DEVELOPMENT OF SHELLFISH PRODUCTION MODELS

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Résumé :

        La modélisation mathématique de processus biologiques est présentée comme un ensemble d'outils de recherche développés en fonction d'un but précis : étude d'impact, bilan énergétique, validation d'hypothèses.

        Son utilisation doit être précédée d'une réflexion sur les mécanismes mis en jeu, selon que l'on s'intéresse à un écosystème ou un individu (échelle biologique), que des phénomènes physiques sont pris en compte (échelle physique), à une échelle de temps donnée. Il ne saurait alors exister de méthode générale d'analyse tant sont variées les conditions d'étude, mais quelques cas types permettent d'illustrer la démarche du modélisateur et les récents progrès de ses outils.

Abstract :

        Mathematical models for biological processes are presented as a set of tools for research, which have been created for specific tasks : impact studies, energy budget, test of hypothesis.

        Before using it, the mecanisms involved must be analysed, depending upon wether a whole ecosystem or one animal is studied (biological scale), physical conditions are taken into account (physical scale), with a predetermined scale for time. The no general method for analysis can be, as conditions of studies are so different, but some typical cases can show the approach of the modelizer and the recent developments of its tools.

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I. INTRODUCTION

The first definition we could give to model is quite general : a model is any representation of the real world or what it is supposed to be at a given moment ; it clearly depends on the knowledge about reality or part of it ; as an abstraction it is necessary based on concepts and assumptions.

This paper deals with mathematical models only and among them, those which try to stimulate biological mechanisms (for about 15 years however, other mathematical approaches have been developping such as adaptative strategies, adapted from economics). Simulation allows to study dynamical behaviour of the elements of the ecosystem (which we denoted the real world) defined by the modeler   Then two main purposes may be reached by the model :

  1) prediction and management of the evolution of the ecosystem,
  2) test of the validity of our knowledge and hypothesis

Consequently model needs both mathematical and biological information.

A classification of the different kinds of models is proposed by Levins (quoted by Wiegert, 1979) according to three criterions : precision, realism and generality, one of these being generally inconsistent with the two others. For instance a realistic and precise representation of a given ecosystem will be probably unvaluable for another one. On the contrary, a general and realistic model will provide qualitative clues about the mechanism studied and poor information for prediction. Nowadays most of (classical) models aim at being general and precise ; common examples are Lotka-Volterra equations (inter- and intraspecies competition) or Von Bertalanffy's growth curve.

Whatever the case, the conception of the model consists in the same few steps. The first step is the definition of the compartements and relationship among them (Wiegert, 1975) ; compartments represent amounts of mass or energy (variables) within trophic levels or foodweb elements (when the model depicts an ecosystem) ; relationships describe the mass or energy flows whereby the variables will change. Forcing functions may be included ; for instance the laws of temperature and light are know, to influence the phytoplankton growth ; a waste water input may bring organic and detritic material. Thus the complexity of the model depends on two factors ; number of compartments (Wiegert, 1975) ; knowledge about interactions and the way to describe them in mathematical equations.

Evolution of all the compartments will be   translated into differential equations. The frame work is thus established.

The parameters are usually provided by experimental or field data. Some of them may be evaluated so that the model results fit the data (optimization). This stage is called calibration.

Once the rationale defined, the acute problem is in fact the validity of the model, coupled to its utilization as a tool for more investigation. The validation consists in comparing the data and the model curves and looking for good agreement. Statistics are rarely employed though classical tests are used by Rice (1984) to evaluate the proportion of the mean square error (MSE) explained by the model.

A sensitivity analysis is often conducted ; here the goal is the study of the model responses to the variation of some parameters values ; such an approach is really useful ; for instance Warwick (1977) tested hypothetical trophic relationship through simulations run with different values of the diet parameters in one compartment. Some models are conceived to study impact of

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disturbances ; Menesguen (unpub) uses a phytoplankton zooplankton model to measure the impact of thermic disturbances created by power plant.

We shall see that models are run with a wide range of issues. Before dealing with production model, I would like to give some information about several kinds of models used either to simulate filtration mechanism or to analyse energy flows.

The former may be integrated in general production model as a submodel. The latter is powerful as soon as the circuit of energy is emphasized. This review also shows that the mathematical description of the process (filtration, growth, production) must be consistent with the different scales involved : time, spatial and biological scale ; a monthly growth will not be depicted by the same equations as a daily one since short term phenomenons shall be erased in the former case ; spatial variability can be integrated when the patchine of the ecosystem is too important (Wiegert, 1975) ; the world of the ecosystem is generally based on tro-phic levels or foodweb elements ; the biological scale is then defined from the lumping of species.

II. FILTRATION, ASSIMILATION

1) Lehman (1976) tries to predict the filter feeder behaviour at both low and high food concentration thanks to an energy optimization assessment. The filter feeder aims at maximizing the quantity $Q = E_A - E_F$, where E_A is the net gain from assimilation and E_F the loss due to the filtration expense. The basic equations enables the author to take various diets into account. Denoting the filtration rate F and the density of particles i, D_i E_A equals $\le E_i D_i$ F   where E_i is the net energy gain from digestion of a particle ; E_F is supposed to be a power function of F, $E_F = aF^b$, F is related to the gut volume, the number of ingested particles of each type, the volume and calorific value of these particles as a function of the time spent inside the gut. Moreover an active or passive selective ingestion is added to the model.

