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International Council for the
Exploration of the Sea

REPORT OF THE WORKSHOP ON MODELLING THE POPULATION DYNAMICS OF HARMFUL ALGAL BLOOMS

Vigo, Spain, 4-7 May 1994

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WORKSHOP ON MODELLING THE POPULATION DYNAMICS OF HARMFUL ALGAL BLOOMS

1. INTRODUCTION

The ICES/IOC Workshop on "Modelling the Population Dynamics of Harmful Algal Blooms" was convened in the Instituto Español de Oceanografía (IEO, Vigo, Spain) from 4 to 7 May 1994, under the co-chairmanship of Wolfgang Fennel (Germany) and Paul Tett (United Kingdom). Twenty nine participants from fifteen countries (including five observers) took part in it. Alberto González-Garcés, Director of the Centro Oceanográfico de Vigo (IEO), welcomed participants and drew attention to the enormous socioeconomic importance of harmful algal blooms in the context of Galicia. Wolfgang Fennel reminded participants of the terms of reference, and that the central aim of the workshop was to establish a common language between biologists and physicists, so that the modelling of harmful algal blooms can be advanced.

Timothy Wyatt acted as a rapporteur.

This workshop involved participants in three distinct activities:

a) Presentation of various viewpoints relevant to modelling phytoplankton-hydrographic interactions;

b) Discussions of modelling procedures and philosophy;

c) Practical exercises in the use of pre-prepared models on PCs.

The list of participants is presented in Annex I. The presentations are collected in Annex II, and the instructional material which accompanied the PC exercises are in Annex III.

Financial support for the organization of the Workshop was provided by D.G. XIV of the CUE (Sponsorship Grant MAC/3/94, AIR Programme)), and by the Instituto Español de Oceanografía. IOC (UNESCO) supported the participation of four observers .

AddLink S.A.-Spain kindly provided twelve licences for a demonstration of the MATLAB programme during the Workshop.

2. TERMS OF REFERENCE

At the 81st ICES Statutory meeting in Dublin (23 September-1 October 1993) the Council resolved (C. Res. 1993/2:49) that:

"A Workshop on Modelling the Population Dynamics of Harmful Algal Blooms will be held in Vigo, Spain, from 4-7 May 1994 under the co-chairmanship of Dr P. Tett (UK) and Dr W. Fennel (Germany) to:

a) investigate the use of numerical models in improving understanding of the dynamics of harmful algal blooms;

b) use the above models to assist in the design of sampling strategies, interpretation, and forecasting of harmful algal blooms;

c) develop a dialogue between physical and biological oceanographers with respect to harmful algal blooms, including the role of physical inputs, and temporal and spatial scales".

3. PROGRAMME

4 May

Morning 10.00-13.30

- Welcome (Director of IEO-Vigo).
- Aims of the workshop (Fennel/Tett).
- Algal bloom models - an overview (Tett).

Afternoon 15.00-18.00

- Modelling the yearly cycle of plankton (Fennel).
- How to built a simple model (seminar with PC/ Fennel).

5 May

Morning 9.00-13.30

- Plankton population dynamics with and without physics (Wyatt).
- Nutrients in buoyant plumes (Osborn).
- Modelling the primary production in the North Sea using a coupled 3D model (Svendsen).
- Numerical experiments with a simple coupled model (Sattler/Fennel).

Afternoon 15.00-18.00

- Working with models (seminar with demonstrations Tett/Burren).

6 May

Morning 9.00-13.30

- A model of the effect of cyst germination on *G. catenatum* populations (Blanco).
- The ecophysiology of exceptional blooms (Tett).
- Dynamic modelling of phytotoxin kinetics in benthic invertebrates (Silvert/Cembella).
- The importance of bio-physical interactions in controlling bloom dynamics in patchy coastal environments (Donaghay).

Afternoon 15.00-18.00

- Diurnal variation and primary production during the spring bloom (Barkmann)
- Towards predictive phytoplankton models (Aksnes)
- Training with PC-programmes (Fennel/Tett)

7 May

Morning 9.00-13.00

- Further exercises in modelling on PCs
- General Discussion.

4. PLENARY DISCUSSION

The objectives of the modelling workshop on HAB, as defined by the terms of reference, were to explore the use of numerical models in improving understanding of bloom dynamics.

An attempt was made to unite phytoplankton biologists, physical oceanographers and modellers to achieve a common definition of the rôle of physical and biological factors integrated over various spatio-temporal scales. A debate arose early in the discussions regarding the appropriate use of ecosystem models. Some participants adopted the approach that numerical models defined by a discrete set of differential equations would serve our purpose; others wished to consider other modelling techniques including *conceptual* (i.e. box or compartment), *analytical*, and even *intuitive* models, the latter of which are employed routinely by phytoplanktologists in formulating and testing working hypotheses.

Existing models of different types might be helpful for crude estimates for risk assessment, however further research is required to refine the underlying assumptions of such models. All participants would welcome an increased participation of phytoplankton biologists in future modelling exercises. It was acknowledged that in general the forcing functions determining the hydrodynamic regime in a given system were better defined and thus more amenable to modelling than the biological determinants leading to HAB formation. At least some of the initial scepticism among biologists towards the utility of numerical modelling in understanding HAB dynamics was due to the belief that biological systems are inherently so complex (involving organismal behaviour, etc.) that the number of functions sufficient to define them could not be successfully incorporated. This was countered by statements that the complexity of a system is not necessarily a fundamental property, hence simple models are not necessarily worse at describing the coupling between physical and biological parameters than more complex ones. In this case, the appropriate level of complexity in the model is that which makes the least number of assumptions while best explaining reality.

One positive outcome of the workshop was the understanding achieved among physical oceanographic modellers and phytoplankton ecologists regarding a common lexicon for their discussions. Thus, physical oceanographers became familiar with the use of terminology associated with growth and primary production (Liebig's Law of the Minimum, cell quota, Michaelis-Menten kinetics, photosynthetic parameters, etc.) while phytoplanktologists were shown the rôle of small-scale turbulence, advective and diffusive flux, barotropic currents, etc., in driving bloom aggregation and dispersion.

The practical examples of extant phytoplankton dynamic models presented to the workshop were essentially oriented towards modelling primary production, biomass, net carbon flux and spring diatom blooms. The implicit assumptions of these models is that there exists a defined suite of first order properties (e.g., nutrient kinetics, photosynthetic rate, etc.) which govern the phytoplankton population growth rate. There was disagreement regarding the utility of general primary production models for understanding HAB dynamics, since the critical property is the harmful effect of such blooms, rather than a common ecophysiology. Biologists also questioned the reductionist approach of the physical modellers towards the biological components; simplifying assumptions such as reducing the primary producer and secondary grazer to single components and fixing the grazing rate as constant in time were considered to be unrealistic. From the point of view of modelling individual harmful species, it was pointed out that individual life history features might be of considerable or even over-riding importance to their population dynamics. On the physical side, while the impact of for example a meteorological front might be adequately known for diagnostic purposes, prognosis would require a detailed ability to predict the time of arrival of that front, which is not generally possible. These views did not immediately deflect the course of the debate, which concerned the mathematical expressions of functional relationships (such as the Michaelis-Menten equation for nutrient kinetics), step functions and truncation procedures, and whether there is a need for feedback between the physical and biological components of models.

