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"Course on Shallow Water and Shelf Sea Dynamics"
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"Transparencies"

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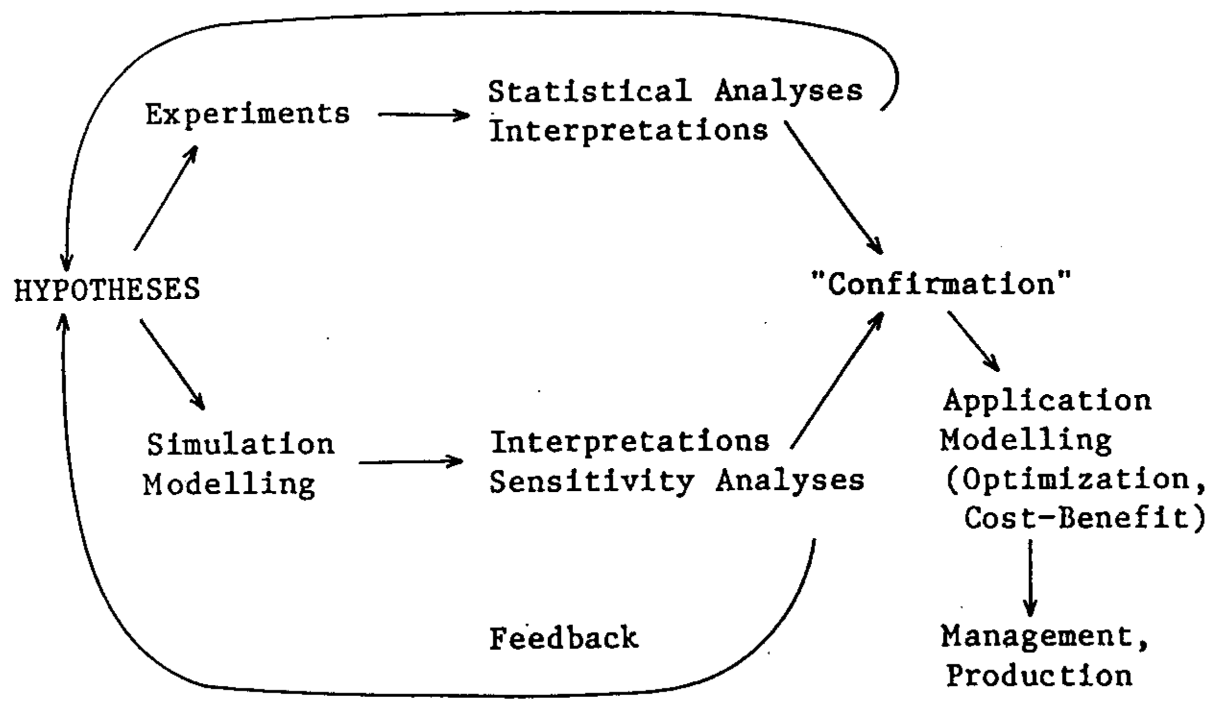


Fig. 1 The role of models in research. Modelling may be seen as analogous to traditional experimental science, with the predictions of the model testing the adequacy of the mathematical formulations (hypothesis) in explaining observations.

