

hours after feeding will lose up to 25% of their HUFA. It is expected that cold storage of enriched *Artemia* juveniles (at 5°C) will allow to maintain initial HUFA levels at their maximum as was proven for nauplii for periods up to 48h by Léger *et al.* (1983).

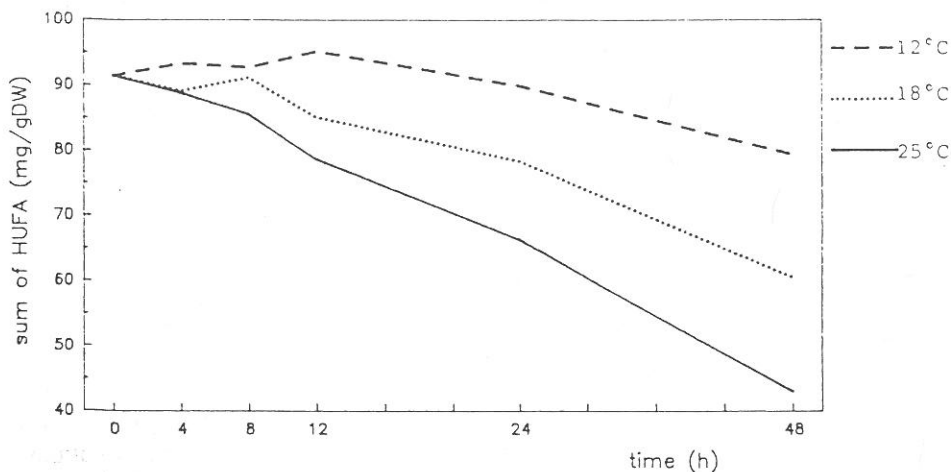


Fig. 1. Change in HUFA level of enriched *Artemia* stored at different temperatures.

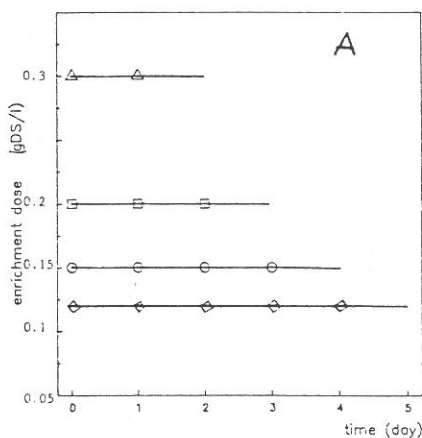


Fig. 2A. Enrichment doses of the different enrichment strategies; total enrichment dose is 0.6gDS/l for all treatments.

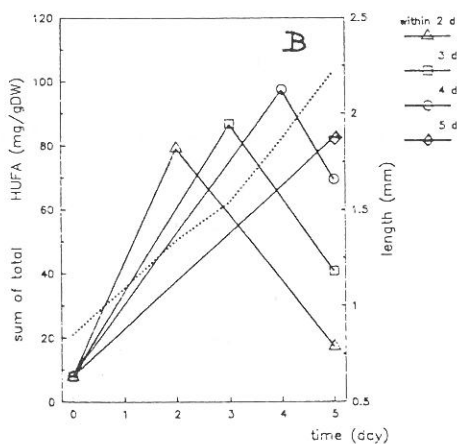


Fig. 2B. HUFA level in *Artemia* enriched within 2, 3, 4, and 5 days; the dotted line indicates animal size.

Enrichment of *Artemia* of various age and size

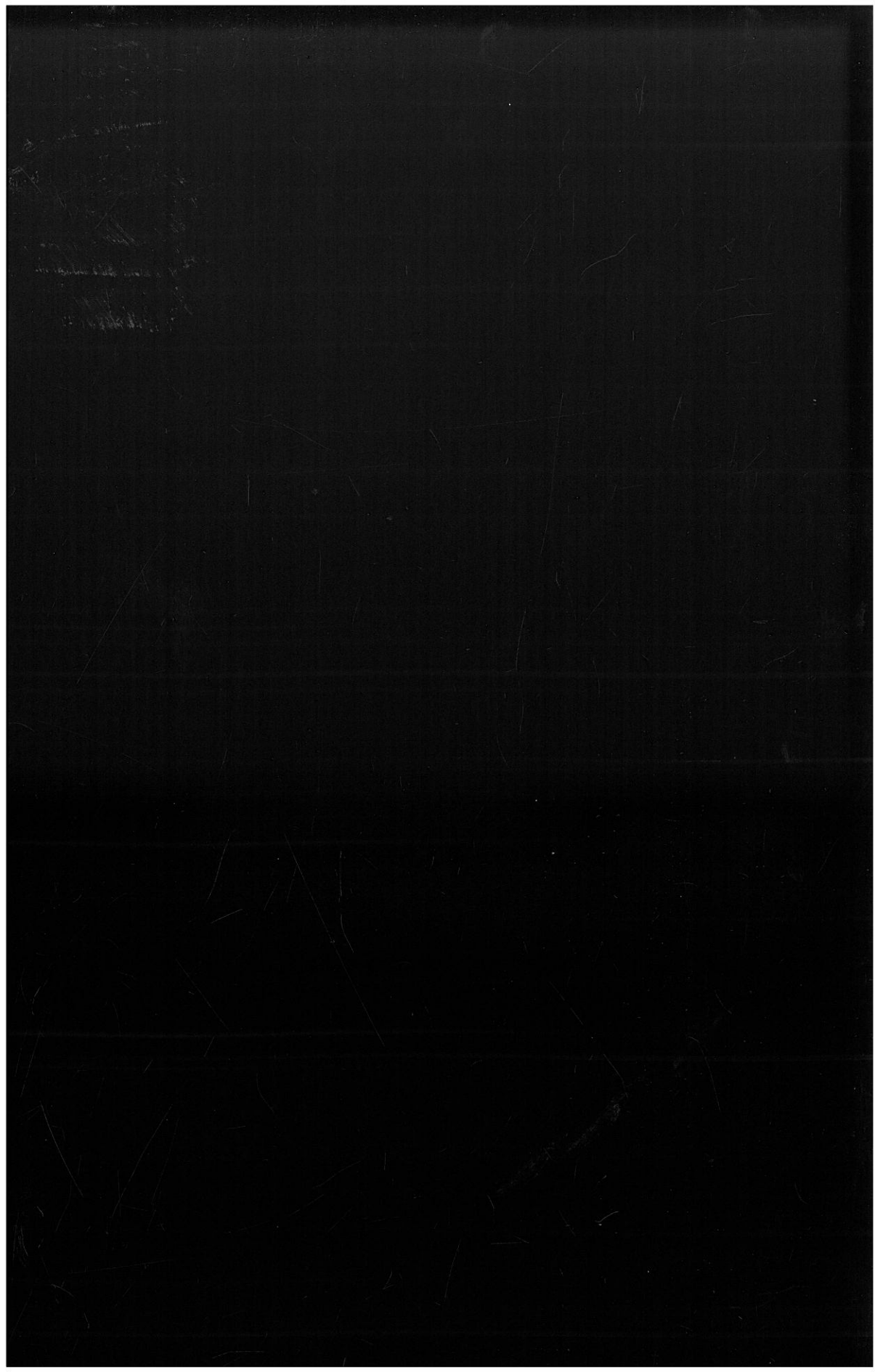
Artemia that received the total enrichment dose during days 0 to 2, accumulated HUFAs in their body tissue at levels comparable to those of gradually enriched 7-day-old *Artemia* (Fig. 2B). On the other hand, final HUFA levels still increased when the enrichment was spread over an extended period. Fig. 2 further shows that HUFA levels dropped drastically as soon as the daily addition of the enrichment medium is ended. This implies that part of the assimilated HUFAs is directly metabolized. As a consequence, an increase in HUFA content will only be realized when the daily HUFA uptake exceeds its decrease through metabolism. This equilibrium determines the minimal effective daily enrichment dose, while its maximum is limited by its negative effect on water quality.

Acknowledgements

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ECOLOGICAL MODELLING OF THE NORTH SEA

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ABSTRACT

North Sea ecosystem models published in accessible literature are partitioned into groups with respect to their emphasis on significance and detail of different trophic levels of the ecosystem. These subsets are treated separately in the three main chapters, which deal with relationships with physical dynamics, lower trophic level interactions and higher trophic level interactions. They are preceded by chapters that introduce the scope of the models, the history of modelling approaches, main purposes and specific aims, general aspects of internal structure, and modelling techniques applied. The main chapters compare the process descriptions characteristic of the subsets of models, and discuss aims and results with emphasis on significance and contribution of the processes considered.

The chapter on plankton dynamics in relation to physical dynamics relates plankton responses in the mixed layer to changes in the physical environment. Attention is given to seasonal forcing functions, the coupling of horizontal and vertical plankton distributions, the flow of matter and the sensitivity of the plankton system.

The chapter on lower trophic levels deals with primary production and its limiting factors, nutrient cycles, eutrophication, the microbial loop, and mineralization of organic matter in the pelagic and benthic compartments.

The chapter on higher trophic levels highlights predator-prey interactions, the impact of grazing, and the significance of predation for system stability.

A final chapter discusses what has been achieved so far with models of North Sea ecosystems and what must be aimed at in the future. It argues for lucidity and more methodology in simplification to the degree allowed by the questions to be solved, more attention for models as carriers of unifying concepts in marine ecological theory, technical solutions in handling differ-

ent time and space scales for different processes and distributions, cooperation of different disciplines to find answers to questions of general importance, and the formation of data bases for model validation.

1. INTRODUCTION

(H.G. FRANSZ)

1.1. SCOPE OF MODELS

Ecological modelling is a method to relate levels, distribution and fluctuations of abundance and production of living organisms to variation in food conditions, predation, and the abiotic environment. In this review only the mathematical approach is considered. To be more specific: only the models dealing with dynamics by integrating expressions for rates of change in system components are reviewed. Those components can be populations of a single species, or higher functional groups such as algae, herbivores or fish. Process models dealing with the functioning of individual organisms will only be discussed if their results are relevant for the definition of rate expressions.

The core of the review is a description and comparison of structure and results of published North Sea models. Estuarine models are not included because estuarine abiotic conditions, transport processes, spatial variation and species composition deviate to such an extent that they create typical ecosystems. Also models for regions outside the North Sea are treated with reserve, and only included to elucidate technical details or general principles.

1.2. DEVELOPMENT OF NORTH SEA ECOSYSTEM MODELS AS TOOLS

During the 1950s the first mathematical description of the seasonal plankton dynamics appeared (RILEY *et al.*, 1949), stimulated by the newly developed ecological theory on the regulation of populations by competition and predator-prey interactions (VOLTERRA

RA, 1926; LOTKA, 1932; NICHOLSON, 1933; GAUSE, 1934).

These lines of thought were followed by STEELE (1958) and CUSHING (1959) in early models of phytoplankton development. Increased knowledge of the biology of the important herbivore *Calanus finmarchicus* led to the development of more detailed models in the seventies (LASSEN & NIELSEN, 1972; STEELE, 1974; HORWOOD, 1974). These models concentrated on the explanation of algal production and development in the northern and western North Sea, but they gradually included more trophic levels to describe the transfer of carbon in the food chains and the productivity at all trophic levels. There was a gradual evolution from STEELE & HENDERSON (1976) through HORWOOD (1982) to JONES & HENDERSON (1987b) in the English tradition. A Belgian school ranged from PICHOT & RUNFOLA (1976) through MOMMAERTS *et al.* (1984) to BILLEN & FONTIGNY (1987) and BILLEN & LANCELOT (1988). The Belgian models were developed for the coastal zone of the Southern Bight and emphasized the nutrient cycles (mainly N) and mineralization at the lower trophic levels, including micro-organisms. A German contribution to the understanding of plankton development in the northern North Sea was given by RADACH (1980, 1983).

In pace with the general trends, but directed at more specific goals, were studies on plankton distribution and patchiness (DUBOIS & ADAM, 1976; EVANS *et al.*, 1977; EBENHÖH, 1980), and eutrophication by riverine nutrient discharge (FRANZ, 1981; FRANZ & VERHAGEN, 1985).

Endeavouring to relate fish production and species composition to basic production processes, fishery research institutes developed a separate line of multispecies models (ANDERSON *et al.*, 1973; ANDERSON & URSIN, 1976). A somewhat simpler model based on community structure and regulation by predator-prey interactions was developed by KOSLOW (1983) to test the validity of some fresh-water paradigms for the marine environment.

The different goals led to highlights on different functional aspects of North Sea ecosystems, which altogether have considerably increased our understanding of their dynamics. In recent years North Sea management has required tools to compare the impact of different scenarios on fish production and environmental conditions. Further development and combination of existing models may ultimately provide such tools. But until now the main achievement has been the provision of coherent scientific concepts relating facts and figures on many different components and processes.

2. IDENTIFICATION OF FUNCTIONAL UNITS MODELLED (J.P. MOMMAERTS)

2.1. INTRODUCTION

Today, efforts towards ecological modelling are being made in virtually all countries around the North Sea. Most of these new generation models have not yet been published and thus escape this review. However, it has been noted that these models tend to become much more biologically and chemically diversified than earlier models, as it is now largely recognized that there is no way to simulate in sufficient detail the ecosystem behaviour without an in-depth treatment of the full cycle of organic matter.

These processes are not foreign to the preoccupation caused by the eutrophication of the sea and its various manifestations.

Indeed, phytoplankton blooms of various nature have been signalled with an increasing frequency in the last ten years in several parts of the North Sea, especially in coastal areas and embayments. In some areas, the regular spring bloom is affected both in a qualitative and a quantitative way: this is the case of the eastern coast of the English Channel and the North Sea, from France to Denmark. The colonial flagellate *Phaeocystis pouchetii* here dominates, provoking conspicuous froth on the beaches and upsetting the ecosystem structure. In other areas, more or less toxic dinoflagellates bloom in late summer, possibly discolouring water, poisoning shellfish, stressing fish and locally contributing to oxygen depletion. Although there is general consensus that the inputs of nutrients to the sea must be reduced, there is so far no firm scientific basis to decide upon the extent of such reductions.

An appropriate way of addressing the problem of eutrophication and of testing nutrient reduction scenarios is to simulate the phenomenon with mathematical models. So far, no so-called eutrophication model (possibly a holistic model) has been applied to the North Sea. On the other hand, it is probably correct to assume that any ecological model with a sufficiently complex internal structure and the multiple relationships that are found at the 'lower trophic levels' (see 4.2.) will come close to an answer, provided the right time scale is applied.

In this chapter we address on the one hand the internal structure and the identification of the functional units to be modelled and, on the other hand, the regional distribution of ecological models. The eutrophication problem is relevant to both aspects.

2.2. INTERNAL STRUCTURE

2.2.1. THE SYSTEM APPROACH AND THE EMERGENCE OF THE CONCEPT OF FUNCTIONAL UNITS OR 'COMPARTMENTS'

Simulation models of ecosystem dynamics existed as early as 1939 (FLEMING, 1939) and were, not surprisingly, contemporary with the famous LINDEMAN's (1942) paper on the 'trophic-dynamic aspect of ecology'. From then on two complementary approaches have coexisted that both may be called 'models': the mass-balance studies and the simulation models.

The two types of models have in common a series of features (including their internal structure) relevant to the system approach:

- system boundaries are defined and enclose the 'universe' at study
- exchanges of matter and energy with the outer world are taken into account
- functional units or 'compartments' (e.g. phytoplankton, zooplankton, limiting nutrient, marine bacteria,

etc.) are identified and supposed to play a prominent enough role to explain most of the behaviour of the whole system, whereas others are discarded from the analysis because they seem to have much less bearing on the system

- pathways connect the functional units and allow fluxes of matter, energy and information between them.

The two types of models differ in that mass-balance models represent a stable balanced diagram of annual fluxes and the simulation models represent a system of time and state dependent fluxes. Thus, simulation models comprise a kinematic dimension, conferring on them a predictive or, at least, an explanatory value.

Therefore, such models often aim at the solving of systems of simultaneous first-order ordinary differential equations (=the conservation equations), each one reflecting the behaviour of a given functional unit (=state variable), usually as a function of time.

