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"Ecological Models of the Marine Environment"

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ECOLOGICAL MODELS OF THE MARINE ENVIRONMENT

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"It is not possible to make an unambiguous picture of reality, as the uncertainty limits our knowledge." Niels BOHR.

1. Introduction

The use of the language of mathematics to model or represent a phenomenon has several advantages. This interdisciplinary approach allows the usage of tools from two disciplines - those of the scientific area plus those of mathematics.

A traditional view of the use of mathematical models is to predict the behaviour of a system. In biology, while prediction is highly desirable, this objective is probably one of the last fruitful avenues of research.

Models are tools for dealing with complexity. For those of us attempting to understand and, perhaps, manage marine ecosystems, they are often useful and sometimes absolutely necessary.

The models used may take a variety of forms, including empirical relationships observed in the field, highly controlled laboratory experiments, flow diagrams, mathematical equations, electrical analogs and computer algorithms for simulation.

This lecture is devoted to the development of numerical simulation models, particularly those which are mechanistic and deterministic in approach.

2. Modelling Aspects in Ecology

The first goal behind the use of ecological models today is related to the question of environmental management. Energy and pollutants are continuosly released into ecosystems, where they cause rapid growth of algae or bacteria, damage species and alter the ecosystem structure. In this sense, the model can been used to select the environmental technology best suited for the solution of specific problems, or legislation reducing or eliminating the emission set up. We shall discuss later these aspects of modelling. Now we want to stress another aspect of modelling studies, that of models as a scientific tool. Models are widely used instruments in science. Nowdays there is a growing interest in methematical models in all the scientific disciplines due also to the development of computers.

Ecological models do not differ essentially from other scientific models not even by their complexity. It is to emphasize that in disciplines like ecology or physical oceanography it is not possible to perform controlled experiments as, for instance, in particle physics. So, mathematical numerical models are the only instruments to supply the lacking of controlled experiments.

In this sense there is a strong similarity of modelling to traditional experimentation. Figure 1 shows the role of models in research.

2.1 Concepts of Modelling

A mechanistic numerical model begins with observations of the ' real world'. From these observations emerge tentative answers to questions about the system which may be appropriate to a modelling analysis. What is our concept of the system ? What are its physical and temporal boundaries? What are the major compartments and how do they vary in space and time? What are the important forcing functions or inputs and outputs from the system? What time scales are involved in the major processes? From these answers starts the modelling procesure. This phase is related to the set up of the so called conceptual model. The main goal of the conceptual model is then to demonstrate connections, causalities, feedback all between part and components of the system of interest. This should be done in such a way that the final result is a help to understanding the functioning of the system. The process of constructing a conceptual model is shown in Figure 2. An example of a conceptual model of a marine system is reported in Figure 3 (from Kremer and Nixon, 1978).

The complete modelling procedure, based on the conceptual model is an iterative process since the conceptual model should be changed according to the comparison to reality of the numerical output of the translation into mathematics of the conceptual model (see Figure 4). We want now to discuss some details of the two flow charts reported in Figures 2 and 4.

The first step in modelling is to identify a system of interest. The identification of the system will depend on many factors including scientific, social, economical and political factors. A system has to be identified in a general way as for instance the eutrophication of an area. Details as physical and temporal boundaries have to be treated in a further step.

It is very important to define the objective of the model. It is to take into account: know-how of the modelling group; data availability; data relevance; computing facilities and last but not least the financial support.

Boundaries of the system should at this step be determined. These boundaries are very important and they determine what is the system and what is out of the system. Ecosystems are open systems, so the interface with the 'external world' have to be precisely defined.

Whenever possible it might be useful to identify subsystems. This approach is helpful for understanding the complexity of an ecosystem and it might be useful to deal with subprograms in the phase of the numerical modelling.

In order to follow the changes of mass and energy within the model it is necessary to know as precisely as possible the inputs and outputs of mass and energy through all the interfaces. External controlling factors as light and temperature, winds, tides and currents have to be determined in order to identify forcing functions which influence the dynamics of the system.

The crucial step in modelling procedure is the choice of the state variables. There is no prescribed way for choosing most characteristic properties of a system. One extreme for the choice of state variables would be to use every chemical and biological species as a state variable. This would result in a model of absolutely unmanageable size. Therefore, groups of organisms have to be combined in one state variable.

The processes defined in the conceptual model have to be represented in the model by mathematical equations. It is not possible to have an equation that represents a given process in all ecological contexts. Most of processes have several mathematical representations, which are equally valid either because the process is too complex to be understood in sufficient detail at present, or because some specified circumstances allow to use simplifications.

By the calibration it is attempted to find the best accordance between computed and observed state variables by variation of model's parameters.

It is of great importance to verify and validate models. Verification is a test of the internal logic of the model. Typical questions are: does the model reacts as expected? Does the model follow the law of mass conservation? and so on. Validation must be distinguished from verification. It consists of an objective test on how well the model outputs fit the data.

The sensitivity analysis attempts to provide a measure of the sensitivity of either parameters, forcing functions or submodels to the state variables in the model. This process not only provides insight into the behaviour of the model, but it also serves as a crucial feedback loop in suggesting sensitive areas where additional research is needed.

2.2 Classes of Ecological Models

The main classification based upon a difference in the scientific ideas behind the model, is between reductionistic and holistic models.

Reductionistic ecological models attemt to incorporate as many details of the system as possible. This approach is based on the fact that the property of a system are the sum of all the details.

On the contrary, holistic models treat the system as a global system. In this case are the properties of the system, not the sum of all the details considered, but the system posseses some additional properties because the subsystems are working as a unit.

In addition, both kind of models can be stochastic or deterministic wether or not they contain input disturbances and random measurement errors.

2.3 Complexity

Nature is too complex to enable us to get a detailed picture of ecosystems. Different models and different degrees of approximation must be developed for different purposes. No model is completely correct, but a good model must give a knowledge of a certain aspect of an ecosystem. A typical question is : How can we describe a such complex system as an ecosystem is? The answer is that it is impossible to include in the model all the interactions among components. When we are choosing for a model we have to simplify the problem by considering the data at disposal and the process we are interesting in.

An interesting concept has been introduced by Jorgensen (1988) concerning with the complexity of ecosystems. Consider for instance two components of an ecosystem. If we want to know all the relations between these two components, we would need at least three observations to be able to state whether the relationship is linear or nonlinear. Correspondingly, will the relations between three components require to know the shape of a plane and we need therefore 3*3 observations. If we have 18 components, we need correspondingly more or less 3**18 observations. This concept can be used to formulate a practical 'uncertainty principle' in ecology:

$$10^5 \frac{\Delta x}{\sqrt{(3^{n-1})}} \leq 1 \qquad (1)$$

where Δx is the relative accuracy of one relationship, and n is the number of components included in the model.

Furthermore, we can use all the observations on one relation or all the observations on all the possible components of the ecosystem. Costanza and Sklar (1985) talk about about the choice between these two extremes: knowing everything about nothing or nothing about everything. It is clear at this point that a compromise has to be done : to balance your selection of complexity in your description.

3. Marine Ecosystem Models

The expression 'ecosystem model' should be properly applied only to the most complex level of models. Actually in this lecture we are dealing with the so called productivity models which take into account only the first trophic levels of the marine system.

These models usually are based on earlier work of Riley, and Steele (1949, 1974). The aim of these models is to simulate the seasonal cycles of phytoplankton and primary productivity, along with the seasonal levels of the limiting nutrient and the zooplankton populations.

3.1 Physical Processes

The relevant physical processes for the biological models are those that cause a redistribution of mass or energy among the components of the system in a non-chemical biological way. The redistribution can be the result of energy or mass forced through the boundaries of the domain or by internal exchanges between components.

Mass in a unit volume of water is accounted for, in the Eulerian frame, by the following equation:

$$\frac{\partial M}{\partial t} = -\vec{\nabla} \cdot (\vec{v} M) + S \qquad (2)$$

where M is a concentration of mass per unit of water volume, $\vec{v}$ the velocity field, and S some internal conversion of mass. The source term is called the non-conservative term in the sense that it includes all the non-physical effects such as biological or chemical conversion of mass from one form to another. The flux divergence term includes the conservative physical processes that affect the distribution but not the form of the mass. The local change is merely the difference between the other two and is, in fact, what is observed in nature. The flux divergence term can be expanded into components as follows:

$$\vec{\nabla} \cdot (\vec{v} M) = \frac{\partial(uM)}{\partial x} + \frac{\partial(vM)}{\partial y} + \frac{\partial(wM)}{\partial z} \qquad (3)$$

Let us examine now one of these components and decompose further as :

$u = \bar{u} + u' \qquad M = \overline{M} + M'$

$$\frac{\partial}{\partial x}(uM) = \frac{\partial}{\partial x}(u'M') + u\frac{\partial \bar{M}}{\partial x} + \bar{M}\frac{\partial \bar{u}}{\partial x} \tag{4}$$

where $\bar{u}$ and $\bar{M}$ refer to low frequency portions of the variables and u' and M' to the high frequency portion. In equation (4) the second term on the r.h.s. is referred as the advective term and the first term as the diffusive one. The diffusion process takes into account the random turbolent processes at small scales. This term is usually parametrized as:

$$\frac{\partial}{\partial x}(u'M') = \frac{\partial}{\partial x}(K\frac{\partial M}{\partial x}) \tag{5}$$

where K is the diffusion coefficient.