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Since it is not clear that the biological forcing functions governing HAB population growth are necessarily those of nutrient dynamics, an overemphasis on nutrient kinetics in modelling may be seriously misleading. Some participants expressed the pessimistic view that HABs will prove particularly intractable to modelling since their net population growth may be a function of *secondary* or *tertiary processes* (allelopathy, water conditioning, complex nutrition or behaviour, etc.) which are currently unknown or at best are ill-defined. Some discussion took place of the different modelling approaches which might emerge depending on whether one took the view that harmful algal events result from the opportunistic behavior of individual species, or alternatively, that they occur as a result of changes to the system at large. It was commented that for example PI curves of harmful species do not appear to differ from those of other species, but that special features such as encystment/excystment cycles, vertical migrations, and heterotrophy need to be incorporated into HAB models.The problems of identifying first and higher order processes were briefly alluded to, with particular reference to the forms of functional relationships, and several people drew attention to biological feedback mechanisms which need to be considered, such as the relationships between algal biomass and light-absorption, or the production of extracellular polymers, viscosity and turbulence. The fact that HABs may arise in response to catastrophic environmental disruptions which are themselves not predictable contributes additional complications.

A fundamental dichotomy was established between *diagnostic* models, for analyzing and explaining bloom events which have already occurred, and *prognostic* models for forecasting and bloom prediction. There was some agreement that diagnostic models need to be developed now to improve our understanding of the ecological and oceanographic mechanisms involved in HAB occurrence, and that prognostic models lie further in the future. But it was also felt that at a practical level, models are required now which will give early warnings of potential dangers to shellfish producers or fish farmers, i.e. real time guidance, and that the kinds of model which are successful in such contexts do not necessarily lead to better understanding of the underlying biological and oceanographic mechanisms. In the interim, greater emphasis should be placed on the development of "species of interest" models to focus on specific harmful species. Furthermore, it was pointed out that it is not necessary to model entire ecosystems to provide useful recommendations to public health officials and fisheries and aquaculture managers. Models capable of generating short-term predictions (over a few days or weeks) based upon risk assessment probabilities generated from monitoring data can assist in the implementation of mitigating strategies for HAB effects. The development of *holistic bloom dynamic models* coupling biology with three-dimensional models of circulation and mixing await further definition of the requisite rate processes and parameters.

Some participants felt that the discussion had not yet succeeded completely in achieving an understanding between physicists and biologists, in part due to the fact that it was being conducted in a language unfamiliar to biologists. Bloom prediction and some other matters already dealt with may belong more properly to a future workshop, while the current session should have addressed fundamental questions about how to begin modelling and the requirements for background information.

Participants felt the workshop was an excellent start towards the goal of strong interaction between biologists, physicists, and modellers on the problems of harmful algal blooms. The multitude of problems associated with the oceanographic complexity of the problem will necessitate many different modelling approaches.

5. CONCLUSIONS

Discussions during the workshop had revealed a diversity of views on the utility and purposes, as well as the methods, of modelling of harmful algal blooms. Some participants remained unconvinced of the value of numerical modelling. In this final remarks, Dr Tett attempted a synthesis of these views. Modelling, he thought, could help in understanding and predicting harmful blooms. Three approaches

seemed likely to be useful.

(1) <u>As part of the scientific process</u>. Relatively simple models of life cycles and biological-physical interactions can act as tools for testing hypotheses about HABS and thus for gaining better understanding of their causes and dynamics.

(2) <u>For risk assessment</u>. Appropriate models could provide objective estimates of HAB risks in particular localities. For example, a 2-D circulation model of a ria coupled with a semi-stochastic model of dinoflagellate population dynamics could be forced with data for a range of typical meteorological and oceanographic conditions to give bloom probabilities for particular locations and conditions.

(3) <u>Day-to-day prediction of bloom evolution</u>. In the same way that it was not possible to predict weather more than a few days in advance, it seems unlikely to be possible to predict particular bloom events any further ahead, if for no other reason that phytoplankton growth was strongly influenced by weather. However, by analogy with modern methodes of weather forecasting, it should be possible to provide forecasts, updated daily, and valid over the next few days, of the evolution and movement of blooms in a given region. The basis for such predictions would be (a) high-resolution, 3D physical transport models, accurate over irregular topography, and tuned to the region in question; (b) numerical models for the dynamics of relevant harmful algae (or cyanobacteria) engineered for modular coupling with the physical model; (c) networks, including remote sensing, for real-time monitoring of relevant aspects of water physics, chemistry and biology; and (d) procedures for combining these real-time observations with the output of a model driven by actual and forecast weather.

Dr Tett distinguished the type of effort and funding necessary to advance each kind of modelling. Type 1 was part of the scientific process, and was taught as such in many institutes of higher education. He hoped that the workshop had successfully given some flavour of this approach to persons who considered themselves not to be modellers. Type 2 could be seen as applied research and as a way of drawing together existing knowledge. Where there was adequate local knowledge of hydrography and biology, a modeller skilled in this approach should be able to provide useful estimates of risk with about a year's work. His experience had been that both types of modelling helped the dialogue between scientists and the fishing and fish-farming industries and their regulators.

Finally, he saw type 3 modelling as an engineering problem, which would draw upon the scientific understanding gained with type 1 models and applied in type 2 models. All parts of the methodology for type 3 models were now available, but implementation for a given location would be costly, and would clearly only be justified in regions where the economic consequences of HABs were large and where such consequences could be ameliorated by predictions of bloom evolution.

6. RECOMMENDATIONS

The dialogues between physical and biological oceanographers, modellers (theory) and non-modellers, laboratory work and studies at sea shoud continue in order to improve our understanding of the scientific principles involved in HAB.

A practical workshop on building models from scratch using participants data sets should be organized.

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ANNEX II: COLLECTION OF SCIENTIFIC COMMUNICATIONS

MODELLING TOXIC ALGAL BLOOMS
A dozen points by way of Introduction

Paul Tett

1. **Simple view** - phytoplankton are green stuff that require light and nutrients. When stratification provides ample light, a bloom will occur if nutrients are sufficent.

2. **Complications** - the bloom might be prevented by grazing, sinking or physical dispersion; the bloom might be concentrated by physical processes; the bloom might contain harmful algae, and their harmfulness [/toxicity] might be enhanced by bloom conditions.

3. **Equation** for rate of change of phytoplankton biomass **X**:

$$\partial X/\partial t = -V{\cdot}\partial X/\partial y \ - \ (W+X_W){\cdot}\partial X/\partial z \ + \ \partial(K_y{\cdot}\partial X/\partial y)/\partial y \ + \ \partial(K_z{\cdot}\partial X/\partial z)/\partial z \ + \ (\mu-G){\cdot}X$$

Where:

    y (horizontal) and **z** (vertical) are spatial co-ordinates;

(a)
    V, W are horizontal and vertical water velocities;
    K_y and K_z are horizontal and vertical turbulent diffusivities;
(b)
    X_W is vertical phytoplankton velocity relative to water;
    μ and **G** are phytoplankton relative growth and grazing loss rate.

(a) terms are physics;
(b) terms are biology, and differ between species; in addition,

$$\mu = f(I,S)$$

and thus depends also on the effect of physical processes on irradiance **I** and on nutrient concentration **S**.

4. **What is best way of describing the physical framework?**:
   - eulerian, fixed Cartesian (or similar) co-ordinates, with time- and depth- varying turbulent diffusivities parameterising small-scale (rapidly fluctuating) velocities [as equation above];
   - time-varying mixed (boundary) layers, transferring water etc. by entrainment;
   - eulerian, fixed compartments, with all transports parameterised as exchange rates between compartments;
   - lagrangian, particle-tracking models, with turbulence/mixing effects represented by time- and depth- varying step length.

