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MODÈLE
MICROBIOLOGIE
PHYTOPLANCTON
REMINÉRALISATION
GOLFE DE FOS
ÉCOSYSTÈME CÔTIER
MÉDITERRANÉEN

RÉSUMÉ – Dans l'optique d'une meilleure compréhension du devenir de la matière organique lors de son transit en zone côtière, une nouvelle approche de type numérique a été tentée dans une baie du sud de la France, le Golfe de Fos, largement ouvert sur la Méditerranée et par lequel transite une partie des eaux rhodaniennes. Le modèle décrit les principaux processus physiques de circulation estuarienne, de stratification thermohaline et de remise en suspension, l'ensemble étant couplé à des processus biologiques de croissance des microalgues, Bactéries et Protozoaires sous le contrôle des sels nutritifs et de la lumière disponible, ainsi que des processus de reminéralisation dans la colonne d'eau et le sédiment. Des simulations ont permis de mettre en évidence : 1) le rôle important que joue le golfe de Fos dans le recyclage des nutrients en provenance du continent, avant leur exportation en direction du large ; 2) l'intervention des processus de remise en suspension, d'une part, dans la limitation de la lumière disponible pour la photosynthèse et, d'autre part, dans l'exportation de matière organique contenue dans les sédiments locaux ; et 3) la variabilité haute fréquence qui caractérise ces systèmes peu profonds et largement forcés par le vent.

MODEL
MICROBIOLOGY
PHYTOPLANKTON
REMINERALISATION
GULF OF FOS
MEDITERRANEAN COASTAL
ECOSYSTEM

ABSTRACT – Numerical modelling provides a means of studying the processes that cycle nutrients and organic material as they pass through the coastal zone on their way from the land to the sea. The Gulf of Fos is an embayment on the Mediterranean coast of France, receiving part of the discharge of the Rhône river. We discuss the design of a simple numerical model for the Gulf. The model couples the physical processes of estuarine circulation, density stratification, and particulate resuspension, with the microbiological processes of light – and nutrient – controlled growth of pelagic micro-algae, bacteria and protozoans, and the detrital remineralisation of nutrients in water-column and sediment. Simple numerical experiments are used to show (1) the rôle of the Gulf in cycling land-derived nutrients before they reach the open sea ; (2) the importance of particulate resuspension in controlling light availability for photosynthesis and the export of organic material ; and (3) the high frequency of variability in this shallow, wind-forced system.

INTRODUCTION

The coastal zone moderates the interaction between land and ocean (Holligan 1990). The inner coastal zone is most subject to terrestrial influence and to extreme marine effects such as stirring by waves, and plays an important role in ameliorating the consequences of anthropogenic discharge. It is thus important to understand the main processes that control the functioning of shallow-water marine ecosystems. It is also important to understand the links amongst these processes, which include water transport, sediment dynamics, and the biological cycling of material. Numerical models provide tools for studying such links, and data to

parameterise and test these models can more easily be acquired in shallow waters than in the deep ocean. In this paper we describe a Mediterranean coastal embayment, the Gulf of Fos, near Marseille, and discuss the factors that led us to choose a particular representation of the physical and microbiological processes controlling the cycling of carbon and nitrogen in this bay. Our case for focusing on the early steps in the development and testing of a coupled model is that these steps are part of the scientific process of forming and testing hypotheses, and are thus useful in developing ideas about ecosystem function, even if the model does not, at this stage, make accurate predictions.

THE GULF OF FOS

The Gulf of Fos is situated on the Mediterranean coast of France at 43.25°N, 4.56°E. It is a semi-enclosed shallow area, influenced by freshwater from the Rhône river and occasionally from the Etang de Berre (Fig. 1). Mean depth is 8 m and the approximate area is 45×10^6 m². A navigation channel divides this area into two parts : the western Carteau Cove, dominated, since 1983, by shellfish farming ; and the north-eastern part, bordered by an important industrial chemical complex.

The discharge of freshwater into the Gulf by the Rhône Canal was estimated by Arfi (1989) as being 1 % of the total Rhône flow. This flow is, however, highly variable with time. During 1986, the mean flow in the Rhône at Beaucaire, near Arles, was 1700 m³ s⁻¹ with spring peaks of up to 6300 m³ s⁻¹ (Fig. 2 A).

The mean tidal range in this region is less than 0.3 m, so tidal forcing is weak, with typical velocities of order 10^{-2} m s⁻¹. Instead, winds provide the main input of kinetic energy. The mean wind speed in 1986 was about 5 m s⁻¹, mainly from the NW and SE (Fig. 2 B), and only 4 % of days were without wind. Physical modelling and current meter studies (Grenz, 1989) show the importance of wind-driven circulation within the Gulf. Salinity profiles sometimes show strong salinity layering (Fig. 3). Salinometers moored in Carteau Cove from 18-29 October and 3-17 December 1993, and recording at 15 minute intervals, showed surface-bottom salinity differences exceeding 4 psu during 30 % of the time.

The sediments are muddy sands (25 % particles less then 63 μm) and sandy muds (50 to 90 % < 63 μm) depending on location and depth (Grenz in Massé, 1993). Water content varies between 35 and 60 % of total wet weight. Organic content in the upper sediment varied over space and time between 2 % and 15 % of ash-free dry weight, with molar C : N ranging from 15 : 1 to 25 : 1 (Plante-Cuny *et al.*, in press).

When winds are strong, stirring suspends inorganic and organic particles (Grenz, 1989). This suspended particulate material (SPM) could be trapped within the Gulf by the local circulation, or exported to the open sea. Conversely, during calm periods, the Gulf could act as a trap for sedimenting material. It seems likely that the alternation of resuspension and deposition is important in controlling production and consumption in the Gulf. Firstly, resuspension could enhances the microbial decomposition of organic detritus. Secondly, although no precise optical data are available, light availability for primary producers must be substantially reduced during periods of high SPM load.

The shallow, organic-rich, sediments of the Gulf sustain a high oxygen demand and nutrient release rate. Measurements during 1987 and 1988, by means of *in situ* benthic chambers, showed typical fluxes of – 2 to – 12 mmol O_2 m⁻² d⁻¹ and + 1.5 mmol nitrate + nitrite + ammonium (dissolved inorganic nitrogen, DIN) m⁻² d⁻¹. The oxygen fluxes represent sediment demand ; they are however less than total respiration because of daytime gross photosynthesis of + 11 to + 26 mmol O_2 m⁻² d⁻¹. The DIN flux, from the sediment to the water, could contribute up to 15 % of the
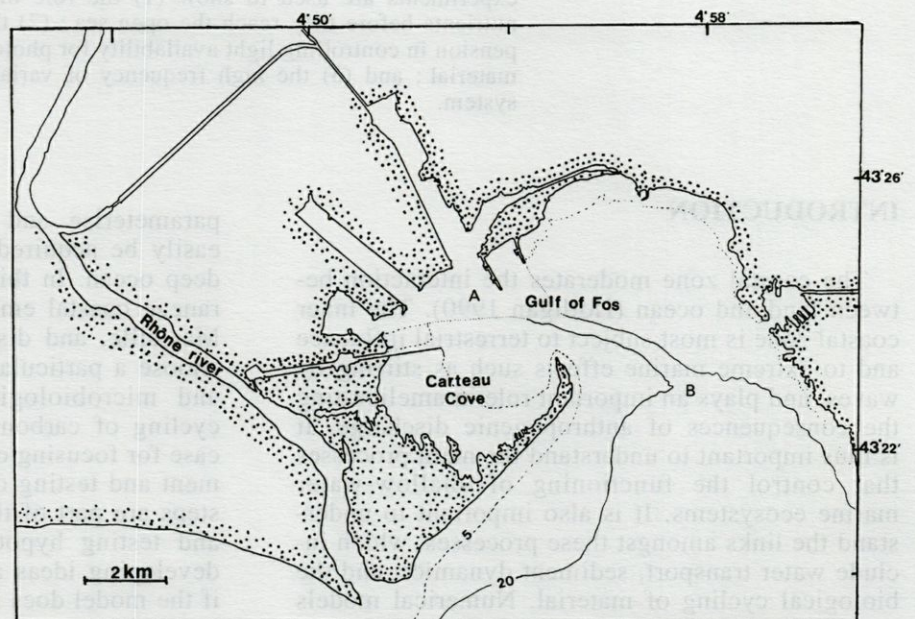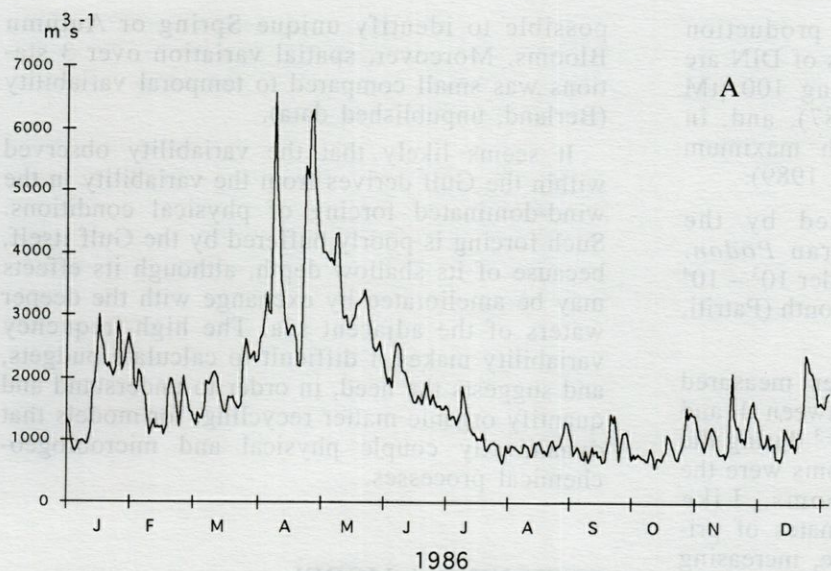