The advective flux (second term in Eq.4) represents changes due to the physical traslation of gradients.

We will review briefly the processes involved in moving the water in coastal situations. It can be useful to distinguish between movements in dynamic balance and those not in balance.

Balanced flows are flows represented by a frictionless balance of forces, such as geostrophic flows, inertial motion, internal waves and tidal flows. They contribute to what is generally referred as mean flow. Unbalanced flows are on the contrary referred to ageostrophic flows, stressed flows or transient flows. Because friction is important these flow are mainly turbolent and are of primary importance near the coastal boundaries.

These different types of flows are discussed in terms of which forces are prevailing. The conventional set of forces is given, for instance, by the following horizontal equation of motion:

$$\begin{aligned}
&\frac{\partial u}{\partial t} - fv = \frac{g}{\rho}\frac{\partial p}{\partial x} - \frac{g}{\rho}\int_0^z \frac{\partial \rho}{\partial x}\,dz + \\
&\frac{\partial}{\partial z}A_v\frac{\partial u}{\partial z} + \frac{\partial}{\partial x}A_h\frac{\partial u}{\partial x} + \frac{\partial}{\partial y}A_h\frac{\partial u}{\partial y} \\
&\frac{\partial v}{\partial t} + fu = \frac{g}{\rho}\frac{\partial p}{\partial y} - \frac{g}{\rho}\int_0^z \frac{\partial \rho}{\partial y}\,dz + \\
&\frac{\partial}{\partial z}A_v\frac{\partial v}{\partial z} + \frac{\partial}{\partial x}A_h\frac{\partial v}{\partial x} + \frac{\partial}{\partial y}A_h\frac{\partial v}{\partial y}
\end{aligned} \tag{6}$$

where : f is the Coriolis parameter; g the acceleration due to gravity; ρ the water density; A_v A_h the vertical and horizontal eddy viscosity coefficients; p is the pressure.

There are two other equations needed i.e. the hydrostatic equilibrium :

$$\rho g = \frac{\partial p}{\partial z}$$

and continuity:

$$\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = 0$$

It is necessary to have some criterion for determining the dominant processes which are important in a given situation. Physical oceanographers usually use scaling procesures to neglegt terms in the equation of motion. This allow to neglect for instance non-linearities or friction forces.

A general treatment of hydrodynamical models is beyond the aim the lecture. The reader can refer for example to the works of Nihoul, 1975, 1981; Nihoul and Djenidi, 1987. Here it is to note that from the numerical point of view, hydrodynamical models being based on partial differential equations, can be solved either by finite difference or finite element methods.

3.2 Bio-chemical Processes

An ecosystem may be regarded as a system in which there is a cyclic interchange of material between the biotic and abiotic components.

Marine ecosystems in particular are normally considered as having four main biotic components: producers, consumers, decomposers and detritus. Detritus, although not being an active component, is often included since it plays a major role in the trophic chain. Producers are organisms that, using sunlight as energy and inorganic carbon and nutrients as building materials, photosinthetize organic matter which is then partly grazed by the consumers and partly converted into detritus. Consumers, partly grazing on the producers and partly preying within their own compartment, also contribute to the detrital component either upon death or by way of their fecal production. Decomposers are mainly bacteria that take energy out and matter from detritus. Along this cycle, carbon and nutrients are taken up by the producers during photosynthesis and released by all three active components in respiration, while oxygen is released to the environment in photosynthesis and consumed in respiration.

The organic matter photosynthesized goes into increasing the biomass of the ecosystem. However, not all the matter remains within the phytoplanktonic organism to be grazed down by the consumers. A fraction of the organic matter is immediately oxidized in respiratory processes; another fraction may be directly excreted and yet another part may go directly into detrital component to be degraded by bacteria. Only the remaining organic matter can be used to increase the size of the cells or to build new ones. Biomass production is therefore only one of the uses given by the ecosystem to photosynthesis, the remaining ones recycle without passing through the higher trophic level components.

3.3 Equations for the Biological Terms

The modelling procedure requires, of corse, mathematical relations between the biological terms considered in the model. Sets of equations are usually required for: growth rate of phytoplankton as a function of incoming radiant energy and a limiting nutrient; ambient radiant energy intensities at physiological wavelenghts; limiting nutrient concentration as a function of uptake, regeneration and supply by mixing of surface waters with deep layers; loss rate of the phytoplankton from grazing, natural mortality, sinking and mixing; activities of zooplankton and higher trophic levels.

Biological modellers have traditionally chosen to carry all biological elements of the model in a single unit, usually energy, carbon, nitrogen or phosphorus. However, since most models include a nutrient term placing limits on photosinthesis, conversion factors must be used, for example from carbon to nitrogen.

We shall see now in some details the most common equations used in biological models.

Phytoplankton terms

The terms affecting growth of the phytoplankton are indicated in the following 'word equation':

change of phytoplankton / time = growth - respiration - sinking - grazing + advection + diffusion - excretion - mortality

Advection and diffusion are taken care of automatically with the definition of hydrodynamic framework and need not to be discussed further. Grazing will be discussed in the zooplankton equation.

For the growth term we consider nutrient limitation and light limitation. Normally, nitrogen and phosphorus are considered as limiting factors. The self-regulatory effect of nutrient concentration on the rate of uptake has been shown to follow the Michaelis-Menten hyperbola :

$$V = V_{\max}\frac{S}{K_S + S} \qquad (7)$$

where S is the ambient nutrient concentration and K_s the concentration at which the specific uptake rate V is 1/2 of the maximum atteinable rate $V_{\max}$.

For the the light limitation a lot of empirical formulations exist. One is, for instance, the following:

$$V = V_{\max}\frac{I_z}{K_L + I_z} \qquad (8)$$

where : I_z is the light intensity at depth z.

Usually an exponential decay of light intensity is assumed through the water depth.

If we consider in the model more nutrients, a Liebig's law of the minumum is usually considered. This means that at each time the growth of the phytoplankton is controlled by only the most limiting nutrient i.e. that having the minimum semi-salutation ratio.

Respiratory and excretion losses. Considerable variation exists in the way these losses are treated in productivity models. Usually these terms are temperature dependent. To see the different approaches see for instance Vinogradov (1972), O'Brien and Wroblewski (1972) and Hendricks (1973).

Sinking. The loss of phytoplankton by sinking from the euphotic layer is sometimes handled directly by the specification of a mean sinking rate. Another approach to sinking losses is that of setting up a term for the detritus production, composed of unassimilated food.

Mortality. This is treated as a linear term in the equation.

Zooplankton terms

The terms affecting growth of the zooplankton are indicated in the following 'word equation':

change of zooplankton / time = growth - mortality - predation

Growth. The term is the result of grazing expressed as intake of energy, carbon or nutrient and respiration and excretion losses. Also in this term a Micaelis-Menten kinetic is usually assumed for the growth of zooplankton due to grazing of phytoplankton.

Respiration and excretion. The amount of carbon and nutrient ingested by herbivores are partitioned into growth, fecal pellets excretion and into respiratory losses. These processes have been modelled using a great variety of approach. See for example Lassen and Nielsen (1972), Steele (1972), Walsh and Dugdale (1971) and O'Brien and Wroblewski (1972).

Predation. Models often are termined at the herbivore level especially when the objective is to simulate phytoplankton dynamics. However a grazing on zooplankton by fishes can be added to the model. A fish predation can be described as:

$$\frac{dZ}{dt} = -\phi F\left(\frac{Z}{Z + \theta P}\right) \qquad (9)$$

where: Z is the zooplankton concentration, F the concentration of fishes, θ the gill raker efficiency.

The intent is to weight the predation as a function of phytoplankton abundance.

In the following pages we present a more detailed analysis of a typical marine productivity model following the model equations by Kremer and Nixon (1978). It is however to remember that in these models the 'correct equations' do not exist. So, a great variability in model formulations can be found in literature.