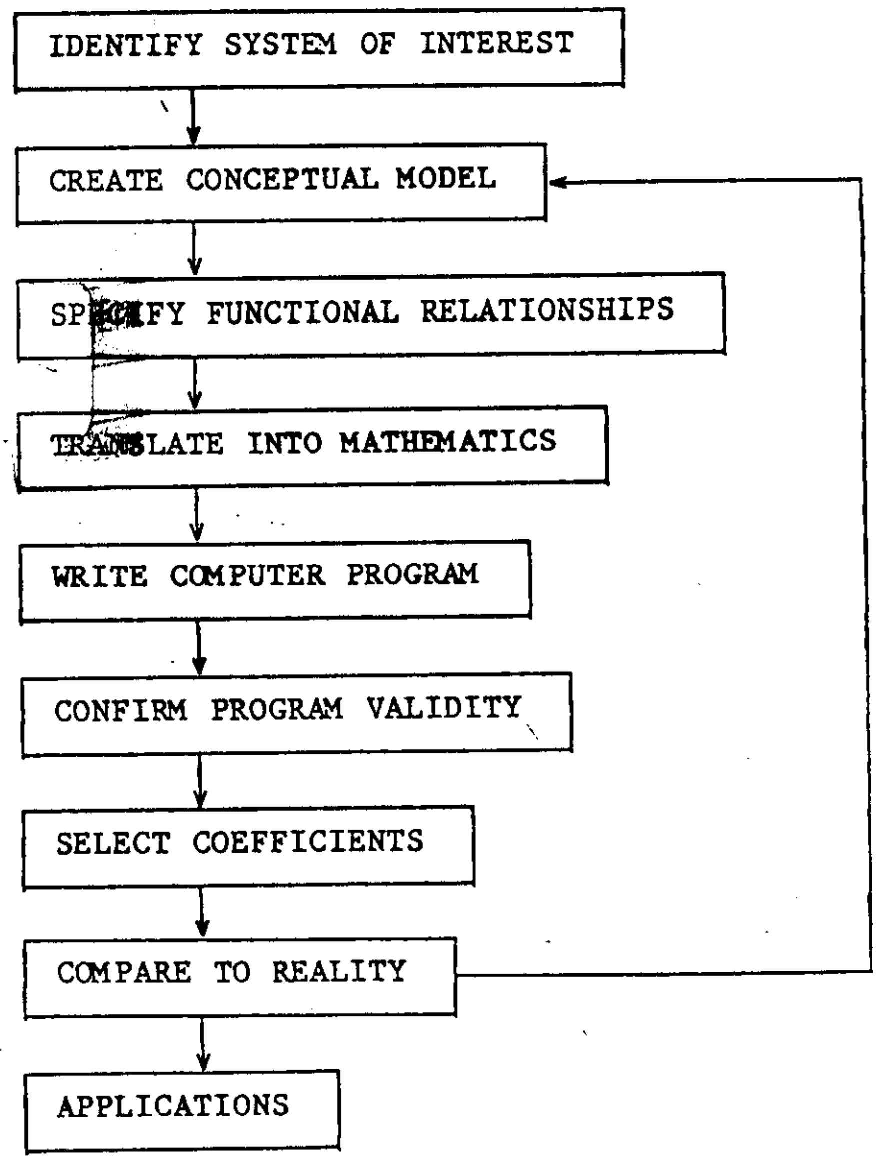


Fig. 4 Iterative processes involved in updating a conceptual model.

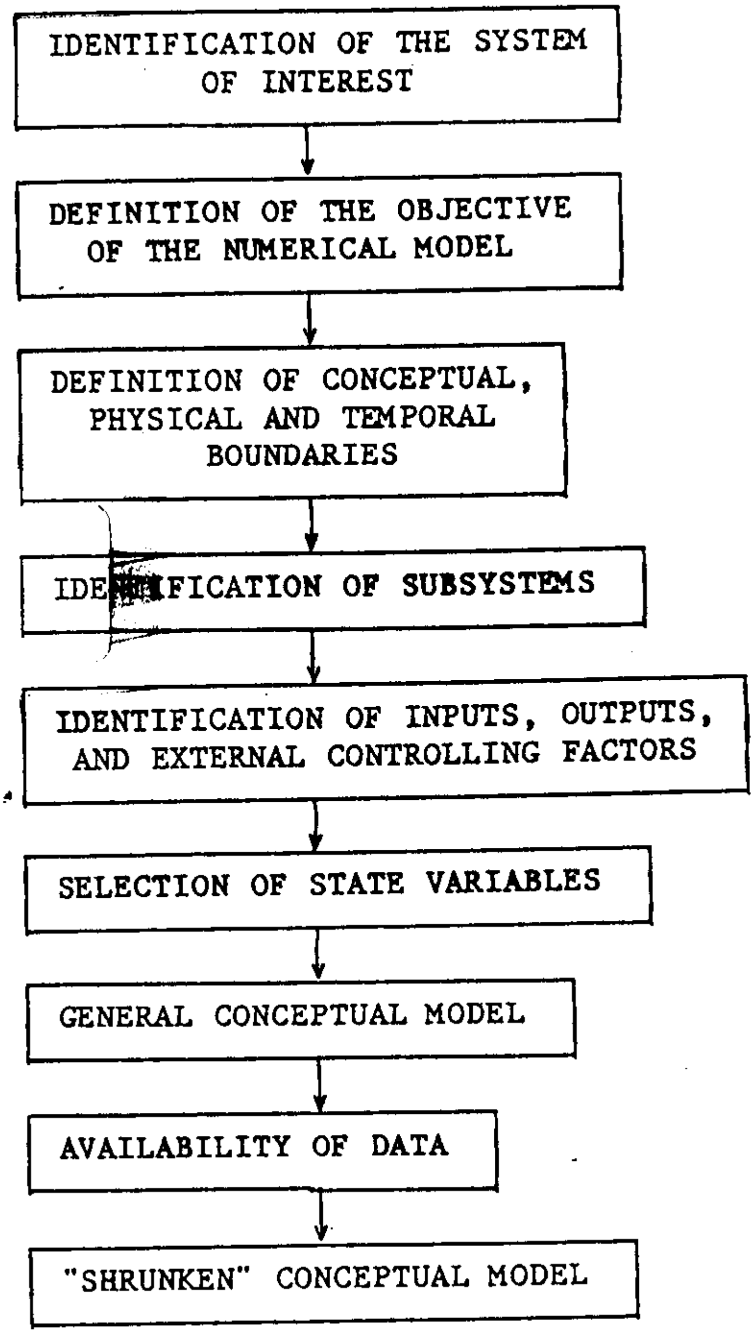


Fig. 2 General scheme for preparing a conceptual model.

Reductionist vs. Holistic Models

- Reductionist approach : Properties of an ecosystem = Sum of all details

  Methods of investigation → as Classical Mechanics

- Holistic approach : Properties of an ecosystem = global behaviour

  Methods of investigation → Statistical Mechanics, Thermodynamics, Information theory.

Complexity

Two components of an ecosystem : 3 observations to state whether the relationship is linear or non linear;
"Uncertainty Principle in Ecology" [illegible]

$$10^5 \frac{\Delta x}{\sqrt{3^{n-1}}} = 1$$

where : Δx is the relative accuracy, n is the number of components of the ecosystem.