This theoretical view of the filtration activity is lowered by the lack of data (Taghon and al., 1978) about such parameters as gut passage time and assimilation efficiency (it is one of the numerous problems the modeler has to face with). However, the first conclusions drawn from the model are consistent with the observations found in the litterature, even if the validity is not proved ; assumption on selectivity and assimilation may be tested by this model which, as its author says, can be used to guide experiments. Goldstein (1971) compares two compartimental models of ingestion and assimilation for fish ; very simple, these predictive models may be extrapolated to other species but more data are needed in order to calibrate and test the parameters which define the kinetics between the compartments. (FIG 1)

FIG 1   Schematic diagrams of two-compartment, three-parameter models for describing the retention of ingested elements by animals. (a) Model commonly used. (b) Model proposed by authors.
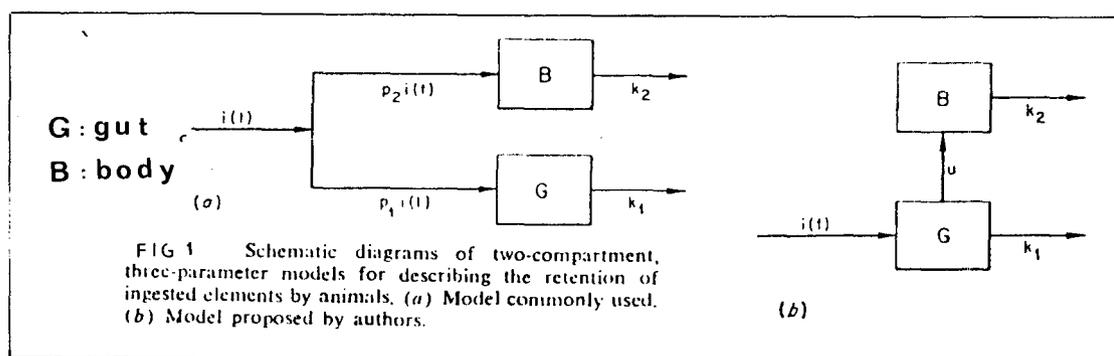
Another descriptive and predictive model is shown by Slagstad (1981), who depicts the dynamics of gut in copepods with hypothesis on assimilation and diets ; the volume of an ingested cell decreases at a constant digestion rate and the assimilation rate is stated to be proportional to the undigested fraction of cells inside the gut ; the digestion rate and the minimum gut passage time are supposed to control the assimilation efficiency.(FIG. 2)

Time (hours)
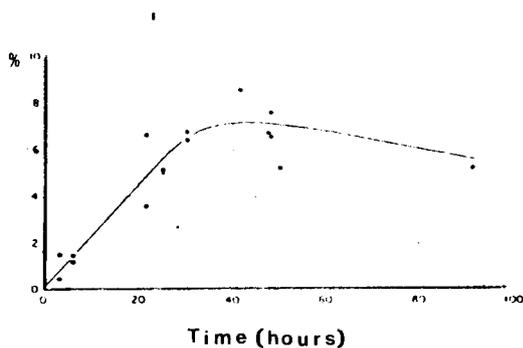
FIG. 2 . Percentage of ingested ^{137}Cs in the body compartment, B, of 10 g bluegills (*Lepomis macrochirus*) after fish were fed a single meal of *Chironomus* sp. larvae labeled with ^{137}Cs (modified from Kolehmainen and Nelson 1969).

The previous models are somewhat theorical and suffer from the paucity of data ; they show that writing mathematical equations may improve one's knowledge about complex mechanisms. The following models are perhaps more classic, as numerous available measurements make calibration possible.

2)Majkowski (1980) has developed an energetic model on the Rotifer Brachionus rubens, on the basis of the wellknown energy budget equation C = P + R = A (faeces are not taken into account) his purposes are :

1) to understand the dynamics of energy flows through the animal
2) to lead comprehensive studies to improve the knowledge about production.

Consequently, such a model should be useful in an ecosystem simulation. The fundamental equations are written :

$$C = C_1 (\emptyset) \ W^{c_2} \quad \text{(allometric relation)}$$

$$\emptyset = \text{food concentration}$$

$$C_1 (\emptyset) = a (1 - k \ e^{-b\emptyset}) \quad \text{(Ivlev relation)}$$

(limitant effect of the food)

$$U = \frac{A}{C} = u_1 + \frac{u_2}{C_1 (\emptyset)} \quad \text{assimilation efficiency}$$

inversely proportional to C_1

$$R = r_1 \ W^{r_2}$$

$$r_1 = r_3 + r_4 \ f^{r_5} \qquad \text{with } f = \frac{C_1 (\emptyset)}{\emptyset}$$

(f is the filtration rate, in volume X time $^{-1}$)