I. PHYTOPLANKTON

1. $\frac{dP}{dt} = \mu P - G - M \pm A$

where: P = phytoplankton biomass, mg C/ℓ
μ = instantaneous daily growth rate, per day

2. $\mu = \mu_{max} \cdot$(Light Limitation)$\cdot$(Temperature Limitation)$\cdot$(Nutrient Limitation)

where: μ_{max} = maximum daily growth rate, per day

3. Light limitation = $\frac{\overline{I}}{I_{opt}} \exp(1 - \overline{I}/I_{opt}) - r \quad (1 + r)$

where:
$\overline{I}$ = mean light in the water column, calculated from $\overline{I} = \frac{\overline{I}_s \, (1 - e^{-Cz})}{Cz}$

$\overline{I}_s$ = average visible light at the surface, which may be taken directly from field measurements or obtained by multiplying an estimate of total incident solar radiation (Ly/day) by 0.85 to correct for reflection, and by 0.45 to eliminate long-wave radiation.
C = diffuse attenuation coefficient (or extinction coefficient), per meter
z = thickness of the water layer, m
I_{opt} = light intensity at which phytoplankton growth is maximum, Ly/day
r = a correction factor allowing for a negative change in biomass at very low light levels, $\overline{I} < 0.01\ I_{opt}$

4. Temperature limitation = $\frac{e^{PK1 \cdot T}}{e^{PK1 \cdot T_{max}}}$

where: $PK1$ = slope of the growth rate as an exponential function of temperature, $^{o}C^{-1}$
T = water temperature, per ^{o}C
T_{max} = maximum water temperature, ^{o}C

5. Nutrient limitation = $\frac{[NH_4 + NO_3]}{PKN + [NH_4 + NO_3]}$ or $\frac{[PO_4]}{PKP + [PO_4]}$ or $\frac{[Si(OH)_4]}{PKSi + [Si(OH)_4]}$

where: The lowest of these three values is used
[ ] = concentration of ammonium and nitrate, phosphate, or silicate in the water, $\mu mol/\ell^{-1}$

PKP, PKP, PKSi = half saturation constant for each nutrient; the concentration at which growth is reduced to half the maximum

6. $G = F_f + F_c$

where: F_f = ingestion by filter feeding zooplankton, mg C/d
F_c = ingestion by ciliates, mg C/d

7. $M = m \cdot P$

where: m = a fractional daily death rate
P = phytoplankton biomass

8. A = advective exchanges according to the physical circulation model

II. MACROPHYTES (*Posidonia*)

1. $\frac{d(CHO\text{-}C)}{dt} = P_{max} \quad \frac{T}{T_{opt}} \exp(1 - T/T_{opt}) \quad \frac{I_z}{k_{PI} + I_z} \, CHNOP - TR$

2. $\frac{d \; CHNOP\text{-}C}{dt} = TR - M - k_d \; (CHNOP\text{-}C)$

3. $TR = 0.022 \; (CHNOP) \; \frac{T}{T_{opt}} \exp(1 - T/T_{opt})$

where: CHO-C = standing crop of *Posidonia* carbohydrate, g C/m^2
P_{max} = the weight specific maximum carbon fixation rate of *Posidonia*, g C/g C/d
T = bottom water temperature, ^{o}C
T_{opt} = the optimum temperature for *Posidonia* photosynthesis, ^{o}C
I_z = visible light reaching the bottom, Ly/d
R_{PI} = visible light intensity at which *Posidonia* photosynthesis is half the maximum, ly/d
CHNOP = the standing crop of *Posidonia* tissue, gdw/m^2
CHNOP-C = the standing crop of *Posidonia* tissue carbon, g C/m^2
TR = the input of carbon from carbohydrate storage, g $C/m^2/d$
M = 0.85 (CHNOP-C) on day 270, g C/m^2
k_d = fractional daily loss to the detrital pool, per day on days 1-270.

III. ZOOPLANKTON

1. $\frac{dZ}{dt} = Z(F - R) - U - D$

where: Z = zooplankton biomass, mg C/ℓ
F = feeding rate, weight specific per day
R = respiration rate, weight specific per day
U = unassimilated food, weight specific per day
D = mortality, weight specific per day

2. $F = F_{max}$ (Food Limitation)(Temperature Limitation)

where: F = feeding rate
F_{max} = maximum feeding rate, mg C/mg C/d
Food Limitation = $\frac{\text{Food Concentration, mg C/ℓ}}{k_f + \text{Food Concentration}}$
and k_f = Food Concentration at which feeding is half the maximum

Temperature Limitation = $\frac{T}{T_{opt}} \exp(1 - T/T_{opt})$

3. $R = r_o \exp(k_r T)$

where: r_o = respiratory rate at 0°C, mg C/mg C/d
k_r = slope of the curve describing respiration as a function of water temperature, per ^{o}C
T = water temperature, ^{o}C

4. $U = F \cdot x$

where: x = the fraction of ingested food which is not assimilated

5. $D = Z \cdot y$

where: D = mortality
y = the fraction of zooplankton biomass consumed by larger predators, per day

IV. DEAD ORGANIC MATTER

1. $$\frac{d(OM)}{dt} = J - X - s + E \pm A$$

where: OM is dissolved and dead particulate organic matter, mg C/ℓ

2. $J = M + U + D/z$

where: J is the input of organic detritus to the water
M = mortality of phytoplankton, mg C/ℓ/d
U = zooplankton feces, mb C/ℓ/d
D = *Posidonia* detritus, kd(CHNOP), g C/m/d
z = depth, m

3. $X = (X_o\, e^{k_x T}) \cdot (OM)$

where: X = the decomposition of organic detritus
X_o = the detrital decomposition rate at 0°C
k_x = the slope of the detrital decomposition rate as a function of temperature, per °C

4. $$s = \frac{W_s}{z} OM$$

where s = the loss by sinking, mg C/d
W_s = sinking rate, m/d
z = depth, m

5. E = inputs from all external sources

6. A = advective exchanges

V. SEDIMENT ORGANIC MATTER

1. $$\frac{dS}{dt} = J' - X'$$

where: S = standing crop of sediment organic matter, g C/m^2
X' = the decomposition of organic detritus on the bottom, g C/m^2/d
J' = input of organic detritus to the bottom, g C/m^2/d

2. and $J' = M + s \cdot z$

where: M = the input of *Posidonia* leaves on day 270, g C/m^2/d
s = sinking of dead organic matter from the water column, mg C/ℓ/d
z = depth, m

3. $X' = (X'_o\, e^{k_x T})S$

where: $X^{o\prime}$ = normalized decomposition rate of sediment organic matter at 0°C, per day
k_x = slope of the sediment organic matter decomposition rate as a function of temperature, per °C

VI. NUTRIENTS

1. $$\frac{dNH_4}{dt} = 12.6\,(Rz + X + \frac{X'}{z} - dP - \frac{dM}{z}) - N + E \pm A$$

where: NH_4 = concentration of ammonia in water, µmol/ℓ/d
12.6 converts stoichiometrically from mg C/ℓ to µmol NH_4/ℓ
Rz = zooplankton respiration rate mg C/ℓ/d
X = decomposition of OM, mg C/ℓ/d
z = depth, m
X' = decomposition of sediment organic matter, g C/m^2/d
dP = phytoplankton growth mg C/ℓ/d
dM = Posidonia growth, d CHNO/dt, g C/m^2/d

N = oxidation of NH_4 to NO_3, calculated by $N = \exp(k_{ox} \cdot T)$
where N_o = oxidation rate at 0°C, µM/µM/d
k_{ox} = slope of the curve expressing the oxidation rate as a function of temperature, per °C
T = water temperature, °C
E = external inputs, µmol/ℓ/d
A = advective transport, µmol/ℓ/d

2. $$\frac{dNO_3}{dt} = N + E \pm A - 12.6(dP + \frac{dM}{z})^*$$

where: N = oxidation of NH_4, µM/ℓ/d
Note: other terms are defined as in Eq. (VI 1).

3. $$\frac{dPO_4}{dt} = 0.8\,(Rz + X + \frac{X'}{z} - dP - \frac{dM}{z} + E \pm A$$

where: 0.8 converts stoichiometrically from mg C/ℓ to µmol PO_4/ℓ
other terms are defined as in Eq. (VI 1)

4. $$\frac{d\,Si(OH)_4}{dt} = 16.6\,(\frac{X'}{z} - dP_d) + E \pm A$$

where: 16.6 converts stoichiometrically from mg C/ℓ to µmol $Si(OH)_4$/ℓ
dP_d = the growth rate of diatoms, mg C/ℓ/d
other terms are defined as in Eq. (VI 1).

