

$$G_1(i,T) = a * e^{[b(i)*To(i)]} * F(i,T(t),To(i)) \qquad (7)$$

where the first term is maximum growth rate for the species, with

a: daily growth rate at To(i)=0 degrees; a constant in the model. The value of 0.059 is frequently suggested in the literature.

b(i): temperature factor, typical of each species, given as input.

The factor F is an almost shape factor, ranging from near 0 to 1, to modulate the first part of the function, which describes maximum growth rate, with temperature T(t). F is a function also of the optimal temperature for the growth of the i-th species, To(i), such that

$$F(i,T(t),To(i)) = e^{[(T(t)-To(i))/DT]} \quad \text{if } T(t) \le To(i)$$
$$F(i,T(t),To(i)) = e^{[-(((T(t)-To(i))/DT))]^n} \quad \text{if } T(t) > To(i) \qquad (8)$$

The second expression in equation (8) fits the rapidly descending tail exhibited by actual growth curves over optimal temperature, and is strongly influenced by n and DT. The default values for the model are respectively 2 (Gaussian tail) and 4 °C. DT expresses the temperature interval for a 63% decrease, from optimum growth rate, under the maximum-growth temperature and an identical decrease in actual growth rate under the maximum-growth temperature; away from this interval the decrease is faster on the

high temperature side. In any case, the user may change these values, species by species, when modeling for species with wider intervals of suitable temperature.

T(t), the water temperature at the point of interest, is evaluated through three forcing functions, two giving the average temperature and its fluctuation for every day of the year, while the third defines the daily cycle within the fluctuation itself. The first function is:

$$T'(t) = Ta - Td * \cos[0.0172142*(dn+m)] \quad (9)$$

with

Ta: yearly average water temperature in Celsius degrees; an input parameter.

Td: yearly maximum departure for Ta; also an input parameter.

dn: day of the year.

m: a parameter derived from a fit procedure giving also the values of Ta and Td. For data within 40° and 45° N latitudes a value m=-30 has performed well in the model.

The third function has the form

$$Tf(t) = A'(t) * \sin(0.2618*h-1.5708) \quad (10)$$

with

h: hour of day

with daily fluctuation having an amplitude computed about (10) on a yearly basis

$$A'(t)=Dmax/4*(1-\cos(0.0172142*(dn+m))) \quad (11)$$

where Dmax is the maximum daily fluctuation measured per annuum which is given to the model as an input datum. So, the temperature is computed as a sum of the daily value from formula (9) plus the fluctuation from (10). Based on these we have

$$T(t) = T'(t) + Tf(t) \quad (12)$$

1.2. We have also the light dependent factor to be considered, which can have optionally three shapes:

$$G_2(i,I)=(Ia(t,z)/Io(t))*e^{[1-(Ia(t,z)/Io(t))-r]} *(1+r) \quad (13)$$

This is Steele's modified factor, with

r=0.027, a factor taking into account negative growth, being the average light intensity Ia(t,z) less than 1% of the optimal acclimation intensity Io(t). Ia(t,z) is evaluated for the water column at the point considered based on the equation

$$Ia(t,z)=Is(t)*[1-e^{-C(t)*z}]/(C(t)*z) \quad (14)$$

where C(t) is the extinction coefficient and z is the water column depth. The surface light intensity Is(t), in ly/day, is another forcing function, given by the relation

$$Is(t) = Imx(t) * Dl(f,h)$$

where Imx(t), is given by

$$Imx(t)=(1-Rf)*(1-Lw)*[600-340*\cos(6.28*(dn+10)/365)] \quad (15)$$

Rf represents the reflected fraction (we use Rf=0.15), while Lw is the long wave fraction (we use Lw=0.55). These values, taken from literature sources, have performed well in the model. dn is the day of the year, counting 365 days. The formula gives correct maximum intensities at Italian latitudes (for others, see Hull and Lagonegro 1988). The daily cycle of day light and night is simulated by another forcing function, Dl(f,h),

$$Dl(f,h) = 0 \quad \text{if } h<d \text{ or } h>s$$
$$Dl(f,h) = abs[1+\sin(h/K+F)] \quad \text{if } d \le h \le s \quad (16)$$

with

$d=13-0.5*[24*f(t)+3]$ (time of dawn)

$s=13+0.5*[24*f(t)+3]$ (time of sunset)

h=hour in the day

f(t) is the photoperiod evaluated by

$$f(t)=0.5-0.125*\cos[6.283*(dn+10)/365] \quad (17)$$

$$K=\frac{6.283}{f(t)*24+3}$$

$$F=7.8537-\frac{6.283*13}{f(t)*24+3} \quad (18)$$

Dl(f,h) has been deduced from experimental data and describes the profile of light intensity at Italy's mean latitude.

$$Io(t)=0.7*I1(dn,z)+0.2*I2(dn-1,z)+.1*I3(dn-2) \quad (19)$$

where

$$I1(dn,z)=Is(t=dn)*e^{-C(t)*z} \quad (20)$$

We use z=1 m, as suggested by Kremer and Nixon in their book (1978). I2 and I3 are the same quantities computed respectively one and two days prior to I1. Io(t) must be given a starting value for which we chose 40 ly/day.

Extinction coefficient C(t) can be computed optionally by two expressions:

$$C(t)=0.04+0.054*cha(t)^{0.667}+0.0088*cha(t) \quad \text{(Riley 1956)}$$
$$C(t)=0.16+0.039*Pht(t)^{0.667}+0.0053*Pht(t) \quad \text{(Walsh 1975)} \quad (21)$$

with cha=0.476*Pht(t).

The other two light factors are

$$G_2(i,I)=\frac{2.718*[e^{[-(Ia(t)/Io(t))*e^{-C(t)*z}]}-e^{-(Ia(t)/Io(t))}]}{C(t)*z} \quad (22)$$

and

$$G_2(i,I)=[1-e^{a*Ia(t)/p}]*e^{-b*Ia(t)/p} \quad (23)$$

G_2 computed with equation (22) is the factor in Di Toro *et al.* (1971), and G_2 computed as in (23) is that given in Platt *et al.* (1982). Most quantities have already been explained. The light intensity is expressed in Watt/m^2 and costants a, b, p wich are computed by averaging alpha, beta and P parameters given in Platt's table, have values 0.05, 0.00147 and 0.85 respectively.

1.3. The nutrient dependent factor is taken from the kinetics of all considered nutrients, that is the kinetics for ammonia and nitric nitrogen, orthophosphate phos-

phorus, reactive silicon and oxygen, following Liebig's law, according to which nutrients are utilized in accordance with minimum concentration levels. The general equation is

$$G_x(i,nut)=\frac{[nut.conc.]}{[0.5\ sat.conc.]+[nut.conc.]} \quad (24)$$

The nutrient concentrations are obviously a function of time, directly, or indirectly, through dependence on time by the consumer species. Details will be shown later in the paper.

2. *Macrophytes equation*

A single entity is considered, representing all benthic plant species. The equation is

$$\frac{dM(t)}{dt}=kM(t)$$

and k holds at

$$k=Gm*\frac{Tb(t)}{Tm}*e^{[1-(Tb(t)/Tm)]}*\frac{Ib(t)}{Im+Ib(t)}*fb(t)-Km \quad (25)$$

for all days of the year before a specified one. After this, we have k=0 and 85% of the macrophytes biomass becomes part of the detrital pool. The remaining 15% represents the starting value for a new simulated year. The quantities in (25) are:

Gm: maximum daily growth rate of macrophytes.

Tb(t): bottom temperature, computed in the some equation at depth z (formula (9)), but with different values for parameters Ta and Td, given as input in the model.

Tm: temperature for optimal growth of macrophytes.

Ib(t): light intensity on the bottom, computed from Is(t), taking into account absorption in the water column according to equation (14) with bottom depth z.

Im: light intensity for half-maximum growth of macrophytes.

fb(t): growth limiting factor, depending on nutrient supply compared with the macrophytes needs from 0 to 1 as parameter fo(t) values in equation (4).

Km: daily fraction of macrophytes biomass added to the detrital pool before the threshold day.

Gm, Tm, Im and Km are part of the data input in the model.

3. *Zooplankton equations*

The equations have the general form

$$\frac{dZ(j,t)}{dt}=kZ(j,t)*Zo(j,t) \quad (26)$$

where

Z(j,t): j-th zoospecies biomass at time t.

Zo(j,t): j-th zoospecies time dependent survival factor; it is computed by a kinetic equation

$$Zo(j,t)=\frac{[O_2\ conc.\ at\ t]}{Szo(j)+[O_2\ conc.\ at\ t]} \quad (27)$$

with

Szo(j): O_2 concentration for 50% survival of the j-th species.

For k we have

$$k=0.8*[Fg(j,t)+Fp(j,t)-Lp(j,t)]-D'(j)-R'(j,T) \quad (28)$$

where

$$Fg(j,t)=\sum_{i=1}^{Np}Gr(j,i)*\frac{P(i,t)*Tz(T(t))}{S(j)+Pht(t)} \quad (29)$$

$$Fp(j,t)=\sum_{m=1}^{Nz}Pr(j,m)*\frac{Z(m,t)*Tz(T(t))}{S'(j)+Zot(t)} \quad (30)$$

$$Lp(j,t)=\sum_{n=1}^{Nz}Pr(n,j)*\frac{Z(n,t)*Tz(T(t))}{S'(n)+Zot(t)} \quad (31)$$

where, besides the already defined terms,

Pr(j,m): predation capability of zoospecies j on zoospecies m, an element in a square matrix given as input in the model.

S'(j): predation half-saturation constant for species j, given as input.

Zot(t): total zoospecies biomass, computed by

$$Zot(t)=\sum_{j=1}^{Nz}Z(j,t)$$

D'(j): natural mortality rate for zoospecies j, an input datum

$$R'(j,T)=Ro*e^{Kz*T(t)} \quad (32)$$

the respiration rate of zoospecies j, depending on temperature. Ro(j) and kz are input data.

The sums in k express the variation in biomass for the zoospecies j. The first one (29) represents the contribution from grazing, already seen in formula (4). The second one (30) is the contribution from predation on other species. The third (31) is the loss from being a prey to other zoospecies. If a species practices cannibalism, the term appears as input on the second term and as output in the third and thus a balance is maintained. The coefficient 0.8 represents suggestion (Kremer in UNESCO, 1983) that only 80% of the ingested food is assimilated, while the remaining 20% goes to the organic dead matter flux.

4. *Dissolved and dead particulate organic matter equation*

The equation takes into account the total organic matter of dissolved and particulate origin (DOM and POM) from the water column and from macrophytes on the day leaves fall, and is:

$$\frac{dDm(t)}{dt}=\sum_{i=1}^{Np}Ph(i,t)*D(i)+\sum_{j=1}^{Nz}Z(j,t)*[D'(j)+0.2*If(j,t)]-$$

$$-Dm(t)*[\frac{Vs}{z}+Dr(T(t))]+Km*\frac{M(t)}{z} \quad (33)$$

where

Dm(t): dead organic matter at time t.

If(j,t) = Fg(j,t)+Fp(j,t)-Lp(j,t)

Vs: sinking rate (in m/day), an input datum in the model.

z': bottom depth, an input datum.

$$Dr(T(t)) = 0.5 * e^{0.09*T(t)} \quad (34)$$

The sinking term describes what is lost from depth z; matter from above enters depth z and sinks further down soon after, thus adding nothing to the balance. The exponential term in (34) is the decomposition rate of dead organic matter dependent principally on temperature. The numerical terms were obtained from various reports (UNESCO 1983). The last term in formula (33) is the average increase of dead organic matter in the water column produced by the macrophytes at bottom level and diffusing through the water column. The first sum is the dead organic matter from dead of phytospecies. The second sum thus comes from dead zoospecies. Fecal pellets of zooplankton are not included since these are thought to be negligible.