A reproduction term is also expressed as a function of $\emptyset$ and including life span and age at maturity. Then the evolution of the total calorific value of the body is simulated.(FIG. 3)
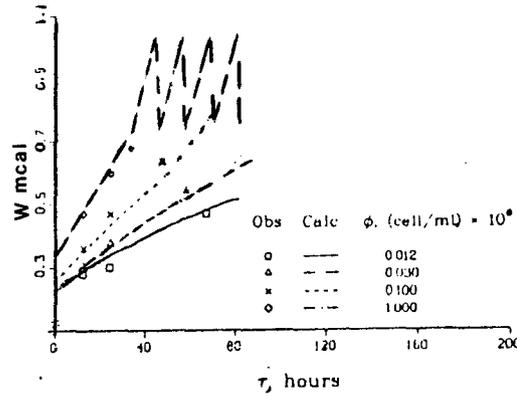
FIG. 3 Relation between the body calorific value of the male rotifer, W, and its age, τ, at various constant food concentrations, ϕ.

The validity of the model is stated for low concentrations since the simulation fits the data quite well-goodness of fit is also seen on C, A, P, R versus $\emptyset$ curves. The sensitivity analysis of this model allows the author to indicate which parameters are important and must be precisely measured (food consumption, respiration and assimilation efficiency). One may wonder whether such a model cannot be applied to molluscs.

Another model designed by Bayne (1976) relates the same mechanisms in a different manner, to food concentration, body weight and temperature. The rationale is logical and corresponds with the widespread hypothesis on filtration. The model excludes pseudofeces and emphasizes the filtration of particles without selection ; dissolved dubstances assimilation and recycling problems are dropped :
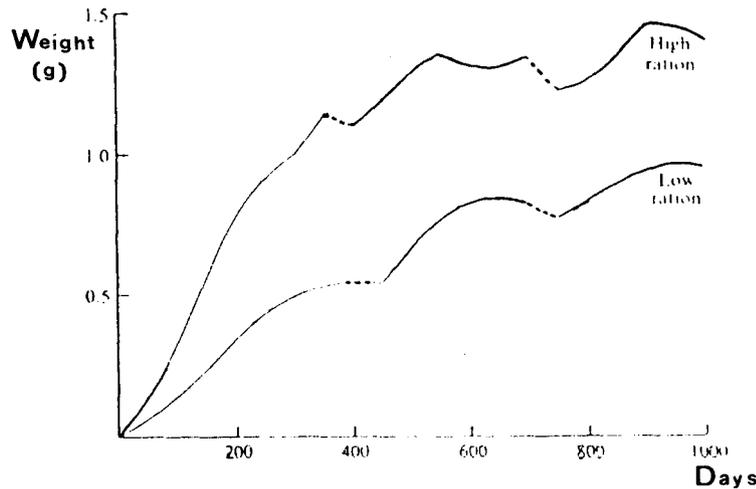
FIG. 4 The growth of *Mytilus edulis* over 1000 days at 'high' and at 'low' ration, as determined by a simulation model. The dashed portions of the curves signify weight loss due to spawning.

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$$f = aW^b \qquad \text{filtration rate (volume X time}^{-1})$$

Only a fraction of the material brought by the filtration is ingested ; the rate of ingestion is a fonction of W (body weight) and $\emptyset$, food concentration. Bayne computed it as a decreasing fonction of $\emptyset$, then $\emptyset$ is greater than a threshold value ; for $\emptyset$ less than $\emptyset_o$ the rate of ingestion equals 1 ; as $\emptyset$ increases the rate reaches an asymptotic value.

This material is partially assimilated ; the assimilation efficiency depends on body weight, temperature and the weight of organic matter intake R. Respiration is an allometric expression ; it varies with temperature and R. An other allometric relation is given for fecundity, though few data are available.

These series of equations are quite general for bivalves ; based on regressions, they should be precise ; they depict the energy flows through the individual according to the balance :

$$C = R + F + P_g + P_s, \text{ so that}$$
$$P_s = C - R - F - P_g \qquad (\text{FIG. 4})$$

A subroutine predicts the variations of the nitrogen contained in the body. As Majkowski's, the model is said to be predictive and useful fo pointing out misunderstanding. For instance everybody will not agree Bayne's equation of the pseudofeces (Widdows, 1979). Nevertheless his fundamentals are admitted by Verhagen (1982) in his population model.

The flaws of models most often correspond with the lack of available data on important biological problems. Thus recycling pseudofeces egestion or dissolved matter impact on filtration are often disregarded. The models may test ideas about these phenomenons provided that data exist. These hypothesis stated from simulations are about to start experiments.