I PHYTOPLANKTON

(2) μ_{max} = 0.3/d for diatoms and for other phytoplankton in summer and winter

(3) r = 0.028, so growth = 0 at 1% I
C = baseline value, m^{-1} =

	summer	winter
coastal	0.27	0.13
offshore	0.02	0.03

must be corrected for increase due to phytoplankton Chl *a* (see text)
I_{opt} = 50% of visible light penetrating the water surface
I light incident on the surface as a forcing function

(4) PK1 = 0.05/°C for diatoms
= 0.06/°C for other phytoplankton
Tmax = 26°C for both
T = water temperature as a forcing function

(5) PKN = 1.0 µM for diatoms
0.5 µM for other phytoplankton
PKP = 0.1 µM for diatoms
= 0.05 µM for other phytoplankton
PKSi = 1.3 µM for diatoms, not considered for other phytoplankton

(6) All terms are simulated

(7) m = unspecified, i.e., no data available

II MACROPHYTES (POSIDONIA)

(1) Pmax = 0.022/d (value quite uncertain)
T_{opt} = 20°C

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*NO_3 uptake only if NH_4 drops below 0.5 µm

(2) R_{PI} = 135 Ly/d
C = see eq. I (3)
z = total depth

(3) T_{opt} = 20°C
K_d = 0.016/d (value quite uncertain)

III ZOOPLANKTON

(2) F_{max} = 0.5 mg C/mg C/d (filter feeders)
= 1.0 mg C/mg C/d (ciliates)
= 0.75 mg C/mg C/d (carnivorous zooplankton)

kf = 0.050 mg C/ℓ (filter feeders)
= 0.075 mg C/ℓ (ciliates)
= 0.0002 mg C/ℓ (carnivorous zooplankton)

T_{opt} = 26°C summer, all groups
15°C winter, all groups

(3) r_o = 0.034 mg C/mg C/d (filter feeders)
= 0.040 mg C/mg C/d (ciliates)
= 0.017 mg C/mg C/d (carnivorous zooplankton)

k_r = 0.10/°C (filter feeders)
= 0.110/°C (ciliates)
= 0.069/°C (carnivorous zooplankton)

(4) x = 0.12 (filter feeders)
= 0.20 (ciliates)
= 0.10 (carnivorous zooplankton)

(5) y = unspecified, i.e., no data available

IV DEAD ORGANIC MATTER

(3) X_o = 0.5 mg C/mg C/d
k_x = 0.069/°C

(4) 0 = 0.3 m/d

V SEDIMENT ORGANIC MATTER

(2) M = 0.85 CHNOP on day 270, g C/m^2

(3) X'_o = 0.02 mg C/mg C/d

VI NUTRIENTS

(1) N_o = 0.03 μM/μM/d
k_{ox} = 0.069/°C

3.4 Coupling between Hydrodynamical and Biological Models

Essentially, there are two main different approaches for coupling the basic hydrodynamic with a biological model. One is related to boxes in which the hydrodynamic fluxes are input- output variables through each box. In the other approach, the biological terms are treated as nonconservative tracers in advection-diffusion equations, and are computed on a regular grid that can be the same grid for the hydrodynamic computation.

Box models are in fact answerable to the same philosophy as depth-averaged hydrodynamic models. When one is particularly interested in the time evolution of biological variables, it seems reasonable in a first approximation, to perform a space integration over the region of interest. In a more refined way, the region can be divided into several individual boxes by their mean or integral properties. A model is then constructed for each box taking into account, in the inputs and outputs, the flows of material and energy from one box to another.

This approach leads to treat, from the mathematical point of view, ordinary differenatial equations which are easily solved by numerical methods. Furthermore, these kind of models can describe more details of the biological dynamics in each box. The drawback is due to the scarce spatial resolution, since boxes are usually large sea areas. If one is more interesting in the spatial distribution of the variables then the second approach is better. This leads to treat completely partial differential equations and the numerical solutions are more time and memory consuming, from the computational point of view, than for box models.

3.5 Examples of Marine Ecosystem Models

A typical and famous example of a box model is that one developed by Kremer and Nixon (1978) for the Narragansett Bay, Rhode Island. Figure 5 shows the area of the investigation and the division of it into eight boxes. Within each box the water properties are considered homogeneous. A sketch of the phytoplankton and zooplankton compartments is reported in Figure 6.

The hydrodynamic fluxes throughout the boxes are obtained by a numerical hydrodynamical model of the basin developed bu Hess and White (1974). This is an extension of the basic two-dimensional long wave propagation model by Leendertse (1967).

Some model results are given in Figure 7.

As an example of a model of the second kind, we report that one of Walsh (1978). This is essentially a model of coastal upwelling (see Figure 8). The basic hydrodynamics is very simple. The considered circulation is the seasonal stationary one. So, the velocities are considered stationary and are inserted into the biological dynamical equations (Figure 9). Diurnal peridiocities are specified in the biological coefficients. The results of this model were in a good agreement with measured data.

4. Applications of Models to Management Purposes

It has been frequently suggested that numerical ecosystem models should be applied directly to problems of environmental management as a tool for predicting the response of natural systems to perturbations and modifications of various kind. However, while such applications may be instructive, the results must be interpreted with caution. There are, after all, many differences between model systems and real ecosystems!

Since many management decisions are tied to questions of large or long term perturbations of the system, it may not be appropriate to extrapolate very far into the future a model that is constrained by being closed and nonevolving. These constraints become less important if the model is used to explore the responses of the present system to relatively small changes in parameters and processes that are specifically included in its formulation.

No matter how realistic the model, the results of simulations do not necessarily suggest the best management strategy. Even if we knew that the model simulations were absolutely correct about what happen, for example, if the sewage input were removed or doubled, it is not clear if either alternative is more desirable than the present situation. The model offer no escape from value judgements and long links of supposition for those involved in management issues.

It is important to emphasize that the interpretation of the model results in management must be closely restricted to effects and relationships deliberately included in the model. For this reason, it is most desirable that the management objectives and related questions to be posed to the model be specified from the outset. Only then can maximum information and confidence be achieved.

4.1 Environmental Management Models

There is no principal difference between scientific and environmental management models. Environmental management models have, on the other side, some characteristic features.

The management problem to be solved can often be formulated as follows: if certain forcing functions (management actions) are varied, what will be the influence on the ecosystem state? The model is used to answer this question or in other words to predict, what will change in the system, when forcing functions are varied with space and time. The term 'control function' is used to indicate forcing functions, that can be controlled by man such is regulation of water level in a river or discharge of pollutants into the sea. A class of environmental management models are in fact control models. They differ from other models by the content of the following two elements: a quantitative description of control processes, a formalization of objective and evaluation of achievements. This leads to consider problems under the framework of control theory. To understand the difference between control models and other environmental management models let us consider the following example. Suppose to have an eutrophication model. If we find the model response to various input of nutrients, we get the corresponding scenarios as model output. Among these scenarios the manager can select the one that he prefers from an ecological-economical viewpoint. This model is used as a management tool but is not a control model which needs within the model the specification of goals. We have then to add a control variable into the model and to find solutions that, for example, minimize the costs of nutrient removal with the constraint of achieving a certain degree of water quality. Control problems are then, from the mathematical point of view, optimization problems.

Where objectives are multiple, not all the formulated goals might be achieved simultaneously. Some of the goals might be even contradictory. Several transformations are available in operation research to solve multi goal problems. Nevertheless, the final selection of a control function may be determined by subjective criteria, such as aesthetic which cannot be precisely formulated. The final decision is in other words political.

A further step in complexity is the construction of ecological- economical models. It is often feasible to find a relation between a control function and the economy, but it is in most cases quite difficult to assess a relationship between the economy and the ecosystem state, What is, for instance, the economy advantages of an increased water transparency?

This presentation of economical-ecological models could give the impression, that environmental models always are more complex than scientific models. This is not true. Environmental management models have often a more clear formulation of the objective of the model than scientific models, which might render it more easy to select the complexity of the model in the first hand.

It is often advantageous to attack an environmental problem in the first hand by the use of simple models. They require very few data and can give the modeller and the decision maker some preliminary results. If the modelling project is stopped at this stage for one or another reason, a simple model is still better than no model, because it will at least give a survey of the problem. The simple model is, furthermore, a good starting point for the construction of more complex models.

4.2 Management Examples

We present now two simple examples dealing with management control models. These constitute only a starting point for further studies based on more complex models. However, they might be interesting to understand what control problems mean in the ecosystem management framework.

- Optimal Policies in Coastal Eutrophication.

This problem is reported in Mosetti (1988). Consider a coastal area on which there is a discharge of nutrients due to industrial activities. Assume that in a standard situation the level of nutrients in the basin has an average value N and that growth of some species of phytoplankton, say red algae, is limited by this nutrient. We assume the following growth model for red algae:

$$\dot{x}(t) = ANx(t) - kx(t) \qquad (10)$$

where: x(t) is the biomass of red algae at time t; A is a constant; and k is the mortality/respiration rate. Assume AN > k, so that there is an increasing of biomass. We postulate that to a growth of red algae corresponds an amount of economic damage for the community living near the basin area. We describe these costs by a function P(x) that is increasing in x and such as P(0)=0.

Suppose now that it is possible to remove nutrients in the basin by acting, for instance, at the source. In this way a control variable can be defined:

$$0 \leq u(t) \leq N = u_M$$

Substituting this into equation (10) we obtain the following control system:

$$\dot{x}(t) = Au(t)x(t) - kx(t) \qquad (11)$$

Nutrient removal has a cost proportional to $1-u/u_M$, that reaches a maximum value C when u = 0. An optimal management of this environmental system can be to minimize over a long time period the sum of the cost due to the environmental damage and the cost of the nutrient removal (cost-benefit analysis) i.e.

$$\int_0^\infty e^{-rt}\{C(1-\frac{u}{u_M})+P(x)\}\,dt \qquad (12)$$

being r the discount rate.