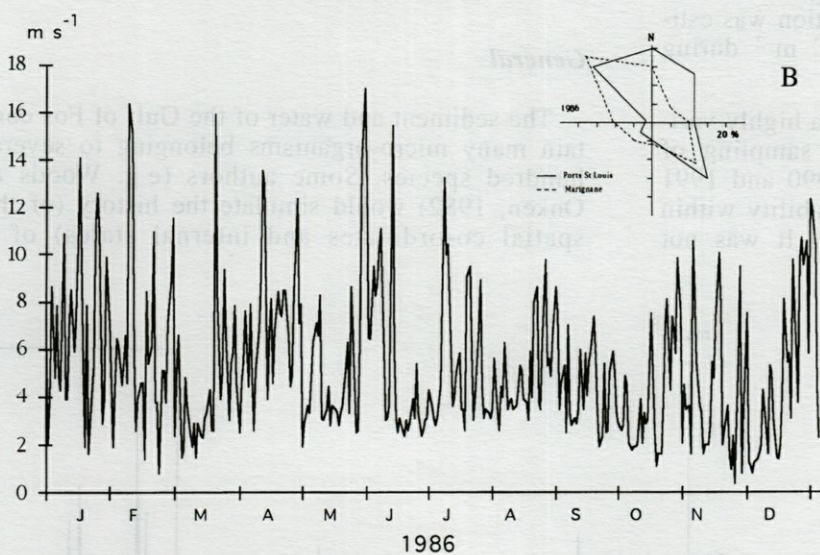Fig. 1. – Map of the Gulf of Fos and position of sampling stations A and B used in April 1991 for data in Figure 4.

Fig. 2. – A, Flow in the Rhône recorded at Beaucaire during 1986 (data from Compagnie Nationale du Rhône-Lyon). B, Wind speed (and directional rose) at Marignane during 1986 (data from Météo France).
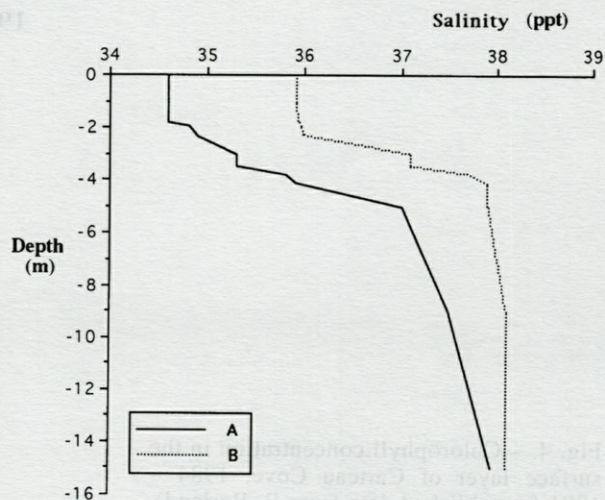

Fig. 3. – Profiles of salinity on 5 April 1991 ; for station positions see Fig. 1.

nitrogen requirement for primary production (Baudinet *et al.*, 1989). Other sources of DIN are the Rhône water, typically containing 100 µM nitrate (El Habr & Golterman, 1987), and, in winter, the Mediterranean sea, with maximum 5 µM nitrate (Cruzado & Velanquez, 1989).

Mesozooplankton are dominated by the copepod *Acartia* and the cladoceran *Podon*. Biomasses during 1980-81 were of order $10^3 - 10^4$ animals m^{-3}, depending on site and month (Patriti, 1984).

Water-column chlorophyll has been measured since 1984. Typical values were between 1 and 5 mg chl a m^{-3}, with up to 22 mg m^{-3} during the Spring Bloom of 1990 (Fig. 4). Diatoms were the main type of algae during blooms. Like chlorophyll concentrations, ^{14}C estimates of primary production were highly variable, increasing during Spring Blooms to 400 mg C m^{-3} d^{-1} (Folack *et al.*, 1989). Annual production was estimated as between 71 and 140 g C m^{-2} during 1984 (Folack, 1986).

As such data indicate, the Gulf is a highly variable environment. High frequency sampling of water column chlorophyll during 1990 and 1991 showed that there was as much variability within a month as during the entire year. It was not possible to identify unique Spring or Autumn Blooms. Moreover, spatial variation over 3 stations was small compared to temporal variability (Berland, unpublished data).

It seems likely that the variability observed within the Gulf derives from the variability in the wind-dominated forcing of physical conditions. Such forcing is poorly buffered by the Gulf itself, because of its shallow depth, although its effects may be ameliorated by exchange with the deeper waters of the adjacent sea. The high-frequency variability makes it difficult to calculate budgets, and suggests the need, in order to understand and quantify organic matter recycling, for models that dynamically couple physical and microbiogeochemical processes.

DESIGNING A MODEL

General

The sediment and water of the Gulf of Fos contain many micro-organisms belonging to several hundred species. Some authors (e.g. Woods & Onken, 1982) would simulate the history (of the spatial co-ordinates and internal states) of a
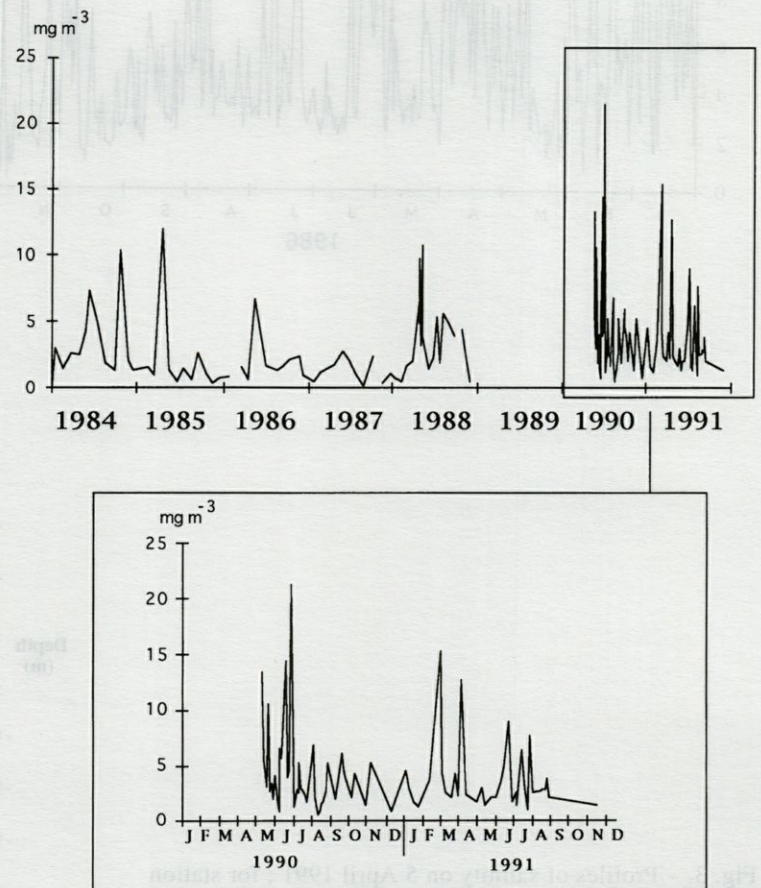

Fig. 4. – Chlorophyll concentration in the surface layer of Carteau Cove, 1984 – 1991 (unpublished data from B. Berland).

sample of typical individuals. Nevertheless, there is, as yet, no evidence that the extra computing costs of such an exercise are justified by substantially better predictions. The conventional approach, which we adopt here, is to group organisms. Each group is described by a time-varying mean state. Rates of formation, transformation and removal are specified by continuous functions of the mean state, and movements are forced by average water motions.

The fundamental problem in designing a biological model is thus to decide how to group the organisms. If the bulking is taxonomic, should it take place at the level of species, classes, phyla or kingdoms ? How many state variables should be used to describe each bulked entity ? Should values of these state variables be calculated at the nodes of a two – or three – dimensional mesh, or averaged over large parts of the Gulf ? Are the mean physical transports best described by applying equations for advection and turbulent diffusion at each node, or by computing exchanges across compartment boundaries ? Should the compartment boundaries be fixed or dynamic ?

Such questions are not easily answered. Nevertheless, a general guide is given by Occam's razor and Popper's epistemology of science (Popper, 1972) : add complexity only when forced by circumstances, but strive to discover such circumstances. For example, our initial physical model did not include exchange between the Gulf and the Mediterranean. Compared with observations, the model predicted water temperatures that were too high in summer, and too low in winter. Adding marine exchange resulted in better agreement (Fig. 5).

This emphasis on avoiding unnecessary complexity led to a model in which :

• variables were averaged horizontally over the Gulf, and vertically over one or two water-column layers of variable thickness, and one sediment layer of constant thickness ;

• physical transports were represented by exchanges between the layers, and between them and the sea, the vertical exchanges including upwelling, entrainment and particulate sinking in the case of the water column, and deposition/resuspension of particulates, and diffusional exchange of solubles, in the case of the sediment-water interface ;

• particulate material was divided into three types : inorganic particulates not subject to biological gains or losses but influencing photosynthesis through effects on water turbidity ; organic detrital material subject to slow mineralisation by associated heterotrophic micro-organisms ; and 'microplankton' including fast-recycling micro-heterotrophs as well as phytoplankton ;

• organic particulates were quantified in terms of carbon and nitrogen, and, in the case of the microplankton, as chlorophyll ; combined nitrogen, was conserved by cycling through ammonium and nitrate ; and the production or consumption of organic carbon, and the oxidation or reduction of nitrogen, were associated with changes in dissolved oxygen.