5. **What other physical processes** (other than transports) must be included?:
   - deposition/resuspension for (a) algae with benthic stage, and (b) light absorbing SPM;
   - optical processes, including effects of algae themselves as well as SPM on light attenuation, leading to prediction of **I**.

6. **How to link physics and biology:**
   - *statically*: take physical parameters either from observation (or deduction from observation), or from physical model run independently of biological model, then applied as time-series to biological model;
   - *dynamically*: solve physical and biological equations simultaneouslv.

7. **The purpose** of models:
   - *diagnostic*: to aid understanding, often by using the model for analysis or what-if questions: needs only typical or generalised initial and forcing data;
   - *prognostic* - to predict what will happen: needs accurate initial and forcing conditions (and may need to make predictions about evolution of forcing - e.g. of weather).

8. Model **time-scales**:
   (not the same as the computational time-step)
   - for understanding/predicting annual cycle - resolve to 1-day time-scale;
   - for understanding/predicting detailed time-courses of blooms - need to resolve physical processes within tidal cycle and day, and diel biological cycles of growth, grazing and vertical movement?
   (the importance of understanding the effect of averaging time-scales for the forcing data)

9. **Biological models**:
   - bulk, or biogeochemical: for total chlorophyll or organic carbon; compartmentalisation on functional basis, e.g. microplankton-detritus;
   - trophic network, representing selection of types of organisms and flows of energy/material amongst them: species differ in terms of: ability to get and use nutrients; use of light; vertical movement; susceptibility to grazing.
   (understanding the biological models - reduce physical effects by simulating laboratory culture, microcosm or mesocosm)

10. **Seeding bloom models**:
    - what (in reality, in a model) controls the biomass or species innocula present at the start of a bloom (at the end of winter; in the case of a summer bloom);
    - seeding from the benthos (e.g. cyst-forming dinoflagellates), or from outside the model domain;
    - importance of individual life-cycles (e.g. *Phaeocystis*);
    - is seeding a largely deterministic or largely stochastic process?

11. **Predicting the consequences** of blooms:
    - development of toxicity;
    - oxygen consumption by bloom biomass;
    - release of organics (e.g. ---> foaming; DMS --> acid ppt.);
    - trophic effects.

12. **Optimism and pessimism** about models:
    - models based on conservation (e.g. potential energy, total nitrogen) can make reliable over-all predictions, even if initial data inadequate: especially when model (and nature) includes stabilising feedback;
    - models based on non-linear interactions with positive feedback (e.g. turbulence-generation, predator-prey) may have chaotic behaviour, so that outcome depends critically on exact knowledge of initial conditions.

MODELLING THE YEARLY CYCLE OF PLANKTON

How to construct a model of a marine ecosystem

Wolfgang Fennel

Models of marine ecosystems require coupling of physical and biogeochemical models.

What is a model? In a formal sense a set of differential equations which describe the dynamic behaviour of a system.

Dynamic Equations - describe changes in time. In physics the changes are caused by forces, and formulation of equations follows from basic laws (conservation of energy, momentum, mass, etc..)

How to formulate dynamical equations of a marine ecosystem? What drives the changes in a marine ecosystem? There is no general rule to formulate the biogeochemical relationships in terms of differential equations. Formulation requires SIMPLIFICATION of a properly addressed problem.

EXAMPLE
'Description of the annual cycle of plankton'
Consider nutrients, plankton, and detritus in terms of concentrations (relative to the concentration of the limiting nutrient)
- N - nutrients
- P - phytoplankton
- Z - zooplankton
- D - detritus

This implies neglect of several dynamical aspects (e.g. individual behaviour)

What drives the changes of N, P, Z, and D in a simple ecosystem?
- growth and loss of phyto- and zooplankton
- redistribution through currents and mixing

$\Delta(N,P,Z,D)/\Delta t =$ (redistribution - currents, mixing)(N,P,Z,D) + (gain and loss) (N,D)+ (growth and loss) (P,Z).

growth of P:
consider one day as time scale,
(physical control - light, temperature, etc. has been summarized under V_{max} ,can be 'zoomed in' by more detailed assumptions) fundamental relationship - nutrient limitation
$growth(N) = V_{max} N^2/(\alpha^2 + N^2)$
low growth rates for low nutrient levels
α = half-saturation constant
$growth (N) = V_{max}$ for $N >> \alpha$
$growth (N) = V_{max} (N/\alpha)^2$ for $N << \alpha$

Dynamical relations
$\Delta P/\Delta t \sim growth(N) P$
$\Delta N/\Delta t \sim -growth(N) P$

LP = loss of phytoplankton (extracelluar release, mortality)
LPN, LPD = loss of P converted to N, D
LP = LPN + LPD

$\Delta P/\Delta t \sim growth(N)P-LP P$
$\Delta N/\Delta t \sim -growth(N) N + LPN P$

$\Delta D/\Delta t \sim LPD\ P$

growth of Z through food limited grazing
$graz(P) = \beta\ [1 - exp(-I\ P^2)\ ]$
I = modified Ivlev constant
$graz(Z) = \beta$ for $P >> 1$
$graz(Z) = \beta\ I\ P^2$ for $P << 1$
$\Delta Z/\Delta t \sim graz(P)\ Z$
$\Delta P/\Delta t \sim -graz(P)\ Z$

LZ = loss of zooplankton (egestion, mortality, etc)
LZN = loss of Z converted to N
LZD = loss of Z converted to D

$\Delta N/\Delta t \sim -growth(N)\ N\ +\ LPN\ P\ +\ LZN\ Z$
$\Delta P/\Delta t \sim growth(N)\ P\ -\ LP\ P\ -graz(P)\ Z$
$\Delta Z/\Delta t \sim graz(P)\ Z\ -\ LZ\ Z$
$\Delta D/\Delta t \sim LPD\ P\ +\ LZD\ Z$

ignore loss of Z by higher predators (included in mortality)

TRUNCATION OF THE HIERARCHY

Coupling of physical and biological dynamics

B = (N, P, Z, D)
$\underline{v}$ = (u, v, w) - current vector
A_h, A_v - horizontal and vertical eddy diffusivities

ADVECTION DIFFUSION EQUATION

$B_t + \underline{v} \cdot \nabla B - A_h\ \Delta_h\ B - A_v \Delta_v\ B$ = biological dynamics
ocurrence of $\underline{v}$ and $A_{h,v}$ requires input from a circulation model

COUPLED MODELLING

Reduction to a simplified BOX MODEL
- integrate horizontally
- consider two vertical layers

$<B_t>$ = $<$biological dynamics$>$ + fluxes through boundaries

upper layer
$N_t = -growth(N)\ N\ +\ LPN\ P\ +\ LZN\ Z\ +\ A_{mix}(D-N)\ +\ SN^{ext}$
$P_t = growth(N)\ P\ -\ LP\ P\ -graz(P)\ Z$
$Z_t = graz(P)\ Z\ -\ LZ\ Z$

lower layer
$D_t = LPD\ P\ +\ LZD\ Z\ -\ A_{mix}(D-N)\ +\ SD^{ext}$
vertical fluxes by sinking - LPD and LZD
$A_{mix}(D-N)$ controls vertical fluxes by mixing
SN^{ext} and SD^{ext} prescribe external fluxes (sources and sinks)

Assume that the biological activity is controlled by physics through formation and destruction of stratification

in the box model - switch from one layer to two layers

for day 92 to day 273:
grow, graz nonzero; A_{mix} zero

for day 0 to 92 and 273 to 365:
grow, graz zero; A_{mix} nonzero

overwintering of P and Z?

assume, that P and Z decrease to a certain low background concentration, P_B, Z_B.