3)This review of individual short term models would be incomplete without an example of the kinetics approach which will lead to further developments. Amouroux (1982) studies the interaction between the Venus Verrucosa, dissolved matter, particulate matter faces, CO_2 and bacteria compartments in a closed system. He finds good agreement between
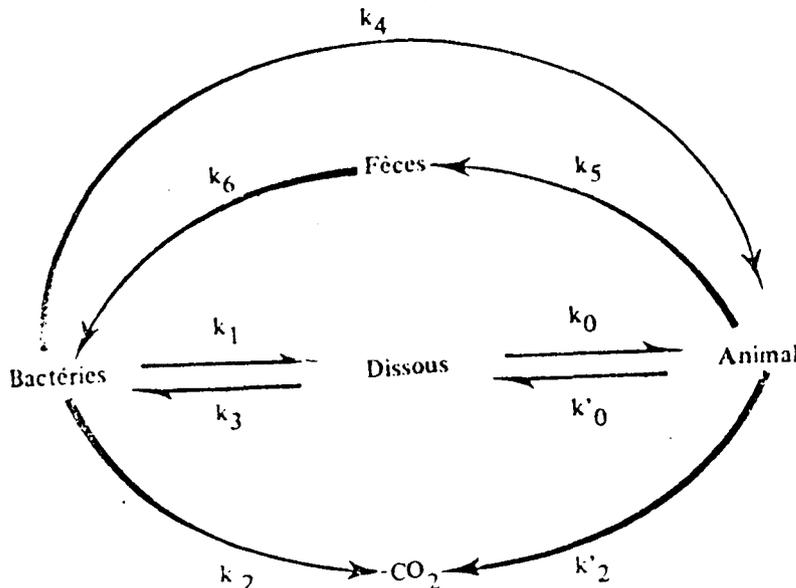
FIG. 5 Flows between compartments

his data and simulation curves on short term experiments (40 hours). Differential equations are assessed to be linear (first order kinetics) and the parameters are evaluated from different submodels results. Amouroux showed that bacteria are quickly consumed and feces are recycled.(FIG.5)

III. ECOSYSTEM

The ecosystem modeling must avoid the danger and the temptation to gather numerous submodels which increases the complexity, the non stability of the model and thus fails in producing adequate simulations (Patten, 1975), though the model seems realistic (Park, 1975). The application of individual and short term growth or filtration model to huge ecosystems doesn't make sense, since the time scale and the number of species integrated are quite different.

Furthermore a complex hydrological structure may interfere with biological mechanism. The movement of particles is derived from physical transport equations, usually solved by numerical calculations.

1) Physics

Denoting · X a particle concentration, the equation of evolution is written :

$$\frac{\delta X}{\delta t} + \overrightarrow{V} \nabla X = \nabla . K \nabla X + \text{sinks} + \text{source}$$

(Chahuneau, 1980)

$X = X(t,x,y,z)$ where x, y, z are spatial coordinates

$\overrightarrow{V} = (V_x, V_y, V_z)$ current speed

$\nabla X = (\frac{\partial X}{\partial x}, \frac{\partial X}{\partial y}, \frac{\partial X}{\partial z})$ diffusion matrix

divergence operator $K = \begin{pmatrix} K_x & 0 & 0 \\ 0 & K_y & 0 \\ 0 & 0 & K_z \end{pmatrix}$

$\overrightarrow{U}.\nabla X$ represents the advection, which is the part of the transport due to the current speed.

$\nabla.K\nabla X$ equals the diffusion term caused by variations of X concentration. This equation is usually integrated on the vertical dimension (z) ; thereby we obtain a similar equation with new terms representing the wind effect and the friction on the bottom (boundary constraints) ; sinks and sources sum up the whole biological interactions wich influence X concentration, and physical forces (sedimentation, Coriolis) coupling the physical and biological submodel allows to classify models according to the complexity degree:number of spatial dimensions and number of trophic levels or foodwebs elements (Chahuneau and al., 1980).

Both physical and biological parameters have to be estimated and the sampling must include the spatial variability in order to keep validation possible. The physical complexity level is connected to the temporal scale and the purpose of the whole model ; a phytoplankton biomass model for a lake will generally refer to seasonal changes ; di Toro (1975) elaborates a rather simple phytoplankton model in a lake divided in seven spatial elements (boxes) ; c_{ij} is the concentration of substance i in segment j :

$$V_j \frac{dC_{ij}}{dt} = \sum Q_{kj} C_{ik} + \sum E'_{kj} (C_{ik} - C_{ij}) + \sum S_{ijk}$$

where V_j is the segment volume,
Q_{kj} the net advective flow rate between k and j
E_{kj} the bulk rate of transport, fonction of the difference of concentration between

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i and a, adjacent segment. These segments are defined from homogenous regions in which advection and mixing flows are measured.

The model simulates the nitrogen and phosphorus circuit through phytoplankton, zooplankton benthic compartments with classical phenomenons : grazing mortality excretion, regeneration from organic to inorganic forms, primary production temperature and light are the (classical) forcing fonctions. The model is neither precise nor realistic but may give information on the evolution of eutrophication with increasing human population.(TAB. 1)

ILLUSTRATIVE APPLICATION OF THE EUTROPHICATION MODEL [a]

Year	Observed [c]	Population accelerated growth [d]	Population moderate growth [d]	Population limited growth [d]	Two foot Lake-level change [d]	Phosphorus removal (50% agriculture)	Phosphorus removal (95% + detergent)	80% P [b]
1930	15 μg liter^{-1}	—	—	—			—	—
1970	25 μg liter^{-1}	—	—		$\Delta 2$ μg/liter [e]	$\Delta 1$ to 2 μg liter^{-1}	—	—
1990	—	37 μg liter^{-1}	30 μg liter^{-1}	—	—	—	10–15μg/liter [c]	15 μg liter^{-1}
2010	—	42 μg liter^{-1}	35 μg liter^{-1}	26 μg liter^{-1} 28 μg liter^{-1}	—	—	15–20μg/liter [c]	20 μg liter^{-1}

  a The information presented should be considered an illustration of the types of results obtainable from application of eutrophication models to analysis of planning problems rather than a projection of future conditions.
  b 'These levels are for the moderate growth population levels.
  c The same algae levels can be obtained with an 80% phosphate removal policy plus 1990—25% nitrogen removal and 2010—50% nitrogen removal.
  d Values are micrograms/liter of chlorophyll for Western Lake Erie in Section 7 of the eutrophication model (near the Maumee River).
  e Change in chlorophyll levels from 1970 conditions.