5. Sediment equation

The sedimented organic matter is due to sinking processes of dead organic matter from above and from macrophytes on the bottom. The last contribute is indirect, with its dead matter, and direct, with the 85% loss of biomass to the detritus pool after a certain threshold day, which is an input datum in the model (UNESCO, 1983). The equation is

$$\frac{dSom(t)}{dt} = -Som(t)*Sd*e^{Sk*Tb(t)} + \sum_{j=1}^{Nd} a(j)*Dm(j,t)*\frac{Vs}{z(j)} \quad (35)$$

where

Som(t): sedimented organic matter on the bottom at time t.

Sd: decomposition rate of sediment at 0 °C.

Sk:dependence of decomposition rate at the bottom temperature.

Nd: number of points along the water column axis where the model equations have been engaged. In our sample it is set to 1. The order is from the surface towards bottom.

Dm(j,t): dead organic matter as in equation (33); here j indicates the point for which it has been computed.

z(j): depth of j-th point

Vs: sinking speed as already defined.

a(j) = 0 if t < t(j) = [z' - z(j)] / Vs

= 1 if t > t(j)

This coefficient multiplies the contribution coming by sinking from the j-th point above. t(j) is the time the sinking dead organic matter needs to reach the bottom starting from depth z(j).

6. Nutrient equations

We consider fluxes of nitrogen (both ammoniacal and nitric) phosphorus, silicon and oxygen, treated as nitrogen equivalent fluxes by means of parameters, characteristic of each plant species, specifying the ratio of each nutrient to nitrogen in the simulated species. These parameters can be edited by the user of the model at each break time, if they are provided when the simulation is launched.

A group of threshold levels is provided to the model which make nutrient concentrations unable to reach unrealistically high values. The difference in excess is considered to be lost to some invisible pool which belongs to the external environment. This strategy should be unnecessary if the model could be coupled inside a wider network program with the hydrodynamic circulation compartments. The thresholds may be chosen by the user when the simulation program is run: this is to make them more adherent to particular known environmental situations.

6.1. Nitrogen equation. The concentration of the nitrogen pool is, below the corresponding threshold (over which the derivative is obviously equal to zero):

$$\frac{dNit(t)}{dt} = Nei(t) - \frac{M(t)}{z'}*Am(t) - \sum_{i=1}^{Np} g(i,t)*P(i,t) +$$

$$+\left[\sum_{i=1}^{Np} R(i)*P(i,t) + \sum_{j=1}^{Nz} R'(j,t)*Z(j,t)\right] -$$

$$- [Nit(t)*0.03*e^{0.063*T(t)} + Dm(t)*0.5*e^{0.069*T(t)} +$$

$$+\frac{Som(t)}{z'}+*Sd*e^{Sk*Tb(t)}]*fo(t) \quad (36)$$

where

Nit(t): nitrogen concentration at time t (in mg/m^3)

Nei(t): external input of nitrogen, if any is involved.

Am(t): growth factor for the macrophytes; which holds:

Am(t) = k - Km as from equation (25)

fo(t): that is a time dependent factor which defines the ratio between available oxygen supply and uptake needs; it can range between 0 and 1; when the level value matches 1 it means that supply exceeds uptake.

The first term refers to the uptake of the macrophytes, at the depth of which the equation is computed, while the first sum refers to the uptake that concerns to all the phytoplanktonic species. In the square bracket the sum of the respiratory loss of phytospecies and zoospecies is first computed and it is added to the nitrogen pool, then the loss for oxidation of ammonia, finally the terms for the decomposition to ammonia of the dead and sediment organic matter. These processes are dependent on the oxygen availability, so the related factor multiplies all these transformation terms.

The numeric terms for this equation were found in literature (e.g., UNESCO report, etc.); if a user can acquire them from field experiments, the new values can be edited in the computer source program.

Nitric and ammonia nitrogen are considered to be the same chemical species; as a matter of fact, over a given threshold it is exactly so for the simulation performances, and all the nitrogen uptake is taken from ammonia. Under this given level, the nitrate shares the consumption proportionally to the respective concentrations. Finally, if ammonia becomes completely exhausted, nitrate tends to satisfy all the phytospecies needs of nitrogen. This treshold level is an input parameter that must be given to the simulation program.

Nitrate nitrogen has also an independent equation that considers a possible external input and the contributions due to all the processes of oxidation of ammonia. This concentration level is lowered only in the case ammonia supply is insufficient for vegetal forms uptake, in any case it cannot go over its upper threshold value discussed above.

6.2. Phosphorus equation. This equation is a little simpler than that for nitrogen. It is, under the corresponding threshold:

$$\frac{dPho(t)}{dt}=Pei(t)-[\frac{M(t)}{z'}*Am(t)]*MPN-$$

$$-\sum_{i=1}^{Np}[g(i,t)*P(i,t)]*PN(i)+$$

$$+[\sum_{i=1}^{Np}R(i)*P(i,t)+\sum_{j=1}^{Nz}R'(j)*Z(j,t)]*DPN+ \qquad (37)$$

$$+[Dm(t)*0.5*e^{0.069*T(t)}+Som\frac{(t)}{z'}*Sd*e^{Sk*Tb(t)}]*fo(t)*DPN$$

where

Pho(t): phosphorus concentration at time t, in mg/m^3.

Pei(t): phosphorus external input.

MPN: macrophytes phosphorus to nitrogen ratio. It comes from an input parameter to the model which can be edited at each break time, if any is provided. If given as zero, the plants do not consume phosphorus as a nutrient, otherwise they take MPN parts of phosphorus for each nitrogen assumed part.

PN(i): the same for the i-th phytospecies.

DPN: ratio of phosphorus to nitrogen in the detritus decomposition. This quantity is computed.

The last two rows in the equation refer to recycled quantities resulting from respiration, both from phytospecies and zoospecies, as well as that coming from decomposition of sediment organic matter.

6.3. Silicon equation. For what regards the recycle of detritus, we assume (UNESCO 1983) that all the reusable silicon comes from sediment decomposition. We have then:

$$\frac{dSi(t)}{dt}=Sei(t)-[\frac{M(t)}{z'}*Am(t)]*MSN- \qquad (38)$$

$$-\sum_{i=1}^{Np}[g(i,t)*P(i,t)]*SN(i)+\frac{Som(t)}{z'}+*Sd*e^{Sk*Tb(t)}*fo(t)*DSN$$

where

Si(t): silicon concentration at time t, in mg/m^3.

Sei(t): silicon from possible external input.

MSN: silicon to nitrogen ratio for macrophytes. Holds true the same that has been said for MPN.

SN(i): the same as for the i-th phytospecies.

DSN: sediment ratio between silicon and nitrogen. It is a computed parameter.

6.4. Oxygen equation. The equation for oxygen is quite complicated because of the very many pathways followed by this chemical element in most of the simulated processes. It is:

$$\frac{dO_2}{dt}=Oei(t)-[\frac{M(t)}{z'}*Am(t)]*MO_2N-$$

$$-\sum_{i=1}^{Np}[g(i,t)*P(i,t)]*O_2N(i)+\frac{M(t)}{z'}*Am(t)*OFM+$$

$$+\sum_{i=1}^{Np}[g(i,t)-R(i)-D(i)]*P(i,t)*OF(i)- \qquad (39)$$

$$-[\sum_{i=1}^{Np}R(i)*P(i,t)*OCP(i)+\sum_{j=1}^{Nz}R'(j)*Z(j,t)*OCZ(j)]-$$

$$-[Nit(t)*0.03*e^{0.063*T(t)}]*fo(t)*OCN-$$

$$-[Dm(t)*0.5*e^{0.069*T(t)}+\frac{Som(t)}{z'}*Sd*e^{Sk*Tb(t)}]*fo(t)*OCS$$

where

$O_2(t)$: oxygen concentration at time t, in mg/m^3.

Oei(t): external possible input of oxygen.

MO_2N: oxygen ratio to nitrogen for macrophytes.

$O_2N(i)$: the same for the i-th phytospecies.

OFM: oxygen generated by macrophytes per unit mass growth.

OF(i): the same for the i-th phytospecies.

OCP(i): oxygen consumed per unit mass in respiration by the i-th phytospecies.

OCZ(j): the same for the j-th zoospecies.

OCN: oxygen consumed per unit mass of oxidized ammonia.

OCS: oxygen consumed per unit mass of decomposed sediment organic matter.

The first row in equation (39) includes, besides a possible external input, the uptake terms. The second one contains the oxygen production terms, the third the consumption through respiration, the following the term for ammonia oxidation, the last the terms for or-

ganic matter decomposition, both for floating and sediment. In all nutrient equations the sediment term is divided by the depth. This is because what is affected is the concentration at a given depth and the sediment contribution therefore has to be diluted through the whole water column.

6.5. External inputs. The model has been conceived to perform computations at various depths but on a single point, where the nutrients are carried in somehow. So the model has to be considered as a part of a wider one with hydrodynamics in a separate package. In any case it had to be validated, and this has been done supposing that there are circumstances when the circulation is slow and regular. Also that the nutrients can be found homogeneously dispersed in the volume of water around the point chosen for simulations, which is an environmental situation often found in shallow water coastal lagoons. The nutrients can be supplied to the aquatic system following three different strategies:

a) they are considered to be residuals left after all vegetal form uptakes have been completely satisfied, as if sampling, for the laboratory analyses, had taken place in late afternoon (*i.e.* at sunset); in this case no limit comes to growth from nutrients and it results the maximum possible under the light and temperature conditions for the given set of other parameters of each species. In this situation the model computes the vegetal form uptakes for the output to the user or for a plot program.

b) they are the concentrations before vegetal form uptakes take their share or consume them completely, this depending on availability, as if sampling had taken place early in the morning. In this case the model computes the actual residuals for the output or for the plot programs.

c) they are daily input rates in a certain period of time. Values for starting concentration conditions are given for all of them at the beginning, then the system evolves with the simulations considering the nutrients incoming at a rate that has to be given as an input to the model. The residuals are given this time as output for printout or plot.

In any of these cases, except in the first where it is useless, changes of the structural parameter values at pre-set break times can be done in order to allow the user to simulate and study possible sudden modifications in the system's behaviour. The first approach can be used in all those simulations where nutrients availability is never thought to be limiting, or to anticipate needs for known phytospecies biomass.