From: Jørgensen, 1990: Fundamentals of Ecological modelling, Elsevier.

of observations:

$$\Delta t \, \Delta E \geq h/4\pi \quad (4)$$

where Δt is the uncertainty in time and ΔE in energy. If we use all the energy that earth has received during its lifetime of 4.5 billion years we get:

$$173 \times 10^{15} \times 4.5 \times 10^{9} \times 365.3 \times 24 \times 3600 = 2.5 \times 10^{34} \text{ J} \quad (5)$$

Δt would therefore be in the order of 10^{-67} s. Consequently, an observation will take 10^{-67} s even if we use all the energy which has been available on earth as ΔE, which must be considered the most extreme case. The number of observations during the lifetime of the earth would therefore be:

$$4.5 \times 10^{9} \times 365.3 \times 24 \times 3600/10^{-67} = 1.5 \times 10^{84} \quad (6)$$

This implies that we can replace 10^5 in equation (2) with 10^{59} since:

$$10^{-17}/\sqrt{1.5 \times 10^{84}} = 10^{-59}$$

If we use $\Delta x = 1$ in equation (2) we get:

$$\sqrt{3^{n-1}} = 10^{59} \quad (7)$$

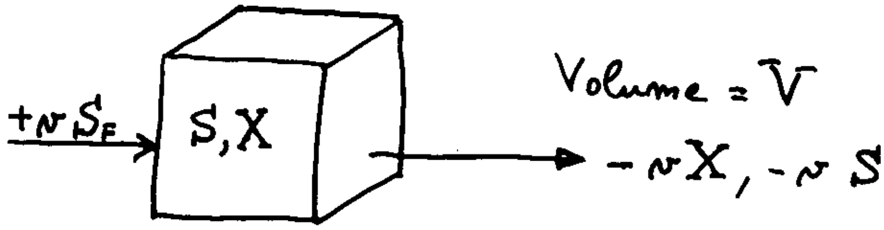
or

$$n \approx 240$$

!

From these very theoretical considerations, it is clear that we shall never get a sufficient number of observations to be able to describe even one ecosystem in detail. These results are completely in accordance with Niels Bohr, who expressed it as follows: "It is not possible to make an unambiguous picture (model) of reality, as the uncertainty limits our knowledge". The uncertainty in nuclear physics is caused by the inevitable influence of the observer on the atomic particles, and in ecology it is caused by the enormous complexity and variability.

A biological reactor.



S = substrate concentration ;
X = microorganism concentration ;
S_F = supply of substrate ;
v = flow rate.

Mass balance for the two components gives :

$$V \frac{dX}{dt} = V\mu X - vX$$

$$V \frac{dS}{dt} = V\mu X / Y + v S_F - v S$$

= specific growth rate ; Y = coefficient (stoichiometry)

Usually $$\mu = \hat{\mu} \frac{S}{K_S + S}$$ (Michaelis - Menten - Monod)

Phytoplankton

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

- Growth

Self-regulatory effect of nutrient concentration on the rate of uptake follows the Michaelis-Menten-Monod law:

$$V = V_{MAX} \frac{S}{K_S + S}$$

S is the ambient nutrient concentration and K_S (semi-saturation constant) the concentration at which the specific uptake rate V is 1/2 of the maximum attainable rate V_{MAX}.

Liebig's law:

If we have more nutrients $S_1, \dots, S_N$ then:

$$V = V_{MAX} \cdot \min \left\{ \frac{S_1}{K_1 + S_1}, \dots, \frac{S_N}{K_N + S_N} \right\}$$

The minimum is "the most limiting nutrient"

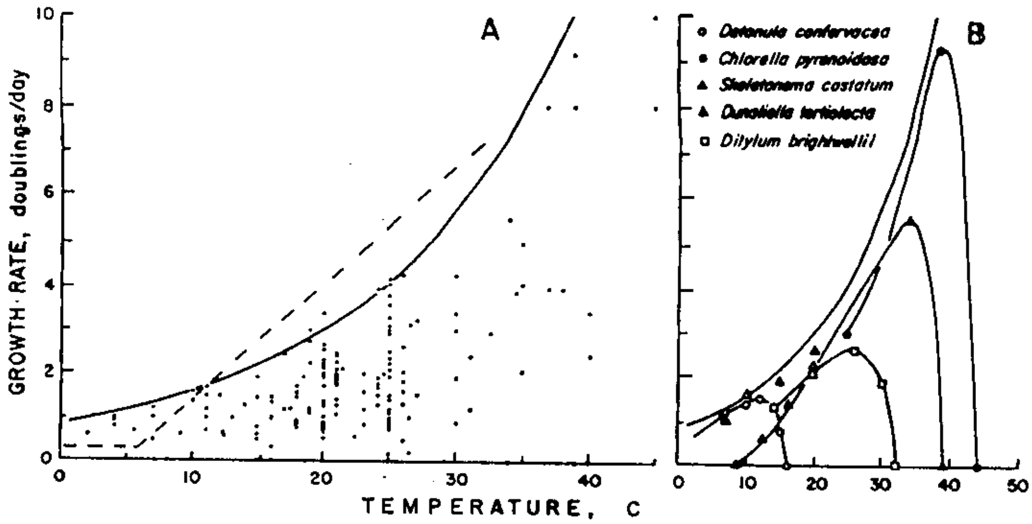


Fig. 15 A and B. Temperature response of phytoplankton growth rate. (A) Measurements of maximum specific growth rate in doublings per day for laboratory cultures largely in continuous light (Epply, 1972). *Solid line:* hypothetical maximum Eq. (7) used in most simulations. *Dashed line:* used in some runs of the model to represent a second, warm-water species-group. (B) Observations of specific growth rates for five species of unicellular algae demonstrating patterns of thermal optima which underlie the hypothetical maximum (Eppley, 1972)