TAB. 1
Effect of population growth, agricultural land use policy or lake-level change on eutrophication.

Beside management purpose, population dynamics may be outlined. For instance, Verhagen (1982) elaborates a coupled biological and physical model about a mussel population evolution. The fundamentals of the biological submodel are derived from Bayne's (1976) to which larval development equations are added. The water circulation is driven by the wind speed and the bottom geography, so that the salt lake may be divided in nearly closed volume elements. Field data show that these elements correspond with the musselbeds and can then be considered as independent boxes. Inside a box, measurements show that the physical transport may be reduced to a vertical dispersion and a constant horizontal advection ; denoting C (z,t) the particular matter concentration at depth z and time t, we have :

$$\frac{\partial C(z,t)}{\partial t} = u(C_0 - C) + D_z \frac{\partial^2 C}{\partial z^2}$$

= advection + vertical diffusion   (FIG. 6)

Water
column

$C_0(t)$ $C(z,t)$

u
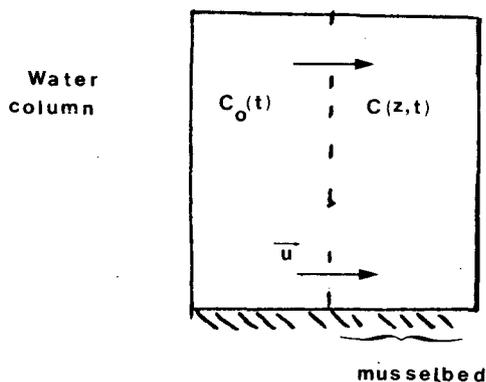
musselbed

FIG. 6 Structure of the water column above a musselbed (see text)

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The integration of this equation provides the amount of available food at the bottom, where the mussels lie. Regarding then the biological model, the ratio of ingestion rate par m^2 per day is estimated and allows to conclude that the primary production is almost completely consumed by the mussels. Short-comings are revealed by the comparison between calculated and extrapoladed cohort evolution (FIG. 7)

Dry weight (mg)

Age (years)
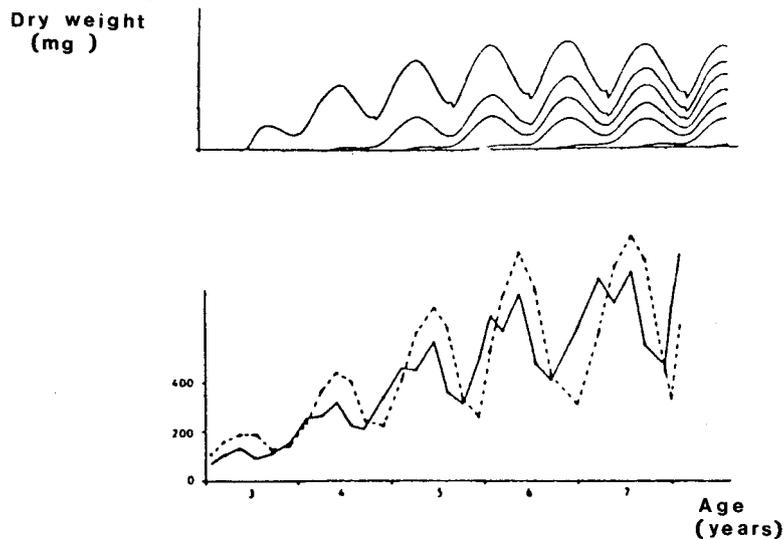
FIG.7--Growth in weight of calculated cohorts compared with measured data from Bayne and Worrall (1980).

However simulations show the same trends as the observed curves. Verhagen outlines the lack of available data about cohort analysis ; this is an acute problem, modelin   are often faced with. Another problem consists in interpretating the mathematical properties of the models provided by the non-linearity structure ; for instance Verhagen finds a good agreement between long term predicted oscillations and observed ones ; but it does not seem reasonable to take into account the long term conclusions of a model previously built to study annual events. Nevertheless, providedthat temporal scale, spatial scale and the rationale are kept in mind, modelisation gives relevant results.