The choice of 3 elements (C,N and O) and two (fast and slow cycling) types of organic particulate, coupled with a simple, boundary-layer physical framework, may be contrasted with the
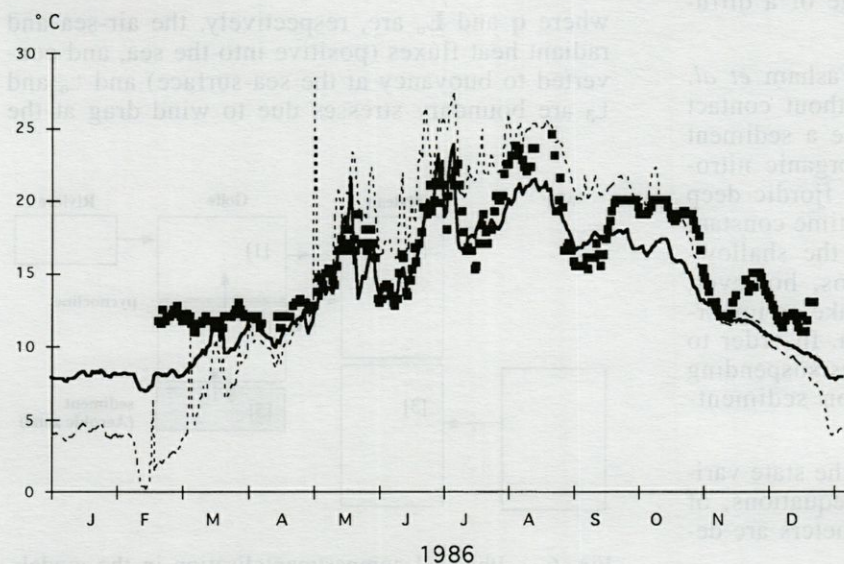

Fig. 5. – Surface temperatures in the Gulf of Fos during 1986. Dots correspond to values observed in Carteau Cove, the dashed line to model-prediction without circulation, and the solid line model-prediction with circulation.

plankton models of Anderson & Nival (1989), Fasham *et al.* (1990), and Ross *et al.* (1993). Anderson & Nival and Fasham *et al.* represent only one element (nitrogen) ; Ross *et al.* also include carbon. All three models explicitly include zooplankton amongst their 4 (Ross *et al.*, Fasham *et al.*) or 8 (Anderson & Nival) types of organic particulate.

Both Fasham *et al.* and Ross *et al.* used a simple physical framework. In the case of Fasham *et al.* this was an oceanic mixed layer with depth variation (and consequent entrainment) supplied as a forcing function. Ross *et al.* described fjordic hydrography by a three-layer structure with fixed compartment volumes and interface depths. Entrainment and diffusional exchanges were supplied as forcing functions. Anderson & Nival's model of a Mediterranean coastal pelagic ecosystem was driven by vertical turbulent diffusion, with time-constant but depth-varying eddy diffusivities. Biological concentrations were predicted at a series of grid points representing a vertical profile, rather than averaged over 1 or 2 boundary layers as in our case.

In none of these models was the biology dynamically coupled to the physics. Observations had shown highly variable density stratification in the Gulf of Fos, which is shallow compared with the systems described by the other models. We thus needed a physical model that allowed a switch from a vertically mixed to a layered water-column, and in which the interface between the layers was free to move as a result of physical forcing that also drove the biological processes through effects on nutrient supply and PAR. A boundary-layer physical model is computationally simpler than a diffusion model. It simulates the transport of water between surface – and bottom – mixed layers by anisotropic entrainment, which may be more realistic, in strongly mixed waters, than the vertically isotropic exchange of a diffusion model.

Finally, Anderson & Nival and Fasham *et al.* modelled deep-water ecosystems without contact with the benthos. Ross *et al.* include a sediment layer which mineralised deposited organic nitrogen and returned it to the overlying fjordic deep water by a first order process with a time constant of about 3 months. In the case of the shallow-water ecosystem of the Gulf of Fos, however, resuspended organic material may make an important contribution to remineralisation. In order to investigate this, we allowed processes suspending inorganic particulates also to act on sediment-layer detritus.

Table I lists the symbols used for the state variables, and Table II gives the main equations, of the model for the Gulf of Fos. Parameters are defined in Table III.

The physical model

The physical compartmentalisation is illustrated in Fig. 6. The first version of the model simulated only the column labelled "Golfe", omitting lateral exchanges. In this case the physics was that of the model L3VMP, as described by Tett (1990a), and was driven by two main processes : surface heating or cooling as a result of solar irradiance and air-sea heat exchange ; and the injection of turbulent kinetic energy (t.k.e.) into surface and bottom layers as a result of boundary stresses. Resulting changes in water-column potential energy and heat content brought about changes in layer temperature and thickness. An increase in, for example, the thickness of the surface layer due to greater wind stirring, resulted in the entrainment into the surface layer of water from the bottom layer. Bottom stress caused particulate resuspension when the stress exceeded a critical value, otherwise particulates were allowed to deposit. Solutes exchanged between pore water and water-column by a diffusional process scaled by an arbitrary parameter representing bioturbation.

The stratification model derives from the mixed-layer model of Kraus & Turner (1967), as modified to include tidal stirring by Simpson & Bowers (1984). Clarke (1986) provided the two-layer algorithms. The potential energy anomaly of a two layer system is defined by :

$$[1] \qquad F = - g \cdot \Delta r \cdot h_1 \cdot (d - h_1)/2$$

where Δr is the density difference (≤ 0) between the two layers. $F = 0$ when the water column is well mixed, and < 0 under stratified conditions. In the absence of salinity variation, changes in the anomaly are given by

$$[2] \qquad dF/dt = - (q + E_0) \cdot d \cdot g \cdot a/(2 \cdot c) + f_0 \cdot |V| \cdot f(t_0) + f_3 \cdot |U| \cdot f(t_3)$$

where q and E_0 are, respectively, the air-sea and radiant heat fluxes (positive into the sea, and converted to buoyancy at the sea-surface) and t_0 and t_3 are boundary stresses due to wind drag at the
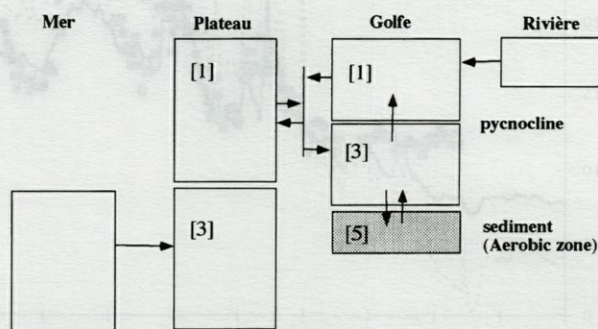

Fig. 6. – Physical compartmentalisation in the model.

Table I. – State, forcing and main intermediate variables.

Symbol	Description	Units
State variables		
A	Concentration of inorganic particles	mg m^{-3}
B	Concentration of microplankton carbon	mmol C m^{-3}
C	Concentration of detrital carbon	mmol C m^{-3}
h	Layer thickness	m
I	PAR irradiance	μE m^{-2} s^{-1}
M	Concentration of detrital nitrogen	mmol N m^{-3}
N	Concentration of microplankton nitrogen	mmol N m^{-3}
O	Concentration of dissolved oxygen	mmol N m^{-3}
NH$_S$	Concentration of dissolved ammonium	mmol N m^{-3}
NO$_S$	Concentration of dissolved nitrate	mmol N m^{-3}
t	Time	d
X	Chlorophyll concentration*	mg m^{-3}
Φ	Potential energy anomaly†	J m^{-2}
θ	Temperature	°C
σ	Salinity	psu

* not independent - function of B and N in layer
† not independent - function of θ, σ and h over water-column layers

	Forcing variables	
D	Elevation rate due to freshwater discharge	m d^{-1}
E$_0$	Sea-surface solar irradiance (all wavelengths)	W m^{-2}
G	Mesozooplankton grazing pressure	0.2 d^{-1}
q	Air-sea heat flux	W m^{-2}
^{tide}U	Maximum tidal current speed	0.01 m s^{-1}
V	Wind speed	m s^{-1}

	Intermediate variables	
E	Entrainment velocities between layers	m d^{-1}
Q	Nutrient quota, N/B	mmol N (mmol C)$^{-1}$
u	Microplankton nutrient uptake rate	mmol N (mmol C)$^{-1}$ d^{-1}
W	Pycnocline elevation rate due to circulation	m d^{-1}
w	Particle sinking speed	m d^{-1}
λ	PAR attenuation coefficient	m^{-1}
μ	Microplankton growth rate	d^{-1}
τ	Boundary stresses	kg m^{-3} s^{-4}

sea surface and tidal and other movements at the sea-bed. $|V|$ gives the absolute wind speed ; because $t_o = {}^{air}p \cdot k_0 \cdot V^2$, the intensity of wind stirring is proportional to V^3. Likewise, the intensity of bottom stirring is proportional to U^3, where, in the original version for North-West European shelf seas, U was the maximum tidal velocity.

Tides are weak in Fos, but wind effects can easily reach the sea-bed in these shallow waters. Thus, we used algorithms from CERC (1974, in Railland, 1991) to compute the additional bottom stress (and consequent t.k.e. injection and particulate resuspension) due to the orbital motion of wind-waves. The joint velocity became :

$$U = \sqrt{({}^{tide}U^2 + {}^{orb}U^2)}$$

where ^{orb}U is the horizontal component of the orbital velocity at the sea-bed.

In our initial 1-site model, simultaneous solution of equations [1] and [2], starting from known initial conditions, predicted $\Delta h_1/\Delta t$ and thus the vertical entrainment velocities E defined in Table II. As already mentioned, the 1-site model failed to predict water temperatures accurately, so we added the circulation shown in Fig. 6, which includes an additional water column ("Plateau") in the Gulf of Lions, and allowed for the effects of freshwater on potential energy in equations [1] and [2] (see Table II). The landwards boundary conditions included a varying discharge of freshwater, which was assumed to be immediately mixed throughout layer [1] of the "Golfe" water-column. Sea-water was introduced as a bottom wedge ; the resulting upwards displacement of the pycnocline was opposed by turbulence in the surface layer, which entrained salt into the surface layer. An entrainment multiplier, computed from

Table II. – Main equations of the model.

The equations are given in two versions. The generalized version is for a mixed water-column and without lateral exchanges; subscripts are mostly omitted. In the detailed equations for stratified conditions, purely numeric subscripts refer to the "Golfe" water column. Layers in adjacent water-columns have complete subscripts. Fig. 7 shows column names and layer numbers. See Tett (1990a) for details of sediment processes, boundary exchanges, and functions not given in full.