Until very recently most ecosystem modellers have not made much effort to introduce more biological

Preliminary diagrammatic representation of the relation of the Herring to the Plankton Community as a whole. Links in the nutritive chains taken from the results of other researches shown in dotted line.

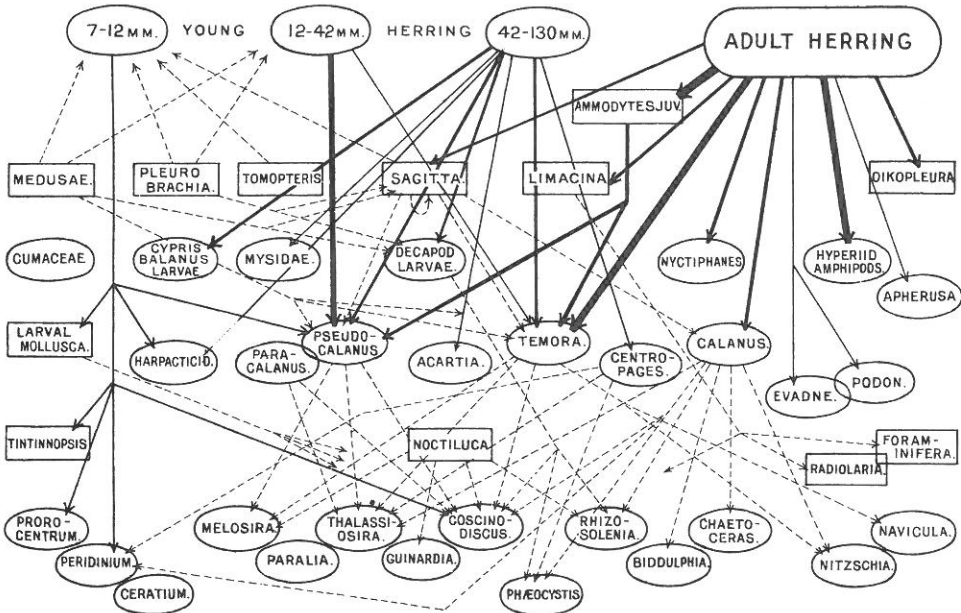


Fig. 1. Feeding relations of the North Sea herring, *Clupea harengus*, during different stages of its life history (from HARDY, 1924).

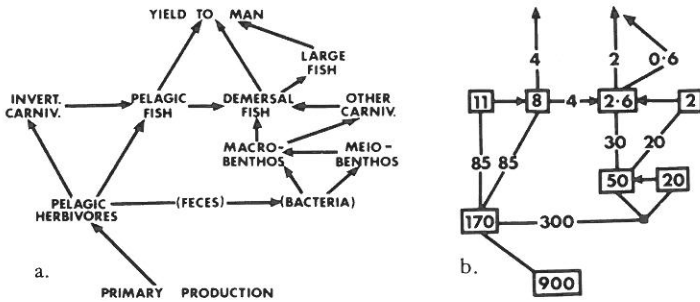


Fig. 2. a. A North Sea food web based on the main groups of organisms. b. Values for yearly productions ($\text{kcal}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) (from STEELE, 1974).

and chemical diversity than found in the classic model of RILEY *et al.* (1949), which is based on a simple three-stage foodchain: limiting nutrient - phytoplankton - zooplankton.

Instead, their explorations have rather tended to address specific aspects related to the connection between that very simple biological model and the physical world. Thus, some models are vertically and others horizontally resolved, whereas some authors try to combine aspects of both approaches.

However, synecological studies demonstrate that the number of functional compartments must be larger, including dissolved and particulate organic matter and the biological compartments which are responsible for its mineralization in water (heterotrophic bacteria, microzooplankton) and in sediments (heterotrophic bacteria, microzoobenthos). Phytoplankton, zooplankton and nutrients themselves can be diversified in a series of more relevant units.

2.2.2. THE TROPHIC-DYNAMIC STRUCTURE AND MASS-BALANCE STUDIES

Prior to simulation modelling comes the identification procedure and the establishment of a balance of all fluxes connecting the identified functional units.

The identification procedure is a critical step in any modelling effort. It starts with a careful inventory job in the field. It continues with some delicate decision-making such as the lumping of several biological populations or chemical species in 'model compartments'. It ends with a thorough evaluation by well-trained synecologists, including the setting-up of mass and flux balances, generally on an annual basis. This whole process is recursive.

Modern mass-balance studies find their origin in the earlier studies of the food-web at sea that abound in the ecological literature. Some of those early descriptions are focused on particular aspects of the system, e.g. HARDY (1924, the food of the herring of

the North Sea) (Fig. 1) and MARE (1942, the role of microbenthos), whereas others are focused on the whole system e.g., BLEGGVAD (1916), PETERSEN (1918, the Limfjord), HART (1942, Antarctic system), SVERDRUP *et al.* (1946) and HARVEY (1945, 1955). Most are purely descriptive or at best semi-quantitative.

Although the wealth of organisms engaged in the marine food-web and the patterns of feeding habits by themselves may in many instances seem to be desperately complex and unstable, most of the functional units as we know them today were already well identified, thus realizing a necessary compromise

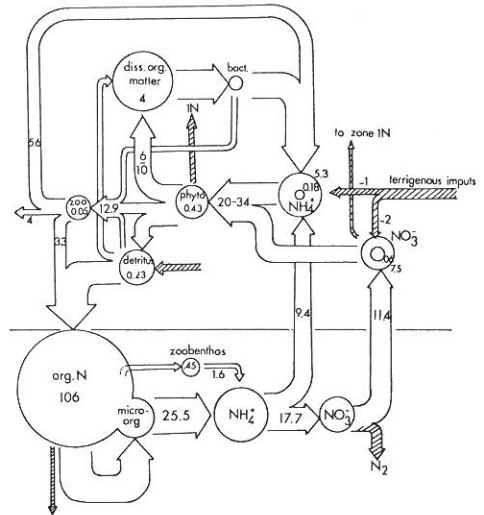


Fig. 3. Diagram of the nitrogen budget for the Belgian coastal zone (from NIHOUL & POLK, 1977).

between reality and simplicity. For instance, in his work on the cycle of phosphorus in the English Channel, HARVEY (1945, 1955) identified the compartments nutrient, phytoplankton, zooplankton, nekton and benthos, organic detritus, dissolved organic matter, marine bacteria etc. Moreover, the choice of a common unit for the biological variables—usually in terms of elemental composition—smeared over species variation to yield presumable properties of a system which has less variance than its component species populations (MANN, 1975).

The paper by LINDEMAN (1942) undoubtedly encouraged ecosystem studies, putting even more emphasis on the functional units and on the quantification of the fluxes of matter and energy between them.

Thus, the attempt by STEELE (1974) to put figures—collected from quite a number of more specialized authors—on a diagrammatic food-web in the northern North Sea is well worth mentioning (Fig. 2). This author has also taken important steps in the direction of simulation modelling.

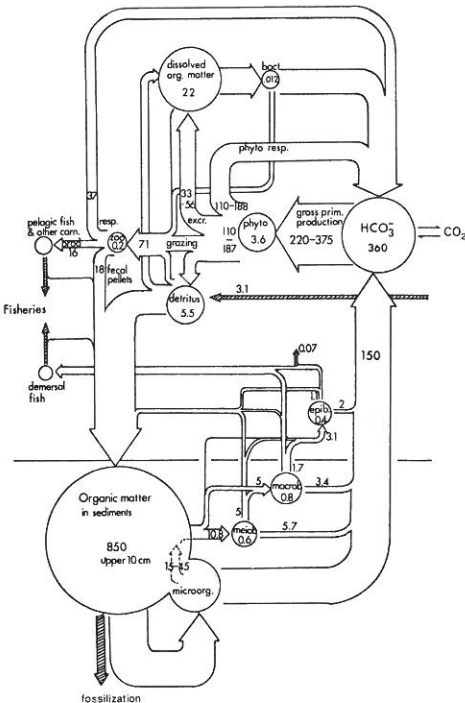


Fig. 4. Diagram of the annual carbon budget for the Belgian coastal zone (from NIHOUL & POLK, 1977).

From 1973 onwards, a Belgian team has been working on the mass-balance of nitrogen in the Southern Bight of the North Sea (BILLEN *et al.*, 1976; JOIRIS *et al.*, 1982; MOMMAERTS *et al.*, 1984). The emphasis was put on field determinations of fluxes (N uptake and losses by phytoplankton, grazing by zooplankton, pelagic bacterial activity, mineralization of organic matter in the bottom sediment). They succeeded in producing a balanced overall picture of production and consumption fluxes in N units as well as in C units (Figs 3 and 4). The simulation model by PICHOT (1980) stems directly from this mass-balance study.

A significant outcome of this work was that, in the eutrophic Belgian coastal area, primary products appear to be diverted from the classic food chain (phytoplankton - zooplankton - fish); instead, they enter a microbial loop with little benefit to the ecosystem diversity. Thus, the new 'paradigm' underlined by POMEROY (1974), and putting the emphasis on the role and turn-over of organic matter in marine ecosystems found justification in these studies.

The same approach has been followed by JONES & HENDERSON (1984, 1987) for an area off the Scottish east coast, with clearly similar conclusions about the important role played by organic matter and the microheterotrophic food chain.

These authors too have taken steps towards simulation modelling.

2.2.3. INTERNAL STRUCTURE OF ECOSYSTEM MODELS

Mass-balance studies have generally been paralleled—with only a short time lag—by simulation models. It follows that the evolution of models has also been characterized by the growing intricacy of their internal structure. For instance, the models by FRANSZ & VERHAGEN (1985) and BILLEN & LANCELOT (1988), which were written for the purpose of eutrophication modelling, have a particularly complex internal structure with over 20 state variables and many more parameters.

There are some problems and dangers, however:

- There is always a loss of information in the process of converting the system picture into a working model. Indeed, it is not possible to meet the validation requirement for all process parameters. Hence, simpler descriptions permit this problem to be evaded but there is a loss of flexibility. Moreover, there are also computer constraints (although these tend to disappear, with the coming of modern super-computers).

- As in the earlier models, the structuration into trophic levels of the more recent models does not go beyond the herbivore level (zooplankton). In other words, there is so far no connection with the fish

compartment(s) although models for fishes and fisheries have existed for quite a long time. However, there are signs that this gap could be filled before long, but no published model is available yet.

- It follows that, with their limited number of functional units, many of the models reviewed (see 4.2.) lack realism with respect to the total behaviour of the ecosystem: the necessity of mass conservation inevitably leads authors to rely on 'source' and 'sink' terms. For instance, the bottom sediment is often simultaneously treated as a source of inorganic nutrient and a sink for detritic matter but there is so far no coupling between detritus deposition and detritus mineralization. In a similar way, 'carnivores' always act as a sink for zooplankton. Although mass conservation is preserved, the use of sinks and sources considerably weakens the value of such models and especially their self-organizing capacity.

- Conversely, the multiplication of parameters can have an adverse effect on the final accuracy of the model. Thus JESTER *et al.* (1977) put forward that, from a certain level of complexity, the accuracy of a model becomes asymptotic to a plateau whereas the uncertainty grows exponentially.

The alternatives proposed by LEVINS (1966) should also be kept in mind, where a choice must be made between realism, accuracy and generality (any combination of two of these properties automatically excluding the third).

The latter observation also indicates that the scope of several simulation models discussed in 4.2. is bound to be regionally limited if some degree of realism and accuracy is to be preserved.

But important progress has also been accomplished: Although more recent models do not simulate an actual food-web—with *i.e.* some functional units pertaining to different trophic levels simultaneously—they come close to this picture in diversifying notably the existing trophic levels. Hence several species of inorganic nutrients are considered simultaneously as well as several groupings of phytoplankton (diatoms, flagellates, *Phaeocystis pouchetii*) and its several internal pools (*e.g.* precursors, storage products, structural products: LANCELOT, 1983; LANCELOT *et al.*, 1986), young cells, senescent cells (FRANZ & VERHAGEN, 1985) etc.

A similar diversification is now considered for zooplankton, where not only several species of copepods would co-exist but where each species would develop through several multi-cohort development stages and generations (BOSSICART, 1980a, 1980b).

Last but not least, significant progress has also been made in the understanding and the modelling of bacterial mineralization of organic matter, the production of inorganic nitrogen in the bottom sediment (through ammonification, nitrification and denitrification) and its diffusion towards the water column

(BILLEN, 1978, 1982; BILLEN & LANCELOT, 1988), as well as bacterial activity (including exoenzymatic activity) in the open water (SOMVILLE & BILLEN, 1983; BILLEN, 1984; BILLEN & FONTIGNY, 1987). There is now an actual coupling in some models between both detritus and dissolved organic matter production, and inorganic nutrient creation.

In such models, the degree of validation of the process parameters has generally improved, benefiting from new methodologies and progress in the understanding of biological and biogeochemical mechanisms. An example of this (not used in the above-mentioned models) is the process model of photosynthesis relying on the activity of the photosynthetic units (FASHAM & PLATT, 1983). Other examples are the well-documented collection of sub-models of photosynthesis, excretion and exchange processes between cells and external mucus in the colonial flagellate *Phaeocystis pouchetii* (LANCELOT *et al.*, 1986).

It follows that the total number of pathways that connect functional units in the system has increased considerably in the more recent models, going far beyond the classic 'prey-predator' step. This increase is also paralleled by an increase in the number of 'negative feedbacks', *i.e.* controls exerted by the prey (or substrate concentrations) on the activity of the predators (or consumers). Feedback loops confer a unique property to models: a self-organizing capacity. One is thus measuring the progress accomplished since RILEY *et al.* (1949) and STEELE (1958) introduced this aspect into simulation modelling. Moreover, as the relations that govern such feedbacks are mostly non-linear (*e.g.* hyperbolic saturation curves, with or without threshold), such properties as system stability and resiliency are re-inforced.

Thus, more information and matter flows within the system simulated. In recent models, there is also more information and control coming from the outer world: for instance, as the resolution in time tends to be finer, diel variations of light must be taken into account. This in turn has a marked effect on the growth strategy of phytoplankton, especially in the model with internal pools. On the other hand, the physical forcing—*e.g.* the vertical structuring resulting from the turbulent diffusion activity in relation with the temperature profile—is also more sophisticated in recent models. This particular aspect is reviewed in chapter 4.1.

Thus, after a period of skepticism there seems to be a revival of the 'reductionist approach', the models being this time based on much firmer physiological and physical grounds. The eutrophication model that is presently being assembled in a joint European study by research teams from almost all countries bordering the North Sea is representative of this approach.

This recent evolution is most welcome at a time when pervading eutrophication is challenging our modern industrial society.

2.3. REGIONAL DISTRIBUTION

It is clear from the analysis of the published models (see also 4.2) that regional differences in the abiotic world have to a large extent determined the type of approach selected.

Thus, models of comparatively deeper ecosystems in most cases belong to the vertically structured type (either divided into 2 homogeneous layers separated by a thermocline, or vertically resolved with the turbulence profile used as a forcing variable). Moreover, eutrophication is generally not a problem in such areas, where the classic food-chain tends to prevail. A simpler internal structure may thus prove sufficient.

The models of STEELE (1958) and LASSEN & NIELSEN (1972) pertain to the two-layered type —inspired by RILEY *et al.* (1949)— whereas those of RADACH (1983) and TETT *et al.* (1986) are vertically resolved. All these models are related to the central North Sea (Fladen Ground) with the exception of the model of TETT *et al.*, which relates to the area of the Scilly Islands as well as to the Sound of Jura (off W. Scotland).

In these models, the horizontal transport (advection and diffusion) is considered to be negligible compared to the vertical exchanges. If not so, the model is established for a shorter period of the year, when such conditions are temporarily met.

Whenever horizontal transport is found to be important, horizontally structured 2-D models provide an alternative. Since there is so far no published 3-D ecological model for the North Sea, such horizontal models imply vertical homogeneity. The models of DUBOIS & ADAM (1976), for the Southern Bight of the North Sea, and of HORWOOD (1982), for an area off the NE of England, belong to that type.

Finally, one observes that whenever biological interactions have received much attention —with respect to number and complexity—, the box-model approach has been elected. This has especially been the case of shallow coastal areas of the North Sea, that include an important benthic component. Here too, the structuration is horizontal but there is no continuity equation to be resolved.