Fig. 1
Model run of the yearly cycle of nutrients, N, phytoplankton , P, zooplankton, Z, and detritus, D, with constant rates.

Fig. 2
Model run of the yearly cycle of nutrients, N, phytoplankton , P, zooplankton, Z, and detritus, D, with time dependent rates.
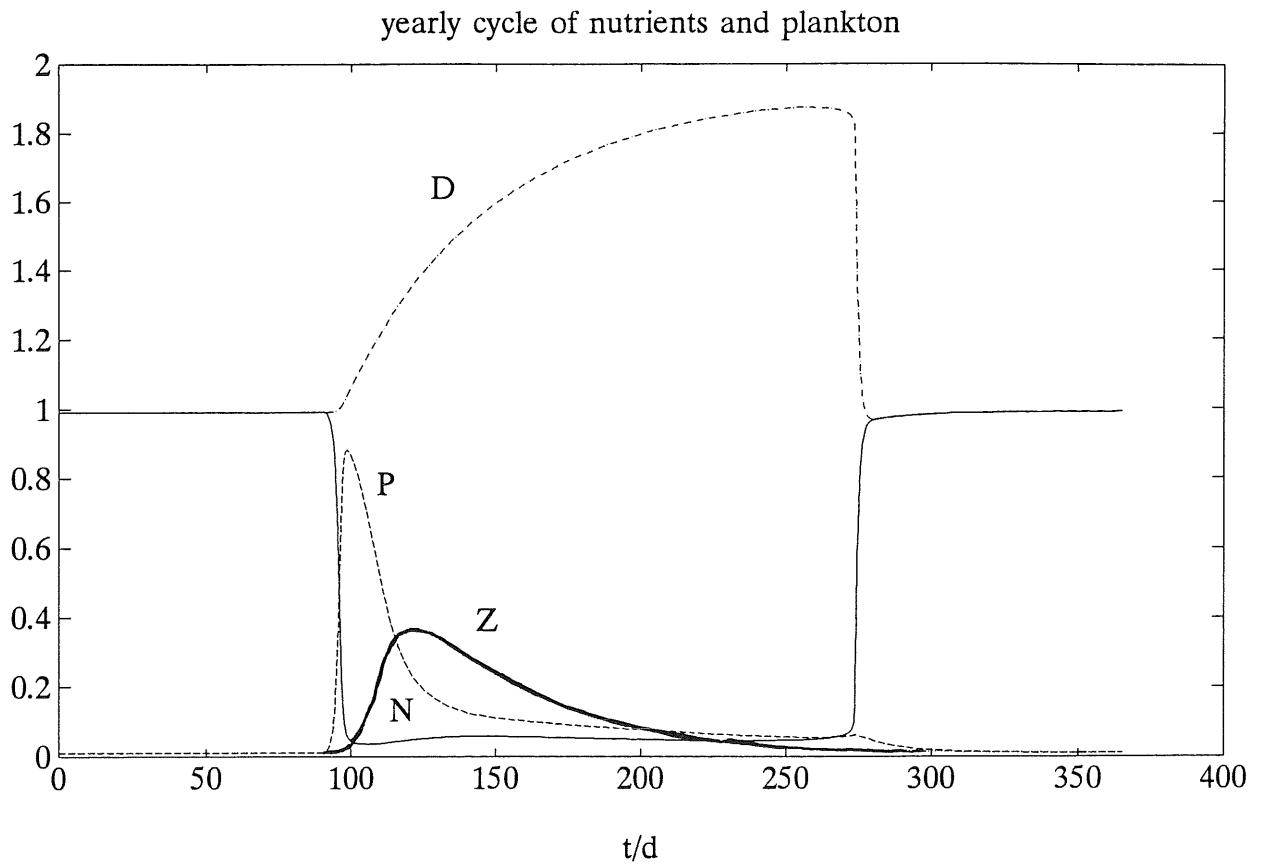
yearly cycle of nutrients and plankton

Fig. 1 (Fennel)
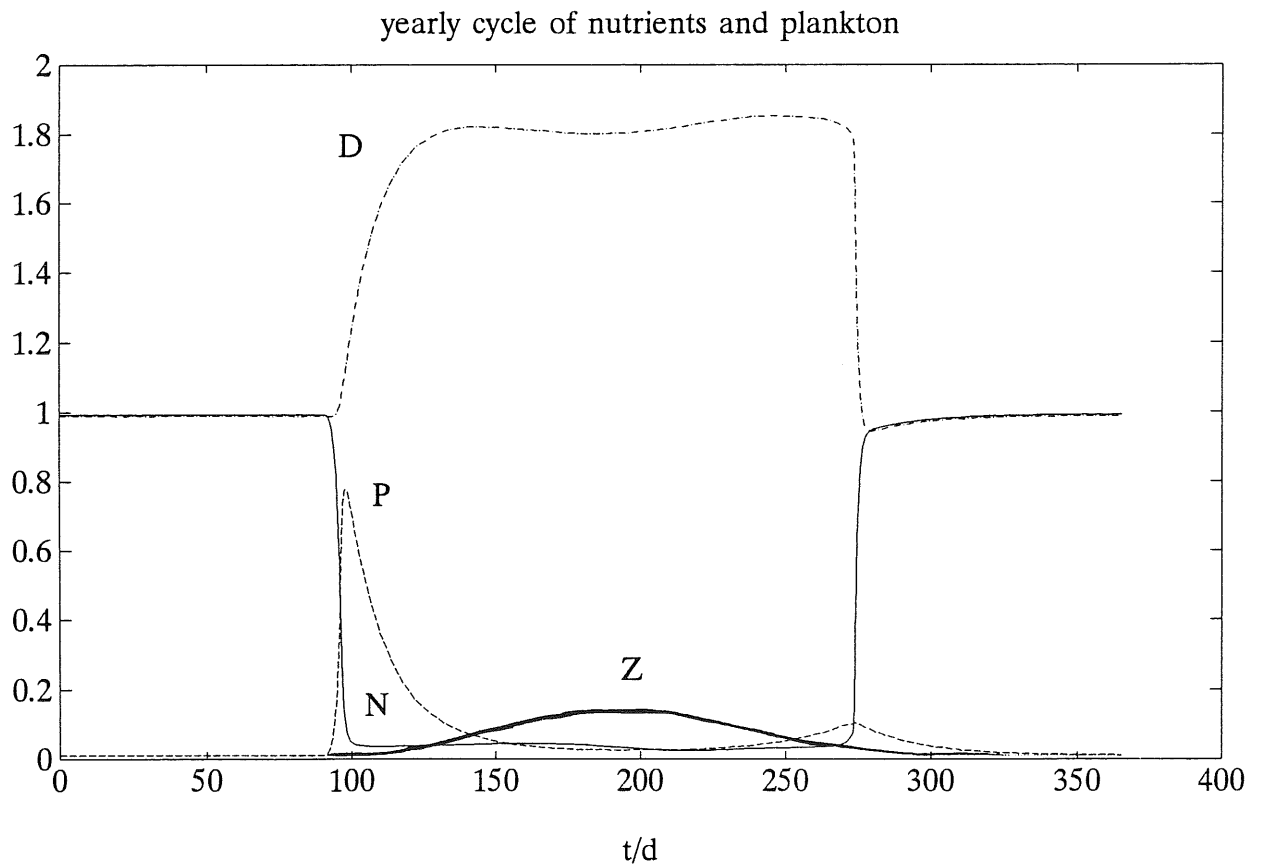
yearly cycle of nutrients and plankton

Fig. 2 (Fennel)

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BUOYANT COASTAL PLUMES: SOME SIMPLE COMMENTS ABOUT THEIR DYNAMICS

Thomas Osborn

The dynamics of coastal currents are much more complicated than the open ocean, due to the significant role of bottom friction and the large variability in temporal and spatial coordinates. However, let us consider very simplified force balances to compare an open ocean front, to a coastal front, and to an estuary.