The problem is therefore to obtain the control law (discharge) that minimize the integral (12). It can be shown that the optimal solution is to reach the equilibrium point $\bar{x}$ defined by the equation :

$$\frac{dP}{dx}(\bar{x}) = \frac{rC}{Au_M\bar{x}}$$

as fast as possible and then, by applying the control value u = k/A, to remain in this point for all the time.

This means that if we start with an initial biomass $x < \bar{x}$ we have to 'pollute' at top level to reach in minimum time $\bar{x}$. If we start with $x > \bar{x}$ we have, on the contrary, to remove all the nutrients until $\bar{x}$ is reached as rapidly as possible. We can see that the larger is r the larger is the optimal equilibrium biomass. This shows the negative effect of the discount rate on the conservation of the environment.

Models of this kind are largely used for fishery management (see Clark, 1976).

- Control of Phytoplankton Growth by means of a Decoupling Feedback.

This second example of control model is taken from Mosetti (1991). The goal of the control action here is to decouple the growth of phytoplankton in an eutrophic environment from the discharge of a certain nutrient.

Let us consider now the three-compartment model with nutrients N_1 and N_2 and phytoplankton P.

The equations are :

$$\dot{N}_1 = -\frac{1}{2}\frac{N_1}{k_1+N_1}\frac{N_2}{k_2+N_2}P + u_1$$

$$\dot{N}_2 = -\frac{1}{2}\frac{N_2}{k_2+N_2}\frac{N_1}{k_1+N_1}P + u_2 \qquad (13)$$

$$\dot{P} = \frac{N_1}{k_1+N_1}\frac{N_2}{k_2+N_2}P - rP = f_3$$

From the application of some control theory it can be shown that if $N_2 \neq 0$ and $P \neq 0$ it is possible to obtain that each control variable acts only on one state variable. The feedback control law that do this is

$$u_1 = \frac{1}{2}\frac{N_1}{k_1+N_1}\frac{N_2}{k_2+N_2}P - P\{\frac{N_1N_2}{(k_1+N_1)(k_2+N_2)} - r\}^2\frac{(k_2+N_2)(k_1+N_1)^2}{k_1N_2P} +$$

$$+\frac{(k_2+N_2)(k_1+N_1)^2}{(k_1N_2P)}v_1 - \frac{k_2N_1(k_1+N_1)}{k_1N_2(K_2+N_2)}v_2 \qquad (14)$$

$$u_2 = \frac{1}{2}\frac{N_1}{k_1+N_1}\frac{N_2}{k_2+N_2}P + v_2$$

Where v_1 and v_2 are the new inputs.

In a new coordinate system our decoupling system becomes explicitly :

$$\dot{P} = f_3 = :\xi$$

$$\dot{\xi} = v_1 \qquad (15)$$

$$\dot{N}_2 = v_2$$

Equations (15) clearly shows the decoupled structure : each of the control variable acts only on one state variable so that, for instance, variations of v_2 do not cause variations of P. This is the essential feature of this technique.

It is to stress that v_1 and v_2 are additional inputs which can be used to regulate further the system once that the decoupling feedback law has been implemented. In fact, to keep the system decoupled, it is sufficient to apply the control law (14) setting $v_1 = v_2 = 0$. On the other hand , v_1 and v_2 can be seen as some noise or fluctuation, which is not controllable, added to the controlled discharge rates of nutrients. We shall use the last approach in what follows.

This suggests the following application. Let $v_1 = 0$ and assume that the concentration of the nutrient N_2 be less controllable and more fluctuating than N_1. Then, the solution for P is :

$$P(t) = \xi(0)t + P(0)$$

being t = 0 a given initial time.

Now if $\xi(0) = 0$, than P(t) = p(0) for every t whatever the fluctuation of v_2 will be. The growth of phytoplankton will not depend upon variations of N_2. This is an important feature mainly if N_2 is the most limiting nutrient.

Remember that for keeping the decoupled structure, the feedback law (14) has to be implemented by some control technique on the discharge rate of u_1 and u_2.

A simulation has been obtained by solving equations (13) with the feedback law (14) by means of a Runge-Kutta fourth-order method. With the following values for the parameters: $k_1 = 1$, $k_2 = 0.6$, $r = 0.1$

Figure 11 shows, for a given initial condition, the time evolution of the three state variables and the two control variables with a constant input rate for both u_1 and u_2.

Since for t = 20 days we have that $\dot{P} = \xi(0) = 0$ we take this time for starting the control action.

Figure 12 illustrates the result of the controlled system if a random fluctuation is added to the discharge of u_2 .

Note that phytoplankton concentration remains unaltered when the control law is acting, and that is not influenced by fluctuations in nutrient supply.

5. Concluding Remarks

It is important to emphasize that ecological models will never be the universal panacea to biological oceanography; nor will they ever replace the need for well-designed observations on the real world. But, if they are used intelligently, good models should help make the observational process more economical, more penetrating and the interpretation of the results more stimulating.

Reductionist models are more commonly used and more readily understood by biologists without a strong mathematical background: they offer the advantage that, given sufficient resources, each component model can be researched in detail.

Holistic approaches the whole ecosystem dynamics, on the contrary, are relatively unexplored so far.

It is however fundamental for all the models,wether holistic or reductionist, to measure physiological rates for the computation of ecological fluxes. Quantification of rates is the only avenue by which models can be driven from the static to the dynamics. A static representation of a dynamic system is of but limited utility.

It is also to fix in mind the idea of scales in time and space. Adequate consideration of scales will help avoid a mismatch between sampling intervals and desired resolution of the data. It should be clear that all processes with characteristic frequency greater than the inverse of the fundamental time-scale of the model will necessarily be parametrized. Processes with lower characteristic frquency may be treated deterministically. Implicit in the choice of time-scale for a model is the decision that processes on a smaller time-scale will be time-averaged. For example, if the fundamental time-step in a dynamic simulation model is one day, the the detailed, nonlinear effects of, say, vertical migration of zooplankton feeding will be averaged out. This is not a bad thing, but the modeller should be aware of this.

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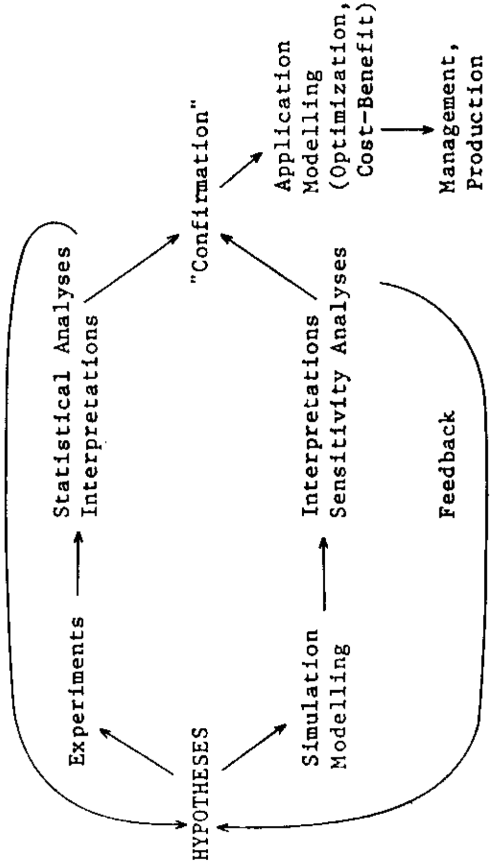


Fig. 1 The role of models in research. Modelling may be seen as analogous to traditional experimental science, with the predictions of the model testing the adequacy of the mathematical formulations (hypothesis) in explaining observations.

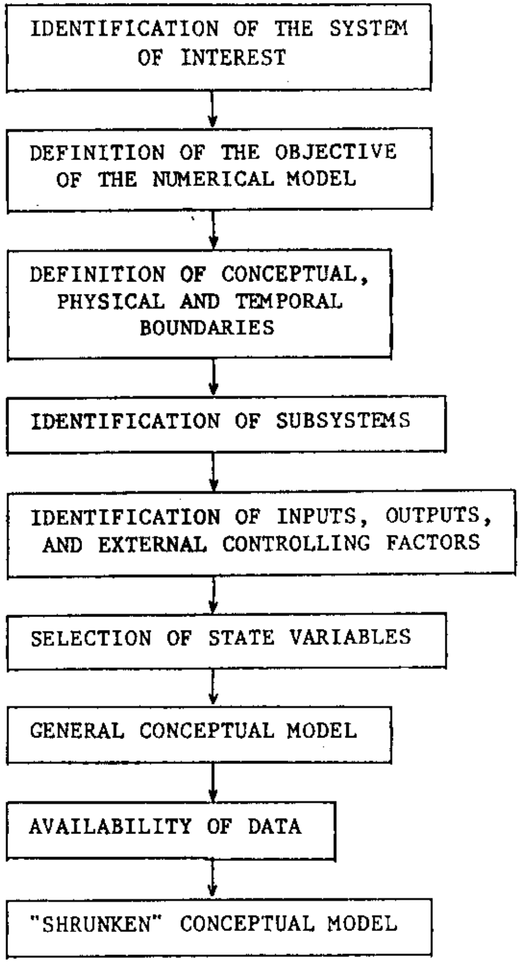


Fig. 2 General scheme for preparing a conceptual model.