Physical model

Structure and transports

h_1, h_3 : thicknesses (m) of layers above and below pycnocline;

d : total depth of watercolumn : $d = h_1 + h_3$

$E_{1,3}$, $E_{3,1}$: 'entrainment velocities' (m d^{-1}), into layer [1] from [3], or *vice versa* :
$$E_{1,3} = \Delta h_1/\Delta t : \Delta h_1 \geq 0 \text{ and } h_1 \leq d; = 0 : \Delta h_1 < 0 \text{ or } h_1 = d;$$
$$E_{3,1} = \Delta h_3/\Delta t : \Delta h_3 \geq 0 \text{ and } h_3 \leq d; = 0 : \Delta h_3 < 0 \text{ or } h_3 = d;$$
$\Delta h/\Delta t$ evaluated by simultaneous solution of equations for potential energy, salinity and temperature.

$E_{3,5}$: sediment erosion velocity (m d^{-1}), the rate at which the water column entrains sediment: a function of tidal and wind-wave stirring at the sea-bed; see also text.

f^d : fraction of sinking material that is deposited, a function of tidal and wind-wave stirring.

W : rate of uplift (m d^{-1}) of pycnocline due to salt wedge intrusion into "Golfe" column:
$$W = m_E \cdot (\sigma_{plateau[1]} - \sigma_1) \cdot D$$

Suspended (fine inorganic) sediment : A mg m^{-3}

$$dA/dt = (E_{3,5} \cdot A_5 - f^d \cdot A_{w} \cdot A)/d$$
$$dA_1/dt = (E_{1,3} \cdot (A_3 - A_1) - {}^{A}w \cdot A)/h_1$$
$$dA_3/dt = (E_{3,5} \cdot A_5 + E_{3,1} \cdot (A_1 - A_3) + {}^{A}w \cdot (A_1 - f^d \cdot A_3)/h_3$$

No lateral exchange of this sediment.

PAR, Photosynthetically Effective IrRadiance : I μE m^{-2} s^{-1} (mean over layer and 24 hr)

$$I = I_0 \cdot (1 - e^{-\lambda \cdot h})/(\lambda \cdot h)$$
I_0 : (photosynthetically active) irradiance at top of layer, 24 hr mean. For sea surface layer,
$$I_{0[1]} = m_0 \cdot m_1 \cdot m_2 \cdot E_0$$
For layer [3], $\qquad I_{0[3]} = I_{0[1]} \cdot e^{-\lambda_1 \cdot h_1}$

λ : diffuse attenuation coefficient (m^{-1}):
$$\lambda = {}^{SW}\lambda + A_\varepsilon \cdot A + X_\varepsilon \cdot X + C_\varepsilon \cdot C$$

Potential energy anomaly : Φ J m^{-2}

$\Phi = 0$ \hfill (mixed)

$\Phi = -g \cdot \Delta\rho \cdot h_1 \cdot (d - h_1)/2$ \hfill (stratified)

$$\Delta\rho = \rho \cdot (a \cdot (\theta_1 - \theta_3) - b \cdot (\sigma_1 - \sigma_3))$$
$$d\Phi/dt = -q \cdot d \cdot g \cdot a/(2.c) - g \cdot \Delta\rho \cdot W \cdot d/2 + \{stirring\};$$
$$\{stirring\} = 0 \qquad\qquad : \Phi = 0;$$
$$\{stirring\} = V^3 \cdot {}^{air}\rho \cdot f_0 \cdot k_0 + f(U) \cdot \rho \cdot f_3 \cdot k_3 \cdot 4/(3.\pi) \qquad : \Phi < 0.$$

where:

$f(U) = {}^{tide}U^3$ ("Plateau"), $= |U| \cdot ({}^{tide}U^2 + {}^{orb}U^2)$ ("Golfe", with wind-wave stirring).

^{orb}U: maximum wind-wave orbital velocity at sea-bed, from wind speed V and fetch and water column depth, using algorithms in Raillard (1991);
$$|U| = \sqrt{({}^{tide}U^2 + {}^{orb}U^2)}.$$

Salinity : σ psu

$d\sigma/dt = 0$ \hfill (mixed, no circulation)

$d\sigma_1/dt = (-D \cdot \sigma_1 + E_{1,3} \cdot (\sigma_3 - \sigma_1))/h_1$ \hfill (stratified, circulation)

$d\sigma_3/dt = (E_{3,1} \cdot (\sigma_1 - \sigma_3) - W \cdot (\sigma_3 - \sigma_{plateau[1]}))/h_3$ \hfill : $h_3 > 0$;

$\sigma_3 = \sigma_{plateau[1]}$ \hfill : $h_3 = 0$.

Temperature : θ °C

$$d\theta/dt = q/(\rho.c.d)$$
$$d\theta_1/dt = (q/(\rho.c) + E_{1,3}.(\theta_3-\theta_1))/h_1$$
(assumes that $\theta_{rivière} = \theta_1$)
$$d\theta_3/dt = (E_{3,1}.(\theta_1-\theta_3) - W.(\theta_3-\theta_{plateau[1]}))/h_3 \qquad : h_3>0$$
$$\theta_3 = \theta_{plateau[1]} \qquad : h_3=0$$

Biological model

Microplankton carbon biomass : B mmol C m^{-3}

$$dB/dt = (\mu - G - (^Bw/d)).B \qquad\qquad\qquad\qquad\text{(mixed)}$$
$$dB_1/dt = (\mu_1 - G - ((^Bw_1+D)/h_1)).B_1 + (E_{1,3}.(B_3-B_1))/h_1 \quad\text{(stratified, circulation)}$$
$$dB_3/dt = (\mu_3 - G - (^Bw_3/h_3)).B_3$$
$$+ (^Bw_1.B_1 + E_{3,1}.(B_1-B_3) - W.(B_3-B_{plateau[1]}))/h_3 \quad : h_3>0;$$
$$B_3 = B_{plateau[1]} \qquad\qquad\qquad\qquad : h_3=0.$$

B_w :(nutrient-dependent) sinking rate of microplankton: between 0 and 5 m d^{-1};
G : zooplankton grazing pressure (d^{-1}) on microplankton - supplied from observations;
μ : microplankton specific growth rate (d^{-1}):
$$\mu = f(Q) \qquad : f(Q) < f(I);$$
$$= f(I) \qquad : f(Q) \ge f(I).$$
where
$$f(Q) = \mu'_{max}.f(\theta).(1-(Q_{min}/Q))$$
$$f(I) = \alpha.I.^XQ^B-r^B$$
$Q = N/B$.
$^XQ^B$: microplankton chlorophyll:carbon ratio (mg chl (mmol C)$^{-1}$);
r^B : microplankton biomass-related respiration (d^{-1}):
$$r^B = r^B_0 + r.\mu \qquad : \mu \ge 0;$$
$$= r^B_0 \qquad : \mu < 0;$$
$f(\theta)$: Arrhenius-type function of temperature.

Chlorophyll concentration : X mg chl m^{-3}

$$X = {}^XQ^B.B$$
where
$${}^XQ^B = Q.(^XQ^N_{max}.Q^* + {}^XQ^N_{min}.(1-Q^*)$$
and $\qquad Q^* = (Q-Q_{min})/(Q_{max}-Q_{min})$

Detrital carbon concentration : C mmol C m^{-3}

$$dC/dt = ((1-\gamma).G + (^Bw/d)).B - (^Cr - (f^d.^Cw/d)).C + (E_{3,5}.C_5/d)$$
$$dC_1/dt = (1-\gamma).G.B_1 - (^Cr_1+ ((^Cw_1+D)/h_1)).C_1 + E_{1,3}.(C_3-C_1)/h_1$$
$$dC_3/dt = ((1-\gamma).G + (^Bw_3/h_3)).B_3 - {}^Cr_3.C_3$$
$$+ (^Cw_1.C_1 + E_{3,5}.C_5 - f^d.^Cw_3.C_3)/h_3$$
$$+ (E_{3,1}.(C_1-C_3) - W.(C_3-C_{plateau[1]}))/h_3 \qquad : h_3>0;$$
$$C_3 = C_{plateau[1]} \qquad\qquad\qquad\qquad : h_3=0.$$

^Cr : detrital C respiration rate (d^{-1}), function of temperature, oxygen, and detrital N:C ratio:
$${}^Cr = f(\theta).(^Cr_{max}.O/(O_{1/2,max}+O).f(M/C) + {}^Cr_{min}.O/(O_{1/2,min}+O))$$
where
$$f(M/C) = (1-(^MQ^C_{min}.C/M))^2$$

Detrital nitrogen concentration: M mmol N m^{-3}

$$dM/dt = ((1-\gamma).G + (^Bw/d)).N - (^Mr - (f^d.^Cw/d)).M + (E_{3,5}.M_5/d)$$
$$dM_1/dt = (1-\gamma).G.N_1 - (^Mr_1+ ((^Cw_1+D)/h_1)).M_1 + E_{1,3}.(M_3-M_1)/h_1$$
$$dM_3/dt = ((1-\gamma).G + (^Bw_3/h_3)).N_3 - {}^Mr_3.M_3$$
$$+ (^Cw_1.M_1 + E_{3,5}.M_5 - f^d.^Cw_3.M_3)/h_3$$
$$+ (E_{3,1}.(M_1-M_3) - W.(M_3-M_{plateau[1]}))/h_3 \qquad : h_3>0;$$
$$M_3 = M_{plateau[1]} \qquad\qquad\qquad\qquad : h_3=0.$$

^Mr : detrital N respiration rate (d^{-1}), function of temperature and detrital N:C ratio:
$${}^Mr = f(\theta).^Mr_{max}.f(M/C)$$