Testing the model

To run the simulation model it is necessary to prepare an input file that must include all parameters and constants for computations. The following shows an input file sample built to put evidence on different performances of the model and how to prepare it with an 'ad hoc' program named AQINPUT10. The input file is in ASCII code, and includes, on different rows, the sequence of data used in simulations.

```
 1)    3     3
 2)    1   1.000         12   1.000
 3)    1
 4)    1
 5)PLO6Y1H
 6)    0
 7)  40.00
 8)    4.000
 9)    3
10)   -30.00
11)    1     1
12)   240.
13)   2190.
15)   4.000        2.000        1.300        2000.
16)   5.000
17)   1.000
18)   .1
19)   .5000E-01    .1000        21.00        .5000E-01
20)   4.000        .5000        .0000        2000.
21)   5.000
22)   0.000
23)   .1
24)   .5000E-01    .1000        .00         .6000E-01
25)   .1000        .5000E-01    .0000         2000.
26)   5.000
```

```
27)  0.000
28)  .1
29)  10.00       .1000E-03  .1000    .4000E-01     0.000
30)  .3000E-01
31)  .3000E-01
32)  .4000E-01
33)  .0000
34)  .0000
35)  .0000
36)  11.00       5.000      .1000    .4000E-01     0.000
37)  .0000
38)  .0000
39)  .4000E-01
40)  .2000E-01
41)  .0000
42)  .2000E-01
43)   6.000      14.00      .1500     .4000E-01    0.000
44)  .0000
45)  .0000
46)  .5000E-01
47)  .3000E-01
48)  .3000E-01
49)  .0500E-01
50)  .3000E-01   .6900E-01   15.    6.    .3
51)  .5000
52)  18.90       8.800      3.00
53)  80.00
54)  40.00
55)  25.00
56)  25.00
57)  12.00
58)  5.000
59)  10.
60)  14.00      113.0      294.0      100.0      1330. 7500.
61)  59.00       90.0       99.0      100.0      991.0 7000.
62)  87.00       95.0       73.0       92.0      990.0 6000.
63)  116.0       94.0       54.0       98.0      995.0 5500.
64)  164.0       94.0       68.0       95.0      995.0 9800.
65)  179.0       94.0       91.0       99.6      994.0 9000.
66)  204.0       90.0      100.0       94.0      992.0 5500.
67)  225.0       99.0       72.3       97.7      994.8 7500.
68)  254.0       95.0       72.5       92.4      990.0 10000.
69)  277.0       92.0       88.0       96.0      994.0 9000.
70)  337.0       97.8       72.5       92.9      996.0 11298.
71)  364.0       91.0      108.0      103.0      994.0 11199.
72)  5.      50.
73)  20.   0.102   0.016   270.   3.    0.   0.   16.02 135.
```

Sample run with simulated data

The input file data displayed above has been used to test the model in order to display its performances on a long- time run, and also to verify its consistency and stability. A similar test, but with the simulations ending after one year, has also been run to test the use of different integration time steps, so as to check the effects of the different values on the structure of the simulated ecosystem and the relative relevance of the yield curves for phytospecies and zoospecies.

Figures referring to these simulations have been produced using two computer programs written in BASIC language: AQUAPLOT and STRAPLOT. The first has been used to plot the yield curves of the biological variables and some important chemical or physical parameters as functions of time. The second has been used to plot variables in pairs, that is one

against another, to check for some trend correspondence between them, or to plot a variable against itself, but with the abscissa value in a given step being the ordinate value in the previous step. This technique is useful to mark the existence of repeating behavioural paths, which could represent some kind of 'state' for the plotted variable in the simulated ecosystem evolution. BASIC language for these programs has been chosen to exploit the simple and easily available graphics of any personal computer operating under MS-DOS.

Figures 1 - 3 show some curves for dt=30 minutes (a), dt=15 minutes (b) and dt=3 minutes (c). The yields of the three phytospecies considered in the sample are shown in Figure 1. In Figure 2 we have only that of the third zoospecies. This is because the curves of the other two, behaving similarly to the first, would have made the plot quite unclear and are therefore not reported.

Figure 3 shows the curve of the residual oxygen concentrations and the yield of the sediment organic matter obtained with the three integration time steps. The flat part of the oxygen curve means that the element has reached its concentration of saturation, and we can suppose that production and external input matched, or surpassed, consumption. Only close to the sediment production peak, in the warm months of the year, a dip in the oxygen curve is remarkable, due to the biochemical decomposition of the sediment, this process is also exponentially dependent on temperature. A similar effect is not remarkable in the last, cold, part of the year, even if the sediment yield is far larger, this because the temperature is low, and also since the mineralization rate and the sediment pile-up are severe.

This behaviour for oxygen is not evident at dt=3 minutes, probably because the phytospecies yield during the warm season, making up for the bigger share of sediment, is relatively low and available oxygen is enough for all processes requiring it.

It can be said that the choice of dt is not influential if the general structure of the yield curves only is concerned, but it becomes vital if a phenomenon like oxygen depletion actually occurs during the warm months. In this case there is evidence that the shortest dt integration time step must be chosen, at least during the critical months, using the break time system, provided in the model's program. It is also obvious that the phytospecies parameters must be adjusted, at least for those blooming during the warm season.

Similar considerations can be made for the zoospecies yields: their general structure remains stable out relative intensity changes must be expected. If the change appears to be of some importance, a trimming must be made on the zoospecies parameters.

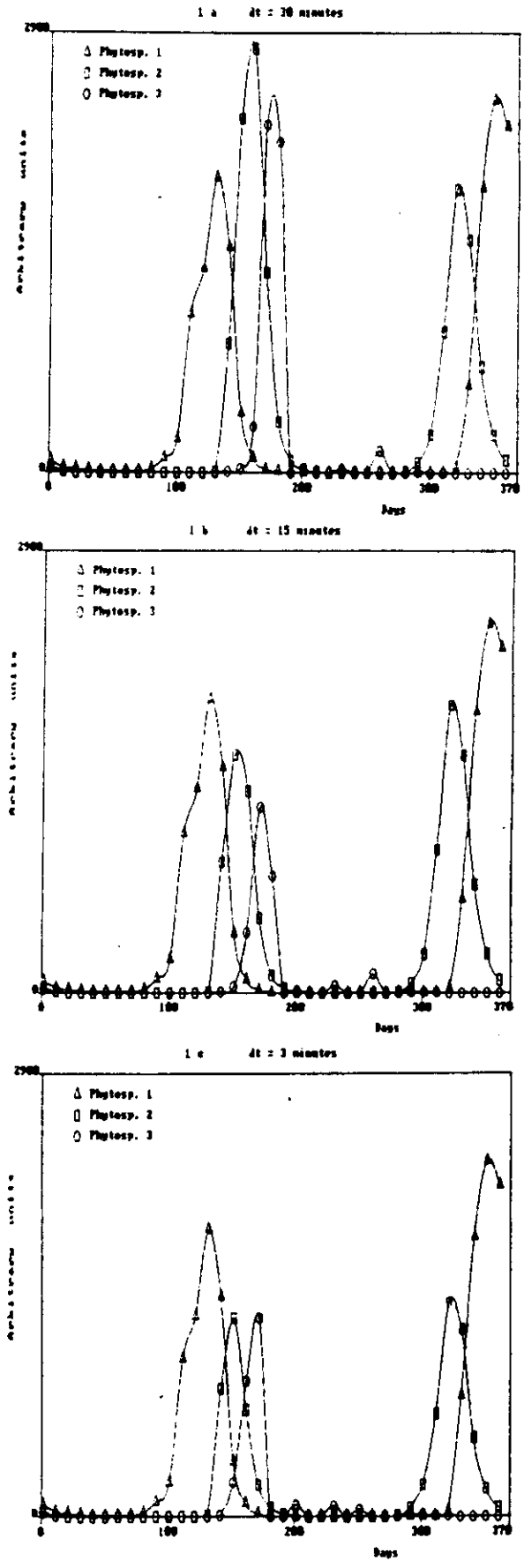

Figure 1. Simulated phytoplankton yields at different integration times.

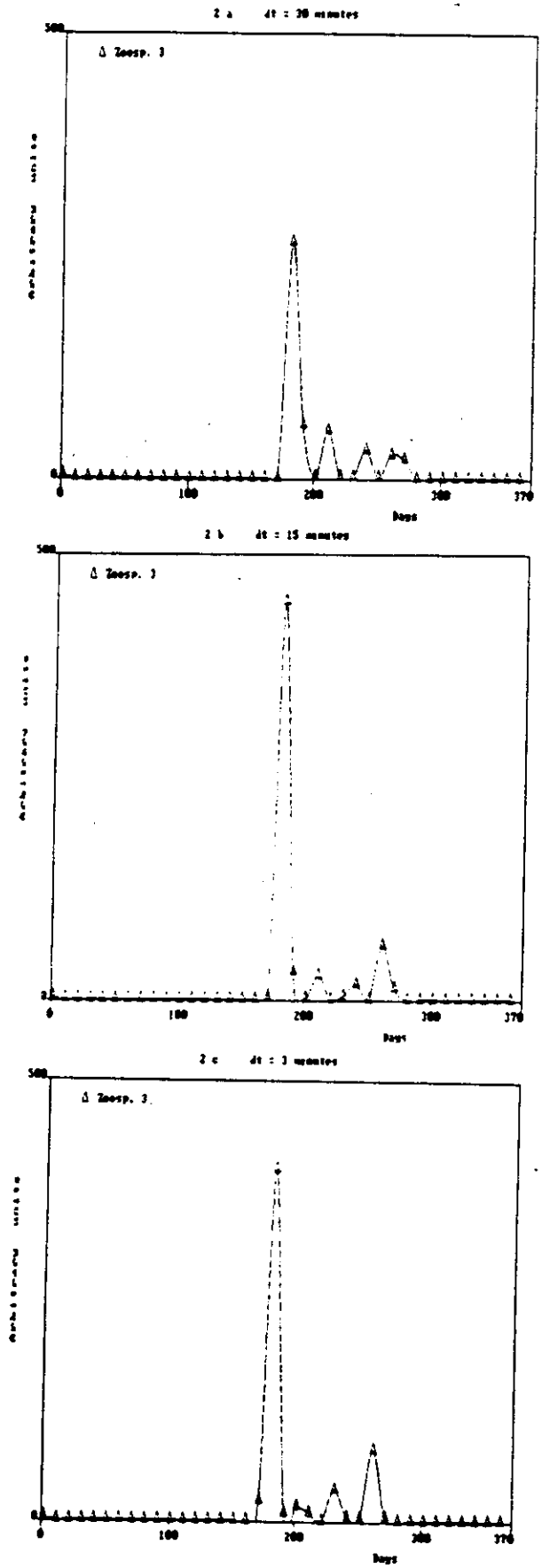

Figure 2. Simulated 3rd zoospecies yields at different integration times.

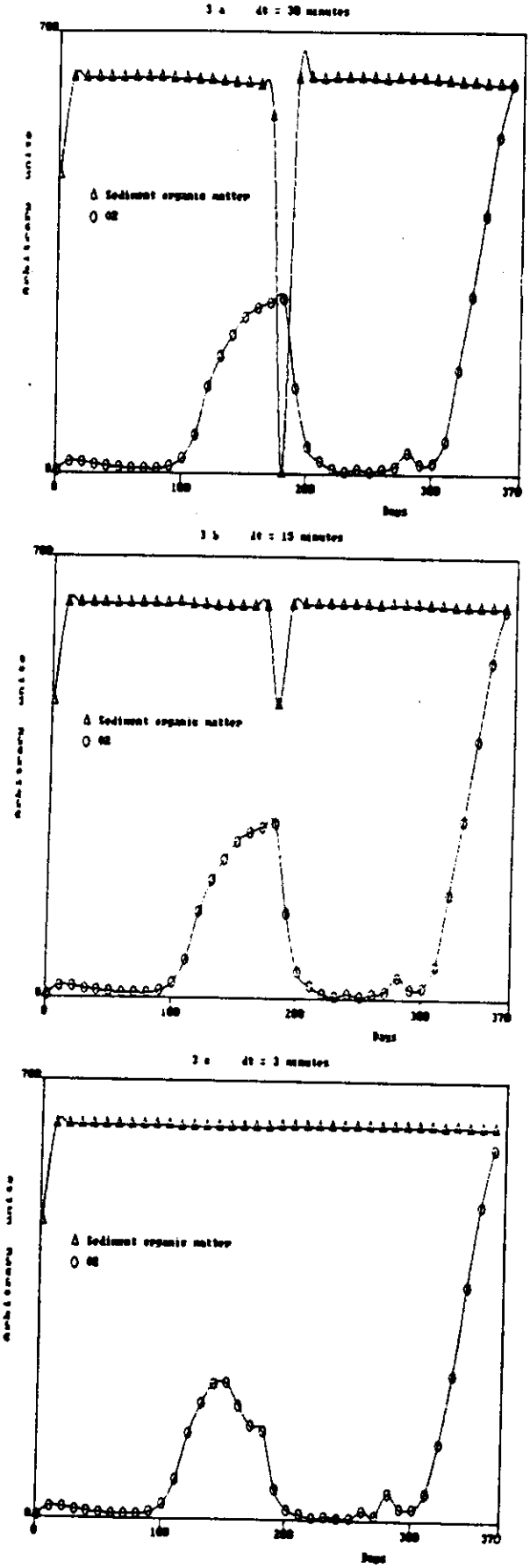

Figure 3. Simulated oxygen and standing crop of sediment organic matter at different integration times.