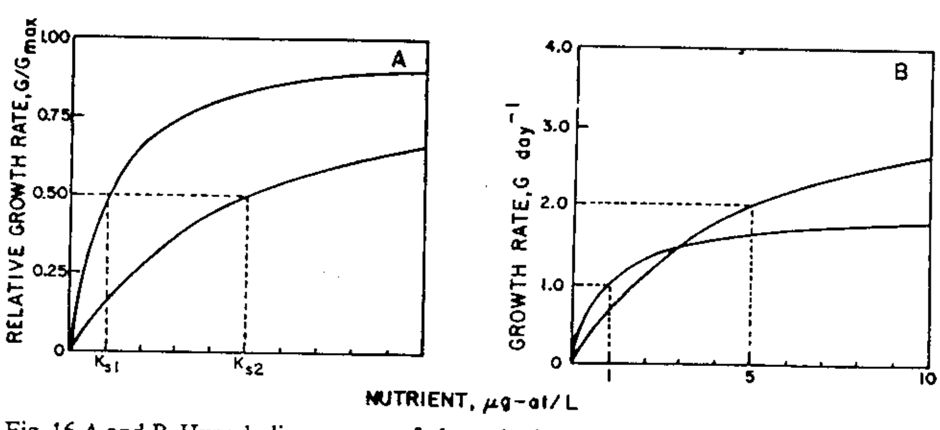


Fig. 16 A and B. Hyperbolic response of phytoplankton growth to a limiting nutrient. The half-saturation constants (K_s) are defined as the concentration at which growth is one-half the maximum. When growth is normalized to a maximum of 1.0, conclusions about the relative competitive advantage of species may be unwarranted. Species 1, with the lower K_s, appears totally dominant in the normalized representation (A). Consideration of the actual growth rates, however, reveals that species 2 grows faster at nutrient levels above 3 µg-at/l (B)

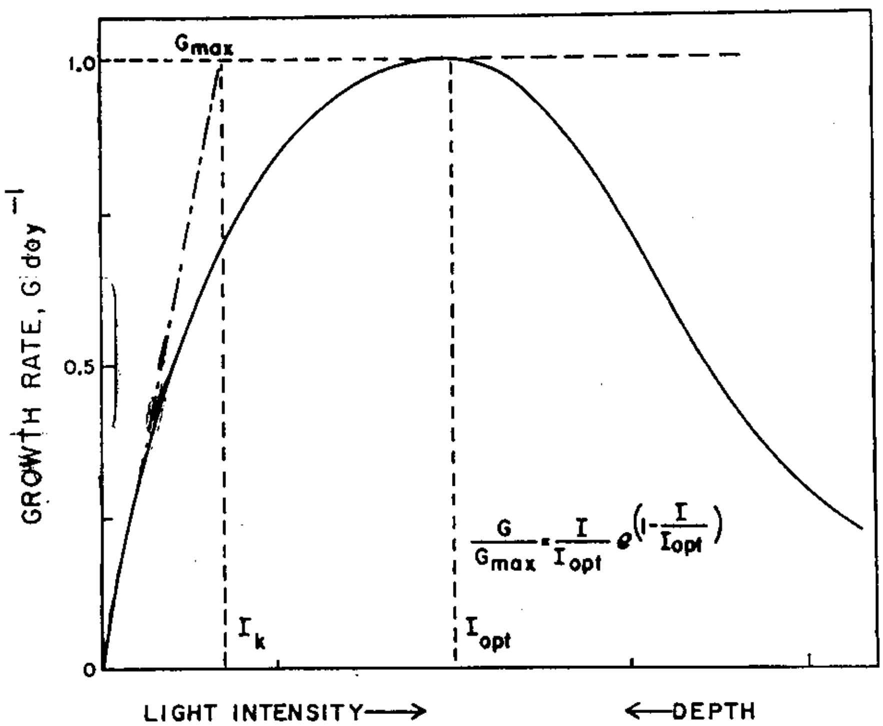


Fig. 17. Theoretical formulation for the instantaneous photosynthesis-light response of phytoplankton (Steele, 1962). The normalized Eq. (12) predicts growth relative to the maximum as a function of the ratio of the incident and the optimum light intensity, I/I_{opt}. Some experimental observations demonstrate a plateau with little or no high light inhibition. In such cases, another measure of light response may be used, with I_k defined as the intersection of the initial slope of the hyperbola with the maximum growth rate

1974, 1974a) and some rather complicated formulations have emerged in order to provide flexibility in curve-fitting the variable degree of high-level inhibition that is observed. Recent work has also produced theoretical analyses suggesting more fundamental expressions of the photosynthetic response to light quanta (Bannister, 1974). The equation proposed by Steele (1962) remains one of the more simple and remarkably versatile:

$$G = G_{max} \times \frac{I}{I_{opt}} e^{(1 - I/I_{opt})} \tag{11}$$

or

$$G/G_{max} = \frac{I}{I_{opt}} e^{(1 - I/I_{opt})}. \tag{12}$$

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 = $\frac{\bar{I}}{I_{opt}} \exp(1 - \bar{I}/I_{opt}) - r \quad (1 + r)$

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

$\bar{I}_s$ = 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, $\bar{I} < 0.01\ I_{opt}$

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

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

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, °C
- T_{opt} = the optimum temperature for *Posidonia* photosynthesis, °C
- I_z = visible light reaching the bottom, Ly/d
- k_{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

$$\text{Food Limitation} = \frac{\text{Food Concentration, mg C/ℓ}}{k_f + \text{Food Concentration}}$$

and k_f = Food Concentration at which feeding is half the maximum

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

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 °C
- T = water temperature, °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/m²
   X' = the decomposition of organic detritus on the bottom, g C/m²/d
   J' = input of organic detritus to the bottom, g C/m²/d

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

   where: M = the input of Posidonia leaves on day 270, g C/m²/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/m²/d
   dP = phytoplankton growth mg C/ℓ/d
   dM = Posidonia growth, d CHNO/dt, g C/m²/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. $$\frac{dNO_3}{dt} = N + E \pm A - 12.6\left(dP + \frac{dM}{z}\right)^*$$

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

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

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

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

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).