Microplankton nitrogen biomass: N mmol N m^{-3}

$dN/dt = u.B - (G + ^Bw/d).N$

$dN_1/dt = u_1.B_1 - (G + ((^Bw_1+D)/h_1)).N_1 + (E_{1,3}.(N_3-N_1))/h_1$

$dN_3/dt = u_3.B_3 - (G + (^Bw_3/h_3)).N_3$
$+ (^Bw_1.N_1 + E_{3,1}.(N_1-N_3) - W.(N_3-N_{plateau[1]}))/h_3$: $h_3>0$;

$N_3 = N_{plateau[1]}$: $h_3=0$.

u : microplankton nitrogen uptake rate (mmol N (mmol C)$^{-1}$ d^{-1}), given by
$u = NH_u + NO_u$
where superscripts **NH** and **NO** refer to ammonium or nitrate; the generalized uptake equation
is:
$u = u_{max}.(1-(Q/Q_{max})).(S/(S_{1/2}+S))$

Dissolved oxygen concentration: O mmol O m^{-3}

$dO/dt = (O_qB.\mu + O_qNO.NO_u).B - O_qNH.NH_r.NH_S - O_qC.C_r.C$
$+ (\{air\text{-}sea\ flux\} - \{sediment\ flux\})/d$

$dO_1/dt = (O_qB.\mu_1 + O_qNO.NO_{u1}).B_1 - O_qNH.NH_{r1}.NH_{S1}$
$- O_qC.C_{r1}.C_1 + (E_{1,3}.(O_3-O_1) + \{air\text{-}sea\ flux\})/h_1$

$dO_3/dt = (O_qB.\mu_3 + O_qNO.NO_{u3}).B_3 - O_qNH.NH_{r3}.NH_{S3} - O_qC.C_{r3}.C_3$

$+ (E_{3,1}.(O_1-O_3) - W.(O_3-O_{plateau[1]}) - \{sediment\ flux\})/h_3$: $h_3>0$;

$O_3 = O_{plateau[1]}$: $h_3=0$.

Ammonium concentration: NH_S mmol N m^{-3}

$dNH_S/dt = -NH_u.B - NH_r.NH_S + e.\gamma.G.N + M_r.C + (\{sediment\ flux\})/d$

$dNH_{S1}/dt = -NH_{u1}.B_1 - NH_{r1}.NH_{S1} + e.\gamma.G.N_1 + M_{r1}.C_1$
$+ (E_{1,3}.(NH_{S3}-NH_{S1}))/h_1$

$dNH_{S3}/dt = -NH_{u3}.B_3 - NH_{r3}.NH_{S3} + e.\gamma.G.N_3 + M_{r3}.C_3$
$+ (E_{3,1}.(NH_{S1}-NH_{S3}) - W.(NH_{S3}-NH_{Splateau[1]}) - \{sediment\ flux\})/h_3$:
$h_3>0$;

$NH_{S3} = NH_{Splateau[1]}$
$h_3=0$.

NH_r : ammonium nitrification rate (d^{-1}), function of temperature and oxygen concentration:
$NH_r = f(\theta).NH_{rmax}.O/(O_{1/2,nit}+O)$

Nitrate concentration: NO_S mmol N m^{-3}

$dNO_S/dt = -NO_u.B + NH_r.NH_S - (\{sediment\ flux\})/d$

$dNO_{S1}/dt = -NO_{u1}.B_1 + NH_{r1}.NH_{S1} + (E_{1,3}.(NO_{S3}-NO_{S1}))/h_1$

$dNO_{S3}/dt = -NO_{u3}.B_3 + NH_{r3}.NH_{S3}$
$+ (E_{3,1}.(NO_{S1}-NO_{S3}) - W.(NO_{S3}-NO_{Splateau[1]}) - \{sediment\ flux\})/h_3$:
$h_3>0$;

$NO_{S3} = NO_{Splateau[1]}$:
$h_3=0$.

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the difference (Δs) between model-predicted salinities in the surface layers of the "Golfe" and "Plateau" columns, coupled the entrained flux of sea water (**W**) to the freshwater discharge (**D**) into the Gulf :

[3] $W = m_E \cdot \Delta s.D$

Both the flux and the discharge are expressed per unit surface area of the Gulf, and are thus best understood as the rate of elevation of the pycnocline by the intruding salt wedge from the "Plateau" site (**W**) and the potential rate of elevation of the sea-surface in the Gulf due to the freshwater discharge (**D**). Since the simulated depth **d** of the "Golfe" water column remains constant, conservation of mass requires that the "Golfe" [1] layer exports water at **D + W** per unit area.

In the absence of data from the Gulf of Lions, the model was run to simulate seasonal cycles of water temperature and thermocline depth for the "Plateau" column, which was given a depth of 50 m. The seawards boundary condition was equivalent to a dilution of the deep water in the Gulf of Lions at about 2 % per day, by water of 10 °C and 38 psu in a Liguro-Provencal current (Massé, 1993) of constant properties.

Table III. – Parameter and initial values.

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physical structure

Surface area of Gulf of Fos and thus of "Golfe" column : 45×10^6 m^2.
d : mean depth of Gulf of Fos and thus of "Golfe" water-column : 8 m.
Depth of "Plateau" water-column: 50 m.
h$_5$: thickness of benthic (oxic sediment) layer in Gulf : 0.05 m.

exact or approximate physical constants

a : coefficient of thermal expansion of seawater (at 15°C and 35 psu): 0.00021 °C^{-1};
b : coefficient of haline contraction of seawater (at 15°C and 35 psu): 0.00078 psu^{-1};
c : specific heat of seawater : 3900 J kg^{-1} °C^{-1};
g : gravitational acceleration : 9.81 m s^{-2};
$^{air}\rho$, ρ : air and seawater densities : 1 and 1025 kg m^{-3};

other physical and optical parameters

A$_5$: concentration of fine inorganic sediment in benthic layer : 200 kg m^{-3}; [1]
f$_0$, f$_3$: efficiencies of surface, wind (0.0029 or 0.0020 [a]) and seabed, tidal (0.004) mixing; [2]
k$_0$, k$_3$: surface, wind (0.0014 or 0.0007 [a]) and seabed, tidal (0.0025) drag coefficients; [2]
m$_0$: 1.91 μE PAR per J total solar irradiance; [3]
m$_1$: optical coefficient (0.95) allowing for surface reflection; [3]
m$_2$: factor (0.37) correcting for near-surface deviations from exponential decay of light; [3]
A$_w$: sinking rate of fine inorganic sediment : 1.5 m d^{-1}. [1]
A$_\varepsilon$: attenuation cross-section of suspended inorganic sediment: 0.1 m^2 g^{-1}; [4]
C$_\varepsilon$: attenuation cross-section of organic detritus: 0.001 m^2 (mmol C)$^{-1}$; [5]
X$_\varepsilon$: attenuattion cross-section of microplankton: 0.02 m^2 (mg chl)$^{-1}$; [5]
SW$_\lambda$: attenuation coefficient due to clear coastal seawater : 0.10 m^{-1}; [4]

[1] : estimated by least-squares fit of model predictions to observed inorganic SPM.
[2] : Clarke, 1986, or [a] reduced from Clarke values in case of shallow water of Gulf.
[3] : Tett (1990b)
[4] : estimated by fitting model to North Sea data - Tett & Walne, submitted.
[5] : Tett (1990a)

microbiological parameters

e : excreted fraction of grazed and assimilated microplankton nitrogen : 0.5;
O$_{1/2,max}$: half-saturation constant for nitrogen-dependent detrital carbon respiration : 10 mmol dissolved oxygen m^{-3};
O$_{1/2,min}$: half-saturation constant for minimum detrital carbon respiration : 1 mmol dissolved oxygen m^{-3};
O$_{1/2,nit}$: half-saturation constant for ammonium oxidation: 30 mmol dissolved oxygen m^{-3};
Q$_{max}$: maximum microplankton nitrogen to carbon: 0.20 mmol N (mmol C)$^{-1}$;
Q$_{min}$: minimum microplankton nitrogen to carbon : 0.05 mmol N (mmol C)$^{-1}$;
O$_q$B : photosynthetic quotient for carbon assimilation : 1 mmol O (mmol C)$^{-1}$;
O$_q$C : respiratory quotient for detrital carbon : 1 mmol O (mmol C)$^{-1}$;
O$_q$NH : 'respiratory' quotient for nitrification : 2 mmol O (mmol N)$^{-1}$;
O$_q$NO : photosynthetic quotient for nitrate assimilation : 2 mmol O (mmol N)$^{-1}$;
M$_Q$C$_{min}$: minimum detrital nitrogen : 0.06 mmol N (mmol C)$^{-1}$;
X$_Q$N$_{max}$: maximum microplankton chlorophyll to nitrogen: 2.0 mg chl (mmol N)$^{-1}$;
X$_Q$N$_{min}$: minimum microplankton chlorophyll to nitrogen: 1.0 mg chl (mmol N)$^{-1}$;
r : factor relating microplankton respiration to growth rate: 0.6; [a]
r$^B_0$: microplankton biomass-related basal respiration : 0.04 d^{-1} ;
C$_{rmax}$: maximum (nitrogen-dependent) detrital carbon respiration at 20°C: 0.08 d^{-1}; [a]
C$_{rmin}$: minimum detrital carbon respiration at oxygen saturation & 20°C: 0.0005 d^{-1};
M$_{rmax}$: maximum relative rate of detrital nitrogen remineralization at 20°C: 0.06 d^{-1}; [a]
NH$_{rmax}$: maximum relative rate of ammonium oxidation at 20°C: 1.0 d^{-1};
S$_{1/2}$: half-saturation constant for nutrient uptake : 0.24 mmol ammonium m^{-3}, 0.32 mmol nitrate m^{-3};
u$_{max}$: maximum microplankton nutrient uptake rate : 1.0 mmol ammonium (mmol C)$^{-1}$ d^{-1}, 0.4 mmol nitrate (mmol C)$^{-1}$ d^{-1};
C$_w$: detrital sinking rate : 0.5 m d^{-1}; [b]
α : microplankton photosynthetic 'efficiency' : 0.07 mmol C (mg chl)$^{-1}$ d^{-1} (μE PAR m^{-2} s^{-1})$^{-1}$;
γ : fraction of grazed microplankton that is assimilated by zooplankton: 0.7; [a]
μ'_{max} : maximum microplankton relative growth rate at 20°C: 2.0 d^{-1};

Source : Tett (1990a) with [a] some modifications; detrital sinking rate [b] estimated for Gulf from least squares fit of model predicted to observed organic SPM.