Two test runs, corresponding to dt=2 hours and dt=1 hour, displayed a performance very near to that for dt=30 minutes, so only this last one has been reported.

Figure 4 shows two curves, the first (a) describes the residual concentration pattern of ammonia in the water, the second (b) that of the nitrate. The deep holes below saturation concentration correspond to the two blooming periods for the phytospecies. The strongest uptake is when all three phytospecies are blooming, that is in the warm season. Similar curves can be obtained for phosphorus and silicon, even if these elements are not consumed at the same rate of

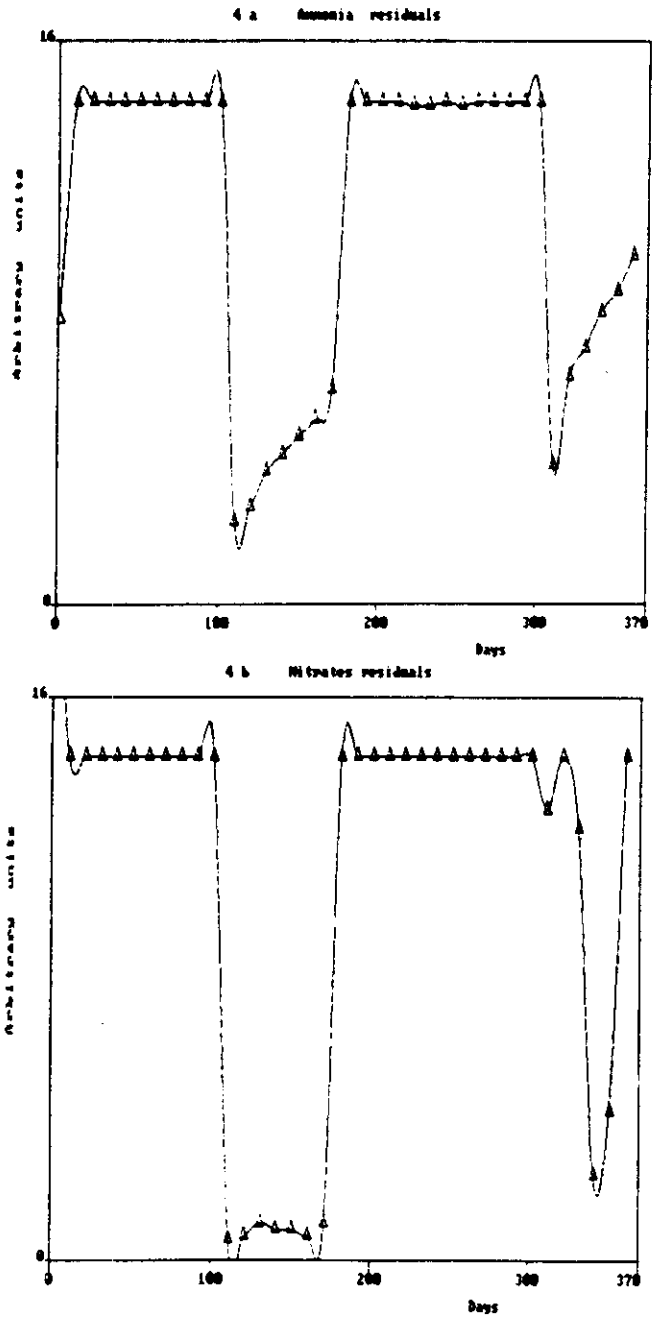

Figure 4. Residual concentrations of nitrogen forms.

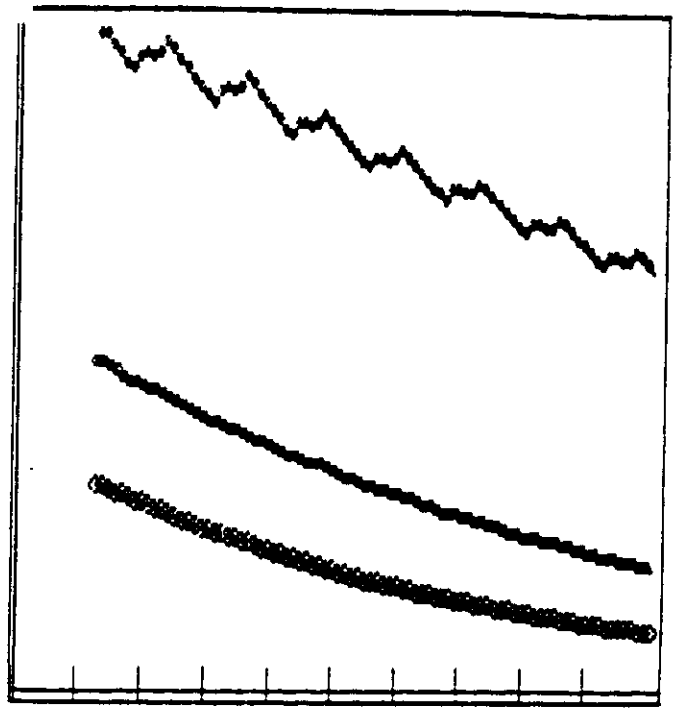

Figure 5. Simulated phytoplankton yields showing day-night cycle for 1st phytospecies.

nitrogen, and this is due to their relative consumption ratios, given as input values for all the species.

Figure 5 reports, amplified, the first 20 days of phytospecies yield curves. The curves clearly show the day-night cycle, especially visible in the curve of the first phytospecies, with its ups and downs.

The following figures are plots of the simulations based on the sample already discussed which ends after a cycle of six years. The purpose of this simulation was not to make forecasts for such a long time, but to test the internal consistency, within the framework of the mathematical relations describing the processes simulated by the model, of an ecosystem having parameter values same as those of the sample described above. If results performed by the model do not crash before simulations ends, it can be said that "ecosystem" is "stable" and "consistent". Otherwise the parameters must be changed, even if they give a reasonable simulation in a short period of time, just after the starting point.

It must be clear that if some parameters have to be changed, just a little change in the others must be expected to accomodate the effect of feedbacks, as a new ecosystem is going to be investigated and a revision of the whole parameters set is clearly advisable. In any case the model takes into account the possibility to change the parameters at some break times, when the user feels the system is going rapidly into changing situations.

Part c of Figures 7 - 10, show the regularly repeating patterns of the yields of the three phytospecies and of the second zoospecies. It can be seen, besides the evidence that the simulated ecosystem is consistent,

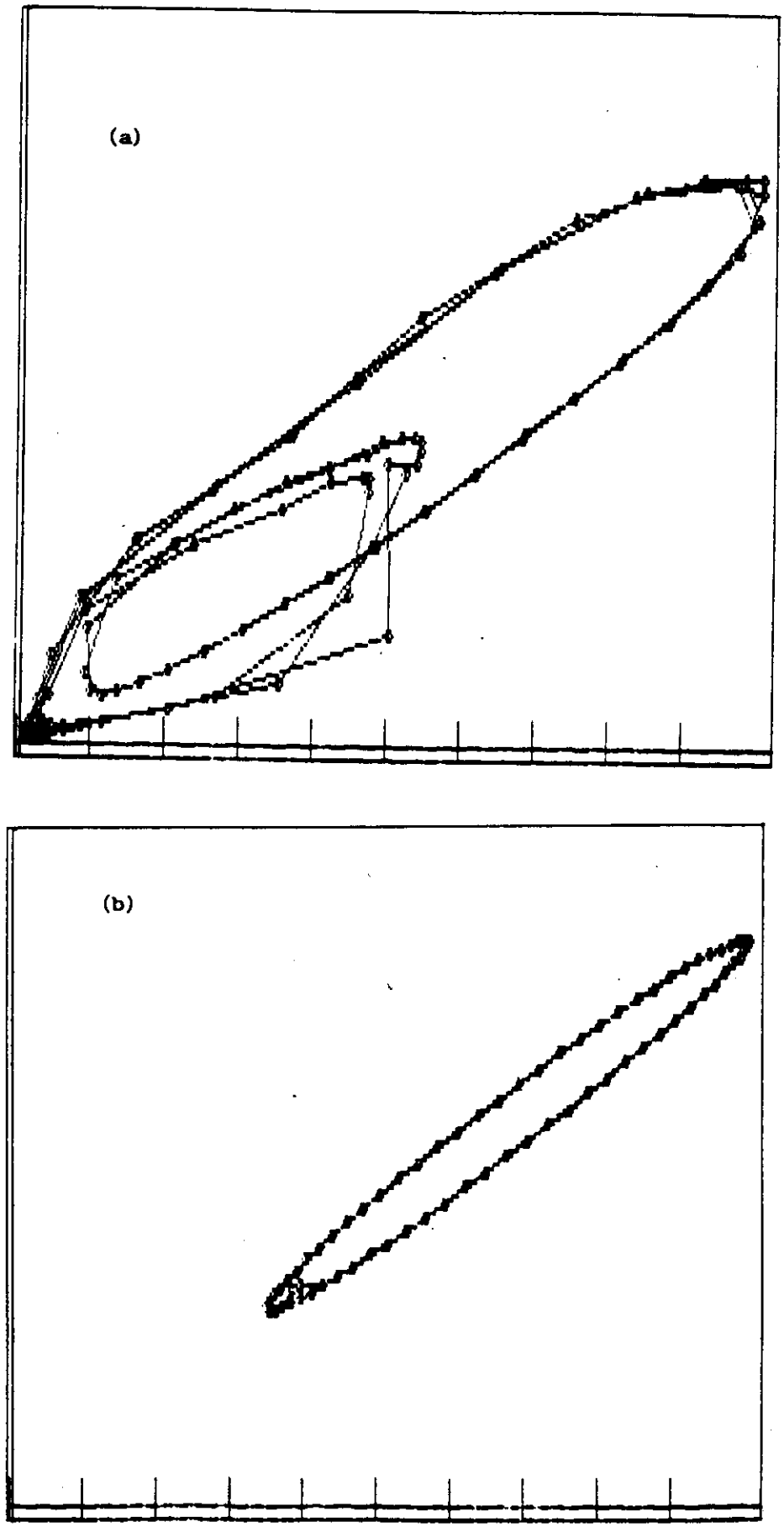

Figure 6. Sediment (a) and temperature (b) at time t plotted against themselves at time t+dt in a 6 years simulation.