2) Ecosystem analysis

The generalization froman individual to a whole population approach is meaningful when a few species are regarded. As soon as a global ecosystem is studied, such a description seems inadequate, for too many non-lineary mechanisms are integrated so that the mathematical properties of the system (stability, periodicity) are not controlled (Patten, 1975). Realism may be integrated at a reasonable degree ; Wiegert. (1975-77 and 79) improves the linear transfer equations by using threshold effects to describe limitant phenomenons, Matter or energy flow from compartment i to j is written :

$$F_{ij} = t_{ij}\, x_j\, f(x_i, x_j) \qquad 0 \leqslant f(x_i, x_j) \leqslant 1$$

$f\left(x_i,\ x_j\right)$ is explicited through the (realistic) definition of two kinds of competition, exploitative and interference competitions which may be separated ; the former is the competition for material resource, the latter the competition for space. Then thresholds are included ; ingestion increases from a saturation to a

refuge level under or upper which the ingestion rate equals zero or one ;
between these two values, the ingestion rate is supposed to be a linear function
of the resource. Applied to a six compartment ecosystem, the model predicts the
evolution of some compartments quite well and then is used to predict the impact
of a perturbation on one compartment (Wiegert, 1977). According to Wiegert, his
rational proves to be general, precise and realistic.

Quite linear systems are also elaborated. They are valuable in so far
as the ecosystem is in steady state (dynamical equilibrium). Under normal condi-
tions, they may fit the observed evolution data but most often provide smooth
evolution curves, due to the averaged parameter values and mainly temperature
forced interactions.

They first aim at test biological hypothesis and emphasize the energy
pathway bewteen the foodweb elements (groups of species showing the same feeding
behaviour).Warwick (1977), for instance, has built a six-compartment model to
simulate the production of the secondary producers ; as other models, the equations
are based on main conservation and include respiration, mortality secretion and
ingestion, activities ; the parameters are derived from the litterature or from
field data ; species are lumped in homogenous compartments (FIG.8)
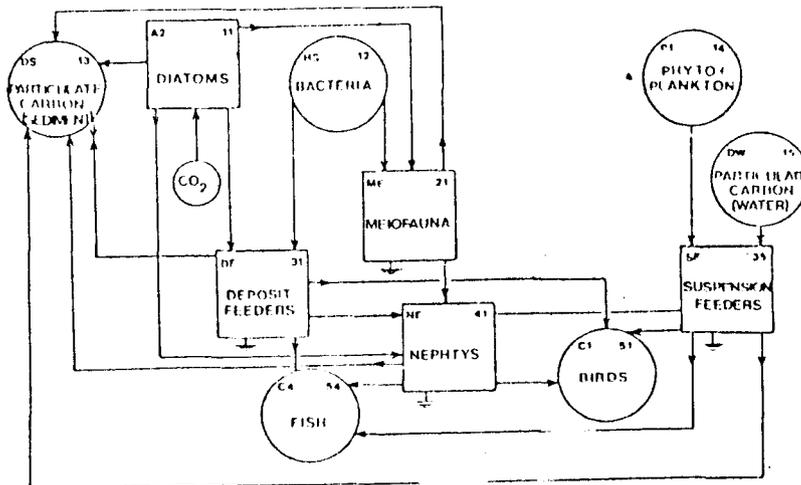
FIG.8 Carbon flow in Warwick's model

resulting from the foodweb structure (biological scale). Simulations give infor-
mation on the tendancy of the carbon flow during the year. Though not precise,
the order of magnitude seem valid. Furthermore biological assessments are
tested such as the effect of different diets on the growth of Nephtys.(FIG. 9)

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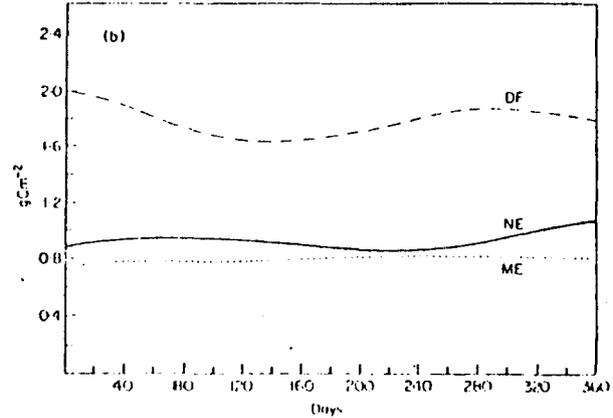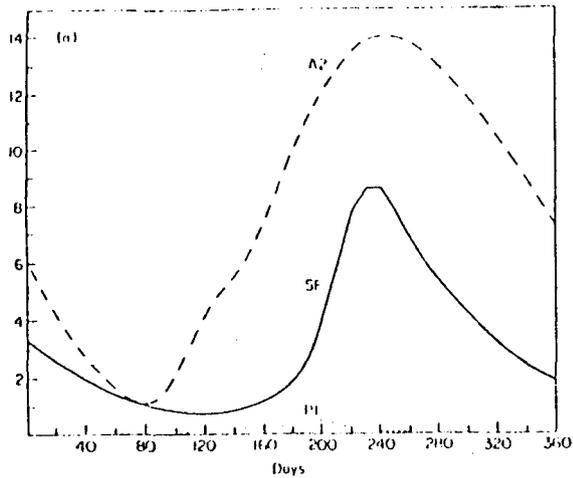
FIG. 9 The results of the dynamic simulation model; (a) for phytobenthos (- - - A2), suspension feeders (— SF) and the values of phytoplankton (···· Pl) supplied as an exogenous variable and (b) for meiofauna (···· ME), deposit feeders (— DF) and Nephtys (— NE). (c) the results of a simulation where Nephtys fed only on meiofauna and deposit feeders and not on phytobenthos and (d) where Nephtys fed exclusively on phytobenthos, and not on meiofauna or deposit feeders.