Thus, the models of PICHOT (1980) (eastern half of the Southern Bight), FRANSZ & VERHAGEN (1985) (Dutch coastal waters), BILLEN & LANCELOT (1988) (eastern coastal sea, from the Western Channel to the German Bight) and also MOMMAERTS (1978) (Belgian coastal waters) and JONES & HENDERSON (1987) (E. Scottish waters) all pertain to that type of model.

3. MODELLING APPROACHES AND TECHNIQUES (G. RADACH)

The simple conceptual ecosystem models and the process models, as well as stochastic models (like uni-variate and multi-variate regression models, autoregressive models or others) are not considered here.

Technical information about the models presented in the papers is usually given low priority, or none at all. In about half of the papers the mathematical solving procedure, *i.e.* the numerics, is not explained, nor is the implementation mentioned or discussed. In nearly all cases the technical solving procedure is not discussed. The numerical methods seem to be self-understanding and self-explaining, which is —of course— not always the case.

3.1. TYPES OF MODELS

The type of models reviewed here is the dynamical simulation model, which allows to simulate the time-dependent development of one or more state variables, either with no space dependence or with one to three space dimensions. Most model simulations yield time series, disregarding space dimensions (STEELE, 1958; LASSEN & NIELSEN, 1972; STEELE, 1974; HORWOOD, 1974; RADACH & MAIER-REIMER, 1975; PICHOT & RUNFOLA, 1976; STEELE & HENDERSON, 1976; EVANS, STEELE & KULLENBERG, 1977; ANDERSON & URSIN, 1977; MOMMAERTS, 1978; RADACH, 1980; KOSLOW, 1983; JONES & HENDERSON, 1987; BILLEN & LANCELOT, 1988). Fewer model simulations deal with spatial distributions in time (DUBOIS & ADAM, 1976; HORWOOD, 1982; MOMMAERTS *et al.*, 1984; FRANSZ & VERHAGEN, 1975). Only very few simulations serve to establish budgets of the model system (*e.g.* HORWOOD, 1982; RADACH, 1983).

3.2. TYPES OF MATHEMATICAL FORMULATIONS

All models considered here consist of time-dependent differential equations. In one case steady state conditions are considered by solving time-dependent equations (TETT *et al.*, 1986).

Ordinary differential equations (ode) are much more frequently used than partial differential equations (pde). This is certainly a consequence of the availability of numerous solving routines for ordinary differential equations and of the greater simplicity of the equations. Reducing the dependence of the state variables to time or to one space dimension yields ordinary differential equations. Including more than one independent variable results in partial differential equations, with much more complication in numerical solving schemes.

Ecological water column dynamics are often treat-

ed by a set of ordinary differential equations, after integrating the original partial differential equations vertically (STEELE, 1958; LASSEN & NIELSEN, 1972; STEELE, 1974; PICHOT & RUNFOLA, 1976; EVANS *et al.*, 1977; ANDERSON & URSIN, 1977; KOSLOW, 1983; JONES & HENDERSON, 1987a, 1987b; BILLEN & LANCELOT, 1988). The number of the equations is very different, ranging from 2 (STEELE, 1958; LASSEN & NIELSEN, 1972) to 4 (PICHOT & RUNFOLA, 1976; EVANS *et al.*, 1977; MOMMAERTS *et al.*, 1984), 7 (BILLEN & LANCELOT, 1988), 9 (JONES & HENDERSON, 1987), 11 (KOSLOW, 1983), 12 (MOMMAERTS, 1978), 17 (FRANZ & VERHAGEN, 1985) to 41 (ANDERSON & URSIN, 1977).

The original vertically resolving equations are partial differential equations of second order due to the vertical diffusion term. They are used by several authors, but usually for small sets of non-linearly coupled equations and often coupled together with a few ordinary differential equations (2 pde and 1 ode: RADACH & MAIER-REIMER, 1975; 2 pde and 6 ode: STEELE & HENDERSON, 1976; 2 pde: RADACH, 1980, 1983; 3 pde: TETT *et al.*, 1986; 2 pde and 2 ode: RADACH & MOLL, 1990).

For horizontally resolved ecosystem dynamics so far mostly simplified equations have been used, by replacing the horizontal second order derivatives through box-averaging by terms which no longer contain derivatives and thus belong to the first group of sets of ordinary differential equations (HORWOOD, 1982; MOMMAERTS *et al.*, 1984; FRANZ & VERHAGEN, 1985). After an early paper (DUBOIS & ADAM, 1976), it is only recently that the partial differential advection-diffusion equations are being solved in their full time and space dependences.

The variety of mathematical formulations mirrors the variety of problems treated in the North Sea. No general guidelines for the mathematical aspects of modelling the North Sea ecosystem can be derived from the existing mathematical formulations.

3.3. TYPES OF SOLVING TECHNIQUES

In the papers that give information about numerical methods different methods for differential equations are used.

Ordinary differential equations were solved by straightforward explicit methods (STEELE, 1974; TETT *et al.*, 1986; JONES & HENDERSON, 1987) or by implicit Runge-Kutta methods (LASSEN & NIELSEN, 1972; ANDERSON & URSIN, 1977).

Partial differential equations were solved by explicit finite difference methods (RADACH & MAIER-REIMER, 1975; STEELE & HENDERSON, 1976 (DuFort-Fraenkel scheme); EVANS *et al.*, 1977; RADACH, 1980, 1983; TETT *et al.*, 1986; RADACH & MOLL, 1990) or by alternating direction implicit methods (ADI; DUBOIS &

ADAM, 1976; HORWOOD, 1982).

In most papers no information is given about the numerical stability of the solving scheme used. Such considerations would be helpful for everybody starting to use numerical methods by providing experience with the different methods. Also, conservation properties of the numerical schemes, like mass conservation, are rarely reported. Such information can be of high value in judging the correctness of the numerical scheme, and *e.g.* mass balances should be calculated (and reported) much more often.

As for the aspects of mathematical formulation, no general rules can be given for the numerical methods to be used in North Sea models. Here we can refer the reader only to the standard literature for numerical methods of ordinary differential equations (HAIRER *et al.*, 1987) and for partial differential equations (SMITH, 1969; ROACHE, 1976).

3.4. IMPLEMENTATIONS

Only half of the papers present information on the implementation of the computer program used for the simulations. Mostly FORTRAN is used for the simulation program. Recently PASCAL has appeared (TETT *et al.*, 1986). While nearly all models were run on mainframe computers (RADACH & MAIER-REIMER, 1975; DUBOIS & ADAM, 1976; ANDERSON & URSIN, 1977; RADACH, 1980, 1983; RADACH & MOLL, 1990), a recent paper reports on simulations on a PC (TETT *et al.*, 1986). This implementation will certainly become a trend, as the power of personal computers increases drastically.

4. PLANKTON DYNAMICS IN RELATION TO PHYSICAL DYNAMICS (G. RADACH)

4.1. INTRODUCTION

Physical processes are important for plankton dynamics on many space and time scales. This has been demonstrated in several past and recent reviews (HAURY *et al.*, 1978; HARRIS, 1980; LEGENDRE, 1981; LEGENDRE & DEMERS, 1984; DEMERS *et al.*, 1986) and will not be repeated here. This chapter deals with plankton models in relation to the physical world; it is centred around models with a strong physical component. Models which focus on biological detail are reviewed in the following sections.

This chapter was originally intended to be restricted to models for the planktonic system of the North Sea, which focus on the effects of physical detail on plankton dynamics. It turned out that only a few physically orientated plankton models have been deve-

loped for problems of the North Sea (DUBOIS & ADAM, 1976; HORWOOD, 1982; RADACH & MAIER-REIMER, 1975; STEELE & HENDERSON, 1976; EVANS *et al.*, 1977; EVANS, 1978; RADACH, 1980, 1983). Many more such plankton models were developed for other regions of the ocean, but bear on the same problems as occur in the North Sea. Therefore, models of plankton systems from other regions are included in the review if they treat physical detail in relation to plankton problems also relevant for the North Sea plankton system. Without being in any way exhaustive, we want to demonstrate the potential of the combination of plankton modelling with physical detail and therefore refer to results obtained for different areas with similar dynamical features.

All the plankton models discussed here were developed and applied for a better understanding of the dynamics of the plankton system, by combining hypotheses about chemical and biological processes with an adequate description of the physical environment. But the ways in which this aim is pursued are very different. There are at least two lines along which plankton models were used: the first sets up exploratory models and seeks to qualitatively and/or quantitatively reproduce certain features of the plankton dynamics. The other line uses models to try to reproduce data sets measured, in the form of hindcasts and of consistency checks between model results and data, in the framework of physical data. The latter approaches are attempts to validate plankton models.

The first to present a mathematical description of plankton dynamics including physical processes in a set of advection-diffusion-reaction equations for the conservation of matter were RILEY *et al.* (1949). Their theoretical formulation is still the basis of most models of plankton dynamics. The models which have appeared since then are either simplified or more complicated versions of the same basic equations, depending on the problem aimed at. The problems of plankton modelling as outlined in the pioneering work by Riley and his colleagues are still the same and cannot be regarded as fully solved. All models reviewed in this section (except one) contain at least a phytoplankton equation. This equation is very often combined with a nutrient equation and one or more zooplankton equations. In a few models other state variables are also predicted, such as various nutrients in the water (*e.g.* KIEFER & KREMER, 1981) or in the cells (*e.g.* TETT *et al.*, 1986), detritus (SJÖBERG & WILMOT, 1977) or underwater light (*e.g.* RADACH & MAIER-REIMER, 1975; WINTER *et al.*, 1975; KIEFER & KREMER, 1981; STIGEBRANDT & WULFF, 1987). Table 1a lists the models reviewed. They resolve the vertical space dimension with respect to their prognostic state variables (which are simulated) and the diagnostic state variables (which are

prescribed), their independent variables, the time and space scales considered in the papers, and area and season for application of the model. Table 1b does the same for the horizontally resolved models.

Details of process formulations will be discussed in this chapter only in so far as physical processes are concerned and effects in combination with these processes appear to be important.

In general, there is a standard theoretical physical oceanographic knowledge, which leaves little room for alternative formulations of physical processes (*c.f.* 4.1.1.). The realization of the physical processes, however, leaves many possibilities for simplification, as can be seen from 4.1.2. The variety of formulations of parameterizations for chemical and biological processes taken into account is greater (see the following sections). In Table 2 the processes involved in the models reviewed are summarized in a simple and simplifying way.

Important features of the models originate from the treatment of the 'bottom' and the 'top' level of the plankton system considered within the ecosystem: the nutrients and the highest trophic level involved. This question is briefly followed up in 4.1.4.

Concerning nutrients, the relevant processes are uptake, remineralisation, excretion and physical exchange. Nutrient uptake is formulated sometimes by multiplicative (*e.g.* RADACH & MAIER-REIMER, 1975), by alternative limitation factors (*e.g.* RADACH, 1980, 1983), or by cell quota kinematics (TETT *et al.*, 1986). These processes are treated in detail in 4.2.

The highest trophic level involved is often zooplankton. The grazing pressure on the phytoplankton turns out to be very important, and so is the grazing formulation imposed. Grazing may be formulated in very different terms. For instance, grazing is assumed to be proportional to constant zooplankton biomass (TETT *et al.*, 1986), or grazing enters the models by prescription of a potential grazing derived from zooplankton standing stocks (RADACH, 1980, 1983). These processes will be treated in detail in 4.3.

The sequence within this section is the following: first, some basic physical process formulations will be given, followed by the variety of practical realizations in the various models discussed; then the effects of physical action will be discussed: first the horizontally resolved models, then a few coupled models, and finally the vertically resolved models.

In each of the following sections I will proceed quasi-historically: because the spring phytoplankton bloom has been in the focus of research first and most extensively, it will be treated first. It is still a main subject of research. After the spring blooms, short-term events, such as storms, will be dealt with. They received attention a few years later, when elaborate mixed layer models became available. Last, models of the full annual cycle come into focus,

TABLE 1a

Comparison of vertically resolved models (ordered historically): prognostic and diagnostic state variables, independent variables, time and space scales, region and season of application of the model.

(#) model, authors	state prognostic	variables diagnostic	x,y,z,t	scales time	space	region/time
(1) RADACH & MAIER-REIMER, 1975	N, P, I	$I_o(t)$ $A_v(z), N(z=B)$	z,t	0.25 h-90 d	2.5-250 m	North Sea spring
(2) WINTER <i>et al.</i> , 1975	P, I	$I_o(t), A_v(t)$ $w(t), Q(t)$ $u(t,z), S(t,z)$ $NO_3(t,z), Z(t,z)$	z,t	0.5-1-35d 0.5-1-75d	0.5-30 m	Puget Sound spring
(3) STEELE & HENDERSON, 1976	N, P, Z_1, \dots, Z_6	$I(t,z), A_v(t,z)$ $N(z=B), C(t)$	z,t	1-300d	2-24m	North Sea year
(4) SJÖBERG & WILMOT, 1977	N,P,D,I	$I_o(t), A_v(z)$	z,t	1?-50d	2?-40 m	Baltic Sea spring
(5) EVANS <i>et al.</i> , 1977	N, P, Z_1, Z_2, Z_3	$U(t,z)$ $N(z=B)$	x,z,t	4h-100d	V:10-40 m H:1-128km	North Sea spring
(6) RADACH, 1980	N, P	$I_o(t), I(t,z),$ $A_v(t,z), N(z=B),$ $Z(t,z)$	z,t	75sec-27d	2.5-150 m	North Sea spring
(7) KIEFER & KREMER, 1981	T, NO ₃ , NO I, PN, Chl	$T(t,z), M(t)$ $I_o(t)$ NH ₄ recycling	z,t	1d-1y	4m?-250 m	Bermuda annual cycle
(8) WOODS & ONKEN, 1982	P	$I_o(t), I(t,z),$	z,t	3min-5d	1-180 m	North Atlantic all year
(9) RADACH, 1983	N, P	$I_o(t), I(t,z),$ $N(z=B), A_v(t,z),$ $Z(t,z)$	z,t	75sec-27d	2.5-150 m	North Sea spring
(10) FASHAM <i>et al.</i> , 1983	N, P, I	$I_o(t), A_v(t,z)$	z,t	1h-3h-5.5d	0.5-95 m	Celtic Sea spring
(11) TETT <i>et al.</i> , 1986	PC, PN, N	$I_o(t), I(t,z)$ $A_v(z), N(z=B)$	z,(t)	0.01-80d	5-100 m	Scilly Islands summer
(12) WROBLEWSKI & RICHMAN, 1987	N,P,Z	$A_v(t,z), M(t)$	z,t	?-5d -40d	2.5?-90 m	Southern California spring
(13) STIGEBRANDT & WULFF, 1987	NO ₃ , NH ₄ , PON, D, O ₂ , H ₂ S	$I_o(t), T(t),$ $A_v(t,z), NIN(t,z)$	z,t	1d-20y	1-250 m	Baltic proper annual cycles
(14) WOLF & WOODS, 1988	N,P	$I_o(t), I(t,z)$ $M(t)$	z,t	1h-50d	1-250 m	North Atlantic spring
(15) RADACH & MOLL, 1990	N,P,D	$I_o(t), I(t,z),$ $N(z=B), A_v(t,z),$ $Z(t,z)$	z,t	75sec-1y	2.5-60 m	North Sea annual cycle

incorporating the achievements of the former models as well as the increased knowledge on the biochemical processes obtained in recent years.

Several papers report on the sensitivity analysis performed with the model (e.g. RADACH & MAIER-

REIMER, 1975; SJÖBERG & WILMOT, 1977; KIEFER & KREMER, 1981; HORWOOD, 1982; EBENHÖH, 1980; FASHAM *et al.*, 1983; TETT *et al.*, 1986). These results will be summarized in 4.1.5. Comparisons will be made as far as possible.

TABLE 1b

Comparison of horizontally resolved models (ordered historically): prognostic and diagnostic state variables, independent variables, time and space scales, region and season of application of the model.

