Production of shellfish production models

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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 simulate biological mechanisms (for about 15 years however, other mathematical approaches have been developing such as adaptive 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 modeliser. 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 characterization 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 studied mechanisms 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 compartments and relationship among them (Wiegert, 1975); compartments represent amounts of mass or energy (variables) within trophic levels or food web elements (when model depicts an ecosystem); relationships describe the mass or energy flown whereby the variables will change. Forcing functions may be included; for instance the laws of temperature and light are known 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 the translated into differential equations. The framework 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 on 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 disturbances; Meneguen (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 to simulate filtration mechanism. 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 whereas short term phenomena shall be erased in the former case; spatial variability can be integrated when the patchiness of the ecosystem is too important (Weigert, ); the world of the ecosystem is generally based on trophic levels or foodweb elements; the biological scale is then defined from the lump of species.

II - Filtration, assimilation

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 \( Q = E - E' \), where \( E \) is the net gain from assimilation and \( E' \) the loss due 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 \( D \), \( E' \) equals where \( E \) is the net energy gain from digestion of a particle; \( E \) is supposed to be a power function of \( F \), \( E = a F^b \) 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 compartmental models of ingestion and assimilation for fish; very simple, this predictive model 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.

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.

The previous models are somewhat theoretical 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.

Majkowski (1980) has developed an energetic model on the Rotifer Brachionus rubens, on the basis of the well-known 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:

$$C = C_0 (\phi)^w C_2$$  (allometric relation)

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

$$C_1 (\phi) = a (1 - k C_i^{-k})$$  (Ivlev relation)

(limitant effect of the food)
A reproduction term is also explicit as a function of $\phi$ and including life span and age at maturity. Then the evolution of the total calorific value of the body is simulated.

$$U - \frac{A}{C} = u_1 + \frac{u_L}{Cl(\phi)}$$

assimilation efficiency

inversely proportional to $Cl$

$$R = r_1 \frac{w}{r_2}$$

$$r_1 = r_3 + r_4 f^3$$

with $f = Cl(\phi)$

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

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 $\phi$ 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 wide spread hypothesis on filtration. The model excludes pseudofeces and emphasizes the filtration of particles without selection; dissolved substances assimilation and recycling problems are dropped.
Physiological integrations

The growth of *Mussel edula* 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.

\[ f = aW^b \]

filtration rate (volume x time \(^{-1}\))

Only a fraction of the material brought by the filtration is ingested; the rate of ingestion is a function of \( W \) (body and weight) and \( \theta \), food concentration. Bayne computed it as a decreasing function of \( \theta \), when \( \theta \) is greater than a threshold value; for \( \theta \) less than \( \theta_0 \) the rate of ingestion equals 1; as \( \theta \) increases the rate reaches an asymptotic value.

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

This 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:

\[ C = R + F + P_s + \text{g} \]

so that

\[ P_s = C - R - F - \text{g} \]

A subroutine predicts the variations of the nitrogen contained in the body. As Najkowski's, the model is said to be predictive and useful for painting 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 phenomena provided that data exist. These hypotheses stated from simulations are about to start experiments.

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 compartment in a closed system. He finds good agreement between 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.

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 so fail 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:

\[
\frac{\partial X}{\partial t} + \mathbf{\nabla} \cdot \mathbf{v} X - \mathbf{\nabla} \cdot \kappa \mathbf{\nabla} X = \text{sinks + sources}
\]

(Chahuneau, 1980)

\[ X = X(t, x, y, z) \]

where \( x, y, z \) are spatial coordinates

\[ \mathbf{v} = (\mathbf{v}_x, \mathbf{v}_y, \mathbf{v}_z) \]

current speed

\[ \nabla X = (\frac{\partial X}{\partial x}, \frac{\partial X}{\partial y}, \frac{\partial X}{\partial z}) \]

diffusion matrix

\[ \tau = \frac{1}{\rho} \left( \frac{\partial \rho}{\partial t} + \mathbf{\nabla} \cdot \rho \mathbf{v} \right) \]

divergence operator

\( \mathbf{v} \cdot \mathbf{\nabla} X \) represents the advection, which is the part of the transport due to the current speed.

\( \mathbf{\nabla} \cdot \mathbf{v} X \) 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 where the variables are averaged and new terms representing the wind effect and the friction on the bottom (boundary constraints; sinks and sources sum up the whole biological interactions which influence X concentration, and physical forces (sedimentation, Coriolis) coupling the physical and biological submodel allows to classify models according to the complexity level (number of spatial dimension, number of trophic levels or foodwebs elements) (Chahuneau and al. 1980). Both physical and biological parameters must 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); \( \mathbf{c}_{ij} \) is the concentration of substance \( i \) in segment \( j \):

\[
\frac{\partial \mathbf{c}_{ij}}{\partial t} = \sum_k Q_{kj} \left( \mathbf{c}_{ik} - \mathbf{c}_{kj} \right) - \sum_k E_{kj} \left( \mathbf{c}_{kj} - \mathbf{c}_{ja} \right) + \sum_k \mathbf{S}_{ij}
\]

where \( V_{ij} \) is the segment volume,

\( Q_{kj} \) the net advective flow rate between \( k \) and \( j \)