A two-layer, open-ocean regime with a frontal region between two water masses with a density difference, is shown in figure 1. Pressure is the weight of water overhead. Since (by definition of the problem) there is no horizontal pressure gradient in the lower layer (below 2000 dbars), the sea surface must vary in height to account for the difference. In the frontal region of the upper layer, where the density transition occurs, there is a sea surface slope. There is a horizontal pressure gradient only in the region below the sloping sea surface (this pressure gradient decreases to zero at 2000 dbars). Due to the geostrophic force balance that exists in the open ocean, there is a frontal jet in the transition region but no flow anywhere else. The geostrophic balance is from the cross-stream component of the equation of motion, i.e., the east-west current is derived from the balance of forces in the north-south direction.

In an estuary, figure 2, the flow is driven by the fresh water flowing 'downhill' along the estuary. Salt water is entrained from below - increasing the volume transport dramatically. The balance of forces is now the downstream pressure gradient, providing acceleration, for the upper layer, and overcoming the interfacial stress between the upper layer and the lower layer.

In the estuary, it is the balance of forces and accelerations along the axis of the estuary which determines the axial velocity. For a simple buoyant coastal plume, it is likely to have most of the pressure gradient balanced by the Coriolis force with a fraction in the downstrean direction to overcome bottom friction. If the plume has a vertical front on the outside edge (figure 3a) then the argument used for the open ocean jet will have the current concentrated in the frontal region. The water flow is not spread across the entire fresh water plume. Intuitively one might expect flow in the plume like water running along a gutter, but rather the fresh water input is a source of buoyancy (appearing as elevated sea level); which leads to a flow in the frontal region. Sloping density surfaces (figure 3b) serve to spread out the surface slope over a wider region than the surface expression of the front. This spreads out the flow but it is still located towards the outside of the plume. Of concern to harmful algal blooms is the question of surface convergence in the frontal region, which when combined with behavioral characteristics, especially vertical swimming, would lead to the concentration of organisms into the region of maximum advection. Such may be the case with *Alexandrium tamarense* blooms in the Gulf of Maine.

In conclusion, the spatial and temporal scales of buoyant coastal plumes imply a geostrophic balance which predicts the main flow in the outer boundary, where there is a horizontal density gradient. Surface convergence into the plume in conjunction with vertical swimming can lead to concentration in the frontal flow.

A SIMPLE MODEL OF COUPLING PHYSICAL WITH BIOLOGICAL DYNAMICS

Carsten Sattler and Wolfgang Fennel

Understanding of complex biogeochemical processes in the sea by means of models requires simplifications to extract the main features of the processes involved.

The physical control of the biology implies that coupled models are necessary. A main problem is that there are no first principles which determine the mathematical relationships of the biological dynamics. We choose an Eulerian continuous model for the dynamics of the biological state variables and connect this to a circulation model. The rationale is to study a simple system where the circulation patterns are well defined and easy to understand. The question to be adressed is: How does the physics affect the biological dynamics?

The biological model was developed by W. Fennel [1] and uses for simplicity only 4 biological state variables: phytoplankton, zooplankton, nutrients and detritus. The model summerizes phytoplankton species by only one state variable and the dynamics is nutrient limited assuming there is enough light.

The circulation model is the GFDL MOM code from Princeton University[1].

The interface between physics and biology is the diffusion-advection-reaction-equation

$$\frac{\partial C_i}{\partial t} + \nabla(\bar{v}C_i) = \nabla(A\nabla C_i) + f_i(C_1,...,C_N,t,...) \quad (1)$$

where C_i is the i-th biological component, $\bar{v}$ is the velocity field, A is the turbulent mixing coefficient and f_i is some source and sink distribution.

In a series of numerical simulations the influence of the initial distribution of nutrients and of the physical dynamics on the biology was studied.

The model basin is a rectangular one with dimension 80 km x 40 km x 40 m.

The initial condition for salinity and temperature corresponds to the mean summer stratification in the Western Baltic Sea. Since only short time scales were taken into account, the mixed layer depth was fixed by a vertical structure of the turbulent mixing coefficient and set to the maximum of the BVF[2], in this case 12 metres. The system is driven by a switch-on wind acting on a fluid at rest and being switched-off after 5 days. The integration time is 10 days.

Several experiments were made for two different cases corresponding to spring and late summer situations. The initial condition for the late summer situation is defined by a zero concentration of nutrients in the mixed layer and a high concentration below. In the spring bloom situation the stratification has just established and the nutrient concentrations are high in the whole water column, which was well mixed before.

Furthermore we assume that the biological processes are active only in the mixed layer. This implies a step function approximation of the vertical variation of the light intensity. The simulations

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[1]   GFDL MOM means General Fluid Dynamics Laboratory Modular Ocean Model developed by Pacanowski, Rosati and Dixon.

[2]   BVF is the Brunt Väisälä frequency.

show that during the first 5 days the physical control is governed by the following key processes:

* coastal jets
* Kelvin waves
* Ekman transport
* upwelling and downwelling

and during the next 5 days (without forcing)

* old Kelvin waves
* new Kelvin waves (excited by switching off the wind)
* currents connected with the decay of the geostrophic pressure gradient
* inertial waves

The nutrient flux into the upper mixed layer in the late summer situation by turbulent mixing processes is increased substantially by upwelling. In all numerical experiments the distribution pattern of the biological tracers were determined by the mentioned physical processes induced by wind forcing. After switching off the wind we find two different cases for the late summer situation. In the case of strong nutrient limitation the distribution patterns are also controlled by the physics. For lower nutrient limitation, these patterns are determined by the biological processes. The spring bloom situation is only slightly affected by the circulation processes.

References

[1] W. Fennel. A model of the yearly cycle of plankton. submitted to Journal of Marine Systems, 1993.

[2] K.H. Mann and J.R.N. Lazier. Dynamics of Marine Ecosystems. Blackwell Scientific Publications, 1991.

[3] B.J. Rothschild (ed.). Toward a Theory on Biological-Physical Interactions in the World Ocean. Kluwer Academic Publishers, 1988.

DIURNAL VARIATIONS AND PRIMARY PRODUCTION DURING THE SPRING BLOOM

Wolfgang Barkmann

The response of phytoplankton photosynthesis to a changing light environment caused by astronomical cycles and vertical mixing has been studied using a one-dimensional Lagrangian modelling approach (Lagrangian ensemble method; Woods & Onken 1982, Wolf & Woods 1988, Woods & Barkmann 1993a). In this method, the phytoplankton biomass is represented by an ensemble of a few thousand particles, each of which contains a population of cells. Each particle follows a trajectory computed from its own sinking speed through the water and from vertical mixing by turbulence. The phytoplankton considered is the small oceanic diatom Thalassiosira pseudonana, which has been studied by Cullen and Lewis (1988).