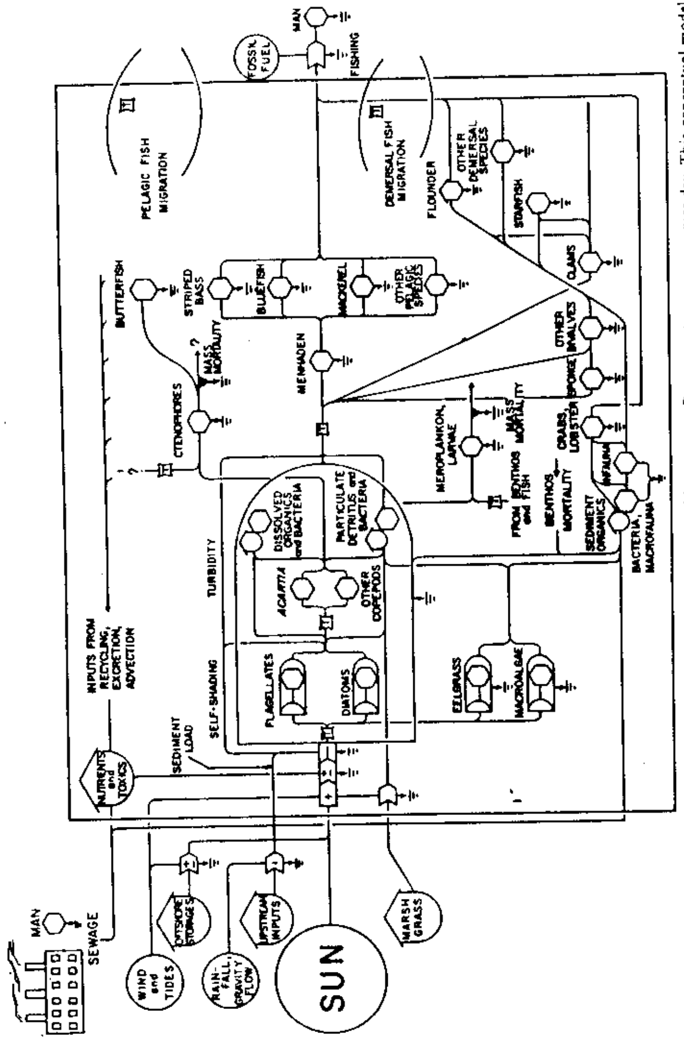


Fig. **3** A complex, but still greatly simplified energy flow diagram for the Narragansett Bay ecosystem on a summer day. This conceptual model was a first step in the process of abstraction that led to development of the numerical model. Symbols follow Odum (1972), and have been used to synthesize past and on-going bay studies by a large number of people

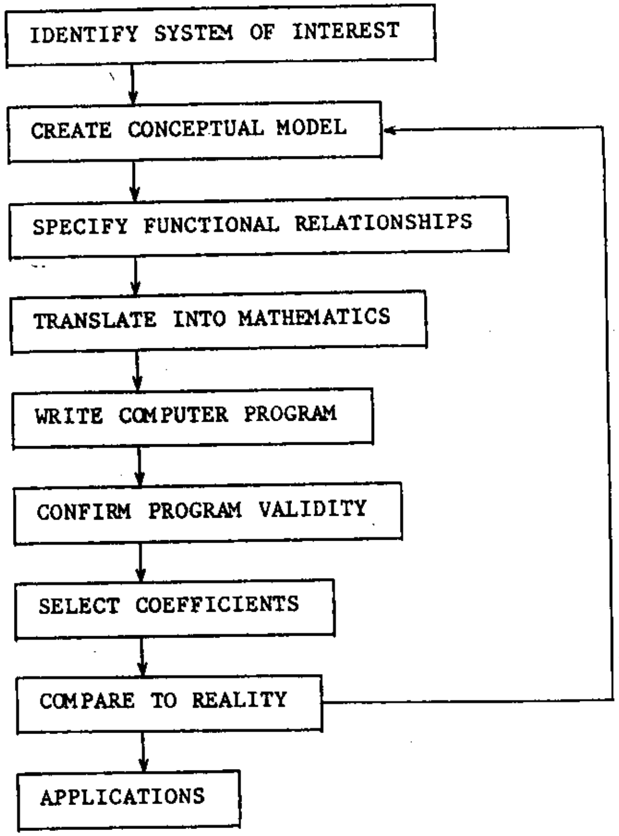


Fig. **4** Iterative processes involved in updating a conceptual model.

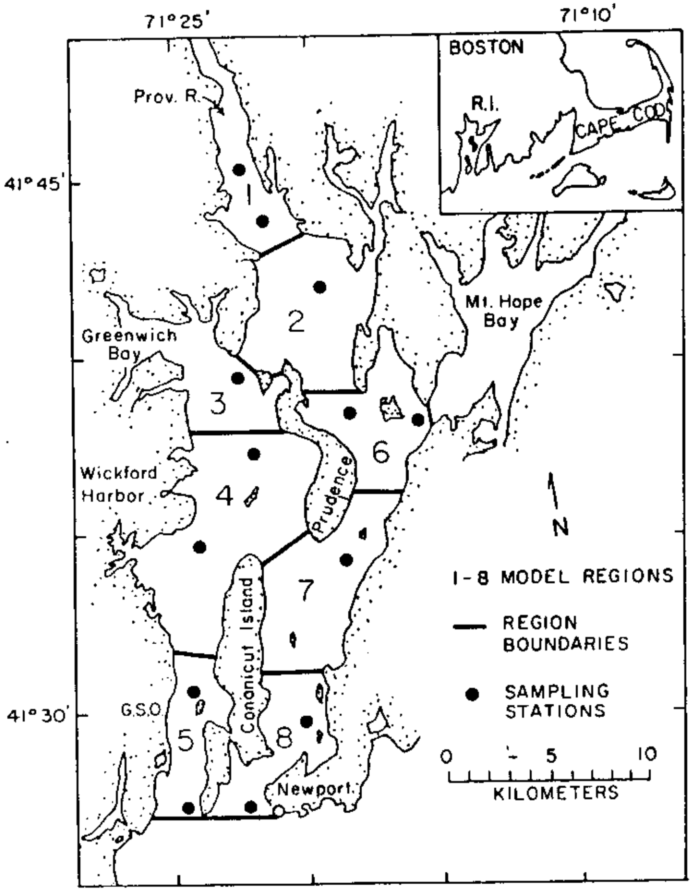
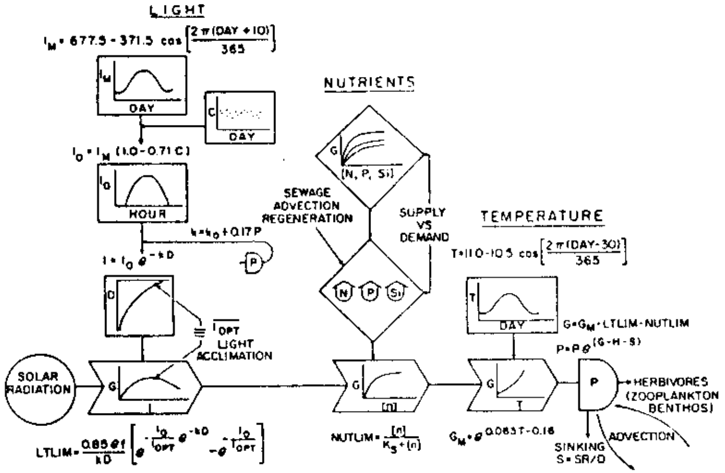
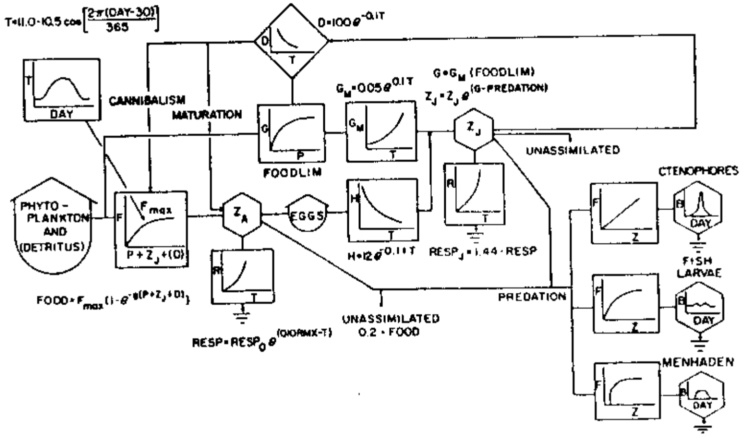