(#) model, authors	state prognostic	variables diagnostic	x,y,z,t	scales time	space	region/time
(16) DUBOIS & ADAM, 1976	P,Z	U(t,x,y) V(t,x,y) C(t,x,y)	x,y,t	0.1-28d	y:6.5-215km x:6.5-345km	North Sea
(17) WROBLEWSKI, 1977	N,P,Z ₁ ,Z ₂	I ₀ (t),N(z=B)	x,t	?-20d	?-20km	subArctic late spring
(18) EBENHÖH, 1980	N,P,Z	I ₀ (t), N ₀ (t), F(t,x,y)	x,y,t	1-90d	1-20km	Barents Sea spring
(19) HORWOOD, 1982	1) N,P 2) N,P	I ₀ (t),T(t,x,y), k ₀ (x),M(t,x,y), u(t,x,y),v(t,x,y) Z(t,x,y), N(z=B)	t x,y,t	1-270d 1-270d	5-300km	North Sea year
(20) KLEIN & STEELE, 1985	N,P,Z	(1) exchange (2) advection, diffusion (3) advection, diffusion	t x,t x,y,t	1h-100d 1h-20d 1h-50d	2.5-200km x,y:2.5-70km	Georges Bank summer

List of symbols:

A _v	vertical turbulent diffusion coefficient	P	phosphorus
B	bacteria	P	phytoplankton, also phosphorus in extensions (e.g. DOP)
C	carbon, also in extensions (e.g. DC, DOC)	PC	phytoplankton carbon
C(t,z)	concentration	PN	phytoplankton nitrogen
Chl	chlorophyll concentration	PON	particulate organic nitrogen
D	dead organic particulate matter (detritus)	O ₂	oxygen
DIA	diatoms	Q	discharge or heat flux
DIN	dissolved inorganic nitrogen	S	concentration of silt, salinity etc., see text
DO	dissolved organic matter	SiO ₄	silicate
H ₂ S	hydrogen sulfide	t	time coordinate
i,j	suffixes	T	time scale
I	light intensity, radiation	T	temperature
I ₀	solar radiation	TON	total organic nitrogen
L	length scale	u,U	velocity component in x-direction
M	mixed layer depth	v,V	velocity component in y-direction
N	nitrogen	w	vertical velocity
N	nutrient, specifically nitrogen, also in extensions (e.g. DON)	W	weight, also in extensions (e.g. ZW)
NH ₄	ammonia	x,y	horizontal coordinates
NIN	nitrogen input	z	vertical coordinate
NO ₂	nitrite	Z	zooplankton concentration,
NO ₃	nitrate	Z ₁ ,Z ₂ ,...	different zooplankton species or stages

TABLE 2

Comparison of vertically resolved models (ordered historically): Complexity of the system simulated, indicated by processes involved in the model.

Equations/Processes	number of model (from Table 1a)														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
nutrient equation	y	n	y	y	y	y	y	n	y	y	y	y	y	y	y
turb. diff.	e	-	e	e	e	e	e	-	e	e	e	e	e	e	e
uptake	e	-	e	e	e	e	e	-	e	e	e	e	e	e	e
regeneration	e	-	i	e	e	e	i	-	e	-	e	e	e	-	e
phytoplankton equation	y	y	y	y	y	y	y	y	y	y	y	y	y	y	y
turb. diff.	e	e	e	e	e	e	e	e	e	e	e	e	e	e	e
production	e	e	e	e	e	e	e	e	e	e	e	e	e	e	e
-light-limitation	e	e	e	e	?	e	e	e	e	e	e	?	e	e	e
-self-shading	e	e	-	e	-	i	e	-	i	e	-	-	e	-	e
-nutrient-limitation	e	e	e	e	e	e	e	-	e	e	e	e	e	e	e
grazing	-	e	e	-	e	e	e	-	e	e	e	e	-	-	e
sinking	e	e	e	e	e	e	?	e	e	e	?	?	e	e	e
death,loss	e	-	-	e	-	e	-	-	e	-	-	e	i	-	e

e explicit formulation

i implicitly included

n not included

y yes, included

4.1.1. THE SCOPE OF THE PHYSICAL WORLD IN PLANKTON MODELS

The physical world enters plankton models in various ways, providing the energy supply for driving the system as kinetic energy, as heat energy and as radiative energy: the environmental conditions act as transport agents by the water movements, given by advection and turbulent diffusion, and they determine the rates of biological and chemical processes by the hydrographic conditions, *i.e.* temperature and/or stratification. Solar radiation acts directly on the phytoplankton in the euphotic zone. The influence of temperature on biochemical processes will be treated in sections 4.2. to 4.4.

The basic knowledge of physical oceanography required for a thorough foundation of the physical input to ecological models can merely be touched upon in this review. Nevertheless it seems necessary at least to mention a few basic equations for creating a common notation. For more details, text books on physical oceanography should be consulted (*e.g.* NEUMANN & PIERSON, 1966; POND & PICKARD, 1978; APEL, 1987).

The change of the concentration of a (living or non-living) substance (state variable) in time is described by an equation of the type

$$dC/dt = \text{turbulent diffusion terms} + \text{action/reaction terms}$$

(4.1.1)

The term on the left-hand side (l.h.s.) is called the total derivative of the state variable C ; it consists of the local change and the changes due to the motions of the water, passing a certain concentration of C by the point of observation:

$$dC/dt = \partial C/\partial t + u \cdot \partial C/\partial x + v \cdot \partial C/\partial y + w \cdot \partial C/\partial z \quad (4.1.2)$$

The first term on the right-hand side (r.h.s.) is called the local derivative of C ; the contribution of advection to C is given by the following three terms, where u , v and w denote the three components of the velocity of the water in x -(eastward), y -(northward) and z -(upward) directions. The equation (4.1.1) is derived for a mean state \mathbf{C} , based on a splitting $C = \mathbf{C} + c'$, where c' is the deviation from a mean state \mathbf{C} and has zero mean. Analogously the velocities are split up into means and fluctuations about the mean

$$\mathbf{U} = \mathbf{U} + u', \quad \mathbf{V} = \mathbf{V} + v', \quad \mathbf{W} = \mathbf{W} + w' \quad (4.1.3)$$

Usually the interval of averaging is defined by the resolution aimed at and by the resulting properties of the fluctuations. (As we deal only with means and fluctuations in the following, we will write normal letters instead fat ones for the mean.) The non-resolved motions will then appear in the second order moments and are usually parameterized by the turbulent diffusion terms, which appear on the r.h.s. in (4.1.1).

The turbulent diffusion terms are very often parameterized by using the gradients of the mean

state, and the diffusion terms on the r.h.s. of (4.1.1) then become

$$\begin{aligned} & \partial(\overline{u'c'})/\partial x + \partial(\overline{v'c'})/\partial y + \partial(\overline{w'c'})/\partial z \\ & = \partial(A_H \cdot \partial C/\partial x)/\partial x + \partial(A_H \cdot \partial C/\partial y)/\partial y + \partial(A_V \cdot \partial C/\partial z)/\partial z \end{aligned} \quad (4.1.4)$$

with horizontal diffusion coefficients $A_H(t,x,y,z)$ and vertical diffusion coefficients $A_V(t,x,y,z)$ (compare the derivation *e.g.* in NEUMANN & PIERSON, 1966, pp 187, 395).

All chemical and/or biological action or reaction is contained in the terms on the r.h.s. of equation (4.1.1), denoted by 'action/reaction terms'.

In many ecological models drastic simplifications are being made. In water column models for plankton dynamics *e.g.*, all horizontal gradients are assumed to be negligible, *i.e.*

$$\partial C/\partial x = \partial C/\partial y = 0, \quad (4.1.5)$$

resulting in the omission of two advective and two diffusive terms in (4.1.2) and (4.1.4). In models treating horizontal dynamics the assumption of vanishing vertical gradients

$$\partial C/\partial z = 0, \quad (4.1.6)$$

which may be justified under certain circumstances, results in neglecting the vertical advective and diffusive terms in (4.1.2) and (4.1.4).

Sinking

Of the great number of action/reaction terms, only the sinking term will be mentioned in this section, because sinking is usually formulated in analogy with an advection term, with a sinking velocity w_s

$$\{\text{sinking}\} = w_s \cdot \partial C/\partial z \quad (4.1.7)$$

The other action/reaction terms in relation to ecological models in the North Sea are given in sections 4.2 to 4.4.

Physical forcing

The physical energy supply acts as forcing on the biological systems. In all the models reviewed in this section, physical variables are the main driving variables. Only in a few cases do nutrients seem to drive the system (*e.g.* exclusively by entrainment from below the thermocline), but then physical energy supply is assumed not to be limiting the biological dynamics in any way.

Meteorological forcing

Meteorological forcing acts as energy supply by wind stress and by heat input at the sea surface, but also within the water, especially by radiation. It will eventually determine the structure of the motions of the water and of underwater light. The obviously most important physical determinants of ecological dynamics are radiation and water movements.

Radiation and underwater light

Underwater light $I(t,x,y,z)$ is the result of the propagation of radiative energy through the water column, and will, of course, be influenced by turbidity. The change of light intensity with depth is described in ecological models mostly by Beer's law

$$dI/dz = -k(z) \cdot I, \quad (4.1.8)$$

where $k(z)$ is the depth-dependent extinction function, which summarizes the effects of the water itself as well as those caused by material in the water, as there is plankton, detritus and inorganic material (*e.g.* clay). The light climate in the water results from solar radiation $I_0(t,x,y)$, usually prescribed at the sea surface $z=0$. Sometimes Beer's model is replaced by models taking different extinction properties of the various wavelengths into account.

Horizontal movements of water

The horizontal movements of water have been included in plankton models as a transport mechanism of matter, either by introducing the water velocity to describe the advection of material, *e.g.* plankton and nutrients, or by admitting horizontal mixing by turbulent diffusion.

For the North Sea very different models are forced by advection, all of them designed for areas of considerable horizontal extent: there are models for plankton dynamics (*e.g.* HORWOOD, 1982) as well as for the full system of the lower trophic levels (*e.g.* MOMMAERTS *et al.*, 1984, 1987), and there are models for the study of effects of eutrophication (*e.g.* FRANSZ & VERHAGEN, 1985). Furthermore there are mainly hydrodynamic models for the study of drifting biota (*e.g.* BACKHAUS & BARTSCH, 1985), as well as models for the study of more basic questions such as the effect of physical impact on plankton dynamics (*e.g.* KLEIN & STEELE, 1985).

Horizontal turbulent diffusion is used in two types of models: those which simulate the formation of horizontal plankton patchiness (*e.g.* DUBOIS & ADAM, 1976; WROBLEWSKI, 1977; EBENHÖH, 1980), and more complex ecosystem models (*e.g.* SCAVIA, 1980), which include horizontal and vertical advection as well as horizontal and vertical turbulent diffusion.

Vertical movements of water and vertical stratification

From the beginning of plankton modelling the outstanding role of mixed layer dynamics for the formation of plankton blooms has been recognized and taken into account. Usually a two-layer system was assumed, the mixed layer itself and the underlying layer (with unlimited nutrient content). Thus stratification was used to avoid the determination of the vertical structure of physical, chemical and biological processes.

The exchange between the layers by vertical diffusion and/or advection was managed by assuming a constant fraction of material being transported upwards or downwards. Here most of the plankton or ecological models must be mentioned (e.g. STEELE, 1956, 1958; LASSEN & NIELSEN, 1972; PARSONS & KESSLER, 1986, 1987). These models will not be reviewed here but in the following sections, as the physical aspect is not their main concern.

Recently, several papers (e.g. KLEIN & COSTE, 1984) have shown that exchange of material in the vertical is far less simple, and a vertical resolution will be necessary for many problems.

Vertical movements of water may enter plankton models as upwelling (e.g. SCAVIA, 1980; ZIMMERMANN *et al.*, 1987; WOLF & WOODS, 1988) or as vertical turbulent diffusion.

The first to take up the lines already designed by RILEY *et al.* (1949), introducing vertical eddy diffusivity profiles as a forcing mechanism for the plankton dynamics, were WINTER *et al.* (1975) and RADACH & MAIER-REIMER (1975). They set up vertically resolved simulation models for studying spring phytoplankton blooms. Their models were soon followed by the models of STEELE & HENDERSON (1976) and EVANS *et al.* (1977). The latter three models were in some way related to the Fladenground Experiment (FLEX'76), a field experiment in the northern North Sea in 1976.

Since then quite a number of papers have presented plankton models designed to incorporate vertical turbulent diffusion as a driving variable in some explicit way, either in the context of ecosystem models for large lakes (e.g. SCAVIA, 1980) or in the context of biological mixed-layer dynamics in strongly stratified upper layers of different oceans. Work related to thermally stratified water is much more frequent than work related to saline stratification (e.g. SJÖBERG & WILMOT, 1977; STIGEBRANDT & WULFF, 1987).

Most work deals with the spring phytoplankton bloom during the formation of the seasonal thermocline (e.g. RADACH, 1980; WOODS & ONKEN, 1982; RADACH, 1982, 1983; TETT *et al.*, 1986), sometimes connected with frontal zone studies (e.g. FASHAM *et al.*, 1983), sometimes with salinity stratification in fjord-like systems (e.g. WINTER *et al.*, 1975; SJÖBERG & WILMOT, 1977). Little work has been done so far on

the annual cycle of the phytoplankton development in relation to the development and erosion of the seasonal thermocline (KIEFER & KREMER, 1981; WOLF & WOODS, 1988; RADACH & MOLL, 1990).

During the last 10 years physical upper layer or mixed layer models have been used in several papers to calculate the temperature profile and either the turbulent diffusion coefficients (varying in time and with depth) or the mixed layer depth as a function of time (then assuming instantaneous mixing within the mixed layer). The simulated quantities are then used as physical forcing in the plankton models. The physical models are driven by (theoretical or actual) wind stress and heat flux or sea surface temperature.

It is not even possible in this review to give an overview of the recent development in modelling the physical upper layer dynamics. A recent review was given e.g. by PRICE *et al.* (1987). Here we can indicate only how complicatedly models of upper layer dynamics are formulated today by citing the equations of a special differential model, e.g. that of MELLOR & YAMADA (1974). The intention is to make clear that a proper modelling of the upper layer dynamics needed for the study of plankton dynamics may necessitate a considerable amount of work by a physical oceanographer.

The model of MELLOR & YAMADA (1974) describes the distribution of heat and momentum in the water column as a consequence of wind and radiative action at the surface.

$$dT/dt = -\partial(\overline{T'w'}) - \chi \cdot \partial T/\partial z / \partial z - \partial I/\partial z / \rho c \quad (4.1.9)$$

$$dU/dt = -\partial(\overline{u'w'}) - \nu \cdot \partial U/\partial z / \partial z + fV \quad (4.1.10)$$

$$dV/dt = -\partial(\overline{v'w'}) - \nu \cdot \partial V/\partial z / \partial z - fU$$

Here U , V and T are the mean velocities and temperature, u' , v' and T' are the corresponding fluctuations around the means. The constant f is the Coriolis parameter. The temperature profile is changed by local absorption of radiation $I(t, z)$, resulting from (4.1.8) by integration,

$$I(t, z) = I_0(t) \cdot \exp(-k \cdot z),$$

where $I_0(t)$ is the incident solar shortwave radiation at the sea surface. The constant c is the specific heat and ρ is seawater density. The second order moments are parameterized by

$$\overline{(u'w')}, \overline{(v'w')} = -l^2 \cdot W \cdot S_m \cdot (\partial U/\partial z, \partial V/\partial z)$$

$$W^2 = (\partial U/\partial z)^2 + (\partial V/\partial z)^2, \quad (4.1.11)$$

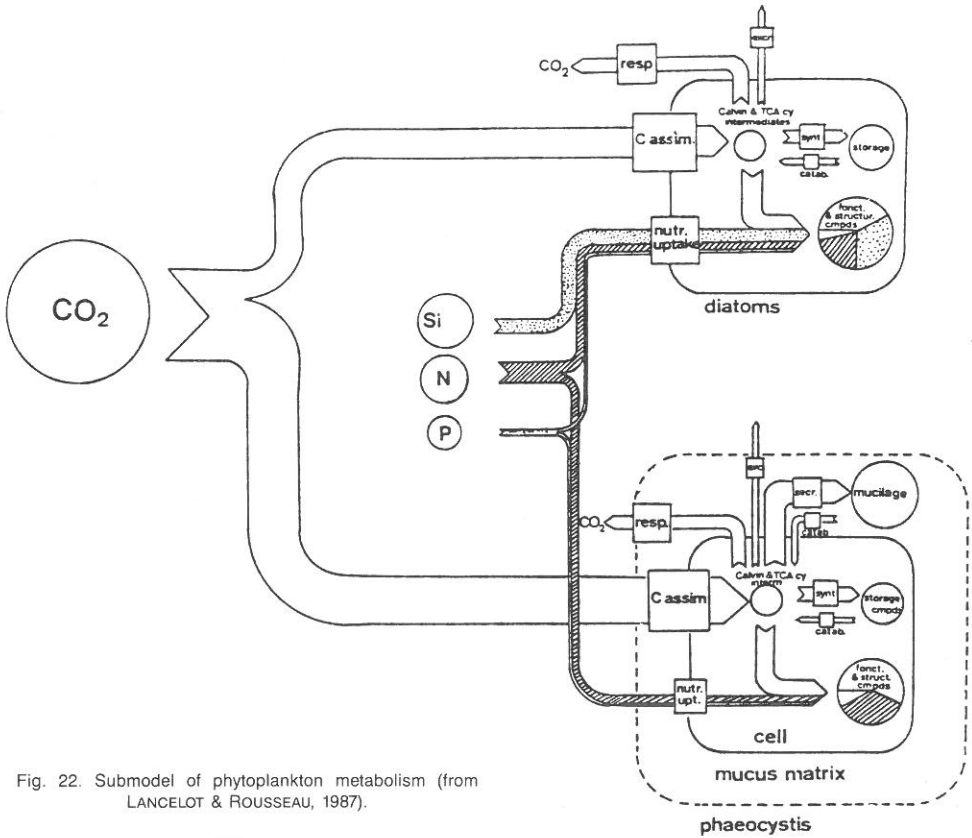


Fig. 22. Submodel of phytoplankton metabolism (from LANCELOT & ROUSSEAU, 1987).