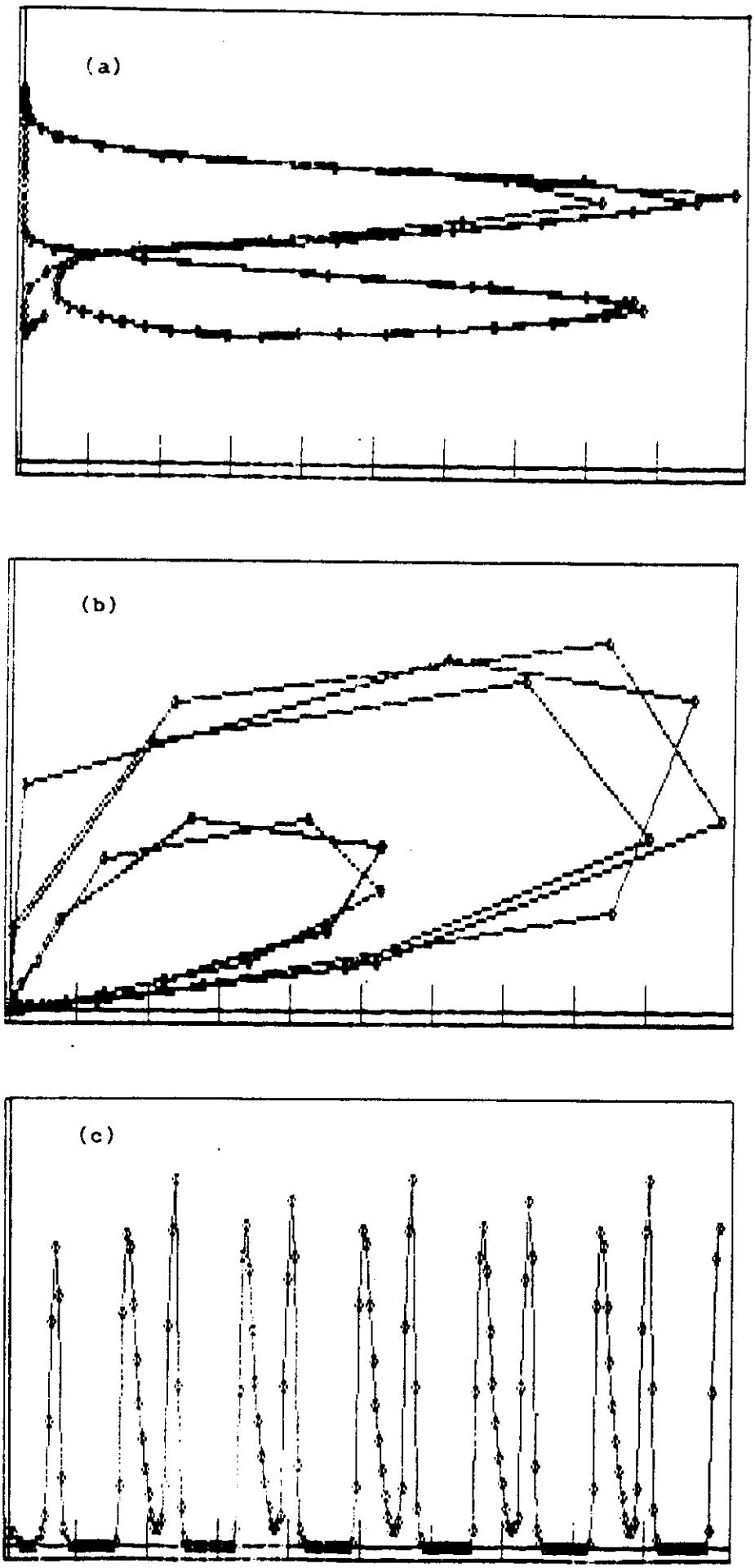

Figure 7. First phytospecies yield as function of time (c), against itself (b) and against temperature (a).

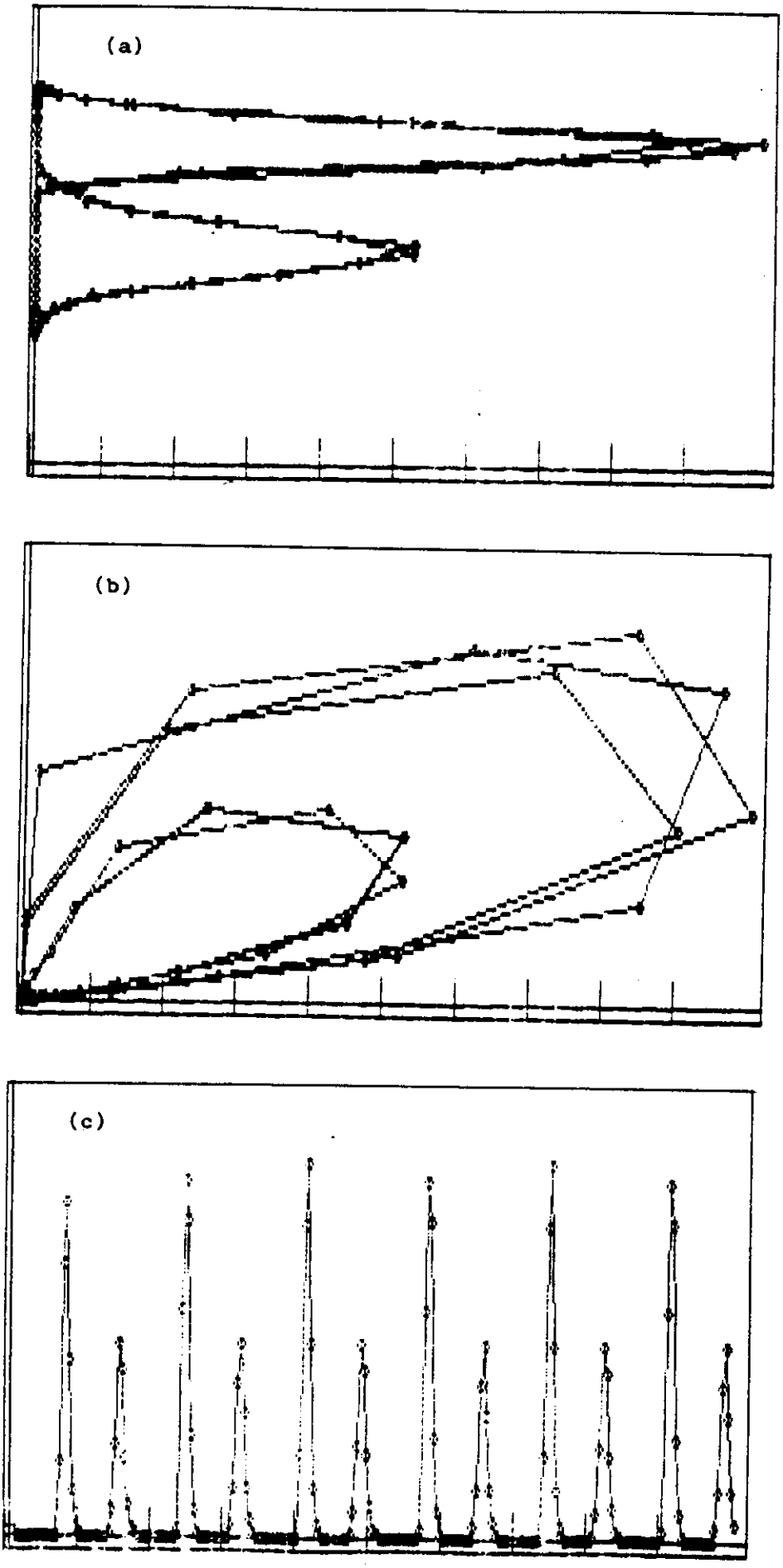

Figure 8. Third phytospecies yield as funcion of time (c), against itself (b) and against temperature (a).

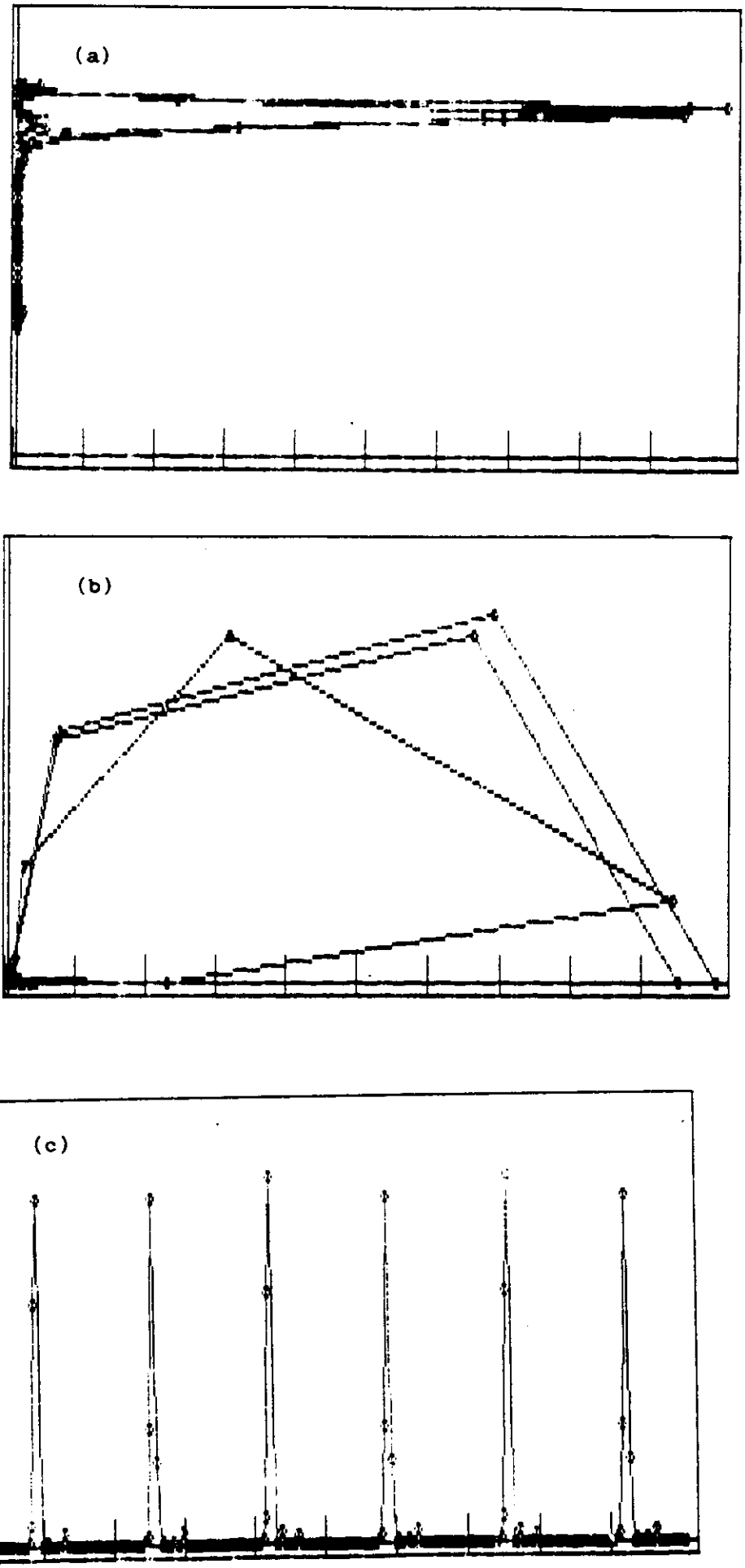

Figure 9. Third phytospecies yield as function of time (c), against itself (b) and against temperature (a).