Initial values of state variables for "Golfe"

$B_1 = B_3$: 1.0 mmol (organic) C m^{-3};

$C_1 = C_3$: 1.0 mmol (organic) C m^{-3};

C_5 : 1.5 kmol (organic) C m^{-3};

$M_1 = M_3$: 0.1 mmol (organic) N m^{-3};

M_5 : 0.093 kmol (organic) N m^{-3};

$N_1 = N_3$: 0.2 mmol (organic) N m^{-3};

$O_1 = O_3 = O_5$: 300 mmol O_2 m^{-3};

$NHS_1 = NHS_3$: 0.0 mmol (ammonium) N m^{-3};

NHS_5 : 10.0 mmol (ammonium) N m^{-3};

$NOS_1 = NOS_3$: 4.0 mmol (ammonium) N m^{-3};

NOS_5 : 10.0 mmol (ammonium) N m^{-3};

Dissolved concentrations in layer [5] refer to pore water, which made up 80% of volume in the layer.

The value of the entrainment multiplier coefficient (m_E) was estimated as 3 psu^{-1}, by least-squares fit of salinities predicted by the model to salinities (n = 10) observed in the Gulf during 1986. The mean dilution time-scale of 20 days for the surface layer calculated for the estuarine circulation in 1986 may be contrasted with the 1 day time-scale estimated (from currents predicted by the 2D, vertically-integrated, model of Millet (*in* Grenz, 1989)) for replacement of the entire contents of the Gulf by a Mistral wind of 15 m s^{-1}. These results imply that periods of slow estuarine circulation (which perhaps exists, in reality, only in the deeper parts of the Gulf) alternate with episodes of rapid, wind-driven flushing.

The microbiological model

The biological model (Fig. 7) is that of L3VMP (Tett, 1990a). It describes autotrophic and heterotrophic microbial processes producing and consuming organic carbon and chlorophyll, and
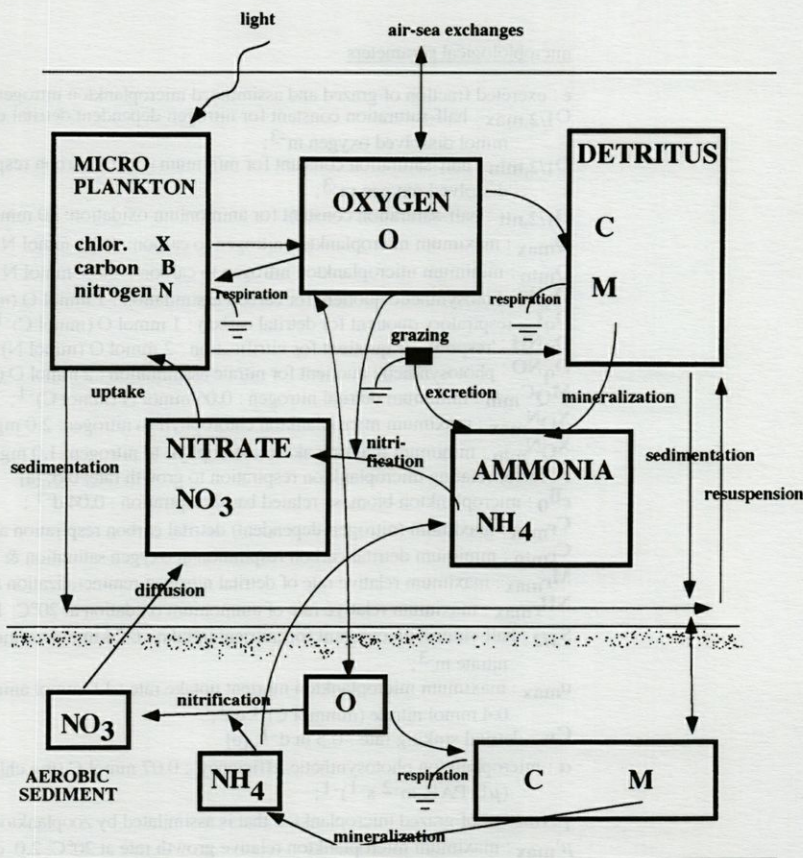
Fig. 7. – Biological and chemical compartmentalisation in the model.

cycling nitrogen through inorganic and organic forms. The fast-cycling compartment is called **microplankton** because it includes water-column micro-heterotrophs as well as micro-algae. The heterotrophs are bacteria and protozoa with growth that depends directly on algal production, and with a growth rate which is sufficiently tightly coupled to algal growth for the micro-heterotrophic metabolism to be treated simply as an extra source of respiration on a one-day time-scale. Ammonium excreted by the protozoa is assumed to be immediately taken up by the algal component of the microplankton.

This combination of phytoplankton and fast-growing micro-heterotrophs avoids the need to model in detail the algal extra-cellular production, and the growth and consumption of bacteria and protozoa, required by an explicit description of the "microcycle" (Williams, 1981). As a result, the primary production predicted by L3VMP, from the product $\mu \cdot \mathbf{B}$ of microplankton relative growth rate and biomass, is "net microplankton community production", approximately what would be measured by the ^{14}C method with 24-hour incubations (Tett *et al.*, 1993).

The microplankton compartment is quantified by concentrations of organic carbon $\mathbf{B}$, nitrogen $\mathbf{N}$ and chlorophyll $\mathbf{X}$. Microplankton growth is predicted with a 'cell-quota, threshold-limitation' equation :

[4]
$$\mu = L\{\mu'_{max} \cdot (1-k_Q/Q),$$
$$(a \cdot \mathbf{I} - r^B_0) \cdot x/(1 + b)\}$$

originally proposed for algae, and here modified from Tett & Droop (1988). In this equation, which assumes linear averaging of relevant processes over 24 hours, the "least-of" operator $L\{...,...\}$ stipulates that the rate of growth is controlled by

either a saturation function of the cellular ratio $\mathbf{Q}$ of nitrogen to carbon, *or* the net rate of photosynthesis, whichever is computed to be the least on a particular day. Net photosynthesis includes losses due to algal and microheterotroph respiration. These losses are assumed to be mainly proportional to growth rate while the 24-hr mean irradiance $\mathbf{I}$ experienced by the microplankton exceeds the compensation irradiance $\mathbf{I_c}$ at which $a \cdot \mathbf{I} = r^B_0$.

Microplankton carbon thus increases as a result of growth, or decreases because of basal respiratory loss when $\mathbf{I'} < \mathbf{I_c}$. Microplankton nitrogen increases as a result of nutrient uptake, which is a saturation function of sea-water concentrations of nitrate and ammonium, modified by the capacity of the microplankton for nitrogen storage. Ammonium uptake is given a lower half-saturation constant than nitrate uptake, but there is no competitive inhibition. Microplankton chlorophyll content $\mathbf{c}$ is made dependent on nitrogen content, with a higher yield of new chlorophyll from assimilated nitrogen when the simulated cells are nitrogen-replete, thus providing as simple mechanism for light and shade adaptation as a response to a changing balance between light and nutrient limitation of growth. Microplankton sinking rate is also made a function of increasing nitrogen content. Pending further investigation, model parameters for maximum cell nitrogen quota, maximum nitrogen uptake rate, and chlorophyll : nitrogen ratios, were made 80 % of values (Tett & Droop, 1988) appropriate for algae, in order to compensate for the inclusion of microheterotroph biomass in the microplankton.

Because the aim is to model microbial dynamics as simply as possible, L3VMP contains no explicit compartment for mesozooplankton. In-
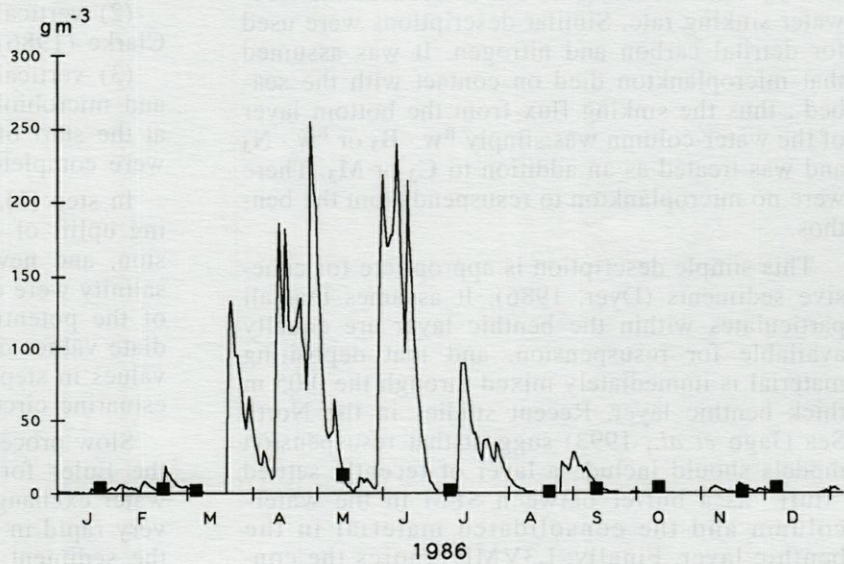

Fig. 8. – Predicted (solid line) suspended particulate matter (SPM) in 1986, compared with observations (squares) in Carteau Cove.

gm^{-3}

1986

stead, the impact of these animals is parameterised by a grazing pressure **G**, which may either be calculated from observed abundances of mesozooplankton (Tett, 1990a ; Tett et al. 1993) or be used as a free variable in fitting the model to observations of chlorophyll concentration (Woods & Tett, submitted). Grazing converts some nitrogen instantly to ammonium, simulating mesozooplankton excretion ; another part of the microplankton particulate material is converted to detritus. All microplankton sinking from the bottom water-column layer are assumed to die, and thus to be converted instantly to detritus, on contact with the sea-bed.