Fig. **5** Narragansett Bay, Rhode Island, and its location on the New England coastline. *Heavy dots:* stations sampled over an annual cycle to collect zooplankton, phytoplankton, and nutrient data for comparison with model simulations. The eight spatial elements or ecological subsystems of the bay were coupled by a hydrodynamic mixing model

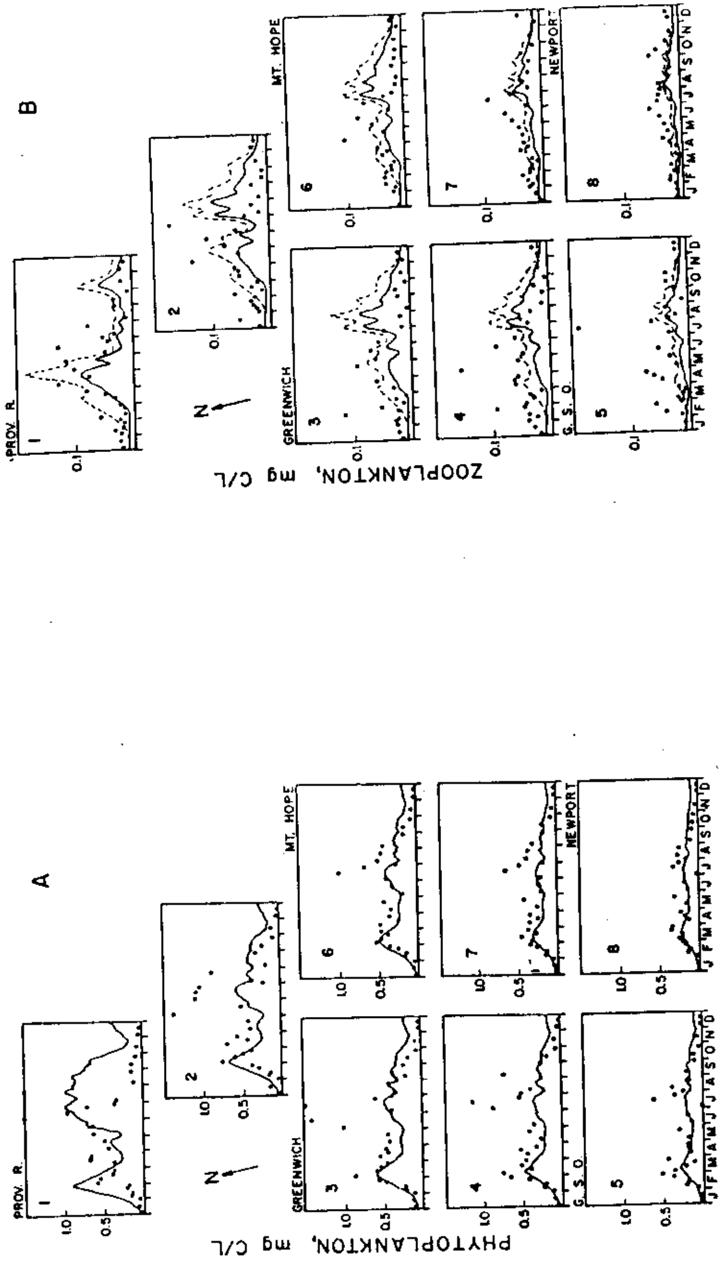


Flow diagram for the phytoplankton compartment showing relationships among the major equations described in text and a graphical representation of their behavior



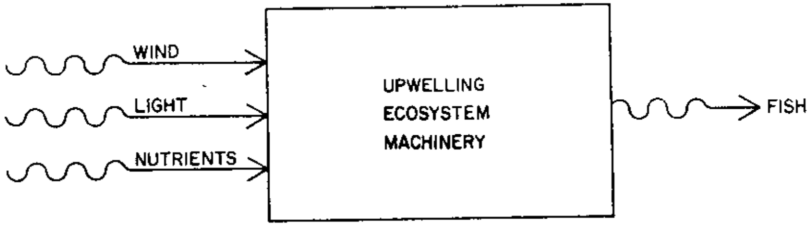
Flow diagram for the zooplankton compartment showing relationships among the major equations described in text and a graphical representation of their behavior

Fig. 6



Comparison of computed (*solid and broken lines*) and observed (●) values in the eight spatial elements of Narragansett Bay (Fig. 1) for the standard run and sample year Aug. 1972–Aug. 1973 (Figs. 4–6). (A) Phytoplankton. (B) Zooplankton adults plus juveniles over 50% mature (*solid line*), and total zooplankton (*broken line*).

Fig. 7



A conceptual black-box model of time dependent interactions within upwelling ecosystems.

Fig. 8

Nitrate

$$\frac{\partial NO_3}{\partial t} = -\frac{\partial uNO_3}{\partial x} - \frac{\partial wNO_3}{\partial z} + \frac{K_y \partial^2 NO_3}{\partial y^2} - \frac{V_m NO_3 P_n}{K_t + NO_3}$$

where $V_m = (0.11 - 0.02\ NH_3) \sin 0.2618t$

Recycled nitrogen:

$$\frac{\partial NH_3}{\partial t} = -\frac{\partial uNH_3}{\partial x} - \frac{\partial wNH_3}{\partial z} + \frac{K_y \partial^2 NH_3}{\partial y^2} - \frac{V_n NH_3 P_n}{K_t + NH_3} + (0.67)\frac{G_z(P_n - P_0)Z_n}{P_k + (P_n - P_0)} + (0.67)\frac{G_f(P_n - P_a)F_n}{P_f + (P_n - P_a)}$$

where $V_n = 0.11 \sin 0.2618t$.

Phosphate:

$$\frac{\partial PO_4}{\partial t} = -\frac{\partial uPO_4}{\partial x} - \frac{\partial wPO_4}{\partial z} + \frac{K_y \partial^2 PO_4}{\partial y^2} - \frac{V_p(PO_4)(0.067P_n)}{K_p + PO_4} + (0.13)\frac{G_z(P_n - P_0)Z_n}{P_k + (P_n - P_0)} + (0.13)\frac{G_f(P_n - P_a)F_n}{P_f + (P_n - P_a)}$$

where $V_p = 0.11 \sin 0.2618t$.

Silicate:

$$\frac{\partial SiO_4}{\partial t} = -\frac{\partial uSiO_4}{\partial x} - \frac{\partial wSiO_4}{\partial z} + \frac{K_y \partial^2 SiO_4}{\partial y^2} - \frac{V_s(SiO_4)(0.67P_n)}{K_s + SiO_4}$$

where $V_s = 0.11 \sin 0.2618t$.

Phytoplankton carbon:

$$\frac{\partial P_c}{\partial t} = -\frac{\partial uP_c}{\partial x} - \frac{\partial wP_c}{\partial z} + \frac{K_y \partial^2 P_c}{\partial y^2} - \frac{G_z(P_c - 5P_0)(5Z_n)}{5P_k + (P_c + 5P_0)} - \frac{G_f(P_c - 5P_a)(5F_n)}{5P_f + (P_c - 5P_a)} + \frac{V_a\{\exp[1 - (I_s/I_m)] - \exp[1 + (I_a/I_m)]\}(P_c)}{rz}$$

where $I_a = I_t\,(0.1309 \sin 0.2618t)$

$I_z = I_a e^{-rz}$

$r = 0.04 + 0.0021P_c + 0.021(P_c)^{0.67}$

Phytoplankton nitrogen:

$$\frac{\partial P_n}{\partial t} = -\frac{\partial uP_n}{\partial x} - \frac{\partial wP_n}{\partial z} + \frac{K_y \partial^2 P_n}{\partial y^2} - \frac{G_z(P_n - P_0)Z_n}{P_k + (P_n - P_0)} - \frac{G_f(P_n - P_a)F_n}{P_f + (P_n - P_a)} + VP_n$$

where V is the minimum of

$$\left\{\frac{V_m NO_3}{K_t + NO_3} + \frac{V_n NH_3}{K_t + NH_3};\frac{V_s SiO_4}{K_s + SiO_4};\frac{V_p PO_4}{K_p + PO_4};\frac{V_a I_z}{K_I + I_z}\right\}$$

with $I_z = I_0 e^{-jz}$

$j = 0.16 + 0.0053P_n + 0.039(P_n)^{0.67}$

Zooplankton nitrogen:

$$\frac{\partial Z_n}{\partial t} = (1.00 - 0.67 - 0.13 - 0.20)\frac{G_z(P_n - P_0)Z_n}{P_k + (P_n - P_0)}$$