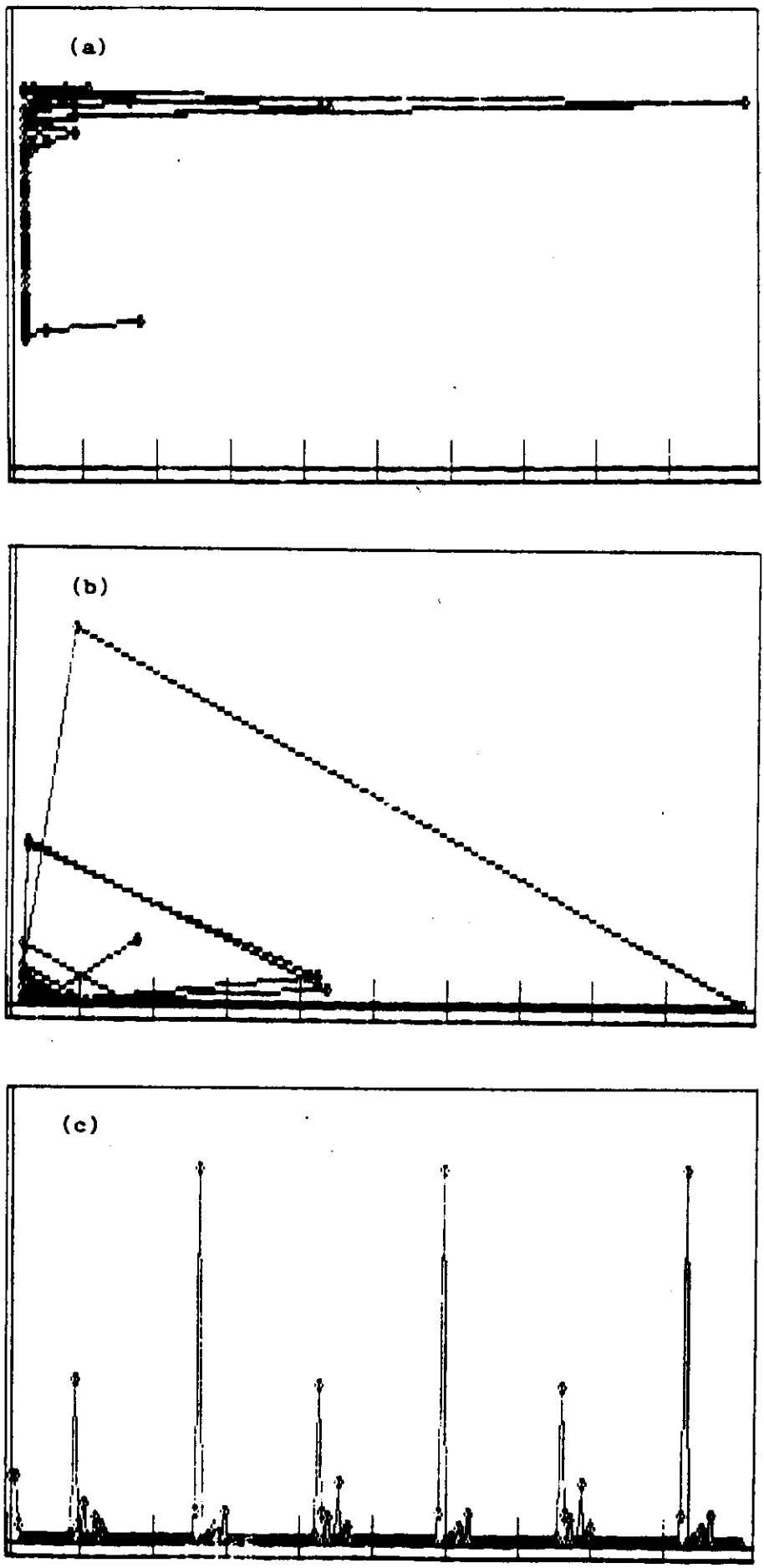

Figure 10. Second zoospecies yield as function of time (c), against itself (b), and against temperature (a).

that some patterns in the yield curves repeat themselves at an interval of two years, even if the maximum period of the harmonic forcing functions (temperature and radiation intensity) is of one year. It looks like a "beat" in the interaction among the parts of the system.

Therefore some more plots have been traced, in which one variable yield is plotted against the contemporary values of another one, or against itself. In this second case we use as plot coordinates, at every output time τ, $X(\tau)$ as abscissa and $X(\tau+d\tau)$ as ordinate value, $d\tau$ being the time interval between two successive outputs. In this case the old ordinate value in a step of the plot becomes the new abscissa in the new step and we can check for some pattern in the "trajectory" the plot describes on the (x,y) plane. The same criteria underlie the comparison of the yields of two different variables: the appearance of some pattern in a trajectory reveals the existence of a sort of "correlation" between the behaviour of the two variables in the flow of time.

Figure 6, part (b), shows temperature against itself in the six years simulation. As expected from a cosine function plotted against another one slightly out of phase with the first, the result is a tight ellipse, which we could consider a sort of "attractor" for this variable, borrowing some jargon from the chaos theory.

In the same figure, part (a), the sediment yield is plotted against itself. A twisted and narrow bunch of curves comes out, exhibiting two main loops, one connected with the other, which we can consider as two "attraction zones", corresponding to the high and low alternating peaks in the plot of sediment yield as a function of time (*i.e.* look at the curve of sediment in Figure 3, repeated along six years).

This operation can be performed with any quantity against itself, or against some other, and not only for computed values. There is nothing against looking for "trajectories" or "correlations" for experimental values of the same variables. It can even give some beautiful pictures.

Figures 7 to 9 show the yields of the three phytospecies as a function of time, part (c), then each species against itself, part (b), finally each against temperature, part (a). The "attraction" zones are clearly marked. Typically we can observe that the species with low or medium optimal growth temperature exhibit two of these zones when compared with water temperature in the simulation (grossly in spring and autumn), but the third one, having a high optimal temperature, shows only one zone of "correspondence" (in summer).

A similar figure has been made for the second zoospecies, Figure 10, but the poor sampling due to the large time interval $d\tau$ between each output does not allow to exhibit a marked pattern as that seen fot the phytospecies, even if it is clearly detectable.

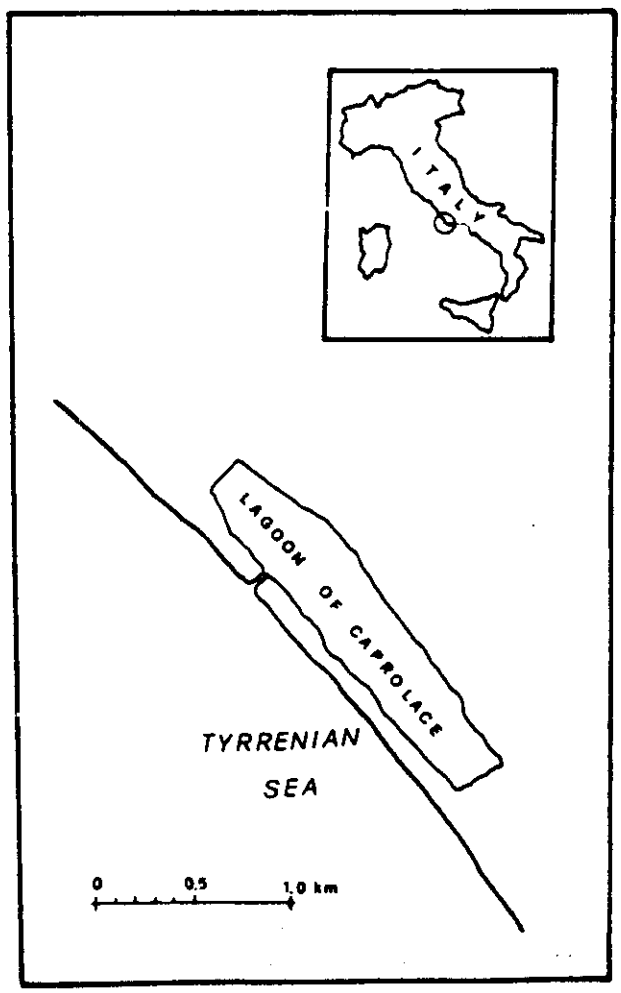

Figure 11. The location of the Lagoon of Caprolace.

Sample run with field experimental data

During 1989 a study of ecological dynamic processes has been carried out on the coastal lagoon of Caprolace (2.5 square km, 1.5 m average depth), located about 100 km south of the city of Rome, Italy. The lagoon is included in the territory of the Italian National Park of Circeo (Figure 11). The environment is isolated from inland fresh waters because they were found to be highly polluted, and only freatic inputs are possible. The water exchange with the sea is insured through a canal with the Tyrrenian, governed by tides. The system is therefore to be considered as a marine lake, marking a nearly null general circulation. Measurements of temperature, salinity, oxygen demand, chlorophyll a content, suspended particulate matter and primary productivity were conducted every 3-4 hours for an over 24-hours period every month. Additional phyto and zooplankton samples were taken for biomass and floro-faunistic composition determinations. The experimental data collections were all addressed to the definition of parameters and constants to set up a numerical simulation model of the trophic dynamics of the lagoon. The trophic structure of the planktonic community of the lagoon of Caprolace is

traced (Figure 12) as a signed digraph in terms of a qualitative loop model (Puccia and Levins 1988); the model marks the complete stability of the population structure, as evidenced by the negative overall feedback. A winter bloom was mainly ascribed to diatoms but also to undetermined forms of microphytoflagellates, a second bloom was of a summer species of dynoflagellates. The zooplankton population showed a bloom of micro scaled animals and of omnivore species (*Acartia* sp.) during the beginning of spring, but never disappeared in the warm season. A macrophytic population of *Zoostera* sp. was present from spring to fall. The phyto and zooplankton biomasses (expressed as chlorophyll a, and as dry weight) are traced against time in Figure 13a and b, oxygen is shown in Figure 13c.

One aspect of the field work that showed some sources of uncertainty was the apparent inconsistency between phytoplankton, and especially phytobenthos yields, and the nutrient concentrations that were found to be very low. Bioassay enrichment experiments on both vegetal forms showed that the mixture of the chemically most important forms (nitrogen and phosphorus) was the best accepted for growth, and that no growth was indeed possible at the lagoon water's concentration levels.

Values of the parameters used to build the input file for the simulation model, as resulting from the output list file performed by it, are reported on pages 50-51.

The goal of the modeling process for this paper is to mark the power of reproduction of the ecological processes observed on the field, and then to supply information about vegetal forms real needs of nutrients.

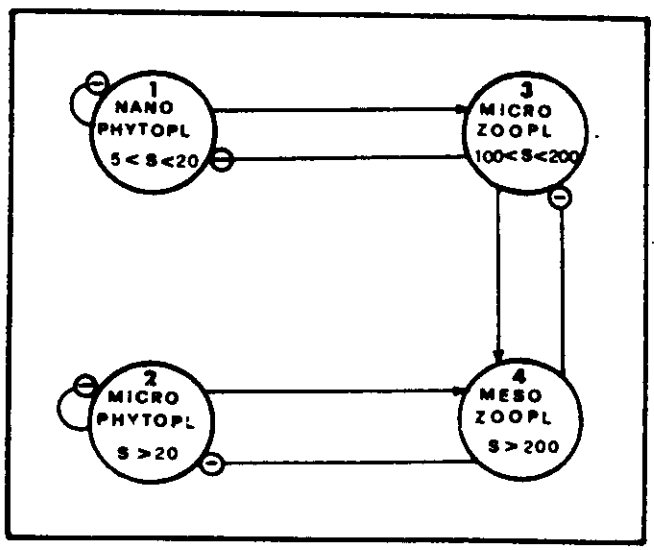

Figure 12. Trophic structure of the planktonic community of the Lagoon of Caprolace (S=size in microns).