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*NO_3 uptake only if NH_4 drops below 0.5 µm

MODEL PARAMETERS

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)
$\frac{I_{opt}}{I}$ = 50% of visible light penetrating the water surface
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

(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

Coupling between Hydrodynamical and Biological models

"Box" Models : Space integration, Fluxes given by an hydrodynamical model ; O.D.E. → more efficient computationally, low spatial resolution.

Advection-Diffusion Models : computation on a grid, P.D.E → time and memory consuming, great spatial resolution.

Let

$$Q_\alpha = \langle R_\alpha \rangle \tag{1.17}$$

$$I_\alpha = \langle J_\alpha \rangle \tag{1.18}$$

and let $\boldsymbol{\sigma}_\alpha$ denote the mean migration velocity, eq. 1.14 gives:

$$\frac{\partial r_\alpha}{\partial t} + \nabla \cdot r_\alpha \boldsymbol{u} = Q_\alpha + I_\alpha - \nabla \cdot r_\alpha \boldsymbol{\sigma}_\alpha + \mathcal{D}_\alpha \tag{1.19}$$

The roles of the different terms of eq. 1.19 are easily identified:

$\nabla \cdot r_\alpha \boldsymbol{u}$ represents the advection by the mean motion. It introduces a coupling with the mechanical variables.

Q_α represents the local inputs and outputs from the exterior world. (Dumpings are in particular included in Q_α.) Q_α must be given before the model can be operated.

I_α represents the chemical, biochemical and ecological interactions. I_α introduces a coupling between the state variables r_α and interacting state variables r_β, r_γ, etc.

$-\nabla \cdot r_\alpha \boldsymbol{\sigma}_\alpha$ represents the migration. The migration velocities are usually expressed in semi-empirical form inferred from observations, and theoretical reflections on the ecological, chemical and physical properties of the compartments (living species, flocculated suspensions, hydrated combinations, etc.). $\boldsymbol{\sigma}_\alpha$ may be regarded as a control parameter.

$\mathcal{D}_\alpha$ represents the molecular and turbulent dispersion. $\mathcal{D}_\alpha$ is expressed in terms of the mean concentration r_α by semi-empirical

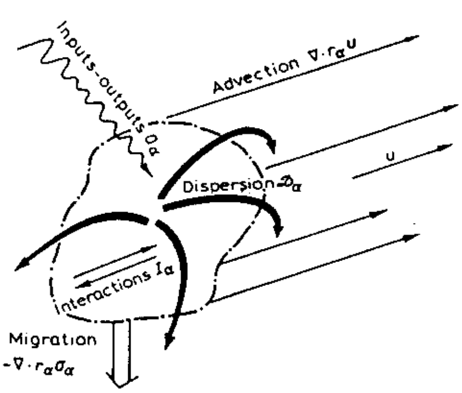
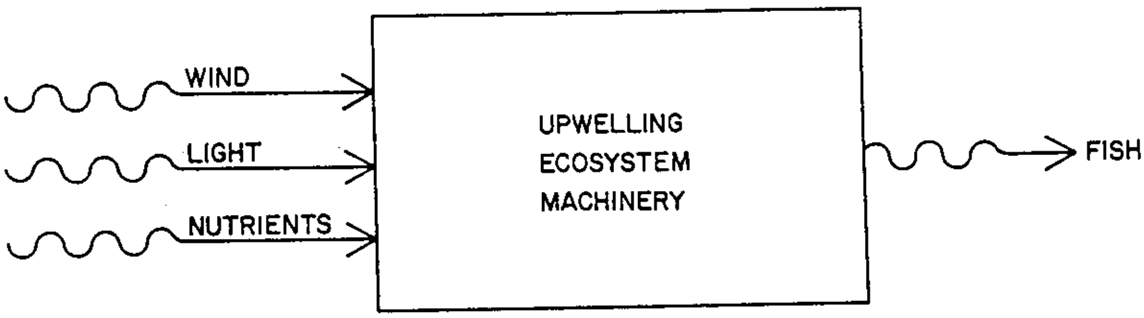


Fig. 1.8. Schematic diagram of the mechanisms affecting the evolution in time of the state variable r_α.

From: Walsh, 1975; In 'The Sea' Vol. 6; Wiley & Sons.