The model results show that the vertical distribution of the photoadaptive parameters (α, P_m, β, light-limited, light-saturated photosynthesis and photoinhibition) is characterized by a strong gradient at the base of the turbulent surface boundary layer. Photoinhibition can become important in the near surface layers during the morning and the early afternoon, when the light adaptation lags behind the ambient light level. Primary production during the spring bloom was found to be sensitive to the adaptive time scale of phytoplankton, but less sensitive to photoinhibition. We conclude that the diurnal variations of vertical mixing may be capable of shifting the onset of the spring bloom towards late winter, i.e. before a density stratification can be established (Woods and Barkmann, 1993b).

REFERENCES

Cullen, J.J. and M.R. Lewis (1988). The kinetics of algal photoadaptation in the context of vertical mixing. J. Plankton Res., 10(5): 1039-1063.

Wolf, U. and J.D. Woods (1988). Lagrangian simulation of primary production in the physical environment - the deep chlorophyll maximun and nutricline. In: Towards a Theory on Biological-Physical Interactions in the World Ocean. B.J. Rothschild (ed.). Dordrecht: Kluwer, pp. 51-70.

Woods, J.D. and R. Onken (1982). Diurnal variation and primary production in the ocean - preliminary results of a Lagrangian ensemble model. J. Plankton Res. 4: 735-756.

Woods, J.D. and W. Barkmann (1993a). The plankton multiplier - positive feedback in the greenhouse. J. Plankton res. 15(9): 1053-1074.

Woods, J.D. and W. Barkmann (1993b). Diatom demography in winter. Fisheries Oceanography, 2:3/4: 202-222.

PLANKTON POPULATION DYNAMICS WITH AND WITHOUT PHYSICS

Timothy Wyatt

1. The process of modelling a single species population trajectory involves several steps, some of which are not always made very explicit. In the first step, a biological problem is <u>translated</u> into mathematical terms, often in the form of differential equations. These equations are then used like a "what if" or "let's pretend" proposition from which some deductions are made. The deductions are then <u>translated back</u> into biological terms to assess their value in resolving the initial problem. Some benefits of these procedures are, to help focus fuzzy ideas, to identify mismatch between model results and the real world (which hopefully can generate new hypotheses), and to help us see in what ways the biological system may be able to escape from constraints imposed by the model. The new views reached can then be used to refine or modify the model (Levins, 1993), or to throw it away.

2. It is obvious that a biological population trajectory (dN/dt) depends on the growth (R) and death (G) rates, and on immigration (I) and emigration (E), so that

    $$dN/dt= N(R\text{-}G+I\text{-}E)$$

    (i)

    The terms R and G are the traditional terrain of ecologists, and in an initial approximation I and E represent the physics, i.e., in a plankton population, the gains and losses due to advection and turbulence. (This equation is formally identical with the more operational equations discussed by Fennel and Tett at this workshop).

    If G, I and E all equal zero, as for example in an axenic culture, equation (i) reduces to

    $$dN/dt= N(R), \qquad (\text{or} \quad dN/dt = rN)$$

    (ii)

    This equation in discrete form was used to describe population growth by Linnaeus in 1744, with $r = 2$. Stewart (1989) traces the earliest use of a "discrete dynamical model" to Leonardo of Pisa in 1220 A.D., who used it to project future population numbers of idealized rabbits.

3. Several things have already happened to the population during the translation which leads to equation (i) or (ii). Amongst these, a) the individuals have all become alike, and there are no distinctions of age, gender, maturity stage, and so on: b) time, whether we write the equations in discrete or continous form, has become homogeneous-there are no distinctions of day/night, summer/winter; c) the growth and death rates, R and G, are defined as density-independent constants; c) a dichotomy has been established between biological and physical processes which tends to constrain future developments of the modelling process. Thus the translation of a biological problem into a mathematically tractable one filters out much of the "reality" perceived by ecologists. This reflects the need for simplification, but there are many ways to do it, and considerable skill is needed to choose an appropriate one. There are also some possibly more fundamental epistemological problems (addressed by Silvert and Cembella at this workshop).

    If, in a particular context, these restrictions are judged to be too severe, then the equations must be modified or substituted by others. Mathematicians might say that equation (ii) is a bad model because it "blows up". Biologists would agree it is bad because the universe is not full of rabbits. But in some circumstances, equation (ii) may be an adequate model of population growth, as in unialgal cultures during the logarithmic phase. The requirement that a model be stable over a

more extensive range than that of the intended application introduces a further dichotomy between the merits of equilibrium and non-equilibrium solutions.

4. To prevent equation (i) from blowing up, we can make the growth rate density dependent. The classical trick is to let

$$dN/dt = rN(1-N/K)$$

(iii)

The new term K is loosely called the "carrying capacity", but is really a mathematical artifice. In some unspecified way, it can be taken to represent light or turbulence or nutrients or any other factor which may control r. In equation (iii), r is now the maximum growth rate, r_{max}, and the realized growth rate is $= r (1-N/K)$. So when $N < K$, r is positive, when $N > K$, r is negative, and there is a stable equilibrium at $N^* = K$. Equation (iii) is known as the logistic, and was introduced to biology by Verhulst in 1838.

Following May (1976), equation (iii) can be written in dimensionless form by letting $N' = N/K$ and $t' = rt = t/T_R$, where $T_R = 1/r$ is the "characteristic return time". Then we have

$$dN'/dt' = N'(1-N')$$

which allows us to separate the factors regulating the magnitude of N^* (K only) from those which control its stability (only r). This is the basis of the well known distinction between r and K selection due to McArthur (1962).

5. In equation (iii), density dependence (1-N/K) operates instantaneously. A conventional way to introduce a time lag is to write

$$dN/dt = rN[1-N(t-T)/K]$$

(iv)

where T is again a mathematical artifice, rather vaguely thought of as "generation time". Regulation now depends on N at a time T earlier, and represents feedback. Equation (iv) provides a rich family of model population trajectories, which can range from monotonic damping (small rT) through damped oscilations ($T \approx T_R$) to limit cycles ($T > T_R$, or $rT > 1$), and so be used to caricature a variety of real time series of population abundance. But this is not the stage at which we should sit back with a virtuous smile, since we have yet to translate the results back to the original biological context. The back translation of the essentially arbitrary devices, K, T, etc is not a straight-forward matter. In equation (iii) for example, this procedure can only lead to the "biological" conclusion that K controls r, since the model provides no alternatives. If the experimental data remains opaque on this basis, we need to recast the biological question. If this step is successfully accomplished, a virtuous smile is briefly allowed! En passent, note that having eliminated the physics from equation (i) and its developments (by setting I and $E = O$), it has to be put back in again (as K) to satisfy biological intuition.

6. A rather different way of making r density dependent was devised by Monod (1950). He wrote

$$r = \frac{r_{max} S}{S + Ks} \quad (v)$$

where S is the substrate concentration and Ks is the half saturation coefficient. We see that the graph of r on S must pass through the origin, which is biologically unrealistic. Nevertheless, like equation (ii), this model is a powerful tool in specific circumstances. Droop (1968) persuaded r to cross the x-axis at positive x by writing $r = r_{max}(1-K_Q/Q)$. Here K_Q is the minimum permissible cell quota for a limiting resource, and Q is the cell quota-cf equation (iii). The virtues of these and other functional forms of nutrient limitation are obviously context dependent. If grazing and regeneration processes allow algae to operate permanently at r_{max}, there is no real need to incorporate this kind of mechanism into a model. Sensitivity tests allow such decisions to be made, and are an integral part of the "let's pretend" step.