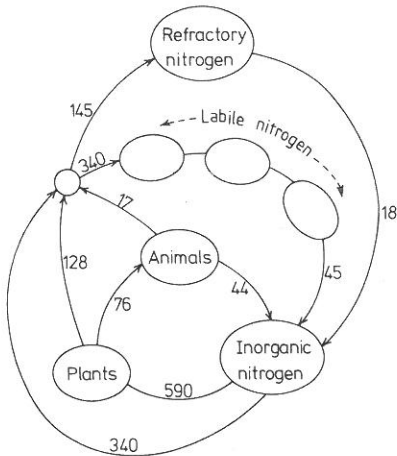


Fig. 23. Daily flows at the height of the spring bloom (after JONES & HENDERSON, 1987).

Pelagic mineralization

Depending on the models, dead organic matter will appear in the pelagic phase under the form of 'dissolved organic matter' (DOM), 'suspended detritus' or several pools of organic matter from highly refractory to highly labile.

MOMMAERTS (1978), PICHOT (1980), FRANZ & VERHAGEN (1985) or JONES & HENDERSON (1987) are among the authors who have taken explicitly the mineralization of such organic matter into account in their models of North Sea areas. However, in each case there is a major short-cut, since pelagic bacteria appear only implicitly in the decay rate that is incorporated in the equation(s) for these compartments.

Conversely, in the model of BILLEN *et al.* (1980), updated by BILLEN & FONTIGNY (1987) (Fig. 24), pelagic bacteria are explicitly modelled together with two other compartments: macromolecular biopolymers and monomeric substrates. Macromolecular biopolymers result from phytoplanktonic excretion or

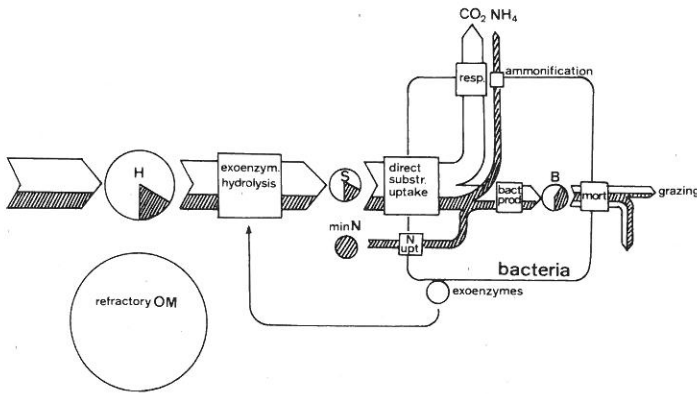


Fig. 24. Diagrammatic representation of the basic processes involved in bacterial utilization of organic matter according to the HBS model. Shaded arrows represent nitrogen fluxes. H: high molecular weight biodegradable organic material (biopolymers); S: directly usable low molecular weight organic substrates (direct substrates); B: bacterial biomass; min N: mineral forms of nitrogen (nitrate, nitrite, ammonium) (from BILLEN & FONTIGNY, 1987).

lysis. In order to be taken up by bacteria, these biopolymers have to be first hydrolysed through the action of exoenzymes and converted into monomeric substrates.

Benthic mineralization

Where bottom sediment or deep layer mineralization are concerned, the relevant processes are generally not simulated in most models, and these compartments mostly appear as a 'sink' term for particulate organic matter and faecal pellets and as a 'source'

term for dissolved inorganic nutrient. For instance, in several models already mentioned above, the nutrients appear from below the thermocline thanks to mixing. Below that boundary layer, the concentration of nutrient is assumed to be constant. In a rather analogous way, PICHOT (1980) assumes that nutrient diffuses according to Fick's law towards the water column, through the sediment-water interface.

In coastal shallow and well-mixed environments, however, the bottom sediment and its important benthic activity cannot be overlooked. The bacterial ac-

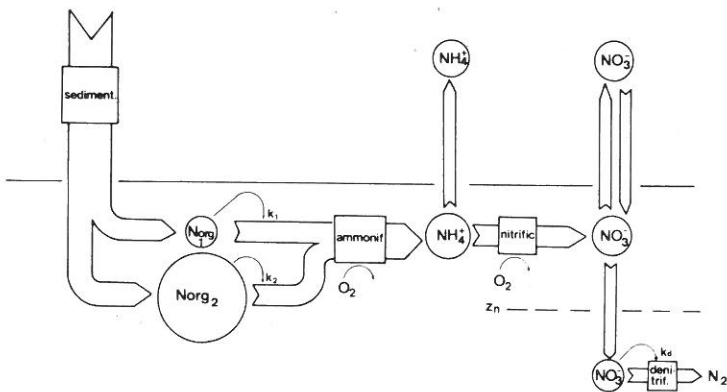


Fig. 25. Diagenetic model of nitrogen mineralization in sediments (after LANCELOT & BILLEN, 1985).

tivity there is largely dominant (so that meio- and macrobenthos activity is generally neglected). It is therefore not surprising that recent models of the Dutch and Belgian coastal areas of the Southern Bight of the North Sea encompass one or more bottom detritus compartments and mineralization processes.

Thus, FRANSZ & VERHAGEN (1985) consider 4 separate pools of bottom detritus (for C, N, P and Si), each being mineralized at a specific rate. These pools result from the sinking of the corresponding pools of suspended detritus, thus originating from naturally dead algae, excretion products and dead organisms from the zooplankton.

On the other hand, VANDERBORGHT & BILLEN (1975), BILLEN (1978), BILLEN & LANCELOT (1988) give a complete treatment to the processes involved in the mineralization of organic matter into the bottom sediment and subsequent diffusion of inorganic nutrient towards the water column, according to Fick's law. The processes taken into account are ammonification, nitrification and denitrification. Hence, organic nitrogen, ammonium and nitrate compartments are explicitly simulated (Fig. 25).

4.2.3. THE CONSERVATION EQUATIONS AND THE MATHEMATICAL DESCRIPTION OF PROCESSES

The processes taken into account for each conservation equation are gradually more complete and more complex. As far as completeness is concerned, we are perhaps nearing a modular view (see our idealized system, section 4.2.2a) where all biological compartments evolve in time as directed by:

1. proper physiological mechanisms *i.e.* substrate (or prey) uptake (u), excretion (e), respiration (if in carbon units) (r) and natural mortality (m)
2. external constraints *i.e.* predation mortality, sinking, advection and diffusion.

In some models, all proper physiological mechanisms are sometimes grouped in one single term for growth:

$$[\text{growth}] = (u - e - r - m)B \quad (4.2.6)$$

4.2.3a PHYTOPLANKTON GROWTH

The degree of complexity today achieved in the equation for phytoplankton, in several models, mirrors well the progress realized in photosynthesis research and plant physiology. Hence, the obvious imbalance, in most general simulation models, between the degree of sophistication achieved with the simulation of phytoplankton growth and that realized for other compartments.

The assimilation term

In the case of phytoplankton, the assimilation term (u), *i.e.* gross primary production, is rendered by a complex function where the rate of C and/or N uptake is altogether controlled by light, nutrient concentration and often temperature.

The photosynthesis-light relationship

The photosynthesis-light relationship (the P/I curve) comes first, chronologically and also by degree of importance in the modelling of phytoplankton growth.

Self-shading comes as a supplementary ingredient into this relationship. It is worth mentioning that self-shading is about the only feed-back that occurs in models, besides the obvious relationship [substrate (or prey) concentration *vs.* rate of uptake] that links trophic levels. Self-shading was introduced by RILEY (1956, 1963) and applied without substantial modification by PICHOT (1980), DUBOIS & ADAM (1976) and HORWOOD (1982) (see also eq. 4.1.30 in chapter 4.1). In the model of FRANSZ & VERHAGEN (1985), the extinction coefficient is allowed to vary seasonally and incorporates a minor contribution from phytoplankton biomass.

The relation of photosynthesis to light was linear in early models (SVERDRUP *et al.*, 1942; RILEY, 1947). The BLACKMAN (1905) formula (linear but with a maximum at some saturating level) has been applied too (*e.g.* LASSEN & NIELSEN, 1972; RADACH, 1983; FRANSZ & VERHAGEN, 1985; TETT *et al.*, 1986). Note that in the most recent models the choice for this very simple expression is deliberate, the authors generally claiming that it is quite sufficient for the purposes aimed at, or advocating methodological reasons.

Nevertheless, non-linear models have been and still are exercising considerable attraction. Non-linearity was introduced by TALLING (1955, 1957). STEELE (1962) and VOLLENWEIDER (1965) added the effect of photo-inhibition. The Steele's expression writes:

$$u = a \cdot I \cdot u_{\max} \cdot e^{1-\alpha I} \quad (4.2.7)$$

or, in the depth-integrated form:

$$\int_{z=0}^{z=\infty} u \cdot dz = \frac{u_{\max}}{\epsilon} \cdot \frac{a}{\alpha} \cdot (1 - e^{-\alpha I_0}) \quad (4.2.8)$$

or, still:

$$\int_{z=0}^{z=\infty} u \cdot dz = \frac{u_{\max}}{\epsilon} \cdot (I_m / I_k) \cdot (1 - e^{-I_0 / I_m}) \quad (4.2.9)$$

with $I_k = 1/ea$ and $I_m = 1/\alpha$.

The Vollenweider's expression writes:

$$u = u_{\max} \cdot \frac{a \cdot I}{\sqrt{1+(a \cdot I)^2}} \cdot \frac{1}{(\sqrt{1+(\beta \cdot I)^2})^n} \quad (4.2.10)$$

or in the depth-integrated form:

$$\int_{z=0}^{z=\infty} u \cdot dz = \frac{u}{\epsilon} \max \cdot \arctg(I_0/I_k), \quad n=1 \quad (4.2.11)$$

or, still:

$$\int_{z=0}^{z=\infty} u \cdot dz = \frac{u}{\epsilon} \max \cdot \frac{I_0/I_k}{\sqrt{1+(I_0/I_k)^2}}, \quad n=2 \quad (4.2.12)$$

After that, the matter became a topic of considerable interest, controversy and progress (see e.g. PLATT & JASSBY (1976), JASSBY & PLATT (1976), MC CAULL & PLATT (1977), FASHAM & PLATT (1983)) among primary production specialists.

Meanwhile, the approach of STEELE (1962) has been utilized in quite a number of North Sea models, either as such in the models by LASSEN & NIELSEN (1972) or RADACH (1983), or under a modified form of the integrated solution in the models of HORWOOD (1982) or DUBOIS & ADAM (1976). The expression for $\int u \cdot dz$ —averaged over several tidal periods— in the latter model is given as an example:

$$\int u \cdot dz = u_{\max} \cdot e \cdot f \cdot (\epsilon \cdot H)^{-1} \cdot \{\exp[-\exp(-\alpha_1 \cdot H)] - \exp(-\alpha_0)\} \cdot f(T) \cdot f(N) \quad (4.2.13)$$

where f is the fraction of daylight, $\alpha_1 = \alpha_0 \exp(-\epsilon H)$ with $\alpha_0 = J_0/I_m$; $f(T)$ and $f(N)$ are respectively the control functions by temperature and limiting nutrient. All other constants and variables are referenced in Table 6.

On the other hand, MOMMAERTS (1978), PICHOT (1980), BILLEN & LANCELOT (1988) preferred to apply the expression of VOLLENWEIDER (1965). An example is given from Pichot's model where an approximated solution is given for the Vollenweider's expression (with $n=2$), integrated on depth and on the day's length:

$$\int u \cdot dz = u_{\max} \cdot \frac{\lambda}{\epsilon H} \cdot \frac{2.6 \cdot 2}{\pi} \cdot \arcsin \frac{c}{\sqrt{1+c^2}} \cdot f(T) \cdot f(N) \quad (4.2.14)$$

$$\text{with } c = \frac{\pi}{2} \cdot \frac{J_0}{2.6 I_m}$$

The nutrient limitation

At an early stage, the nutrient limitation concept appeared in a rather simple way since photosynthesis (or uptake) was linearly related to the limiting nutrient, with a maximum at some saturating concentration. For instance, STEELE (1962), LASSEN & NIELSEN (1972) have used this approach for the North Sea.

Following the work of DUGDALE (1967), non-linear dependency according to Michaelis-Menten kinetics appeared quickly in many models, as related in a hyperbolic way to extracellular nutrient concentration:

$$u^N = u_{\max}^N \cdot \frac{N}{K_N + N} \quad (4.2.15)$$

Actually, the Michaelis-Menten expression proved so successful that it was not only applied to nutrient uptake but in many cases also to photosynthesis or grazing. Scientific justification for the Michaelis-Menten kinetics has been provided, since the enzymatic mechanism of NO_3^- transfer through biological membranes has been shown to obey these kinetics (FALKOWSKI, 1975). Matters were, however, not always so clear since there exists such phenomena as luxury uptake, inhibition of ammonium uptake in the presence of nitrate (DUGDALE & MACISAAC, 1971), adaptive or genetic variations of the saturation parameters (EPPLEY & MCCARTHY, 1969).

In the North Sea situation, non-linear dependency appeared for the first time as an alternative process in the model of LASSEN & NIELSEN (1972). Since then the Michaelis-Menten kinetics has been applied in all recent models of North Sea areas, with one exception, the model of HORWOOD (1982), where this expression is found inadequate since it gives noticeable reduction in phytoplankton reproduction rate for smaller reductions in nutrient. To avoid this, HORWOOD (1982) uses a more pragmatically based function:

$$u^N = u_{\max}^N \left(\frac{N}{N_{\max}} \right)^{0.15 + 1.5 p} \quad (4.2.16)$$

where both N and N_{\max} are expressed in $\mu\text{g at}^{-1} \text{N}$, N_{\max} is the winter or deep water maximum of nitrate nitrogen and p is a parameter controlling the shape of the function.