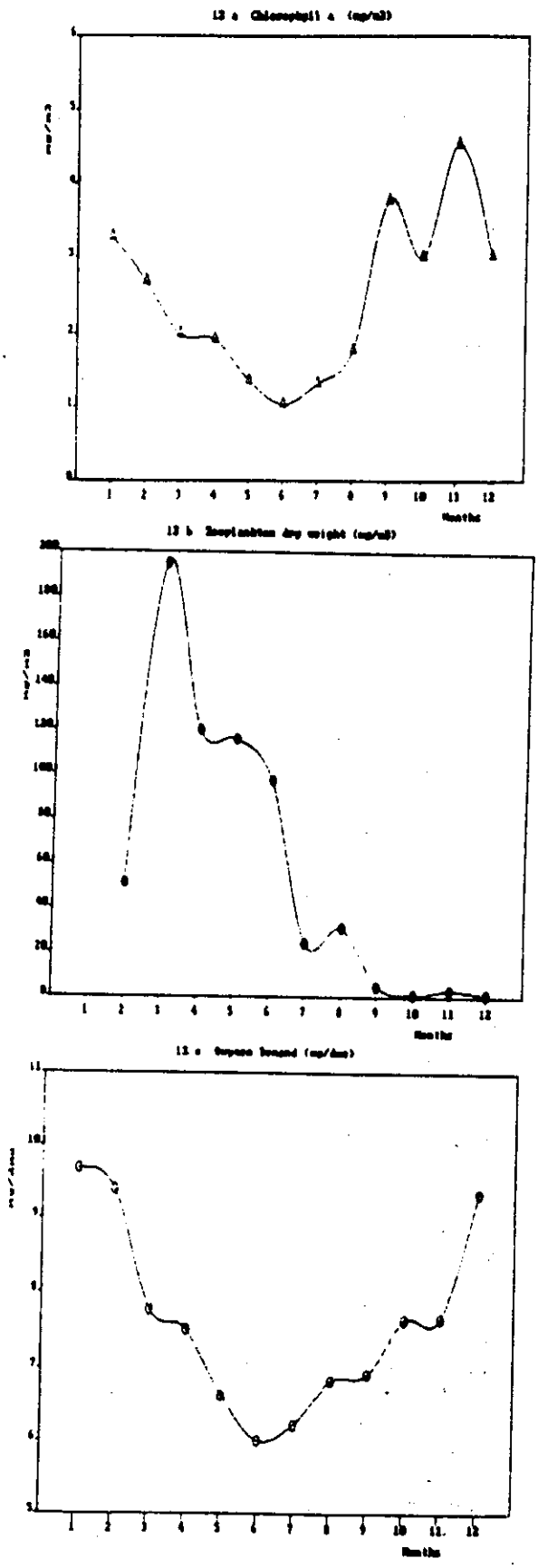

Figure 13. Field data: phytoplankton biomass (as chlorophyll a), zooplankton biomass (as dry weight) and oxygen.

```
 INPUTFILE NAME                              CAPMOD
 CONSIDERED N.OF PHYTOSPECIES                     3
 CONSIDERED N.OF ZOOSPECIES                       2
 BOTTOM DEPTH(M):                                 3.0000000
   LIGHT F.-STEELE(1)/DITORO(2)/PLATT(3)
   EXT.COEFF.-RILEY(1)/WALSH(2)
  3   1
 CHOSEN FILENAME FOR PLOT/NO
CAPMOD.PLT
  PRINT SUPPLY LIMITS-Y(1)/N(0)
  0
 MIN.ACCL.LIGHT I-(FROM AQINPT)          40.0000000
SWITCH LEVEL FROM NH4 TO NO3           14.0000000
NUTRIENTS IN INPUT ARE-MEAS.CONC.(1)
                      -RESIDUALS(2)
                      -INPUT RATES(3)
  1
PHASE CONST.(FROM AQTEMP)FOR TEMP.CURVE IS: -20.0
 MONTH,DAY TO START MOD.RUN:                1              1
COMPUTATION TIME SPAN,IN DAYS: 360.1
TIME INTERVAL FOR OUTPUT,IN HOURS 240.0
PHYTOSPECIES  1
RESPIRATION AND MORTALITY:  .4000E-01  .8000E-01
MAX.GROWTH TEMP.:   11.00     GROWTH COST.=  .8500E-01
HALF SAT.CONST. FOR N,P,SI,O2: .5000 .5000E-01 .1000E-02  100.0
PHYTOSPECIES  2
RESPIRATION AND MORTALITY:  .4000E-01  .7000E-01
MAX.GROWTH TEMP.:   12.00     GROWTH COST.=  .8500E-01
HALF SAT.CONST. FOR N,P,SI,O2: 1.000  .1000  1.300  100.0
PHYTOSPECIES  3
RESPIRATION AND MORTALITY:  .5000E-01  .1000
MAX.GROWTH TEMP.:   25.00     GROWTH COST.=  .6000E-01
HALF SAT.CONST. FOR N,P,SI,O2:.5000  .5000E-01 .1000E-02 100.0
 P/N RATE IN DEAD AND SED.MATTER RECYCLING:  .2000
SI/N RATE IN SED. MATTER RECYCLING:  .2000
ZOOSP. N.  1
GRAZ. ON PHYTO:  1 0XRATE:  .3500     H1/2:  3.000
GRAZ. ON PHYTO:  2 0XRATE:  .0000     H1/2:  3.000
GRAZ. ON PHYTO:  3 0XRATE:  .0000     H1/2:  3.000
PREYING ON ZOO:  1 0XRATE:  .0000     H1/2:  .0000
PREYING ON ZOO:  2 0XRATE:  .0000     H1/2:  .0000
MORTALITY:  .9000E-01 0XC RESPIRATION:  .4000E-01
O2 CONSUM.RATE:  16.02     O2 H1/2 CONST.:  .0000
ZOOSP. N.  2
GRAZ. ON PHYTO:  1 0XRATE:  .0000     H1/2:  4.000
GRAZ. ON PHYTO:  2 0XRATE:  .1500     H1/2:  4.000
GRAZ. ON PHYTO:  3 0XRATE:  .0000     H1/2:  4.000
PREYING ON ZOO:  1 0XRATE:  .5000E-01 H1/2:  1.000
PREYING ON ZOO:  2 0XRATE:  .0000     H1/2:  1.000
MORTALITY:  .1000     0XC RESPIRATION:  .5000E-01
O2 CONSUM.RATE:  16.02     O2 H1/2 CONST.:  .0000
0 DEG.SEDIMENT DECOMP.RATE(1/DAY):  .5500
ITS EXP.COEFFICIENT:  .9000E-01
TM AND TSC AT BOTTOM:  14.00      6.000
SEDIMENTATION SPEED(M/DAY):  .3000
TM(  1)AND TSC(  1)ARE   17.8  10.4
AT DEPTH N.  1 OF METERS     .1
WHERE NITRIFICATION O2/NH4 RATE IS:  4.450
```

```
 AND MAX.TEMP.DAILY FLUCT. IS    2.500
 STARTING VALUE FOR PHYTO SP.  1 IS    30.00
 STARTING VALUE FOR PHYTO SP.  2 IS    300.0
 STARTING VALUE FOR PHYTO SP.  3 IS    1.000
                FOR ZOOSP.N.   1 IS    1.000
                FOR ZOOSP.N.   2 IS    1.000
  STARTING VALUE FOR D.O.M. IS           5.0000000
 OPTIMAL I FOR PHYTO  1 AT START TIME:  40.00
 OPTIMAL I FOR PHYTO  2 AT START TIME:  40.00
 OPTIMAL I FOR PHYTO  3 AT START TIME:  40.00
  TIME(D) NH4,NO3,PO4,SI,O2 (MG/M3)
  LAST COLUMN IS PROFILE OF SED.FACTOR
   15.0   50.40   30.80   9.300   100.0    9504.    1.132
   46.0   63.00   33.60   9.300   100.0    8704.    1.192
   74.0   30.80   30.80   6.200   100.0    7776.    1.404
  108.0   49.00   4.200   6.200   100.0    7472.    1.881
  192.0   72.80   26.60   1.550   100.0    6800.    3.298
  350.0  140.0    84.00  12.40    100.0    8208.    1.243
  START VALUES FOR S.O.M. AND MACRO:
            20.00       50.00
 OPT.TEMP.(*C) FOR MACRO.  20.00
 THEIR GROWTH RATE (1/DAY)  .2000
 THEIR LOSS RATE TO DETRITUS(1/DAY)  .1000E-01
 YEAR DAY OF GROWTH END (USUALLY 270)  270.0
 FOTOEFFICIENCY   16.02
 HALF-MAX. MACRO GROWTH LIGHT INTENSITY(LY/DAY)  70.00
 ..................................
```

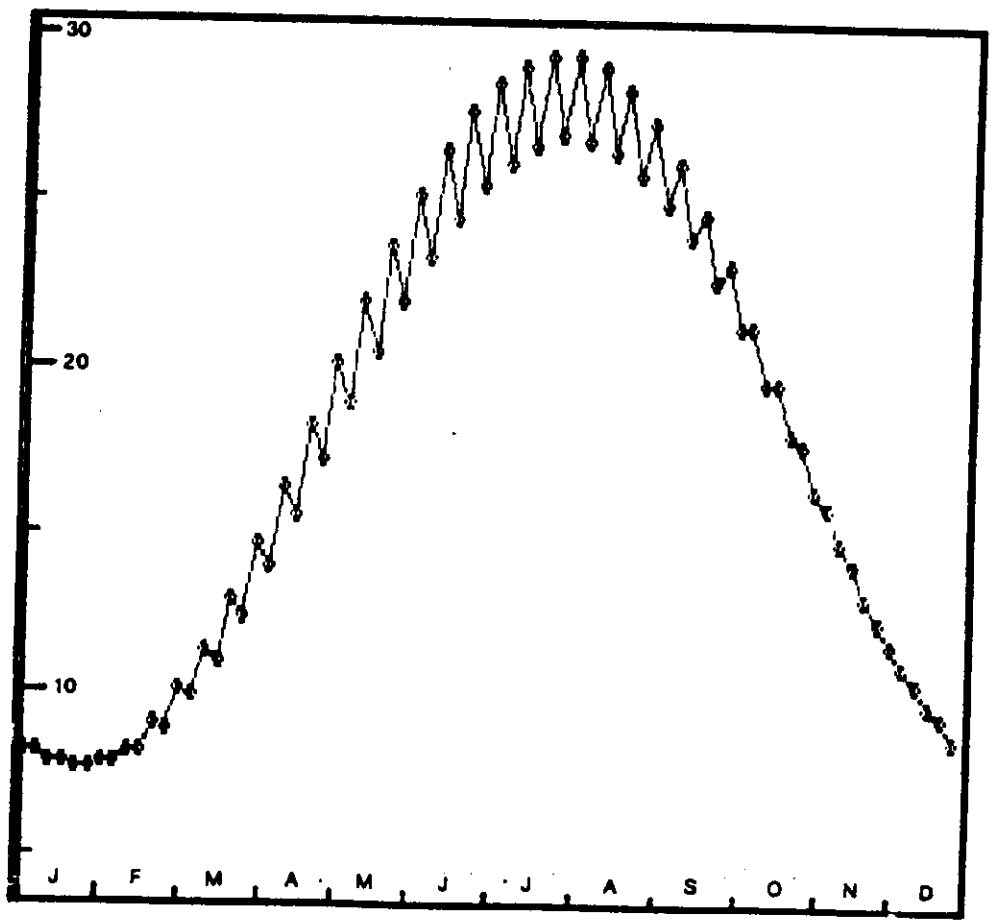

Figure 14. Temperature simulated by the model. Output at noon and midnight.

We share, in fact, the opinion of a very low nutrient limitation to algal growth in shallow water lagoons, as supported by Harris (1986) and discussed by Sommer (1989). Therefore the nutrients for vegetal growth must be from sediment recycling. In this view, limitation to growth for nutrients exists only if the availability is low in comparison with the specific vegetal uptake capacity at given meteo-climatic, physical and chemical conditions.

The temperature curve simulated by the program is shown (Figure 14) with its day-night cycle. The phytoplankton species yields are shown in Figure 15a; the winter bloom is more depressed than expected because of the zooplanktonic pressure of predation on it. The macrophyte species yields are plotted in Figure 15b. The zooplanktonic productions are shown in Figure 15c. All bloom periods substantially complied with simulations, return the consistency of interactions built in the model with the real system.

Nutrients are graphed in Figures 16 (a, b ,c, d) including oxygen; dead organic matter and sedimented matter are traced in Figure 17a and b.