Analysis of such linear systems is developed by Hippe (1983) and Hannon (1973) who use matrix calculation to investigate the properties of the flow circuit through the ecosystem. The general mass conservation equation is written :

$$\dot{x}_i(t) = z_i(t) + \sum f_{ij}(t) - \sum f_{ji}(t) - y_i(t)$$ x_i is the amount of

energy in compartment i
and $\dot{x}_i = \dfrac{dx}{dt}_i$ the rate of change.
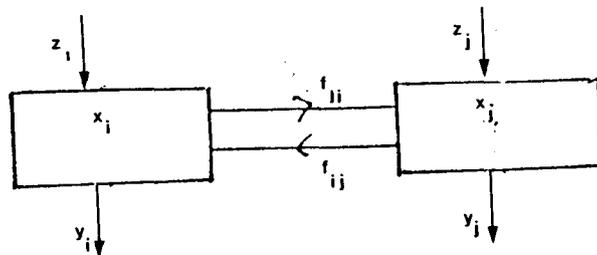
FIG.10 Flow circuit in a quite general compartment model (see text)

y_i represents the output outside the system from i, and
z_i the input toward i, f_{ij} is the flow relating j to i. Hippe defines
the through flow T_k as the amount of energy which passes through the compartment
k, supposing that in a steady state (s_{ik} = 0) inflow equals outflow ; in the
dynamical case $T_k(t) = \sum f_{kj}(t) + z_k(t) - x_k = \sum f_{jk}(t) + y_k(t)$

The basic hypothesis of the model is that the flow f_{ij} from j to i equals a
fraction q_{ij} (t) of the flow through i (donor controlled interaction). Matrix
calculation enables the author to write then $(T_1 \ldots T_n) = (Y_1 \ldots Y_n)(I - Q)^{-1}$

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I is the identity matrix and $Q = (q_{ij})$, $(I - Q)^{-1} = (a_{ij})$
then the relation $f_{ij} = q_{ij} T_i$ may be written $f_{ij} = \sum_k (q_{ij} a_{ki'}) y_k = \sum_k f_{ij}^k y_k$,

Thus f_{ij}^k is the value of f_{ij} when $y_k = 1$ and $y_{k'} = 0$ for $k' \neq k$,
Consequently it represents the intercompartmental flow between j and i, contributing to one unit of outflow y_i (t). Hannon (1973) points out that this approach shows the "energy flow interdependence of each species upon the other" ; it reveals the structure of the ecosystem, eluded in the classical differential equations such as predator-prey ones. System analysis completes the realistic and precise modelisation. Dame (1977, 1981) has applied this procedure to a marsh - estuarine system ; the equations of his models are linear and involve 23 compartments that can be clumped in three submodels. The complexity of the biological structure is shown by a relation matrix displaying the interrelationships between all the compartments.(TAB. 2)

TAB.2 The relation matrix for the total North Inlet model. A positive relation is noted with a 1

The ecosystem reaches a steady-state level consistent with the observed stability. Energy flow analysis is conducted through a six-compartment sub-model.(FIG. 11)
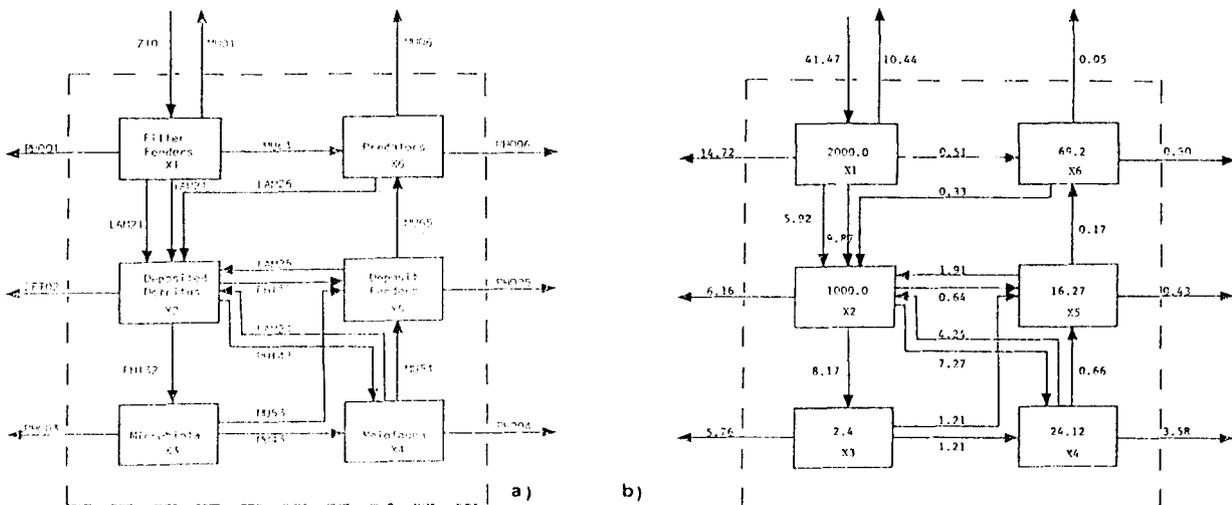
FIG. 11   a Numbers associated with each symbol denote a to/from relationship; for example, MU61 indicates mortality by predators X6 on filter feeders X1 or a flow to X6 from X1

b Energy flows (Kcal m⁻² d⁻¹) and standing crops (Kcal m⁻²) in an intertidal oyster reef