The double limitation problem

The problem of how photosynthesis (*i.e.* carbon assimilation), nutrient uptake and growth are related is a major one in phytoplankton modelling. Several system modellers assume that nutrient uptake is linearly coupled to net photosynthesis: all rates can even be expressed in the same nutrient-units (*e.g.* PICHOT,

1980). Hence, the effects of light and nutrient concentration are often multiplied by each other, although some authors prefer to consider the minimum of the two limitations (e.g. RADACH, 1983), i.e. they apply a 'threshold hypothesis':

$$u = u_{\max} \cdot f(I) \cdot f(N) \quad (4.2.17)$$

or

$$u = u_{\max} \cdot \min \{f(I), f(N)\} \quad (4.2.18)$$

where:

u = (carbon) uptake rate i.e. gross photosynthesis rate (actually, taken as growth rate in several models)

u_{\max} = maximum uptake rate

$f(I)$ = function of light intensity (varying between 0 and 1)

$f(N)$ = function of limiting nutrient concentration (varying between 0 and 1)

Note that in the model of FRANSZ & VERHAGEN (1985), the photosynthetic assimilation rate is multiplied by the lowest Michaelis-Menten function of the different nutrients (N, P, Si): the two approaches are thus here combined.

Other authors, however, make a clear-cut distinction between carbon assimilation (mostly controlled by light variation) and nutrient uptake (mostly controlled by external nutrient concentration). Moreover, they realize that growth depends essentially on internal resources. These views have been encouraged by the work of CAPELON & MEYER (1972) and that of DROOP (1970, 1973, 1975). They have been incorporated in the theoretical model for nutrient limited phytoplankton growth of NYHOLM (1977) and the models of MOMMAERTS (1978), TETT *et al.* (1986) and LANCELOT & ROUSSEAU (1987).

In the model of MOMMAERTS (1978), applied to a marine lagoon connected with the Southern Bight of the North Sea, a symmetrical treatment is given to the expressions for carbon and nitrogen assimilation, respectively:

- the gross uptake of carbon is assumed to be forced by light (according to the VOLLENWEIDER (1965) function) and to be influenced in a less straightforward way by the limiting nutrient (here nitrogen):

$$\frac{dPC}{dt} = u \cdot PC = u^C_{\max} f_1(I) \cdot f_2(N) \cdot PC \quad (4.2.19)$$

- whereas the uptake of nutrient is assumed to be forced by external limiting nutrient concentration (according to a Michaelis-Menten function) and to be influenced in a less straightforward way by light:

$$\frac{dPN}{dt} = u^N \cdot PC = u^N_{\max} \cdot f_1(N) \cdot f_2(I) \cdot PC \quad (4.2.20)$$

- and the coupling between the two expressions is realized by an equation for Q , the nitrogen cell quota (i.e. the N:C ratio), like in DROOP (1973):

$$\frac{dQ}{dt} = u^N - (u^C - r_p)Q \quad (4.2.21)$$

This approach provides a mechanism for phytoplankton excretion. Indeed, Q is allowed to vary between a minimum Q_0 and a maximum Q_m : if $Q < Q_0$, some carbon must be excreted under the form of DOM (thus, no 'luxury uptake'). Conversely, if $Q > Q_m$, nitrogen uptake must cease.

Moreover, the function $f_2(N)$ in the expression for carbon uptake is the same as Droop's expression $(1 - Q_0/Q)$ for limited growth control.

The same Droop's function is applied in the vertically structured model of TETT *et al.* (1986), applied to the English Channel and the Sound of Jura (Scotland). The authors favour simplicity for methodological reasons (there is no complex formulation for photosynthesis).

The 'threshold hypothesis' prevails i.e. only one factor controls at any given instant the rate of phytoplankton growth. The equation for phytoplankton (P) can be simplified to:

$$\frac{dP}{dt} = \frac{\partial}{\partial z} \left(K_z \frac{\partial P}{\partial z} \right) + \mu P - gP \quad (4.2.22)$$

Following the threshold hypothesis, the growth rate μ is either controlled by light:

$$\mu = (aI - r_p) \quad (4.2.23)$$

or by the nutrient quota Q in phytoplankton biomass:

$$\mu = \mu_m \left(1 - \frac{Q_0}{Q} \right), \quad Q_0 \leq Q \leq Q_m \quad (4.2.24)$$

Next to this, nutrient uptake is controlled by the external nutrient concentration:

$$u^N = u^N_{\max} \cdot \frac{N}{K_N + N}, \quad Q \leq Q_m \quad (4.2.25)$$

and uptake ceases when Q exceeds Q_m .

The work of LANCELOT *et al.* (1986) and LANCELOT & ROUSSEAU (1987) provides a closer look at the actual physiological mechanisms: thus, the synthesis of protein in the colonial flagellate *Phaeocystis* is under the double control of light and of external N concen-

tration: day synthesis depends on light intensity whereas night synthesis depends on the pool of energetic substrates, the synthesis of which is regulated by light.

Protein synthesis depends on external N in a Michaelis-Menten way whereas night synthesis depends linearly on the duration of exposures higher than $12 \text{ J} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$. This methodology is claimed to lead to accurate estimates of net primary production, a goal that has never been achieved in 30 years of primary production modelling. In this model (Fig. 22), the following fluxes are presented separately:

- external $\text{CO}_2 \rightarrow$ small metabolites (S):

$$= u_{\max} \cdot f(l) \cdot P \quad (4.2.26)$$

- small metabolites (S) \rightarrow storage products (R):

$$= \gamma_{\max} \cdot \frac{S}{K_S + S} \cdot R \quad (4.2.27)$$

- small metabolites (S) \rightarrow proteins (PROT):

$$= \mu_{\max} \cdot \frac{S}{K_S + S} \cdot \frac{N}{K_N + N} \cdot \text{PROT} \quad (4.2.28)$$

- storage products (R) \rightarrow small metabolites (S):

$$= k_R \cdot R \quad (4.2.29)$$

- respiration:

$$= \text{MAINT} \cdot \text{PROT} \cdot [u_{\max} \cdot f(l) \cdot P] \quad (4.2.30)$$

- excretion:

$$= \text{PER} \cdot [u_{\max} \cdot f(l) \cdot P] \quad (4.2.31)$$

where k_R is a constant of R catabolism, MAINT a constant of maintenance of basal metabolism and PER the percentage of excretion.

The temperature dependency

Photosynthetic assimilation, specific nutrient uptake rates or simply the growth rate have also been explicitly made dependent on water temperature in many models. Therefore, an exponential relationship—either an application of the 'Q10' rule (e.g. PICHOT, 1980; FRANZ & VERHAGEN, 1985) or the function put forward by EPPLEY (1972) (e.g. HORWOOD, 1982)—has very often been assumed. Even more complex relationships are described in the literature, e.g. the LASSITER & KEARNS (1975) function, and are readily available for simulation modellers.

The excretion and respiration terms

In contrast to the accumulated wealth of details available in the terms for carbon and nutrient assimilation, the simulation of excretion and respiration appears very dim. As far as these rates are taken into account, they appear rather as constants or as a fraction of gross photosynthesis in most models.

Excretion (or exudation) is normally supposed to produce a flux of dissolved organic matter. Eq. 4.2.31 (LANCELOT & ROUSSEAU, 1987) is a good example of how this flux is simulated in most models. In the model of FRANZ & VERHAGEN (1985), however, soluble excretion products return directly to the dissolved nutrient pools; moreover, nutrients are also regenerated through respiration, applying the appropriate nutrient:carbon ratios.

A respiration term can appear in carbon-based models. It has been widely assumed that basic dark respiration can be related to maximum gross photosynthesis, following the work of STEEMAN NIELSEN & HANSEN (1959):

$$r_p = r_{\max} \cdot u_{\max}, \quad r_{\max} = 0.1 \quad (4.2.32)$$

Unlike this, in the model of HORWOOD (1982), respiration proceeds at a constant rate of 0.1 d^{-1} times the biomass. In the model of LANCELOT & ROUSSEAU (1987), the respiration term encompasses the photosynthesis rate as well as the proteinic pool (see Eq. 4.2.30)

Although photorespiration could presumably vary between a few and nearly 100% of total CO_2 fixation, this factor has not yet been taken into account for a North Sea model.

The natural mortality term

Phytoplankton autolysis has been shown to be a significant phenomenon in the marine ecosystem (JASSBY & GOLDMAN, 1974). Recent evidence from the Southern Bight of the North Sea indicates that much of the *Phaeocystis*-dominated bloom decays in this way and is partly mineralized in the pelagic phase (LANCELOT *et al.*, 1987).

In earlier models, natural mortality was not considered at all: being grazed by zooplankton or sinking to the deeper layers of the sea seemed to be the fate of all phytoplankton cells. In the models of RADACH (1983) and PICHOT (1980), however, a mortality rate—proportional to phytoplankton biomass—is taken into account. This rate is usually zero (RADACH, 1983) but also allows the option to serve as general loss term in the process of fitting the model.

On the contrary, in the model of FRANZ & VERHAGEN (1985), natural mortality plays a particular and prominent role in the phytoplankton sub-model: each category of phytoplankton—*i.e.* 'diatoms' and

'others'— is in turn split into 'young' and 'old'; 'old' phytoplankton dies one order of magnitude faster than 'young' phytoplankton; 'young' phytoplankton becomes 'old' whenever it meets a situation of nutrient limitation; however, a small portion of 'young' escapes this change so that it will again increase in biomass if the environmental conditions become favourable again. According to the authors, this concept makes it possible to simulate satisfactorily the observed rapid wax and wane of phytoplankton biomass, especially during early spring.

Autolysis is also taken into due account in the model of MOMMAERTS (1978), where the mortality rate incorporates a measure of the physiological state of phytoplankton, based on the N:C ratio (*i.e.* Q from eq. 4.2.21).

$$m_p = \sigma \cdot \frac{1}{f(Q)} \quad (4.2.33)$$

$$\text{with } f(Q) = \theta + \left[\frac{(1-\theta)(Q-Q_0)}{Q_m - Q_0} \right]$$

and σ and θ are constants.

4.2.3b MINERALIZATION OF ORGANIC MATTER IN THE PELAGIC PHASE

In most models nutrient replenishment in the pelagic phase is made possible thanks to a mixing process across a thermocline boundary layer (see section 4.2.2c) or via zooplanktonic excretion.

On the other hand, explicit mineralization of dissolved organic matter (DOM) or particulate organic matter (POM) is not frequently taken up in general models.

When taken explicitly, mineralization in its simplest form affects DOM or POM according to first order kinetics, much like in the river quality model by STREETER & PHELPS (1925). This is *e.g.* the case in the models of PICHOT (1980) or FRANZ & VERHAGEN (1985), where temperature also acts as a forcing function for this mineralization. Although bacteria do not appear as a biological compartment of their own, the model of Pichot comes close to it as the 'mortality' coefficient that affects DOM in his model also produces detritic matter (*i.e.* 'dead bacteria') and thus no nutrient:

$$\frac{d \text{DOM}}{dt} = + \{\text{excretion}\} - c_1 \cdot f(T) \cdot \text{DOM} - c_2 \cdot \text{DOM} \quad (4.2.34)$$

where c_1 is the rate coefficient for mineralization and c_2 is the rate coefficient for 'bacterial mortality'.

In the model of JONES & HENDERSON (1987), mineralization proceeds as a 'cascade' from the most refractory organic matter pool to the most labile: at each step of the cascade, less refractory matter is passed on to the next pool and organic matter is accepted from the previous one:

$$\frac{d \text{DOM}}{dt} = +k_{(l-1)} \cdot \text{DOM}_{(l-1)} - j_{(l)} \cdot \text{DOM}_{(l)} \quad (4.2.35)$$

The nutrient pool benefits from the degradation of the last pool (=most labile DOM pool) only. All degradation constants ($k_{(l-1)}$, $j_{(l)}$) are first-order constants.

A substrate-consumer couple is fully restored in the semi-theoretical model of BILLEN *et al.* (1980). The bacterial biomass appears as such and organic matter (here low molecular weight substrates) is mineralized according to a Michaelis-Menten kinetics. The model demonstrates how the environmental levels of DOM can remain relatively constant—an observation previously made by WILLIAMS (1975)—in an environment characterized by strongly fluctuating values of nutrient, phytoplankton, bacteria numbers. This model has been updated by BILLEN & FONTIGNY (1987), who manage to couple it with that of the phytoplankton dynamics during the spring bloom in the Southern Bight of the North Sea. In this model, biodegradable organic matter in the sea is mostly supplied under the form of macromolecular biopolymers (H). These cannot be directly taken up by bacteria and have first to be hydrolysed through the action of exoenzymes (SOMVILLE & BILLEN, 1983) and converted into monomeric substrates (S). Exoenzymatic hydrolysis therefore often constitutes the limiting step of the whole process of organic matter utilization. Once taken up by bacteria, direct substrates can either be catabolized and respired or used for biosynthesis. The ratio between biosynthesis (*i.e.* production of bacterial biomass (B)) and total rate of organic matter utilization defines the growth yield (Y). This ratio, along with the C/N ratio of the substrates used determines the extent of ammonification, or of mineral nitrogen uptake when nitrogen-deficient organic substrates are used. Moreover, the bacterial biomass (B) formed is subject to mortality caused either by microzooplankton grazing or by spontaneous or virus-induced lysis (SERVAIS *et al.*, 1985). The equations of this model, based on the dynamics of proteins alone, write:

$$\frac{dH}{dt} = \alpha \cdot k_f \cdot F - e_{\max} \cdot \frac{H}{H + K_H} \cdot B \quad (4.2.36)$$

$$\frac{dS}{dt} = e_{\max} \cdot \frac{H}{H + K_H} \cdot B - b_{\max} \cdot \frac{S}{S + K_S} \cdot B \quad (4.2.37)$$

$$\frac{dB}{dt} = Y \cdot b_{\max} \cdot \frac{S}{S + K_S} \cdot B - k_d \cdot B \quad (4.2.38)$$

where:

- H = macromolecular biopolymers (dissolved protein)
 S = monomeric substrates (amino-acids)
 B = biomass of bacteria (carbon)
 F = biomass of phytoplankton (protein)
 Y = yield (i.e. ratio of C production to amino-acids taken up)
 α = fraction of released proteins utilized
 k_f = rate of release by phytoplankton (1st order)
 e_{\max} = maximum rate of exoproteolysis
 k_H = half-saturation constant
 b_{\max} = maximum rate of uptake
 K_S = half-saturation constant
 k_d = mortality constant (1st order)

4.2.3c MINERALIZATION OF ORGANIC MATTER IN THE BOTTOM SEDIMENT

As stated in section 4.2.2c, biological mineralization in the sediment is not frequently taken into account, at least in models of deep stratified environments such as the northern North Sea.

In contrast, in the model of FRANZ & VERHAGEN (1985), detritic matter pools in the bottom sediment vary seasonally as a result of the balance between sinking, resuspension and mineralization. Mineralization obeys specific first-order kinetics constants (for each of the four pools: C, N, P and Si) that are a factor of 10 lower than those applied to the corresponding suspended detritus pools 'to account for the exchange barrier between bottom and water'.

In the model of PICHOT (1980), the sediment is the source of a nitrogen flux regulated, according to Fick's law, by the difference between the concentration of inorganic nitrogen in the water column (a state variable) and that —supposed constant— in the pore water of superficial sediments.

$$\frac{dN}{dt} = c_3 \cdot (c_4 - \frac{N}{H}) \quad (4.2.39)$$

where c_3 is a diffusion rate ($m \cdot d^{-1}$) and c_4 the nitrogen concentration in pore water.

Pichot has of course been influenced by the diagenetic model of VANDERBORGH & BILLEN (1975) and BILLEN (1978), who used a much simplified version of the mathematical treatment developed in detail by BERNER (1971, 1974, 1975) and others: for a dissolved species in the pore water of a sediment, submitted to a Fickian dispersion process, to various

biological or chemical consumption-production processes, and in the absence of important adsorption-desorption processes, the expression for the mass balance of this species can be written:

$$\frac{\partial C}{\partial t} = D_s \frac{\partial^2 C}{\partial z^2} - \omega \frac{\partial C}{\partial z} + r(z) \quad (4.2.40)$$

where

- C = the concentration per unit sediment volume
 D_s = apparent dispersion coefficient of the sediment
 ω = deposition rate
 z = the depth in sediment
 $r(z)$ = the resultant rate of all production or consumption processes

In most situations, the advection term $\omega(\partial C/\partial z)$ can be neglected.

Furthermore, it is assumed that the concentration profile observed corresponds to a steady state situation:

$$0 = D_s \frac{\partial^2 C}{\partial z^2} + r(z) \quad (4.2.41)$$

If the assumption of stationarity is valid and D_s and $r(z)$ are known, the diagenetic equation can be solved and, hence, a dispersive flux across the sediment-water interface can be calculated.