where $G_z = 0.03 \cos(0.2618t + 1.571)$ if $z < 30$ m

$= 0.03 \sin 0.2618t$ if $z > 30$ m

Nekton nitrogen:

$$\frac{\partial F_n}{\partial t} = (1.00 - 0.67 - 0.13 - 0.20)\frac{G_f(P_n - P_a)F_n}{P_f + (P_n - P_a)}$$

where $G_f = 0.008 \cos(0.2618t + 1.571)$ if $z < 30$ m

$= 0.008 \sin 0.2618t$ if $z > 30$ m

Detrital nitrogen:

$$\frac{\partial D_n}{\partial t} = -\frac{\partial uD_n}{\partial x} - \frac{\partial wD_n}{\partial z} + 0.2\frac{G_z(P_n - P_0)Z_n}{P_k + (P_n - P_0)}$$

$$+ 0.2\ G_f(P_n - P_a)F_n \quad \partial D_n$$

Fig.9

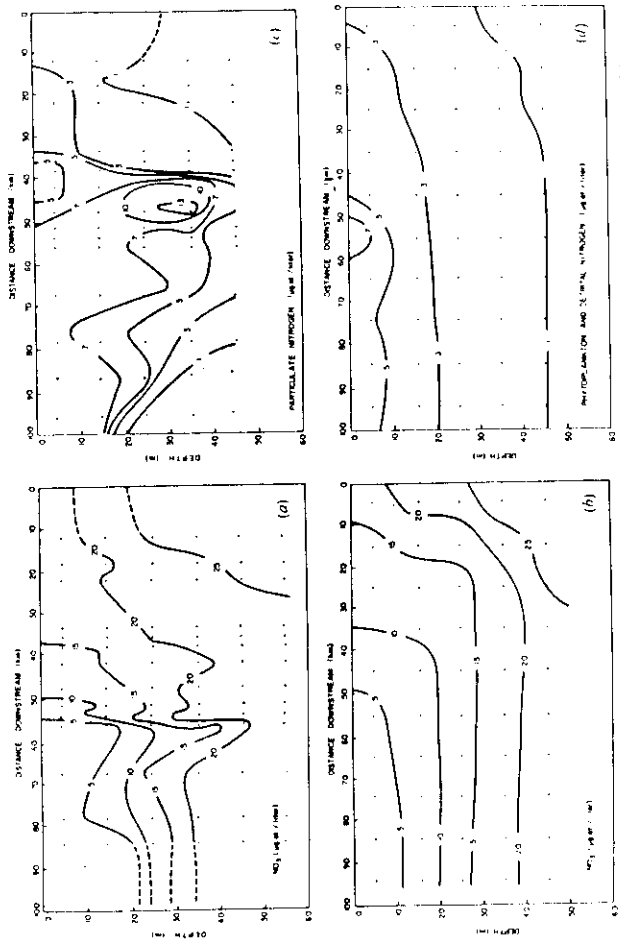
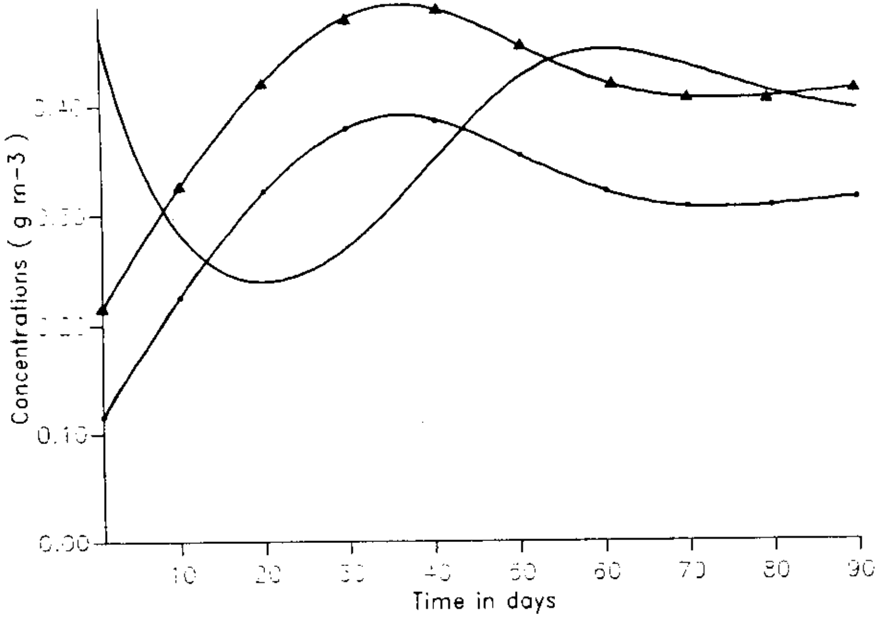
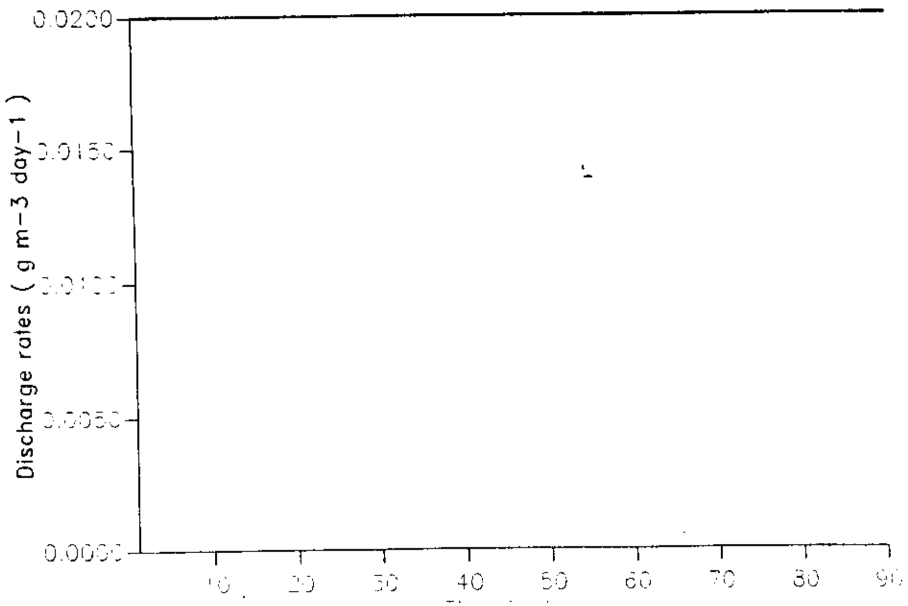
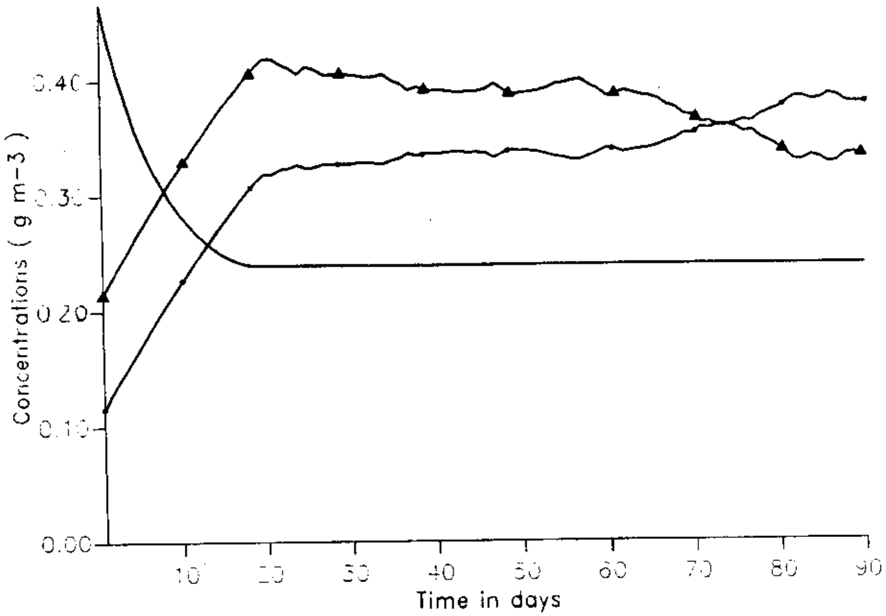


Fig 10 A comparison of observed (*a*, *c*) and simulated (*b*, *d*) nitrate and particulate nitrogen (detritus and phytoplankton) over 0 to 50 m of the autumn water column off Peru (after Walsh, 1975c).



- **Figure 11** Evolution of phytoplankton P (——), nutrients N_1 (—•—) and N_2 (—▲—) and constant discharge rates u_1 (——) and u_2 (—··—) . No control action.





- **Figure 12.** Evolution of phytoplankton P, nutrients N_1 and N_2 and discharge rates u_1 and u_2 under control operations starting at t=20 with $v_1 = 0$ and v_2 random.