As already mentioned, detritus may deposit into the sediment layer, or be resuspended, according to the bottom stress. Detrital mineralisation processes are assumed to be qualitatively similar in the water-column and in the benthos, but to take place more slowly in the latter because of the lower concentrations of oxygen in the sediment pore-water. Details are given by Tett (1990a). At this stage the model does not include anoxic processes such as denitrification, and hence the simulated sediment cannot act as a nitrate sink.

The resuspension model

We modelled the net sediment-water flux of a particulate as the difference between deposition and resuspension. Under stratification, the resuspension flux of inorganic sediment is $f_e(t_3,t_c) \cdot A_5$, and the deposition flux is $f_d(t_3,t_c) \cdot {}^Aw.A_3$, where A_5 is the concentration in the benthic layer and A_3 is the concentration in the overlying water layer. Erosion takes place when the actual bottom stress t_3 exceeds a critical stress t_c ; otherwise there is deposition. The erosion function f_e has the units of velocity, whereas the deposition function f_d is a fraction (0-1) which reduces the free-water sinking rate. Similar descriptions were used for detrital carbon and nitrogen. It was assumed that microplankton died on contact with the sea-bed ; thus the sinking flux from the bottom layer of the water-column was simply ${}^Bw \cdot B_3$ or ${}^Bw \cdot N_3$ and was treated as an addition to C_3 or M_3. There were no microplankton to resuspend from the benthos.

This simple description is appropriate for cohesive sediments (Dyer, 1986). It assumes that all particulates within the benthic layer are equally available for resuspension, and that depositing material is immediately mixed through the 0.05 m thick benthic layer. Recent studies in the North Sea (Jago et al., 1993) suggest that resuspension models should include a layer of recently settled "fluff" as a buffer between SPM in the water-column and the consolidated material in the benthic layer. Finally, L3VMP ignores the con-

tribution that the micro-phytobenthos makes (Plante-Cuny & Bodoy,1987) to production in these shallow waters.

Optical model

In shallow, potentially turbid or potentially eutrophic waters such as the Gulf of Fos, it is important to take into account the contributions of phytoplankton and suspended particulates to light attenuation. Following Tett (1990b), mean photosynthetically available radiation (PAR) in the surface layer was calculated from

$$[5] \quad I_1 = m_0 \cdot m_1 \cdot m_2 \cdot E_0 \cdot (1-e^{-11 \cdot h_1})/(11 \cdot h_1)$$

where E_0 is the 24-hour mean of the total solar irradiance at the sea surface, and PAR diffuse attenuation is given by

$$[6] \quad l_1 = {}^{sw}1 + {}^Xe \cdot X_1 + {}^Ae \cdot A_1 + {}^Ce \cdot C_1.$$

which shows the contributions of particle-free sea-water, chlorophyll, inorganic SPM, and organic detritus. The e terms are attenuation cross-sections, the amount of diffuse attenuation caused by unit concentration of each light absorber.

USING THE MODEL

Numerical methods

Solutions to the equations were found by numerical integration, forced by time-varying boundary conditions, and starting from the initial conditions given in Table III. The equations were separated into groups of terms, which were then solved sequentially for a time-step of 1 day. The order was :

(1) lateral inputs and estuarine circulation, using Euler forward-difference ;

(2) vertical mixing, using algorithms based on Clarke (1986) ;

(3) vertical (boundary fluxes, layer exchanges) and microbiological processes, preserving values at the start of the time-step until all calculations were completed.

In step (1), h_1 was replaced by h_1-**W**, simulating uplift of the pycnocline by salt-wedge intrusion, and new values of layer temperatures and salinity were calculated, leading to a revised value of the potential energy anomaly. These intermediate values of h_1 and **F** were then used as initial values in step (2). Step (1) was omitted when the estuarine circulation was "turned off".

Slow processes in group (3) were integrated by the Euler forward-difference method. Sediment-water exchanges of oxygen and DIN, which were very rapid in relation to the buffering capacity of the sediment pore-water, were integrated by the

same method, but with reduced time-step to avoid instability. Equations for 'fast' microplankton processes such as growth, or nutrient uptake, were integrated analytically to allow calculation with a time-step of 1 day (corresponding to the process time-scale assumed by the cell-quota, threshold limitation, model) without numerical instabilities. For example, in the case of microplankton biomass, the change ΔB was calculated from :

[7] (a) $B' = B_t \cdot (exp((\mu\text{-}G) \cdot \Delta t) - 1)/(\mu\text{-}G)$

(b) $\Delta B = (\mu - G) \cdot \Delta t \cdot B' - \phi/h$

where B' is the mean biomass over the time-step Δt, at the beginning of which the biomass was B_t. The sinking flux from unit surface area of, for example, layer [1] was computed from :

(c) $\phi_1 = (1 - exp(-{}^B w_1 \cdot \Delta t/h_1)) \cdot B_1' \cdot h_1.$

The scheme for separating the main terms of the equations implies that model predictions were not necessarily precise for any one time-step ; however, the property of conserving carbon and nitrogen ensured the accuracy of predictions on longer time-scales.

The solutions were written as a Pascal program to run on an Apple Macintosh computer using the 'Think Pascal' programming environment. Initial values and forcing meteorological and grazing data were read in from text files. Daily values of the state variables and derived fluxes were stored as text files, and subsequently further processed using Microsoft 'Excel'.

Parameter values and boundary conditions

As noted in Table III, most parameter values were taken from the literature. The boundary conditions were the concentrations in the "Rivière" and "Mer" boxes in Fig. 6, and the inputs from these to the "Golfe" [1] and "Plateau" [3] layers. As already mentioned, the freshwater discharge for the standard simulation was assumed to be 1 % of the Rhône flow, taking the latter from the 1986 data shown in Fig. 2 A. The nitrate concentration in this freshwater was taken as a constant 100 μM (El Habr & Golterman, 1987). Temperature, salinity and nitrate in the "Plateau" [3] layer were forced towards the constant 10 °C, 38 psu and 5 μM nitrate assumed for the "Mer" box by a simple relaxation condition, exemplified for temperature by

[8] $d\theta_{plateau[3]}/dt = -\ k \cdot (\theta_{plateau[3]} - \theta_{mer})$

where k was 0.02 d^{-1}. Meteorological data for 1986 (Fig. 2 B) were obtained from Météo France at Marignane, close to the Gulf of Fos. A test of the stratification and circulation models is shown in Fig. 5, which compares observed and predicted temperatures in the surface layer of the Gulf. Additionally, forcing the model with 1990 meteorological and river data predicted salinity stratification in the Gulf exceeding 4 psu on 20 % of days, and less than 1 psu on 34 % of days. The mean difference between layer [1] and [3] was 2.3 psu. This may be compared with the short-period observations in Carteau Cove during Autumn 1993, which showed the mean surface-bottom difference as 3.7 psu, with > 4 psu in 30 % of records and < 1 psu in 38 % of records.

Parameter values for detrital mineralisation and pore-water exchange were adjusted to give nutrient fluxes corresponding to those observed during the 1987 studies with benthic chambers (Baudinet et al. 1989 ; Barranguet & Aliot, ms). Resuspension parameters were estimated by least-squares fit of model predictions for inorganic and organic SPM to observations in 1986. As Fig. 9 shows, the observations were made during periods
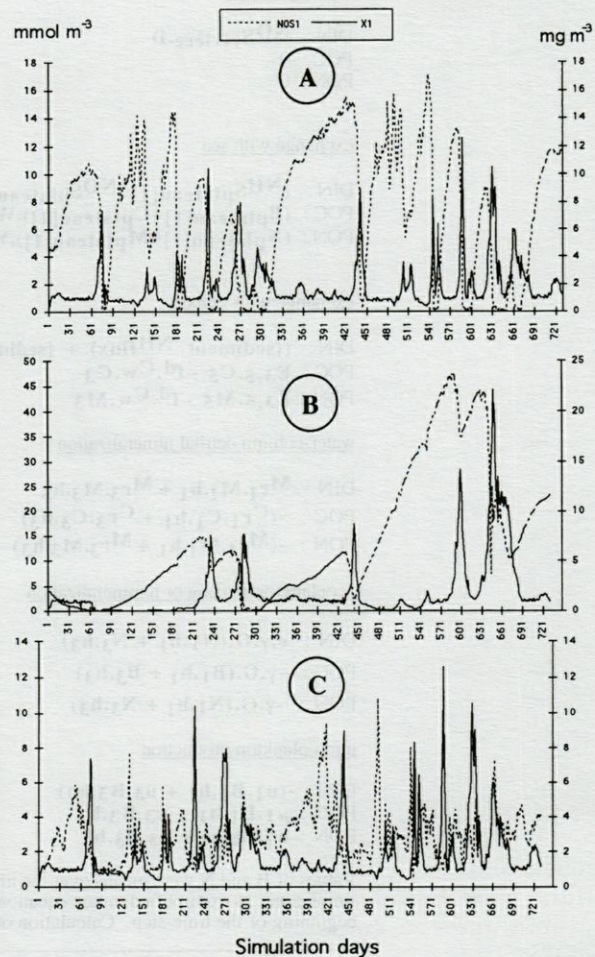

Fig. 9. – Chlorophyll and nitrate predicted over 2 years from 1986 meteorological and river flow data : A : standard run ; B : without circulation ; C : without resuspension of inorganic sediment.

of fair weather, and we have no way of checking the predictions for periods of high wind stirring.

It was decided not to impose a seasonal cycle of mesozooplankton grazing at this stage. Instead, the grazing pressure, **G**, was estimated as a constant 0.2 d¹ on the basis of mean abundances in Patriti (1984).