The production-consumption processes $r(z)$ relate to:

- ammonification: the organic material deposited on the sediment is considered to comprise two fractions, differing in their first-order degradation constant and C:N ratio;
- nitrification: is considered to be proportional at each depth to ammonification, but is restricted to the oxygenated layer ($z < z_n$);
- denitrification: is restricted to the anoxic layer ($z > z_n$) and considered to be first-order with respect to nitrate concentration.

Hence, the diagenetic equation for nitrate in the sediment can be written:

$$\frac{\partial C}{\partial t} = D_s \frac{\partial^2 C}{\partial z^2} + \epsilon \cdot k_n - (1 - \epsilon) \cdot K_d \cdot C \quad (4.2.42)$$

with

- $\epsilon = 1$ for $z < z_n$ (nitrification layer)
- $\epsilon = 0$ for $z > z_n$ (denitrification layer)
- k_n = rate of nitrification
- $K_d = V_{\max}/2K_m$ = first-order constant of denitrification used instead of the second-order constant when $C \leq 2K_m$.

4.2.4. DESCRIPTION AND ACHIEVEMENTS OF THE MODELS REVIEWED

4.2.4a THE MODEL OF BILLEN & LANCELOT (1988)

The model of BILLEN & LANCELOT (1988) aims at the simulation of the seasonal variations in nitrate concentration and phytoplankton biomass in seven geographical entities (boxes) from the Western Channel to the German Bight.

The emphasis is put on the effects of nutrient enrichment on the coastal zones and their role in the proliferation of the colonial flagellate *Phaeocystis pouchetii* during the spring bloom, as part of the several indications of eutrophication that have been collected for the eastern coasts of the North Sea.

The model is a continuing construction with many co-workers: in its present stage of development, it assembles a mosaic of submodels (for phytoplankton, pelagic mineralization, benthic mineralization) which have been described in a number of separate papers. Note that the zooplankton is believed to play only a limited role in the area at study, especially in spring. Hence, this compartment has not been modelled so far.

Boxes are portions of space for which state variables are assumed to be homogeneous. The models of PICHOT (1980) and of FRANSZ & VERHAGEN (1985) are other examples of box-models reviewed in this paper. Each of the seven geographical entities or boxes has its specific morphological characteristics but also terrigenous inputs, water residence time, salinity, sedimentation rate and water transparency. The Western Channel box serves as general boundary condition. Further on, each box sets the boundary condition for the next box.

The evolution of the system is represented by a set of first-order ordinary differential equations. There are seven state variables: limiting nutrients (actually, C, N, P and Si are distinguished), phytoplankton, DOM, bacterial biomass, POM, rapidly degraded sedimented organic matter and slowly degraded sedimented organic matter. The conservation equations and processes—including biochemical steps—have been reviewed in sections 4.2.2 and 4.2.3.

Besides considering compartments that are often overlooked, this model includes new features like the particular—and efficient—strategy of colony-forming *Phaeocystis* in response to the reduction of nutrient concentrations, which occurs in late spring. Also the relative importance of slowly and rapidly degradable organic matter pools in the sediments determines the extent to which the phytoplankton can grow in summer. These new features are believed to account for the fairly good results of this first version of the model.

4.2.4b THE MODEL OF DUBOIS & ADAM (1976)

Most theoretical models describing the evolution of biological populations only deal with time fluctuations. However, patchiness is known to occur in the mesoscale (beyond 5 km and up to 100 km). KIERSTEAD & SLOBODKIN (1953) were the first to propose an equation describing plankton blooms by adding diffusion to the usual growth term. This problem has also been considered by STEELE (1974), and more recently by HORWOOD (1982).

DUBOIS & ADAM (1976) here consider the case of the prey-predator system constituted by phytoplankton and zooplankton and the horizontal structuration of a patch during its drift in the Southern Bight of the North Sea.

This is an example of a vertically integrated and horizontally resolved model. The advection by residual currents and dispersion by eddy diffusion are taken into account.

Based on a prey-predator interaction (cf. Steele's model of 1974), this model comprises only two partial differential equations: one for phytoplankton and one for zooplankton. No regeneration of nutrient is taken into account, the nutrient being here a forcing variable. In contrast to a simple Lotka-Volterra system, this model encompasses many physiological processes (see section 4.2.3a).

During its drift in the Southern Bight, the horizontal structuration of the patch is given by a growing circular disc which loses its center and breaks into segments (Fig. 5). This result is matched by the observations by WYATT (1973).

A fascinating aspect of this model is the generation of an 'ecological wave' due to the prey-predator effect itself. This wave contributes to the structuration of the patch and propagates at some velocity, independently of the advection/diffusion motions.

4.2.4c THE MODEL OF FRANSZ & VERHAGEN (1985)

Like the model of BILLEN & LANCELOT (1988), the model of FRANSZ & VERHAGEN (1985) endeavours to understand the production and eutrophication processes in the eastern coastal area of the Southern Bight of the North Sea, heavily subjected to riverborne P- and N-loads. It thus aims at the simulation of the seasonal cycle of phytoplankton biomass and composition and nutrients (N, P and Si) in seven parallel and adjacent compartments (boxes) from the Dutch coast to some western boundary in the middle of the Southern Bight.

This model—called SEAWAQ—combines biological information contained in earlier models with the model DELWAQ for two-dimensional residual transport by the Delft Hydraulics Laboratory (Netherlands).

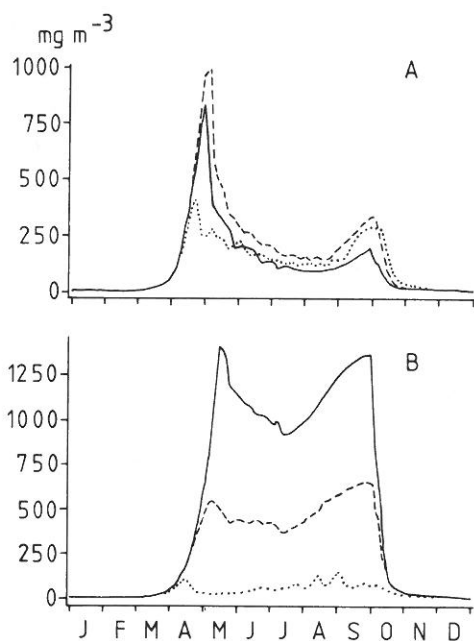


Fig. 26. Seasonal variation of diatoms (A) and other phytoplankton (B) carbon (in $\text{mg}\cdot\text{m}^{-3}$) as computed by the model for the first compartment for three situations: — (full line) river discharge and influx of 1980 — (broken line) river discharge of 1930 and influx of 1980 (stippled line) river discharge and influx of 1930 (from FRANZ & VERHAGEN, 1985).

The seven parallel boxes are considered homogeneous with respect to depth and turbidity. A constant advective residual transport in all boxes was assumed with velocities after the transport model. A constant dispersion of $150 \text{ m}^2\cdot\text{s}^{-1}$ was applied perpendicular to the coast. The rivers Rhine, Meuse and Scheldt discharge fresh water loaded with nutrients into the coastal zone.

There are 17 state variables (see Table 7). The formalism used makes it difficult to clearly distinguish the conservation equations (first-order ordinary differential equations). Nevertheless all processes are clearly described (see also sections 4.2.2 and 4.2.3): the model considers 3 dissolved nutrients to be essential to pelagic algae. Si is only used by diatoms. Zooplankton (a forcing variable) grazes on algae, but the filtering by benthic organisms is ignored. Dead organic matter is pooled in a compartment 'detritus', which partly sediments to the bottom. The

model distinguishes the carbon and the nutrients in the detritus.

This model was applied to compare the phytoplankton and nutrient conditions in 1980 with the hypothetical conditions in 1930. In spite of some imperfections discussed in the paper (chlorophyll is overestimated, particularly during spring and autumn and the phosphate concentration in the coastal area is much higher in summer and autumn than expected), several aspects of eutrophication emanate clearly from the model results: e.g. from 1930 to 1980, primary production is increased by a factor of two and a shift from a diatom to a flagellate community is simulated (Fig. 26).

4.2.4d THE MODEL OF HORWOOD (1982)

The purpose of the model of HORWOOD (1982) is to interpret the amplitude and timing of the two-dimensional distributions of algal standing stock as observed in an area approximately $300\times 250 \text{ km}$ off the north-east coast of England from March to November. This is another example of a horizontally resolved model (*cf.* DUBOIS & ADAM, 1976).

This model has been designed in two stages since a simpler version—integrated over depth and with horizontal gradients considered to be zero—is used for parameter optimization.

The model comprises two vertically integrated first-order ordinary differential equations in the simpler version—each having its partial differential equation counterpart, with proper advection and eddy diffusion terms—in the two-dimensional version. Two current fields (winter and summer residual circulation patterns) are used. In addition, the average depth of the mixed layer is prescribed. Nutrient is allowed to diffuse across the thermocline, at a rate determined by a mixing coefficient.

The state variables are phytoplankton biomass and limiting nutrient (here nitrogen). The status of zooplankton as forcing variable or state variable is not quite clear. Anyway, it appears as forcing variable in the simpler version. Nutrient regeneration is possible via excretion from the zooplankton and diffusion from below the thermocline.

The spatial patterns up to 10 July, 160 days after the start of the simulation, are generally similar except for the large concentrations in the shallow south and southwest areas of the domain modelled (Fig. 17). After this, the model lacks some important late summer and autumn features.

The author not only deals with the differences observed between observational data and model results but also endeavours to start an interesting discussion of the production flow through the ecosystem.

4.2.4e THE MODEL OF JONES & HENDERSON (1987)

The model of JONES & HENDERSON (1987) attempts to simulate the annual nutrient cycle in a mixed water column off the Scottish east coast, 50 m deep, assumed to be independent of adjacent water masses.

The emphasis is put on the understanding of the formation and breakdown of dead organic matter. Indeed, the authors have observed that a large part of the winter nitrate nitrogen is in the form of dead organic matter during summer, since its decrease from winter to summer appears to be four or five times greater than the corresponding increase in animals and plants.

Since there is no vertical nor horizontal structuration, the model appears to belong to the single-box variety of ecological models.

In its annual cycle scenario (the 'seasonally perturbed' version), the model is driven by the incident light cycle.

This model comprises 9 conservation equations with an integration step of one day and apparently no numerical correction scheme. These equations refer to nutrient, phytoplankton, five categories of dissolved organic matter (from highly labile to highly refractory) and 'animals'. Much emphasis is put on the mineralization processes and the 'cascade' that occurs between the five DOM pools. On the other hand, processes such as nutrient and light limitation of primary production, sinking, excretion and/or natural mortality, grazing, etc. are taken into due account.

The model is still very closely related to the mass-balance study (JONES & HENDERSON, 1984) which has served to reveal the major role played by dead organic matter in the ecosystem at study: much information is derived from the period of about 100 days that follows the spring bloom and during which a steady state seems to prevail.

The results of the model cannot be interpreted in the same way as those of most other models reviewed here. Besides its capacity to generate plausible seasonal variations of the main state variables, this model must rather be viewed as a laboratory programming aid, *i.e.* a tool for the authors to explore the ecological mechanisms at work in the system studied. In that respect, the paper of JONES & HENDERSON (1984) is mainly a discussion paper with a wealth of information on the ecosystem dynamics in the eastern Scottish shelf area.

4.2.4f THE MODEL OF LASSEN & NIELSEN (1972)

The model of LASSEN & NIELSEN (1972) is similar to STEELE's (1958) first type of model and simulates primary production as a function of irradiance, phosphate concentration and standing crop of

phytoplankton. The model applies to the central North Sea situation.

It is a two-layer model with provisions for the development and breakdown of the thermocline and mixing between water layers.

The thermocline—placed at a fixed depth—divides the water column into two different layers, assumed to be homogeneous. The bottom layer is assumed to have constant properties. The mixing coefficient is varied in the course of the year, thus simulating the development of the thermocline in the springtime and its breaking down in autumn. Furthermore, the mixing coefficient is allowed to reach a high value for a short while in late summer so that an autumn production outburst can follow.

The equations of the model are first-order ordinary differential equations. There are only two state variables taken into consideration: phytoplankton and phosphate. The equation for phytoplankton comprises a primary production term, depending on light according to an expression derived from STEELE's (1962) formula, and on nutrient concentration according to BLACKMAN's (1905) formula or according to an alternative non-linear relationship. Moreover, there are loss terms for mixing, sinking and grazing. The latter is assumed proportional to the number of phytoplankton units simulated and the number of copepods from a fitted function. Replenishment of nutrient is taken into account by the process of mixing, but there is no mineralization as such.

The results of the model are found to be mostly in agreement with the field phytoplankton and phosphate data. The spring outburst is poorly simulated though. A change in the nutrient limitation function gives a more realistic level of the phosphate concentrations but needs an extra parameter.

This early model has probably achieved the best possible results attainable with a system of two equations only and a simplified two-layer approach. However, it is interesting to note how rigorous is its construction. On the low trophic level, it is a remarkable early attempt to simulate the non-linear nutrient limitation of primary production.

4.2.4g THE MODEL OF MOMMAERTS (1978)

The model of MOMMAERTS (1978) is a fairly complex 12-state variable model, and as many diagnostic variables, primarily designed to simulate the cycle of nitrogen in a lagoon connected with the southern Bight of the North Sea. One attempt has been made to adapt this model to the North Sea area off the Belgian coast.

Much emphasis is put on the biological aspects related to primary production, turn-over of organic matter and zooplankton development and grazing.

The model appears as a single-box model. The

physical forcing comes from light and temperature. Light is allowed to vary at random between deterministic upper and lower diel and seasonal curves. On the other hand, the lagoon model takes water level variations and exchanges with the sea into account.

The equations of the model are first-order ordinary differential equations. The equation for phytoplankton comprises more complex terms than usual for primary production (actually, distinct functions for carbon assimilation, nutrients uptake and growth, taking the existence of an internal nutrient pool into account), excretion and natural mortality. Two kinds of dead organic matter (with rapid and slow turn-over) are considered. Two species of zooplankton are modelled, with several cohorts and development stages. Many other compartments—especially from the bottom community and from the diagenetic sediment model of BILLEN (1978)—appear as diagnostic variables.

The very particular evolution of phytoplankton standing stock in the lagoon is well rendered over the 180 days of the simulation. The model also generates an acceptable spring bloom when configured to North Sea conditions.

This experimental model deserves attention in that—being essentially biologically oriented—it cumulates many features that have appeared since then in more recent models (especially from the 'Belgian school'), as yet more biological processes were taken into account.

4.2.4h THE MODEL OF PICHOT (1980)

In his box model for the eastern half of the Southern Bight of the North Sea, PICHOT (1980) is aiming at the simulation of the seasonal evolution of the nitrogen cycle. The model is also described in MOMMAERTS *et al.* (1984, 1987).

At the time of its publication, this model reflected well the recent evolution of a Belgian team work (BILLEN *et al.*, 1976; JOIRIS *et al.*, 1982), endeavouring to study the mass-balance of the eutrophied coastal sea.

The model covers the eastern half of the southern Bight of the North Sea, off the Belgian and Dutch coasts. It is subdivided into 30 boxes that are interconnected by advection and diffusion flows. The boundaries of the boxes are based on the configuration of the stream lines yielded by a mathematical model of residual circulation (NIHOUL & RONDAY, 1975). Some boxes receive the nutrient inputs from rivers and channels. The model is driven by climatic forcing (light and temperature) and other forcing functions such as bottom nutrient concentration.

First-order ordinary differential equations describe the evolution of the four state variables in each of the

30 boxes: dissolved inorganic N, phytoplankton biomass, zooplankton biomass and dissolved organic matter. The sediment acts as a source term for inorganic nitrogen. Note that specific vertical diffusion coefficients are attributed to the sediments of each box. The sediment acts also as a sink term for all fluxes of dead organic matter.

The processes incorporated in the four conservation equations have been reviewed at length in section 4.2.3.

An extensive analysis of dynamical sensitivities of the system is also presented.

The model reproduces reasonably well the observed seasonal evolution of the four state variables. Moreover, spatial patterns that are consistent with the field observations have been obtained.