7. The contributions of Monod and Droop are just two well-known examples of how more realistic functional relations can be added step by step to very simple models. They can both be viewed as responses to the limitations of the elementary equations from which they stem, limitations which are revealed by the back translation process. They also illustrate the interplay between theoretical and empirical studies of population dynamics, since it is the models which directly suggest what new kinds of information may be required in pursuit of more adequate descriptions of population regulation.

REFERENCES

Lewis R., 1993. Quart. Rev. Biol., 68: 547-555.

Stewart I., 1989. Does God Play Dice? The Mathematics of Chaos, (Blackwell).

May R.M.(ed.), 1976. Theoretical Ecology. Principles and Applications, (Blackwell).

MacArthur, R.H., 1962. Proc. Natl. Acad. Sci., 48: 1893-1897.

Monod J., 1950 Ann. Hist. Pasteur Lille, 79: 390-410.

Droop M.R., 1968. J. Mar. Biol. Ass., U.K., 48: 689-733.

A MODEL OF THE EFFECT OF CYST GERMINATION ON THE DEVELOPMENT OF THE *GYMNODINIUM CATENATUM* POPULATIONS ON THE WEST COAST OF THE IBERIAN PENINSULA

Juan Blanco

Usually when trying to model harmful algal blooms, some aspects of the biological system or the biological-physical coupling are not known. This may be due to a clearly defined gap -in which case it is possible to focus additional research on the subject- or, in some other cases, to a lack in wider areas of knowledge. In this latter case, we have to decide which one of the multiple choices to study or at least which one to study first. Simple -and in most cases speculative- models may help in making this decision.

Gymnodinium catenatum dynamics on the Atlantic coast of the Iberian peninsula and more concretely in Galicia, is one of these cases and we have developed a simple model of cyst germination along the coast in order to have an idea of the possible importance of this mechanism of water inoculation. There is some controversy about the source of motile cells used to inoculate the water masses in the area. Some hypothesize that the populations are initiated by cysts (Figueiras and Fraga, 1990) and others suggest that the motile cells are always present in the water mass (Fraga et al., 1990,1993).

The resting cyst population in the sediments of the area studied is not very abundant (Blanco, 1988; Bravo and Anderson 1994). If we consider an enclosed area, germination, even of the top several centimetres of sediment, is not enough to explain the local increases of motile cell populations. This situation opens two possibilities: a) they are not important, or b) a different mechanism exists, and if we found it we will have an idea of the actual importance of the resting stages.
In the case of the Iberian Peninsula several papers have suggested that *G. catenatum* populations are associated with a warm water mass(sometimes referred to as poleward current) that during the summer or autumn goes to the north, and reaches the Galician coast(Fraga et al., 1990,1993;Moita, 1993).

We hypothesize that the warm water mass affects the shelf bottom in a way that is proportional to the downwelling intensity during an upwelling-downwelling cycle, assumed to be 3-7 days. The effect of the warm water mass on the sediment is to produce cyst germination (at rates given in Bravo et al. 1994) and the subsequent incorporation of the motile cells to the water mass. We also assumed very conservative concentrations of cysts in the sediments, and that only the cysts in the top millimetre of sediment can germinate.

When we compare the estimated development of the population in the foremost area of the warm water mass due to this kind of process to the possibility of a small (1 cell/m^3) motile phase inoculation in the early progression of the water mass, assuming the growth rate to be constant (0.3 day^{-1}), final cell concentrations are higher in the case of cyst inoculation, lending support to the view that inoculation from the sediment cannot be discarded as a fundamental mechanism, and that it too must be studied.

If the hypothesis on which this model is based were true, then an interesting aspect of the dynamics would emerge that would have great importance when trying to obtain a predictive model: the final cell concentration would be very dependent on the phase and period of the upwelling-downwelling cycles and, because of that, it would be very difficult to obtain a predictive model.

References

Bravo,I. and Anderson, D.M. 1994.- The effects of temperature, growth medium and darkness on excystment and growth of the toxic dinoflagellate *Gymnodinium catenatum* from northwest Spain. Journal of Plankton Research, 16(5): 513-525.

Figueiras, F and Fraga, F., 1990.- Vertical nutrient transport during proliferation of *Gymnodinium catenatum* GRAHAM in the ría de Vigo. In: Granèli, E., B. Sundström, L. Edler and D.M. Anderson (eds.), Toxic Marine Phytoplankton. Elsevier, New York, 554 pp.

Fraga, S., Reguera, B. and Bravo, I., 1990.- *Gymnodinium catenatum* bloom formation in the Spanish rías. In: Granèli, E., B. Sundström, L. Edler and D.M. Anderson (eds.), Toxic Marine Phytoplankton. Elsevier, New York, 554 pp.

Fraga, S. Bravo, I. and Reguera, B., 1993.- Poleward surface current at the shef break and blooms of *Gymnodinium catenatum* in the ría de Vigo (NW Spain). In: Smayda, T. and Y. Shimizu (eds.), Toxic Phytoplankton Blooms in the Sea. Elsevier, New York, 952pp.

Moita, T., 1993.- Development of toxic dinoflagellates in relation to upwelling patterns off Portugal. In: Smayda, T. and Y. Shimizu (eds.), Toxic Phytoplankton Blooms in the Sea. Elsevier, New York, 952pp.

NOTES ON PATCH DYNAMICS AND ASSOCIATED PROBLEMS

Percy Donaghay

There are at least 35 hypotheses about the patchiness of plankton organisms, and none of them can be rejected or proved. All are fully 3-dimensional problems. Retention in patches may derive solely from biological mechanisms, and thus features such as the swimming speeds of dinoflagellates become critical.

Furthermore, in this example, the uncertainty of prediction may be dominated by variations in the swimming speed, so that not only do we need to know its mean value, but also how it varies.

There is a growing recognition that the vertical distribution, abundance, and behavior of motile plankton is not only related to the coarse scale (meters to tens of meters) distribution of parameters, but also to the fine scale (cm to tens of cm) features of the environment, including its biological components. Direct measurements of physical, chemical, and biological parameters are needed, on scales relevant to organisms and processes, as a first step to defining the scales of interest for modelling the in situ population dynamics of species of interest.

Reference

Donaghay P.L., H.M. Rines and J.McN. Sieburth. 1992. Simultaneous sampling of fine scale biological, chemical, and physical structure in stratified waters. Arch. Hydrobiol. Beih. Ergebn. Limnol., 36: 97-108.

Modelling the Shelf Break Ecosystem.

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ABSTRACT

Interactions between vertical mixing and biological production in a shelf sea environment have been investigated through the development of a one dimensional model capable of simulating the dynamics of suspended particulate matter (SPM) and the evolution of the vertical distribution of phytoplankton. The model, which employs turbulence closure physics, cell-quota threshold limitation biology (Sharples and Tett, 1994), and deposition and resuspension of SPM from a bottom 'fluff' layer (Jones et al., 1994), has been used to simulate seasonal cycles of chlorophyll on the Malin Shelf, to the west of Scotland. Model results predict a spring phytoplankton bloom shortly after the water column becomes stratified in April, which continues until nutrient levels in the surface waters become depleted. As the thermocline becomes weaker in autumn, a smaller bloom occurs lasting until the water column becomes completely mixed during winter. Vertical profiles of SPM show periodic entrainment from the seabed, with material confined to the bottom 10m over most the of annual cycle due to weak tidal currents.

Comparisons of model results with observational data of chlorophyll, nutrients and temperature show good qualitative agreement. No data exists to compare SPM concentrations with model output. Despite the numerous research cruises undertaken in this area, the phytoplankton spring bloom event has not yet been fully observed. It is suggested that either these discrete observational programs have missed the periods of highest phytoplankton biomass or that the spring bloom is subject to heavy grazing pressure in this region.