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:

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

where $I_a = I_t\ (0.1309 \sin 0.2618t)$
$I_s = I_a e^{-rz}$
$r = 0.04 + 0.0021P_c + 0.021(P_c)^{0.67}$

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

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

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:

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

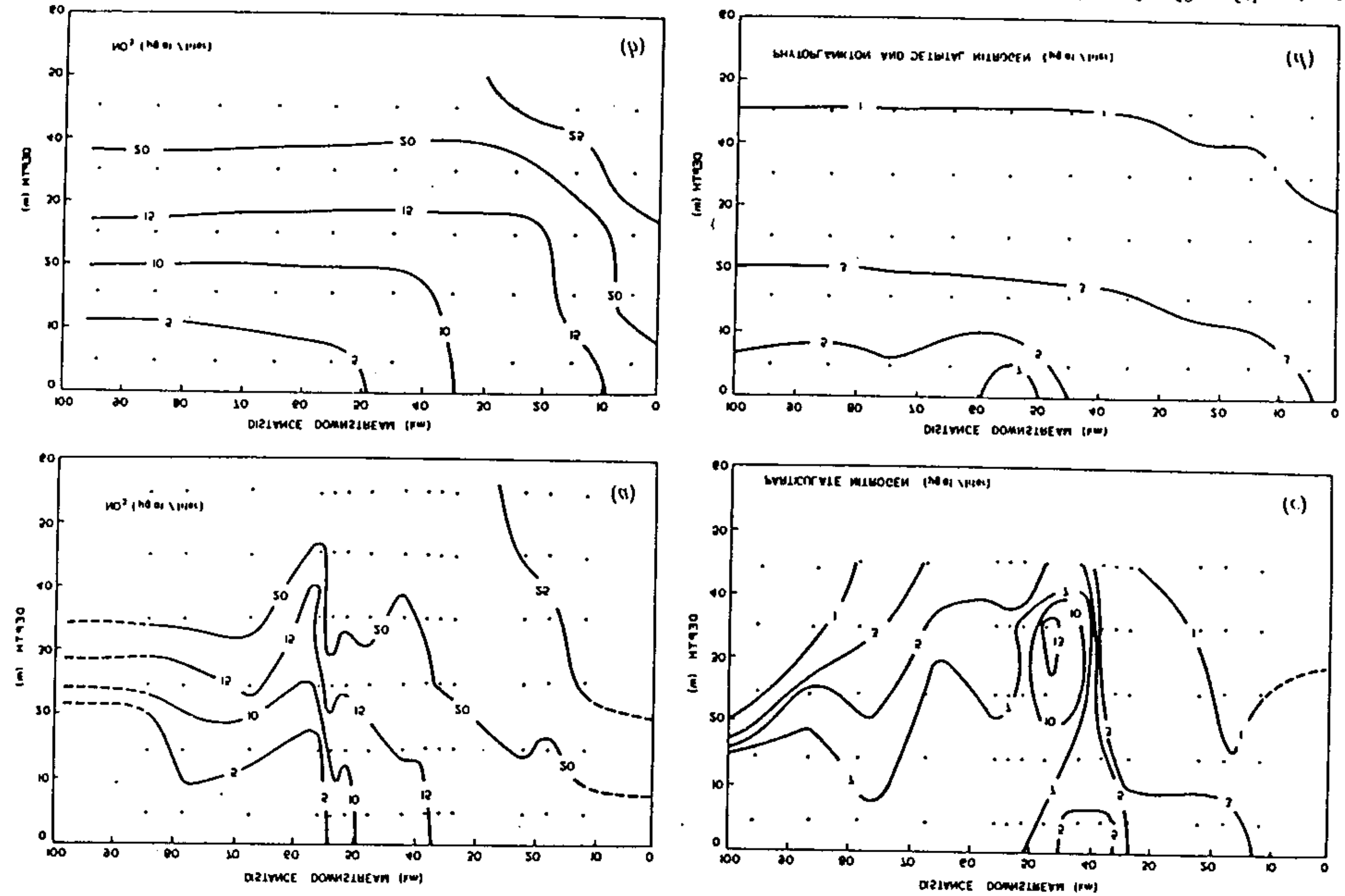
where $G_f = 0.008 \cos(0.2618t + 1.571)$ if $z < 30$ m
$= 0.008 \sin 0.2618t$ if $z > 30$ m

Detrital nitrogen:

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

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).



From: Kremer and Nixon, 1978:
"A Coastal Marine Ecosystem", Springer Verlag.