This ecological simulation model of the Southern Bight of the North Sea was probably the most complete and elaborate for the North Sea at the time of its publication. Especially the lower trophic levels (primary production, organic matter production and degradation, bottom sediment mineralization) have received much more attention than usual. There are several weak points and/or new facts that require a revision of the model. For that, the '*Phaeocystis* project' (see also BILLEN *et al.*, 1988) offers a special opportunity.

4.2.4i THE MODEL OF RADACH (1983)

The model of RADACH (1983) concentrates on the phytoplankton-nutrient dynamics during the spring bloom in the central North Sea, in relation to the formation of the seasonal thermocline. The author attempts to reconcile the different data sets (especially primary production and grazing) obtained during the Fladen Ground Experiment (FLEX '76) on the one hand, and his model, on the other hand.

It is a vertically resolved model, using the vertically structured turbulence profile as forcing variable. Thus, turbulent diffusion influences primary production by determining the residence time of phytoplankton in the upper region of the ocean. At the bottom a vanishing gradient has been assumed for phytoplankton and a constant concentration for phosphate.

This model comprises two partial differential equations: one for phytoplankton and one for the limiting nutrient (here phosphates). Moreover: zooplankton (a diagnostic variable) is used to define the grazing pressure; detritus acts as a sink only; dissolved organic phosphorus is neglected; bacteria act indirectly via assumptions concerning the regeneration of nutrients.

For the particular purpose of the author, four different functions are tested for the photosynthesis-light relationship.

Various processes are reviewed in section 4.2.3.

The equations have been applied for the period from 19 April to 16 May 1976, for which horizontal advective and diffusive transport is of minor importance relative to the local biological terms and the vertical transports.

Phytoplankton and phosphate concentration isopleths in the depth-time field are produced. Visually they match the measured values fairly well. The post-bloom phase is more difficult to simulate since the regeneration of nutrient is not adequately represented in the model.

Surprisingly enough, none of the functions with light-limitation (e.g. from BLACKMAN (1905), TALLING (1957) or STEELE (1962)) allowed primary production in the model to reach the levels measured in the field. Only the fourth function, with no light limitation, allowed the author to succeed in reconciling not only the state variables with the measurements but also processes such as primary production and grazing. Several problems still have to be followed up, as discussed by the author.

This paper illustrates quite well the problem of model validation and that of the consistency of the data themselves.

4.2.4j THE MODEL OF RILEY *ET AL.* (1949)

The classical model of RILEY *et al.* (1949) needs no further description here. The review of it by PATTEN (1968) has inspired some of the comments given in section 4.2.2b. A more general comment would be that forty years after its publication, much more recent models still retain most of its basic structure and even formulation of processes.

4.2.4k THE MODEL OF STEELE (1958)

The approach of RILEY *et al.* (1949) has greatly inspired Steele, who was thus the first author to transpose their approach to the North Sea situation. Two conservation equations (for phytoplankton and phosphate) are numerically integrated in a thermally-stratified sea where the exchanges between the two homogeneous layers are governed by a mixing coefficient. The model by LASSEN & NIELSEN (1972) (see above) is a straightforward application of Steele's equations, with a few improvements.

4.2.4l THE MODEL OF TETT *ET AL.* (1986)

The model of TETT *et al.* (1986) describes the steady-state vertical distribution of phytoplankton biomass near the Scilly Isles, England, and in the Sound of Jura, Scotland, in summer as a function of vertical turbulent diffusion, incident light, grazing pressure and deep-water nutrient flux.

The model is described by 3 partial differential equations in which the state variables are phytoplankton biomass (chlorophyll), phytoplankton nutrient (internal pool) and dissolved nutrient (nitrogen).

Like the model of RADACH (1983), this model is vertically structured, with vertical transport of the system's variables due to turbulent mixing.

There is moreover an attempt to simulate the horizontal organization of the system e.g. along a transect: this is done by eliminating time from the equations, assuming that shelf-sea water columns are in a steady-state in summer and in particular that the vertical distribution of turbulence remains constant over several generations of phytoplankton growth.

On the other hand, the authors justify, by methodological arguments, their choice for an extreme simplicity in the processes modelled: indeed they deliberately ignore self-shading, saturation and inhibition of photosynthesis, sinking and vertical migration, detailed description of grazing.

Steady-state space-depth isopleths of dissolved nutrient and chlorophyll concentrations are produced that fairly well match the field data collected along an east-west 150 km transect, tangential to the northern rim of the Scilly Isles. A chlorophyll maximum shows just above the thermocline, where nutrient diffuses upwards, as revealed by its concentration profile. Such a phytoplankton maximum is believed to 'absorb' the nutrient diffused upwards, thus blocking the supply of deep water nitrate to the upper euphotic zone, where algal growth appears to be nutrient-limited.

The results are much less satisfactory for the Jura Sound simulation. An in-depth discussion follows.

From the point of view of the ecosystem dynamics at low trophic levels, the interesting aspect of this model is that it promotes the internal pool of nutrient in phytoplankton to the status of state variable. The mechanisms of 'luxury' uptake and internally defined growth control thus provided are liable to enhance significantly the 'behavioural quality' of the phytoplankton compartment in ecosystem models, as also demonstrated in MOMMAERTS (1978) and BILLEN *et al.* (1988).

4.3. HIGHER TROPHIC LEVEL INTERACTIONS (H.G. FRANSZ)

4.3.1. INTRODUCTION

The role of animals in grazing, predation and nutrient recycling has received attention in models of North Sea ecosystems with a variable degree of detail. Only few models are most concerned with the seasonal and annual fluctuations of animal popula-

TABLE 8

Comparison of models including higher trophic level interactions: variables, scales and scope.

(#) <i>model, authors</i>	state variables		<i>x,y,z,t</i>	scales time res./dur.	space res./dur.	region/season
	<i>prognostic</i>	<i>diagnostic</i> ¹⁾				
(1) HORWOOD, 1974	N, P, Z ₁ -Z ₁₃	I ₀ (t), M(t), T(t), pr	t	1h-220d	-	Loch Striven spring/summer
(2) STEELE, 1974	N, P, Z	vertical mixing rate e, h, pr	t	1d-365d	-	North Sea year
(3) PICHOT & RUNFOLA, 1975	N, P, Z, Do	N(x,y), P(x,y) T(t), I ₀ (t), h, pr	t	1d-365d	-	Southern Bight year
(4) FRANSZ, 1981	N ₁ , N ₂ , P ₁ , P ₁ , Z, Car ₁₋₃ B, Do, D	N(x,y), P(x,y) I ₀ (t), T(t), S(x,y), depth(x,y) h	t	0.1d-365d	-	Southern Bight year
(5) KOSLOW, 1983	Z ₁₋₂ , Car ₁₋₂	P	t	1d-100d	-	North Sea and Northeast Atlan- tic stability
(6) RADACH, 1983	N, P	I ₀ (t), I(t,z), A _v (t,z), N(Z=B) g(t,z), Z(t,z), e, h	z,t	75s-27d	2.5-150 m	North Sea spring
(7) FRANSZ & VERHAGEN, 1985	N ₁₋₃ , P ₁₋₂ , D	g(x,y,t), h I ₀ (t), T(x,y,t) depth(x,y)	x,y,t	0.1-365d	6-150km	Southern Bight year

¹⁾ Symbols not explained in Table 6 are: e: feeding threshold and h: half saturation constant.

tions and the significance of predation and yield for stability, regulation and biomass distribution. Such models (e.g. ANDERSEN & URSIN, 1977) stress the food-web relationships of animal components and sometimes reduce the fundamental lower trophic levels to a simple herbivore carrying capacity (KOSLOW, 1983).

Most models tend to describe how the productivity and stability of an ecosystem is related to plant nutrients and the physical environment, represented by stratification, transport processes, light conditions and temperature fluctuations. Such models were presented by HORWOOD (1974), STEELE (1974), PICHOT & RUNFOLA (1975), FRANSZ (1981), RADACH (1983) and FRANSZ & VERHAGEN (1985) with different degrees of complexity of the environment. In this group the processes defining phytoplankton are described in most detail.

But grazing by herbivores was not neglected. It can play a dominant role in keeping the phytoplankton at a low and stable level (STEELE, 1974; RADACH, 1983). The mortality of these grazers must in some way be related to predators. The response of grazers

and predators to prey density is often considered to be positively accelerating, e.g. by the introduction of feeding thresholds. This enhances the model stability. Here it is an important consideration how to delimit the number of trophic levels and how to parameterize the highest level. The latter usually is not considered a state variable, but manifests itself as a density-dependent or constant mortality of the prey. Sometimes the density or ingestion rate is given as a forcing function (RADACH, 1983; FRANSZ & VERHAGEN, 1985).

The number of trophic levels considered to be state variables and the degree of stabilization by predators have important consequences for the significance of nutrient depletion in a model (e.g. STEELE, 1976). This is demonstrated by GREVE'S (1981) PO₄ - phytoplankton - copepod - Pleurobrachia - Beroe model. During one season this system evolves gradually from 1 level to 5 levels, causing a sequence of alternating nutrient-limited and down-grazed phytoplankton stocks. In the food web of the North Sea model of KOSLOW (1983) with dominating 3-level sequences phytoplankton - small

herbivores - invertebrate carnivores, and phytoplankton - large herbivores - fish, predatory interactions tend to regulate the zooplankton community structure. However, according to actual observations in North Sea and Northeast Atlantic all components declined during recent decades in concert with phytoplankton, which points to a general food limitation. The removal by fishing of many predators from the North Sea did not increase the density of their prey. Most probably the North Sea ecosystems are not ruled by a sequence of stabilized predator-prey interactions, but rather derive structure and stability from a seasonal sequence of food pulses enabling production, growth and survival of a limited number of individuals in each developmental stage of the many species.

In the next sections the modelling of the limited number of higher trophic levels in simplified North Sea models with lumped groups instead of species will be discussed. Hence the typical multi-species models (e.g. ANDERSEN & URSIN, 1977) will not be considered here. The description of different processes affecting animal number or biomass will be compared. The processes considered are population growth and development, grazing and ingestion, assimilation, respiration, and mortality. The models compared differ strongly in scope and number of variables (Table 8), as well as in complexity of the processes involved (Table 9).

TABLE 9

Comparison of models including higher trophic level interactions: Complexity of the systems simulated, indicated by processes involved.

Equations/Processes	number of model from Table 8						
	1	2	3	4	5	6	7
nutrient equation	y	y	y	y	n	y	y
regeneration by zooplankton	e	e	e	e	-	e	e
phytoplankton equation	y	y	y	y	n	y	y
grazing by zooplankton	e	e	e	e	-	e	e
herbivores equation	y	y	y	y	y	y	y
growth and development	e	e	e	e	e	-	-
ingestion	e	e	e	e	-	-	-
assimilation	e	e	e	e	-	-	-
respiration	e	e	e	e	-	-	-
excretion	e	e	e	e	-	-	-
mortality	e	e	-	e	-	-	-
predation	i	i	e	e	-	-	-
carnivores equation	n	n	n	y	y	n	n
growth and development	-	-	-	e	e	-	-
ingestion	-	-	-	e	e	-	-
assimilation	-	-	-	e	e	-	-
respiration	-	-	-	e	e	-	-
excretion	-	-	-	e	-	-	-
mortality	-	-	-	e	-	-	-
predation	-	-	-	e	e	-	-
planktivorous fish equation	n	n	n	y	y	n	n
growth and development	-	-	-	e	e	-	-
ingestion	-	-	-	e	e	-	-
assimilation	-	-	-	e	-	-	-
respiration	-	-	-	e	-	-	-
excretion	-	-	-	e	-	-	-
mortality	-	-	-	e	-	-	-
predation	-	-	-	e	-	-	-

e explicit formulation

i implicitly included

n not included

y yes, included

4.3.2 BASIC PROCESSES IN HIGHER TROPHIC LEVEL INTERACTIONS

Population growth and development

Herbivores and carnivores can each be lumped into a number of biomass pools, whose growth rate equals ingestion rate minus respiration, mortality and defaecation rate. Sometimes these state variables were structured by distinction of age, size or weight classes (HORWOOD, 1974; STEELE, 1974; FRANSZ, 1981; KOSLOW, 1983). FRANSZ (1981) even applied a two-dimensional structure in age classes of developmental stages (Fig. 27). In such structured population models both number and mean weight of individuals in the classes must be updated.

Most often age-structured herbivores were presented with the behaviour of copepods (HORWOOD, 1974; STEELE, 1974; KOSLOW, 1983). HORWOOD (1974) and STEELE (1974) assumed a succession of 3 generations of copepods (*Calanus finmarchicus*) in separate cohorts. They calibrated development parameters purposely to arrive at 3 generations per year. Steele achieved this by assuming a gross growth efficiency of 39% and a 100% utilization of the volumes filtered by the animals. The correspondingly high growth rate (not corrected for temperature) enables an initial nauplius pulse (triggered by a minimum food availability in spring) to reach the adult stage in due time. Then the adults accumulate excess food over a fixed period of time (about 7 d). This was converted to a number of viable nauplii of the next generation by taking 10% of the accumulated food divided by initial nauplius weight. Then the sequence was repeated. Multiple cohorts were possible by triggering more than one pulse of nauplii initially. HORWOOD (1974) related the number of eggs laid per female per d (E) for 7 d to a maximum number ($M=40$) and to the average number of algae (P) per cm^3 over the previous 2 weeks according to

$$E = M[1 - 0.82 \exp(-c \cdot P)] \quad (4.3.1)$$

where c is a constant depending on food quality. He related development time (d) to temperature (T) and to the ratio (b) of total time from egg to adult and egg development time, according to the Bêlehrádec function

$$d = 27.7b/(T + 4.57)^{1.1} \quad (4.3.2)$$

where b is chosen to make the copepods develop at observed rates. Such a Bêlehrádec function was also used by FRANSZ (1981) to relate development rates to temperature.

In the zooplankton community model of KOSLOW (1983) herbivore numbers (Z) in certain size classe (i) grow in relation to weights (W), herbivore carrying capacity ($K=25$ to 200 mg C m^{-3}) and total herbivore biomass (H) according to:

$$Z_{i+1} = Z_i + k_{i-1}L \cdot W_{i-1}Z_{i-1}/(W_i - W_{i-1}) - k_iL \cdot W_iZ_i / (W_{i+1} - W_i) \quad (4.3.3)$$

where L is a saturation function:

$$L = (K - H)/K \quad (4.3.4)$$

and k is a coefficient of maximal growth (0.26 in small and 0.35 to 0.11 declining with size in large herbivores). Growth in size structured invertebrate carnivores (*Sagitta*) equals assimilated food minus metabolism. The fish density is constant ($3.3 - 330 \text{ mg C m}^{-2}$).

When a gaussian time distribution of hatching nauplii can be assumed, multicohort models of copepod populations describing the seasonal development in all stages can be derived. Such models can be used to estimate biological parameters by fitting them to observed time series of developmental stage densities (BOSSICART, 1980a and b, 1984). In this way Bossicart estimated life span, growth rates, mortality rates, and number of viable eggs in *Temora longicornis* and *Pseudocalanus elongatus* in the Southern Bight, and *Calanus finmarchicus* in the Fladen Ground area. Value ranges found can be valuable for parametrization and calibration of ecosystem models.

Grazing and ingestion

In some cases, when observed time series of zooplankton density and ingestion rates were available and the aim of the model was only the explanation of phytoplankton development, grazing was directed by a forcing function. RADACH (1983) and RADACH *et al.* (1984) applied 4 different methods to estimate ingestion (g) by copepodite stages of *Calanus finmarchicus*: a. from body weight (W), density (Z) and daily ingestion as percentage of body weight ($p=31$ to 148% depending on stage) as

$$g = p \cdot W \cdot Z \quad (4.3.5)$$

b. from filtration rate ($f=11.7$ to $100 \text{ ml d}^{-1} \text{ ind}^{-1}$) and

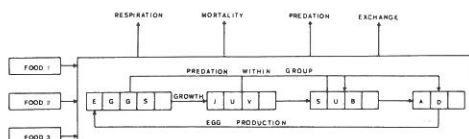


Fig. 27. Synoptical flow diagram of animal submodels with age classes of developmental stages (from FRANSZ, 1981).