\( E_{kj} \) the bulk rate of transport, function of the difference of concentration between \( i \) and \( a \), adjacent segment. These segments are defined from homogenous regions in which the 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 functions. The model is neither precise nor realistic but may give useful information on the evolution of eutrophication with increasing human population.
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 Baynes'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 \( C(x,t) \) the particular matter concentration at depth \( z \) and time \( t \), we have:

\[
\frac{\partial C}{\partial t} + \mathbf{u} \cdot \nabla C = D \frac{\partial^2 C}{\partial z^2} + \text{advective + vertical diffusion}
\]

![Diagram](image-url)
The integration of this equation provides the amount of available food at the bottom, where the mussels lie. Regarding the biological model, the ratio of ingestion rate per m²/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 extrapolated

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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, modelisers are often faced with. Another problem consists in interpreting 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, provided that temporal scale, spatial scale and the rationale are kept in mind, modelisation gives relevant results.
2) Ecosystem analysis

The generalization from 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-linear 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; Weigert (1975–77 and 79) improves the linear transfer equations by using threshold effects to describe limiting phenomenon. Matter or energy flows from compartment $i$ to $j$ is written:

$$ F_{ij} = \chi_{ij} \alpha_i \int (\alpha_j \chi_j) \quad \text{for} \quad \alpha_i \leq \int (\alpha_j \chi_j) \leq 1 $$

$f (\chi_i, \chi_j)$ is explicit through the (realistic) definition of two kinds of competition, exploitative and interference competition which may be separated; the former is the competition for material resource, the latter the competition for space. The thresholds are integrated; ingestion is a function of saturation and refuge levels 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 rationale 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 conditions, 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 between the foodweb elements (groups of species having 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 literature or from field data; species are lumped in homogenous compartments.
resulting from the food web structure (biological scale). Simulations give information on the tendency of the carbon flow during the year. Though not precise, the order of magnitude seems valid. Furthermore, biological assessments are tested such as the effect of different diets on the growth of Nephtys.

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:

\[ \dot{x}_i(t) = \sum_j x_j(t) + \sum_j \int_{t-h}^{t} x_j(t) - \int_{t-h}^{t} x_i(t) - \eta_j(t) \]  

where \( x_i \) is the amount of energy in compartment \( i \), and \( \dot{x}_i \) is the rate of change.

![Diagram of mass conservation equation](image)
The author represents the output outside the system from i, and 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 $T_k(t)$ is.

The basic hypothesis of the model is that the flow $f_{ij}$ from j to i interaction is stated $q_{ij}(t)$ of the flow through i (thus a donor controlled interaction is stated). Matrix calculation enables the author to write then $T_i = (Y_1 \ldots Y_n) (I - Q)^{-1}$ $I$ is the identity matrix and $Q = (q_{ij}), (I - Q)^{-1} = (aij)$ then the relation $f_{ij} = q_{ij}T_i$ may be written $f_{ij} = \sum_{k=1}^{n} (a_{ij} - a_{ik}) Y_k = \sum_{i=1}^{n} q_{ij} y_i$

Thus $f_{ij}^n$ is the value of $f_{ij}$ when $y_i = 1$ and $y_j = 0$ for $k \neq n$. 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.

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.

Throughflows are examined for different input and output vectors. The average path length of an inflow (AP L2) is the number of compartments crossed by a given input. Energy cycling can be estimated through the efficiency

\[ RE = \frac{Tii-1}{Tii} \]

when \( Tii \) represents the flow through \( i \) (see table).

**ILLUSTRATIVE APPLICATION OF THE EUTROPHICATION MODEL**

<table>
<thead>
<tr>
<th>Year</th>
<th>Observed</th>
<th>Population accelerated growth</th>
<th>Population moderate growth</th>
<th>Population limited growth</th>
<th>Two foot Lake level change</th>
<th>Phosphorus removal (50% agriculture)</th>
<th>Phosphorus removal (95% + detergent)</th>
<th>80% P*</th>
</tr>
</thead>
<tbody>
<tr>
<td>1930</td>
<td>15 µg liter⁻¹</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>1970</td>
<td>25 µg liter⁻¹</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>1990</td>
<td>37 µg liter⁻¹</td>
<td>30 µg liter⁻¹</td>
<td>—</td>
<td>—</td>
<td>10 to 15µg/liter⁻¹</td>
<td>10 µg liter⁻¹</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>2010</td>
<td>42 µg liter⁻¹</td>
<td>35 µg liter⁻¹</td>
<td>20 µg liter⁻¹</td>
<td>—</td>
<td>15 to 20µg/liter⁻¹</td>
<td>20 µg liter⁻¹</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

* The information presented should be considered an illustration of the types of results obtainable from application of eutrophication models to analyses of planning problems rather than a projection of future conditions.

1 These levels are for the moderate growth population levels.

2 The same algae levels can be obtained with an 80% phosphate removal policy plus 1990—25% nitrogen removal and 2010—50% nitrogen removal.

3 Values are micrograms/liter of chlorophyll for Western Lake Erie in Section 7 of the eutrophication model (near the Maumee River).

4 Change in chlorophyll levels from 1970 conditions.

Thereby structural properties of the ecosystem are outlined and reveal the main flows.
IV - Marenes-Oléron estuary

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 deserved 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 functions, 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.

We are trying to modelize the Marenes-Oléron 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 populations, 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.
4) A high turbidity prevents the primary production from occurring in the major part of the estuary; the high concentration of non-biotic particles probably lower 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 function (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 function 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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