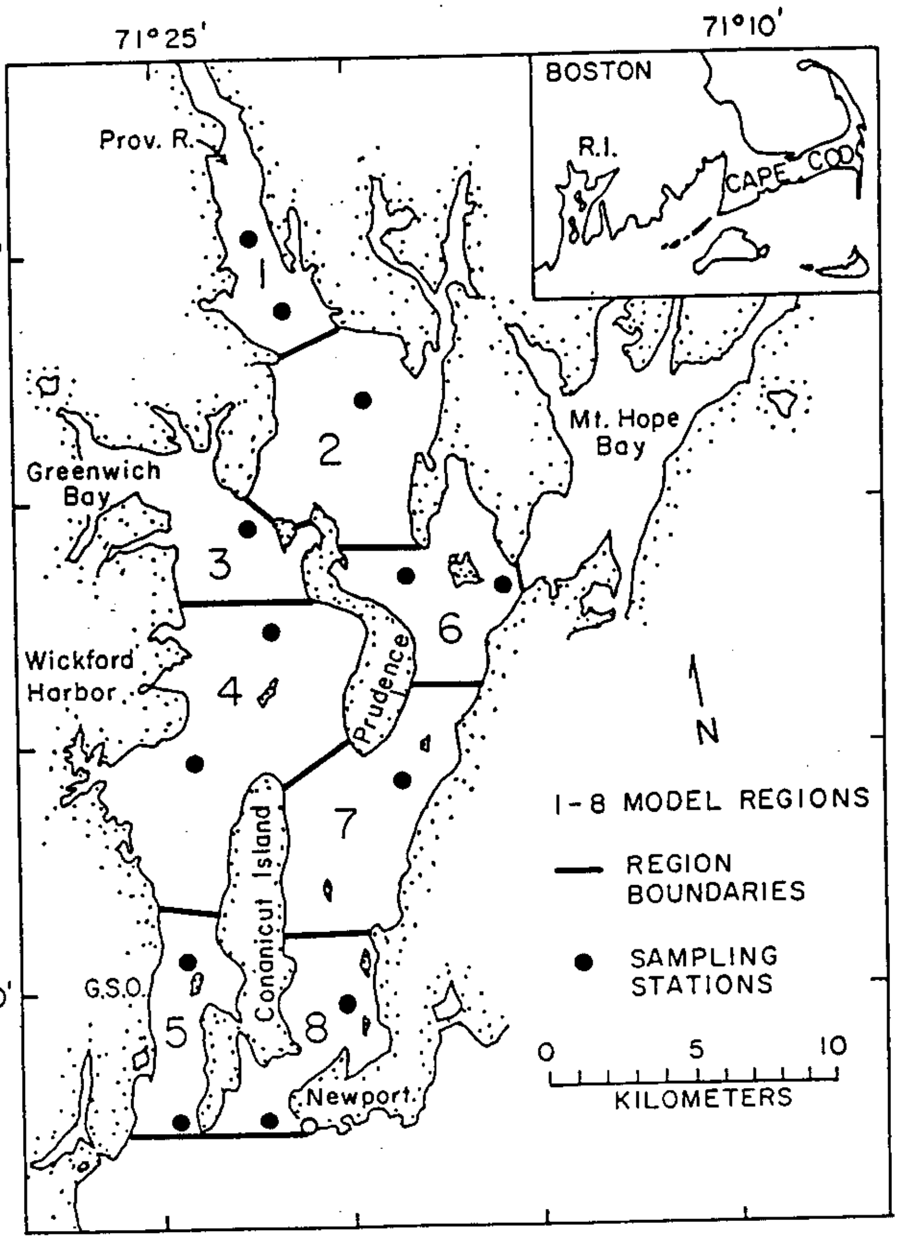
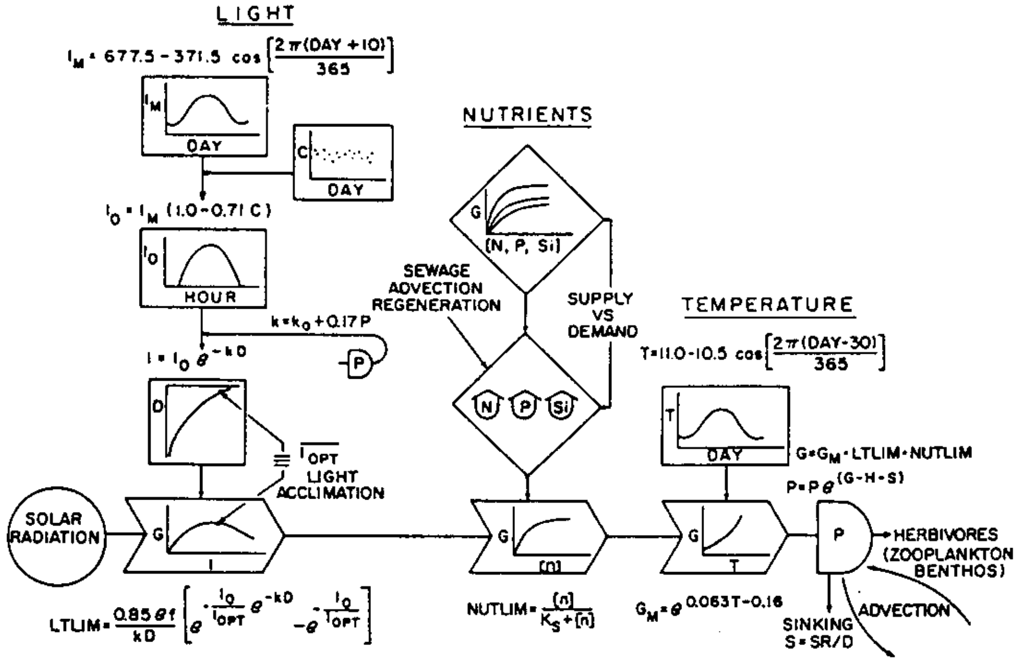
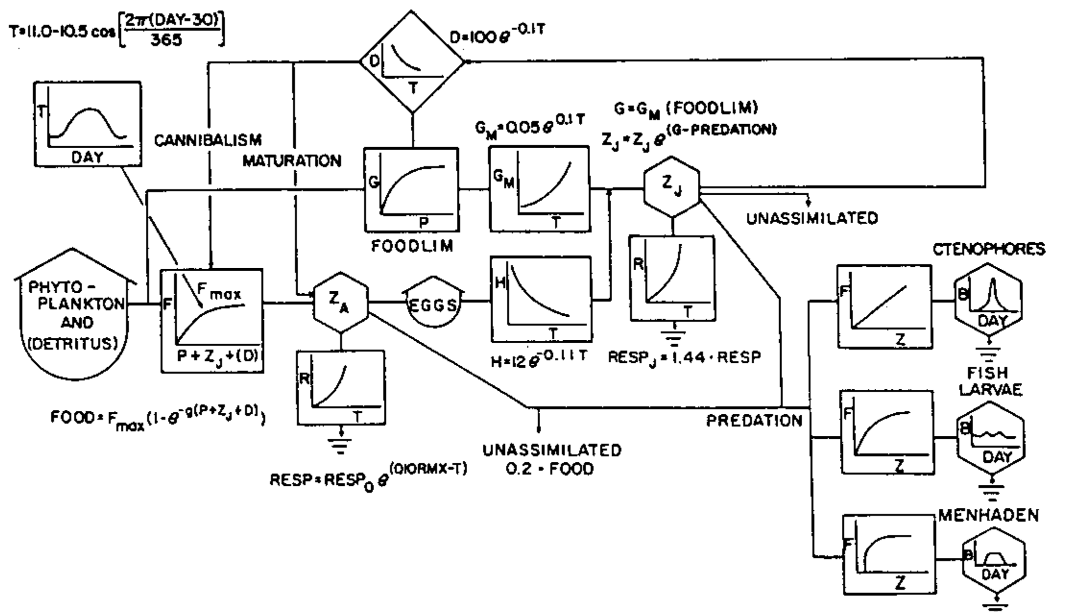