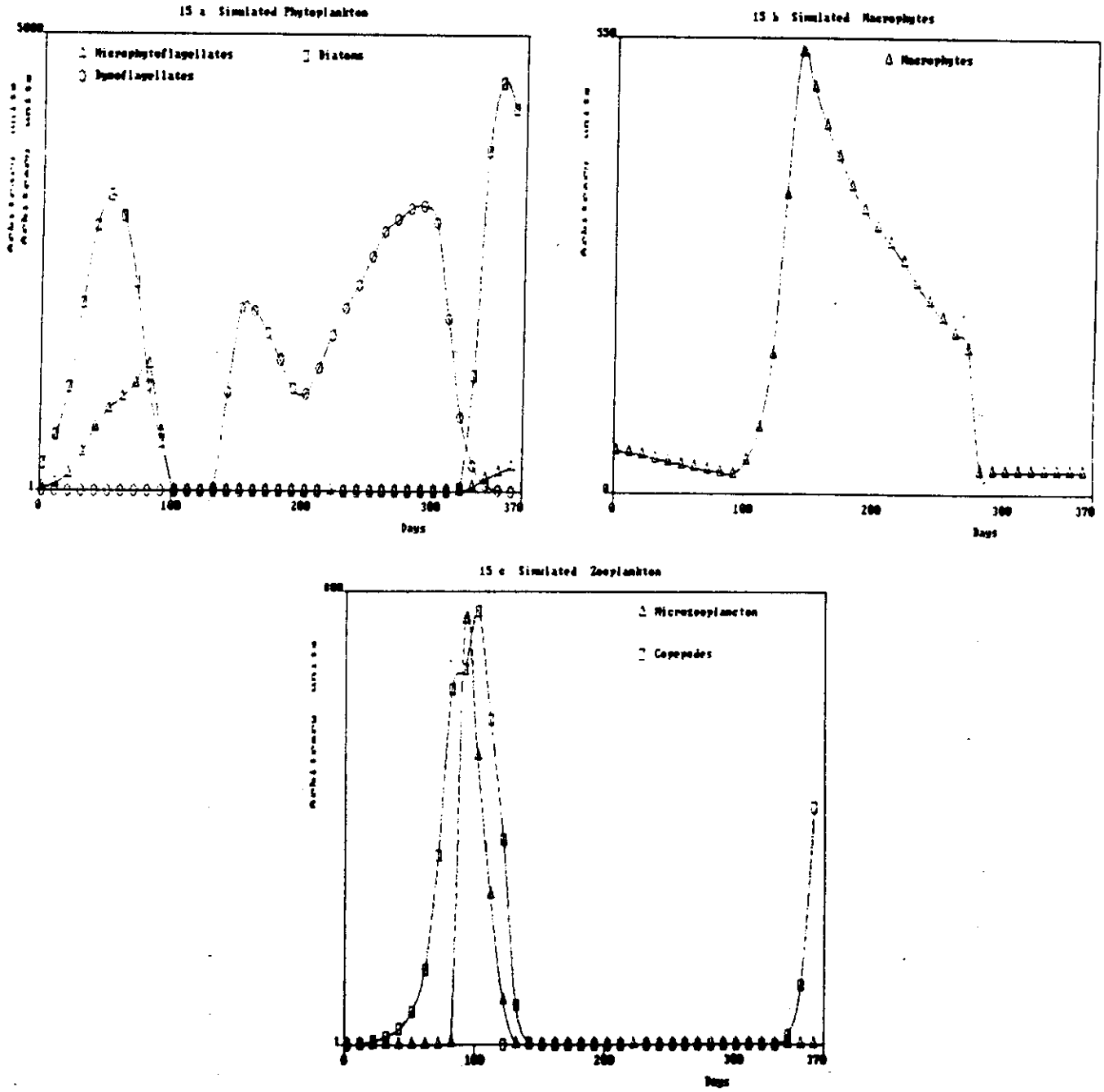

Figure 15. Simulated yields of phytoplankton, zooplankton and macrophytes.

The simulations strengthened the belief that the nutrient concentrations measured in the waters are insufficient to allow micro and macroalgal growth, and that therefore consistent amounts must be realesed from sediments, which assume great importance in shallow water basins.

This first result of the modeling process, and the following considerations are discussed in detail just to mark the model's distinctiveness, but also rise new and more pressing questions. Can the environment be artificially eutrophized to investigate the joined ecological processes? If so, which are the constants or parameters that must be changed to achieve this result? Microalgal growth constants, half saturation constants, or even, the nutrient concentrations? What will happen to the stability of the planktonic population of the Lagoon if the mistivore will prey heavily on the dynoflagellates? Will this leave the overall feedback

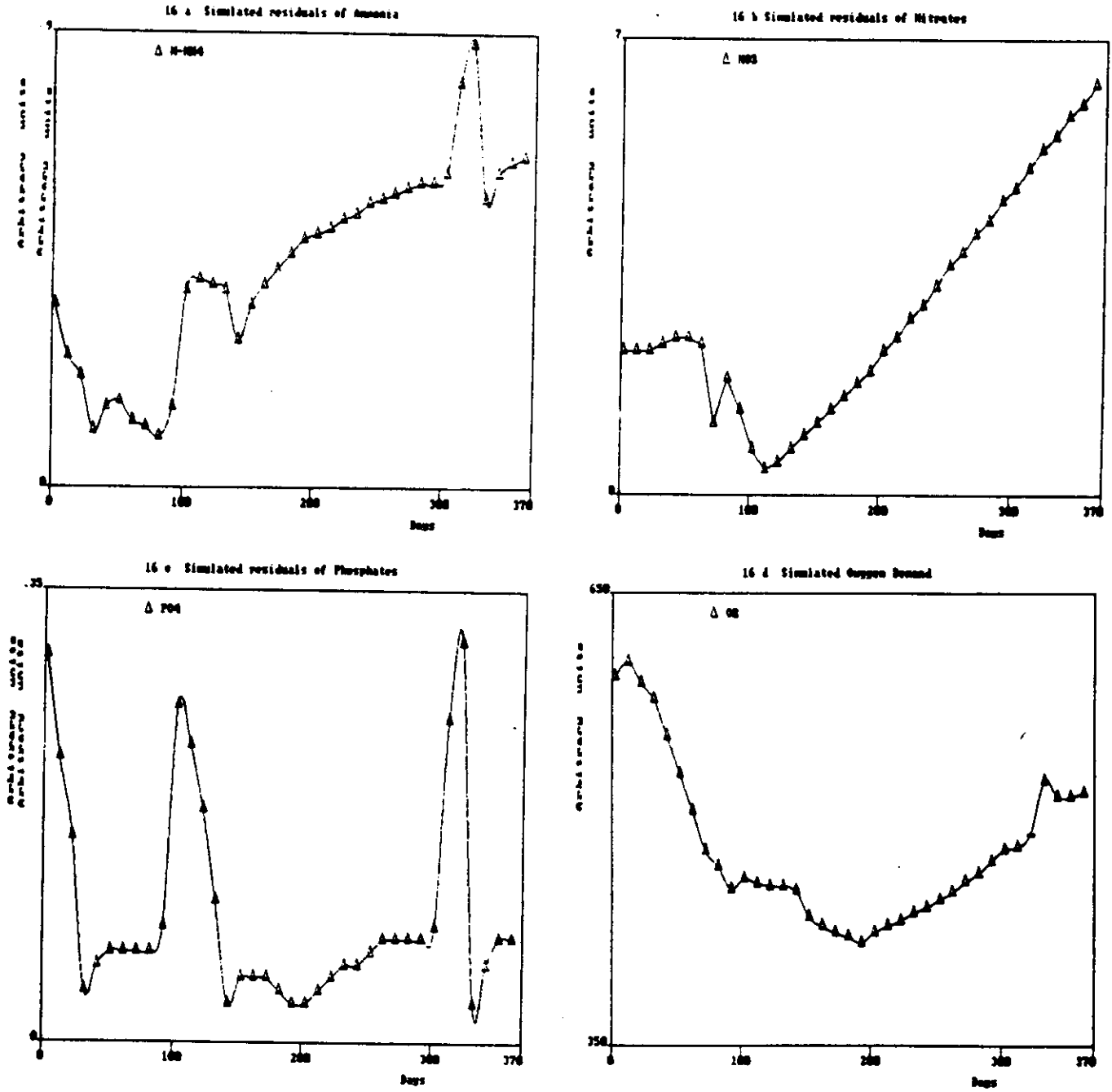

Figure 16. Simulated residual concentrations of nutrients.

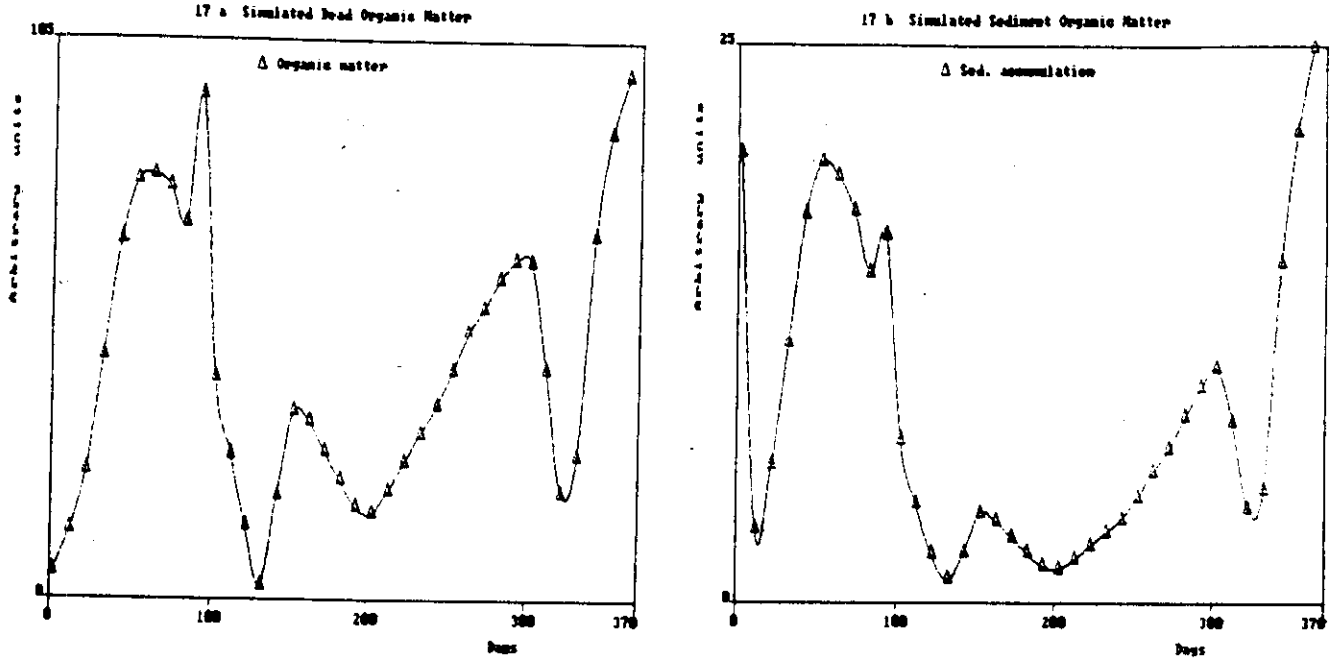

Figure 17. Simulated production of dead and sediment organic matter.

negative? Can an anoxic crisis be simulated, and which parameters have to be increased or changed to do this?

All these examples, and possibly others, can be tested with the model, but are left to the imagination and sagacity of the users.

Request of copies of the model (computer programs and manual) on 5.25 or 3.5 in. diskettes can be addressed, together with a new disk, to the Laboratorio Centrale di Idrobiologia.

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