References

Jones, S.E., C.F. Jago and J.H. Simpson, 1994. Modelling suspended sediment dynamics in tidally stirred and periodically stratified waters: progress and pitfalls. Physics of Estuaries and Coastal Seas, in press.
Sharples, J. & Tett, P. 1994. Modelling the effect of physical variability on the midwater chlorophyll maximum. Journal of Marine Research, 52, in press.

ECOLOGICAL MODELLING IN COASTAL WATERS: TOWARDS PREDICTIVE PHYSICAL-CHEMICAL-BIOLOGICAL SIMULATION MODELS.

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ABSTRACT

A simple, but general, simulation model is specified according to the state-of-the-art within phytoplankton modelling: Process representations are based upon prevailing theoretical and empirical representations given in the literature, and a set of earlier published values of model coefficients that have demonstrated good fit to reliable observations was selected. The emerging phytoplankton model was then validated against data obtained from enclosure experiments with light-, N-, P- and Si-limitations. No tuning of the coefficients were applied as the purpose of this test was to estimate the predictability of the proposed model. The general standard deviations between model predictions and observations were on the range 0.04-0.36 and 0.13-0.42 for the nutrient and phytoplankton state variables respectively. Not surprisingly, these values are higher than those obtained in tuned simulations. Nevertheless, several characteristics such as growth rates and the balance between diatoms and flagellates were predicted by the model. The phytoplankton model was then set up and driven by a 3-dimensional physical model for the North Sea. The period February-June 1988 was simulated and forced with realistic topography, meteorological data, riverine freshwater and nutrient input. Simulated development in nutrients, diatoms and flagellates are presented with references to actual observations and the *Chrysochromulina polylepis* bloom in 1988. Several important characteristics, such as the timing of two diatoms blooms in March and April and one flagellate bloom in May together with vertical and horizontal distributions of nutrients, were simulated quite realistically without any tuning of the model to the actual observations. The present simulations support the general idea that flagellates in the coastal areas of the North Sea are stimulated by anthropogenic nutrients, but more specifically that a strong flagellate bloom in the Kattegat-Skagerrak area, corresponding to the observed *C. polylepis,* was stimulated by such nutrients in May 1988. Although the model should be improved before it is applied in a management context, the potential of using such models is demonstrated.

DYNAMIC MODELLING OF PHYCOTOXIN KINETICS IN BENTHIC INVERTEBRATES

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ABSTRACT

Modelling the uptake and detoxification kinetics of phycotoxins in benthic invertebrates is discussed and illustrated by a case study involving blue mussels (*Mytilus edulis*) in the lower St. Lawrence estuary in eastern Canada. A dynamic model was fit to empirical data acquired during a study of differential responses of mussels transplanted from sites characterized by differing history of exposure to toxigenic blooms responsible for paralytic shellfish poisoning (PSP). Although it is difficult to collect sufficient data to calibrate complicated models, it appears that one- and two-compartment models are fully adequate for this type of modelling. Measuring phycotoxin levels in shellfish can be a useful and cost-effective way to monitor phytoplankton toxicity in the water column, since continuous filtration by shellfish provides an integrated estimate of the toxin levels to which they are exposed.

MODELING THE PRIMARY PRODUCTION IN THE NORTH SEA USING A COUPLED 3 DIMENSIONAL PHYSICAL CHEMICAL BIOLOGICAL OCEAN MODEL

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ABSTRACT

A coupled 3-dimensional physical-chemical-biological model system, is implemented and for the first time applied to study mass and volume transports and primary production throughout the North Sea. The model is run twice for 1985 with specified (for the North Sea Task Force) time series of riverine and atmospheric inputs of nutrients, and also with these nutrient inputs reduced with 40 and 50 % respectively. Especially the evolution of the chemical and biological variables in the two situations is studied.

The model output agrees quite well with the general quantitative and qualitative knowledge of the total yearly production. The intercomparison with some salinity profiles also indicates that the model fairly well handles the large scale circulation and vertical mixing. Estimates for the transport of excess nutrients to Skagerrak and Kattegat in the highly pulsating Jutland coastal current are given, and demonstrates the need for such models for calculating transport of matter from one area to another. Significant reductions in both primary production and transport of matter is seen from comparisons between the two runs.

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COMPLEXITY

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ABSTRACT

Complexity is presented as a property of models, not of systems. It is shown that the complexity of a system is not a well- defined quantity, and that the complexity implicit in a model is connected to the amount of information about the system that the model is able to process.

ANNEX III: INSTRUCTIONAL MATERIAL FOR PC EXERCISES

USING UCNW BIOLOGICAL MODELS ON MACINTOSH COMPUTERS

Paul Tett

Algal bloom models - an overview

- The basic components of a physical-biological model.

- Seasonal cycle models provide context for short-period algal bloom models? The seasonal models must include water-column, and in some cases, sediment mineralization processes. In estuaries and upwelling regions, must take account of lateral inputs of buoyancy and nutrients.

- Algal bloom models need only simulate periods of a few days, so do not need to include remineralization; they must, however, include an adequate description of the response of water-column structure to short period (including sub-diurnal?) changes in physical forcing, and of x-z circulations that may transport and concentrate biomass.

- Physical frameworks can be (i) fixed compartments with time-varying exchanges taken from separate physical model or observations; (ii) dynamically coupled, using either (a) slab-mixing or (b) turbulence closure for vertical structure; (iii) particle-tracking.

- Optical models must include self-shading effects.

- Is there an agreed, general-purpose algal model that can be used to provide a basis for bloom simulation? Should it include sub-diurnal effects (such as the unlinking of photosynthesis and nutrient uptake from population growth)?

- Biological component of bloom model should: (a) allow vertical motion; (b) include one or several species of alga? (c) include life history e.g. *Phaeocystis*, *Alexandrium*? (d) parameterise grazing from mesozooplankton and planktonic protozoans? (e) deal with postbloom - e.g. development of toxicity or of harmful organic material (which may require sedimentation submodel)?

Familiarity with "windows" is assumed.

1. Open the 'Biological models' folder.

2. 'Double-click' the appropriate icon; the program will then start to run. Respond to prompts as necessary. At the end of use, the program will return control to the operating system.

Each simulation outputs, or can be directed to output, an ascii text file (with comma-separated values) to the folder containing the application. These files can be read into standard spreadsheets, such as EXCEL.

The following are available:

   CULTURE: a menu-driven simulation of the growth of a single species of alga in laboratory culture, You can alter the algal and culture parameters interactively. The program contains a complete explanation of the model used.

   POLYCULTURE: a menu-driven simulation of the growth of 5 competing species of algae in laboratory culture. You can select which species to use, and change culture parameters, interactively. The program contains some explanations.

   L3VMP 94: a batch-job simulation of the microbiological-detritus model, with 2-layer physics and sediment resuspensión, of Tett (1990, Proudman Oceanographic Laboratory report 14), forced by

sine functions for meteorological and tidal variables. Model parameters cannot be changed, but initial and forcing conditions can be altered by editing the (ASCII) text files L3-INIT.TEXT and L3-PARAM.TEXT (which must be in the same folder as the application icon).

These applications were compiled from Pascal source code using the THINK Pascal programming environment. Source code is available for L3VMP. Model parameters can be changed by editing the source code file L3-PARAMETERS (which contains a Pascal **unit** of the same name) and recompiling. In this case it is possible to run the program from within THINK. Consult P. Tett for details.