Fig. **5** Narragansett Bay, Rhode Island, and its location on the New England coastline. *Heavy dots:* stations sampled over an annual cycle to collect zooplankton, phytoplankton, and nutrient data for comparison with model simulations. The eight spatial elements or ecological subsystems of the bay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

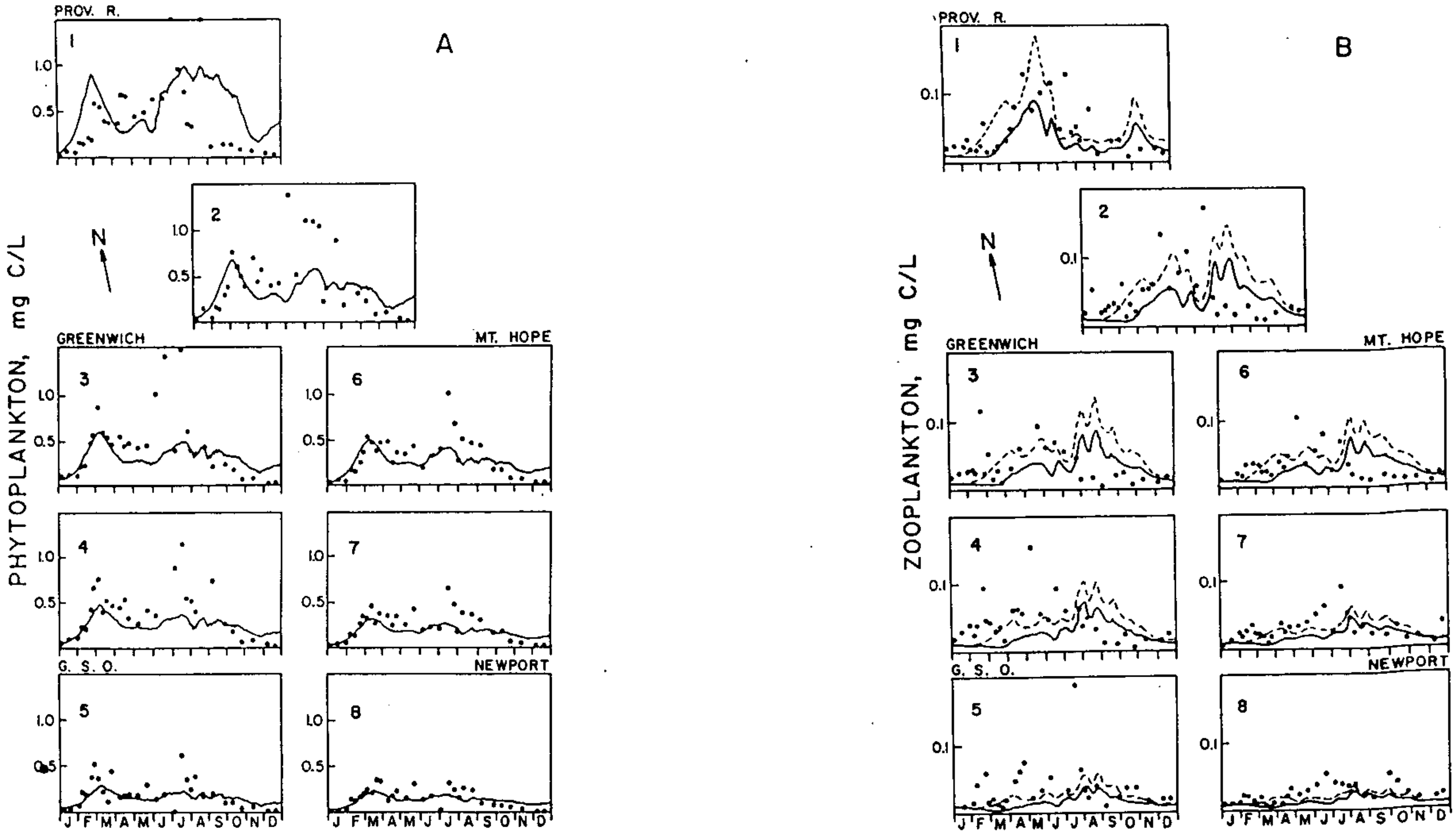


Flow diagram for the phytoplankton compartment showing relationships among the major equations described in text and a graphical representation of their behavior



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