Throughflows are examined for different imput and ouput vectors. The average pathlenght of an inflow (AP LZ) is the number of compartments crossed by a given imput. Energy cycling can be estimated through the efficiency $RE = \dfrac{Tii-1}{Tii}$

when Tii represents the flow through i (see table 3)

Measure	State					
	Filter feeders (X1)	Detritus (X2)	Microbiota (X3)	Meiofauna (X4)	Deposit feeders (X5)	Predators (X6)
Throughflow (Ti)	41.47	22.27	8.17	8.48	2.51	0.69
Average pathlength of a unit input (APLZ)	2.02	2.59	1.84	2.54	3.12	2.23
Average pathlength of a unit output (APLY)	1.00	2.93	3.93	4.07	4.71	2.93
% Total system throughflow-inflow	100.00	–	–	–	–	–
% Total system throughflow-outflow	30.10	21.66	27.10	17.45	2.43	1.26
Recycling efficieney (RE)	0.00	0.28	0.09	0.23	0.11	0.01

Total system throughflow (TST) = 83.58; Total system throughflow straight (TSTs) = 74.33; Total system throughflow cycled (TSTc) = 9.21; Average pathlength (APL) = 2.02; Average pathlength straight (APLs) = 1.79; Average pathlength cycled (APLc) = 0.22; Cycling index (TSTc/TST = CI) = 0.11

TAB.3 Computation of throughflows, pathlengths and recycling

Thereby structural properties of the ecosystem are outlined and reveal the main flows.

IV. MARENNES-OLERON ESTUARY

A) We have reviewed some examples of model applied to population biomass evolution ; here, population defines a species or a part of the ecosystem ; production is the difference between the outflows and the inflows from or to the population. The wide range of patterns we have seen deserves to be introduced for it gives some idea on recent development of modelisation. To sum up this investigation, the consistency of the model depends on :

1) The structure of the ecosystem : exogenous fonctions, time and spatial scales, number of compartments and relation matrix have to be examined.

2) The purpose of the simulation : prediction, management, or trophic relations study

3) The rationale of the model : linear or non linear equations, coupled physical – biological interactions, thresholds

4) The available data

Among the tools that can be used to draw conclusions from the simulation, the most powerful are : systems analysis, sensitivity analysis, disturbance effect, validation, tests of hypothesis.

Generally speaking, the complexity of the model must be slowly increased. It is a wise rule which should avoid uncontrolled simulated behaviours.

Scale / Goal	Temporal scale	Spatial scale	Biological scale
Prediction	1	0 - 1	0 - 1
Energy flow study	1	0	1
Mecanism	0	0	0
Interrelationship	0 - 1	0 - 1	0 - 1

TAB.4 0 : short term, uncoupled physics or individual level

1 : long term, coupled { physics / biology   or   { food web / trophic levels

B) We are trying to modelize the Marennes-Oleron estuary in order to study
the interaction between the growth of oysters and the available food.

Environmental conditions may be outlined as following :
1) Short term physical transport of particles occur ; the water flow is
staying for about 10 days in the estuary and this residual movement is an
average of all the tidal fluctuations.

2) The whole oyster population reaches about 80 000 tons ; the mussel biomass
is given to be 5 000 tons ; beside these cultured population, wild species are
to be estimated but they probably are negligible competitors.

3) A phytoplankton bloom is observed in April or May in the North of the
estuary ; during the year successive detritic (in winter) or living matter
(in summer) inflows take place ; these materials are brought to the oysters
by the residual movement, from North toward South.

A high turbidity prevents the primary production from occuring in the
major part of the estuary ; the high concentration of non biotic particles
probably lowers the oysters ingestion efficiency ; moreover little information
exists about the rejected part of food (pseudofeces).

The model will aim at high-lighting the limitant effect of food on
oyster growth ; in a first stage, the estuary may be compared to a raceway
with boundary constraints (food current) and a forcing fonction (temperature)
Because of the environmental conditions the time scale is about three months
(March, April, May). The second step should study the growth - decreasing food
relationship more precisely thanks to a coupled physical - biological model.
The physical model has already been achieved ; it computes the water level
and the streamline at about 1000 points of a grid ; it has to be adapted to
foresee the particle pathway through the estuary during a tidal cycle (14 days).

Some data are or will be soon available ; the dispersion of oysters,
primary production, growth as a fonction of the tide and the geographical place,
filtration parameters and the water composition. However lack of information
on gametogenesis and food recycling must be pointed out.

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