The standard simulation

The "standard run" of the model (Fig. 9 A) included all the features already mentioned, including freshwater-driven circulation, and wind-wave-driven resuspension of particulates at the

"Golfe" site. In order to initialise conditions at the "Plateau" site the model was run for this site alone for a preliminary two years. Table V gives the predicted organic carbon and nitrogen budgets for the "Golfe" site during the next two simulated years, starting from typical observed mid-Winter values of the state variables. Equations used for calculating fluxes are listed in Table IV. At 69 to 86 g C m⁻² yr⁻¹, predicted microplankton production was at the lower end of the range of 71 to 140 g C m⁻² yr⁻¹ estimated using $_{14}$C by Folack (1986).

All simulated years were forced by 1986 meteorological and river flow data in order to test the long-term stability of the model. Consequently, the decrease in total nitrogen at the

Table IV. – Flux equations.

POC : particulate organic carbon (in microplankton and detritus);
DIN : dissolved inorganic nitrogen - nitrate and ammonium;
PON : particulate organic nitrogen (in microplankton and detritus);

Terms are given for stratified conditions and predict fluxes in mmol m⁻² d⁻¹. A positive value indicates a gain by the "Golfe" water-column.

input from river

DIN : $NOS_{rivière}.D$
POC : 0
PON : 0

exchange with sea

DIN : $(NHS_{plateau[1]}+NOS_{plateau[1]}).W - (NHS_1+NOS_1).(D+W)$
POC : $(B_{plateau[1]}+C_{plateau[1]}).W - (B_1+C_1).(D+W)$
PON : $(N_{plateau[1]}+M_{plateau[1]}).W - (N_1+M_1).(D+W)$

exchange with seabed

DIN : $(\{sediment\ NH_{flux}\} + \{sediment\ NO_{flux}\})$
POC : $E_{3,5}.C_5 - f^d.C_w.C_3$
PON : $E_{3,5}.M_5 - f^d.C_w.M_3$

water-column detrital mineralization

DIN : $M_{r1}.M_1.h_1 + M_{r3}.M_3.h_3$
POC : $-(C_{r1}.C_1.h_1 + C_{r3}.C_3.h_3)$
PON : $-(M_{r1}.M_1.h_1 + M_{r3}.M_3.h_3)$

zooplankton grazing or remineralization

DIN : $e.\gamma.G.(N_1.h_1 + N_3.h_3)$
POC : $-\gamma.G.(B_1.h_1 + B_3.h_3)$
PON : $-\gamma.G.(N_1.h_1 + N_3.h_3)$

microplankton production

DIN : $-(u_1.B_1.h_1 + u_3.B_3.h_3)$
POC : $\mu_1.B_1.h_1 + \mu_3.B_3.h_3$
PON : $u_1.B_1.h_1 + u_3.B_3.h_3$

Values of **B** and **N** were means over the time-step (Δt = 1 day) used in the numerical simulations, as exemplified in text equation [6]. Other concentrations were those at the beginning of the time-step. Calculation of uptake rates obeyed: $u.B.\Delta t < S$.

"Golfe" site, from an initial value of 4.7 mol N m^{-2}, to 1.7 mol N m^{-2} after two years (Table V), shows that the model is not able, with current parameter values, to provide an explanation for the maintenance of nitrogen in the Gulf of Fos which can be deduced from observed long-term constancy in mean sediment and water-column organic content.

The explanation is that the model exports more nitrogen from the "Golfe" site than is imported in freshwater. This loss is most evident in particulate organic nitrogen. The error seems to lie mainly in the resuspension model, which injects large amounts of benthic detrital nitrogen into the water-column during periods of strong wind-stirring. Much of this suspended particulate nitrogen is exported by the simulated estuarine circulation. In reality, the benthos should, during a year, receive a net input of particulate organic nitrogen, as sedimenting detritus, sufficient to compensate for the export of mineralised DIN from the sediment into the water-column.

Some simple numerical experiments

Despite this fault, which itself gives some insight into the importance of organic deposition and resuspension in shallow-water coastal ecosystems, we can still use the model to carry out simple numerical experiments. Two obvious tests are to remove (1) the estuarine circulation, and (2) the resuspension of light-absorbing inorganic particulates.

The effect of turning off the estuarine circulation is to reduce primary production in the first simulated year (to 38 g C m^{-2} yr^{-1}). Production is however restored (to 75 g C m^{-2} yr^{-1}) during the second year. As Fig. 9 B shows, the explanation is that nutrient levels are decreased in year 1 by the lack of a contribution from the Rhône, but that more nutrients are available in year 2 as a result of sustained benthic remineralisation without export of water-column DIN or particulate nitrogen.

The effect of turning off the resuspension of inorganic particulates (Fig. 9 C) is that now only self-shading or nutrient depletion can limit microplankton growth. Predicted chlorophyll concentrations are generally higher, and annual production is more than doubled (130 - 190 g C m^{-2} yr^{-1}).

Short-term dynamics

The difficulties in creating a long-term balance in nitrogen do not prevent us employing the model to gain insights into the short-term dynamics of microplankton. Model results emphasise the high-frequency variability of the pelagic ecosystem in the Gulf of Fos. The pattern of change is very different from the seasonality expected at this latitude. In the case of the oceans, deep mixing in Winter prevents phytoplankton growth until the vernal onset of stratification allows the Spring Bloom. Nutrient depletion thereafter restricts microalgal biomass in the surface mixed layer until

Table V. – Results of the standard run.

A. Total nitrogen budget		at day	0	365	730	
	in water-column		34	130	128	mmol N m^{-2}
	in sediment layer		4651	2840	1526	
	total		4685	2970	1654	
	change over year			-1715	-1316	
	explained by fluxes			-1714	-1317	
	numerical error			-1	1	

B. Annual fluxes	Exchanges		from Benthos		In water column		
	from River	from Sea	Suspension	Pore water	Detrital mineralization	Zooplankton grazing/remin.	Microplankton production
day 1-365							
Particulate organic C	0	-27989	26537	0	-1813	-2262	5739
Nitrate + ammonium	1198	-878	0	386	127	182	-951
Particulate organic N	0	-1852	1422	0	-127	-364	951
day 366-730							
Particulate organic C	0	-14906	12962	0	-2361	-2889	7142
Nitrate + ammonium	1198	-1149	0	719	200	234	-1199
Particulate organic N	0	-1132	598	0	-200	-468	1199

Notes
1. Fluxes are given in mmol m^{-2} yr^{-1}. Positive values are gains by "Gulfe" water-column.
2. Total nitrogen is sum of microplankton N, detrital N, nitrate, and ammonium.

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thermocline ventilation encourages an Autumn Bloom. In the case of the Gulf of Fos, however, shallow waters potentially allow phytoplankton growth at any time of the year. Restrictions are imposed by turbidity and nutrient depletion.

A characteristic sequence of events is thus as follows. (1) High SPM levels following storms cause a decrease in submarine PAR, with the result that microplankton growth rates are less than losses due to grazing and export. Benthic and water-column remineralisation, and the Rhône inflow, bring about an increase in water-column DIN. (2) As particulate material is exported, or re-deposited to the sediment, the water clears, resulting in rapid growth of phytoplankton. (3) Chlorophyll concentrations increase until self-shading, or nutrient depletion, restricts further growth. Fig. 10 shows a predicted sequence of such events, each lasting 10 - 30 days and separated by 30 - 80 days. These time-scales must result from the interval between major storms and from the typical 20 days residence time of water in the Gulf. Of course, these predictions do not include the effects of wind-driven water exchange, but these latter are likely to intensify the episodic nature of change.

CONCLUSIONS

Although, as Fig. 10 demonstrates, detailed agreement between simulated and observed chlorophyll concentrations was poor, the Figure

does suggest that the simulated timescale of chlorophyll variability is about right. Precise prediction was not the aim at this stage. Instead, the construction of a simple, holistic, model that coupled physical and microbiogeochemical processes has given us some important insights into ecosystem function in the Gulf of Fos and has provided guidance about sampling strategies. The insights concern (1) the rôle of the Gulf in cycling land-derived nutrients before they reach the open sea ; (2) the importance of particulate resuspension in controlling light availability for photosynthesis and the export of organic material ; and (3) the frequency of variability in a shallow, wind-forced system. The third insight has, in particular, shown the need to sample more frequently than the monthly intervals initially employed to study conditions in the Gulf. Our new knowledge of the importance of high-frequency variation also emphasises the requirement to take account of wind-driven lateral exchange. Finally, the difficulties in maintaining the long-term constancy of ecosystem nitrogen point to the need for a better resuspension model.

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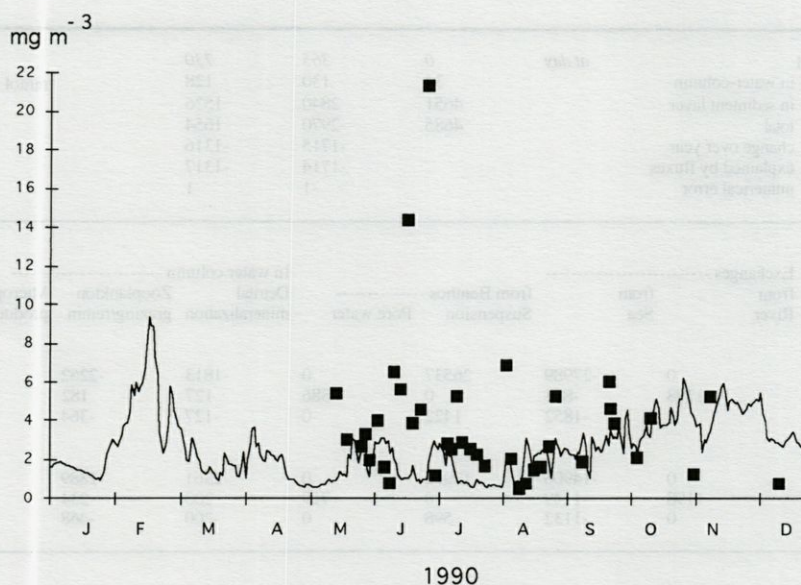
Fig. 10. – Chlorophyll concentrations during part of 1990. Predictions (solid line) forced by 1990 meteorology and river flows. Observations in Carteau Cove shown by squares.

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